Una aproximación eco-evolutiva a las redes ecológicas mediante simulación

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A todos los que un día pusieron la mano para que
no cayera o me la brindaron para levantarme.

"Dicen que el talento es algo innato, puede que sea cierto,
pero riégalo a diario o habrá muerto,
cincuenta por ciento suerte, cincuenta por ciento curro,
no presumo, aquí el curro es noventa y nueva, la suerte es uno".

Pensando en voz alta, Mejor que el silencio
Ignacio José Fornés Olmo 2011

CONTENIDOS

Resumen

Uno de los principales desafíos en ecología es comprender la persistencia y estabilidad a largo plazo de redes tróficas complejas en el espacio y el tiempo. Las interacciones depredador-presa, así como la variabilidad genética intraespecífica y cómo esta afecta a dichas interacciones determinan la estructura y dinámica; y son muy importantes para entender cómo esto mejora la robustez y estabilidad de las redes tróficas. Cabe decir que en ecología los individuos se consideran como la unidad básica de construcción de los sistemas ecológicos ya que tanto sus características como su comportamiento determinan las propiedades del sistema que los compone. Por ello, los Modelos Basados en Individuos (IBMs), también llamados Modelos Basados en Agentes (ABMs), son un tipo de modelos que simulan poblaciones o comunidades compuestas de organismos individuales discretos donde el comportamiento de las poblaciones emerge de las interacciones entre los individuos (factores bióticos) y de éstos con las características físico-químicas del sistema (factores abióticos). Todo esto ha dado pie a que se desarrolle una nueva forma de aproximación para el estudio y modelización de los sistemas ecológicos llamada Ecología Basada en Individuos (IBE).

Dentro del contexto de los Modelos Basados en Individuos la presente Tesis Doctoral tiene como objetivo fundamental el estudio mediante simulaciones de las dinámicas eco-evolutivas de múltiples especies embebidas en complejas redes tróficas de la hojarasca de los hayedos (*Fagus sylvatic*a L.), mediante el uso de un nuevo Modelo Basado en Individuos de Nueva Generación (multi-locus, multi-rasgo, multi-trófico y espacialmente explícito), modificado y mejorado del modelo mini-AKIRA, llamado WEAVER 1.0 **(Capítulo 1)** así como, hacerlo más realista basando la parametrización del modelo en datos reales obtenidos de revisiones bibliográficas **(Capítulo 2)** y de estudios de mesocosmos de campo **(Capítulo 3)**, contribuyendo así a un Programa de Investigación Retroalimentada que ya está en marcha. Finalmente, mostramos las nuevas funcionalidades, implementaciones, y recopilación de estudios para la parametrización e implementación de una nueva red trófica de la hojarasca de los hayedos únicamente de artrópodos con la última versión de WEAVER 1.0, el modelo WEAVER 2.0. Además, mostramos la capacidad de este tipo de modelos para funcionar como un laboratorio virtual en el que podemos desarrollar experimentos “in silico” para responder a una gran cantidad de preguntas, y también cómo diseñar este tipo de experimentos siguiendo las mismas directrices que establece el método científico para experimentos de campo “in situ” o de laboratorio “ex situ” **(Capítulo 4)**.

En resumen, esta tesis aporta una amplia perspectiva sobre el diseño e implementación de complejos modelos de simulación basados en individuos que se han desarrollado con gran velocidad y de forma revolucionaria en los últimos 40 años gracias a los rápidos avances computacionales. Siguiendo los pasos del Ciclo de la Modelización veremos la evolución desde el sencillo IBM mini-AKIRA hasta el modelo de nueva generación WEAVER 2.0. A lo largo de esta evolución se han utilizado estos modelos como laboratorios virtuales para testar hipótesis que serían imposibles abarcar con estudios tradicionales de mesocosmos como el efecto de la conectancia, la variabilidad

genética intraespecífica, la distancia entre islas ricas en recursos o la variabilidad en la productivdad primaria de un micro-corredor ecológico en las dinámicas eco-evolutivas de una compleja red trófica de la hojarasca de los hayedos. Además, cabe destacar como los estudios y esfuerzos de parametrización en este tipo de modelos pueden generar estudios paralelos como consecuencia intrínseca del planteamiento de nuevas preguntas e hipótesis ante tal cantidad de datos obtenidos durante dicho proceso. Gracias a esto desarrollamos un base de datos sobre alometrías longitud-peso desde 1967 hasta 2017, de gran importancia específicamente en los modelos descritos en dicha Tesis Doctoral, de artrópodos del suelo y encontramos evidencias de que la productividad primaria del ecosistema, la temperatura, la precipitación, la latitud, la altitud y el bauplan morfológico de cada grupo taxonómico tienen un gran efecto en los parámetros alométricos, un resultado nuevo y nunca antes contrastado en el mundo científico. Otro gran hallazgo, gracias al proceso de parametrización que necesita poder documentar la actividad de las especies en campo, es que la metodología tradicional de medición de abundancia y actividad en artrópodos del suelo mediante trampas de caída o "pitfalls" es realmente ineficiente para medir actividad frente a dos nuevas trampas desarrolladas por el grupo de investigación altamente recomendables en este tipo de estudios y extrapolables a otros sistemas ecológicos.

Podemos concluir que la modelización ecológica hoy en día ha alcanzado un nivel de madurez tal que nos permite estudiar sistemas ecológicos "in silico" con un gran nivel de realismo, sin olvidar que la creación y utilización de estos modelos debe dirigirse hacia grandes preguntas de la Ecología como, por ejemplo, la estabilidad y resiliencia de los ecosistemas, entendimiento de mecanismos, el papel de la biodiversidad, el papel de la variabilidad genética en las dinámicas eco-evolutivas o cómo los servicios ecosistémicos se pueden ver afectados ante el Cambio Climático.

Introducción General

La ecología es la rama de la biología que estudia las interacciones de los seres vivos con su hábitat. Esto incluye tanto factores bióticos; o conjunto de organismos con el que los seres vivos establecen interacciones, como factores abióticos, esto es, las principales características físicas y químicas del hábitat en el que viven, tales como la climatología (temperatura o precipitación), la geología o la edafología del mismo (tipo de suelo, humedad relativa, cantidad y tipo de nutrientes). La ecología es, por tanto, el estudio de los sistemas en el que los individuos pueden ser considerados elementos de interacción, ya sea entre ellos (factores bióticos), ya sea con las características físico-químicas del sistema (factores abióticos). Los sistemas a este nivel se denominan ecosistemas y la ecología, es por ello, la biología de los ecosistemas (Margalef 1978). Los procesos del ecosistema, como la producción primaria, la pedogénesis o el ciclo de nutrientes regulan los flujos de materia y energía, siendo estos sustentados por la variedad de organismos, es decir, la biodiversidad del ecosistema. Por esta razón, y por ocuparse de las interacciones entre los individuos y su ambiente, la visión integradora de la ecología hace que sea una ciencia multidisciplinar que utiliza herramientas de otras ramas de la ciencia, especialmente geología, meteorología, geografía, sociología, física, química y matemáticas. Esto conlleva que los trabajos de investigación en esta disciplina se diferencien de los trabajos del resto de las ramas de la biología por su mayor uso de herramientas matemáticas, como la estadística y los modelos matemáticos (Blanco 2013).

En ecología, un modelo matemático es una representación abstracta de un sistema ecológico real (que varía desde una escala de población hasta una comunidad ecológica, o incluso un bioma completo), que se estudia para comprender mejor, describir, predecir y/o controlar el comportamiento del sistema real como consecuencia de su complejidad (Hall *et al*. 1990). De forma general se recurre a ellos cuando es más fácil trabajar con una representación simplificada de la realidad que con el sistema verdadero (Ford 1999). Un modelo se construye siguiendo cuatro pasos básicos: 1) delimitación precisa del sistema, 2) caracterización de los elementos del sistema y de las relaciones entre ellos, 3) formulación matemática de estas relaciones y 4) validación del modelo por comparación entre las estimas del mismo y medidas de las variables de estudio (Caselles-Moncho 2008). Dependiendo del tipo de formulación de las relaciones entre los elementos del sistema de estudio los modelos pueden ser: a) teóricos, si se basan en las leyes físicas y biológicas que rigen los procesos y por ello, se fundamentan en la deducción a partir de conceptos o ideas, b) semi-emprícos, que son similares a los teóricos pero incluyen algunos parámetros de ajuste y c) empíricos si se basan en relaciones estadísticamente relevantes y significativas entre variables o factores ambientales que son válidas para el contexto en el que se calibraron, y por ello, se fundamentan en datos experimentales. En general, independientemente del tipo de formulación matemática, estos modelos reciben el nombre de modelos mecanicistas (también llamados de procesos), ya que pueden utilizarse como modelos exploratorios para predecir como un ecosistema (o una parte del mismo) podría funcionar si existe un cambio en las condiciones ambientales. En el caso de que el

modelo no incluya una representación matemática explícita de los mecanismos implicados se denominan modelos descriptivos o fenomenológicos (Begon *et al*. 1999; Smith & Smith 2004).

Los modelos ecológicos mecanicistas pueden clasificarse dependiendo de una serie de características dicotómicas: a) según las características de las variables: si representan el tiempo como un continuo (modelos continuos) o como momentos determinados del sistema (modelos discretos); b) según las características de las ecuaciones pueden ser modelos lineales o no lineales; c) según la dependencia temporal, si los modelos incluyen una representación matemática de los estados futuros del sistema (modelos dinámicos) o no la incluyen (modelos estáticos); d) según si representan de forma explícita el espacio, los modelos pueden ser homogéneos o heterogéneos (si el espacio está representado en bloques o puntos distintos en el espacio); e) según su propia naturaleza, los modelos pueden ser deterministas si dado un conjunto de parámetros y variables de entrada producen siempre el mismo conjunto de variables de salida o estocásticos, si incluyen una fuente de aleatoriedad dentro del modelo que hace que para un mismo conjunto de datos de entrada genere salidas diferentes, y f) según la resolución de las ecuaciones, esta puede ser analítica, que se utiliza para estudiar sistemas relativamente simples que pueden describirse con precisión mediante un conjunto de ecuaciones matemáticas cuyo comportamiento es bien conocido; o de aproximación numérica o simulación, en que los modelos utilizan técnicas numéricas para resolver problemas para los cuales las soluciones analíticas son poco prácticas o imposibles (Fedra 1980; Kimmins 2004). Los modelos de simulación tienden a ser más utilizados por su capacidad para estudiar sistemas complejos, mientras que los modelos analíticos se caracterizan y valoran por su poder explicativo (Grant & Swannack 2008, Jørgensen 1996).

El método de resolución de un modelo es una característica muy importante, pues los pros y contras de cada tipo de modelo analítico o numérico (mediante simulaciones) determina qué clase de modelo necesitamos según nuestro objetivo de estudio. Hay que destacar que la resolución analítica del modelo proporciona una fórmula como solución mientras que mediante simulaciones obtenemos una solución computacional aproximada. Los modelos analíticos se caracterizan por su generalidad, proporcionar un mensaje más claro, no estar sujetos a ruido y no depender de un gran coste computacional. No obstante, en ocasiones pueden ser conceptualmente difíciles, no tener una solución analítica o ser imposibles de utilizar en situaciones complejas. Los modelos numéricos por simulación requieren un menor esfuerzo conceptual, son posibles de resolver, aunque no exista una solución analítica, y muy apropiados y factibles en situaciones complejas. Sus principales contras vienen dados por un gran coste computacional, aunque en los últimos 30 años la tecnología se ha desarrollado rápidamente y hoy en día podemos tener acceso a supercomputadoras con muchos nodos, los resultados sólo son válidos para cada caso concreto y puede tener problemas de ruido y de convergencia. Además, llevan añadidos en muchos casos problemas derivados de la falta de comunicación entre los modelizadores informáticos y los ecólogos experimentales pues se trata de

modelos interdisciplinares, además de una falta de base empírica para testar los modelos mediante datos experimentales (Billie 2007). Por ello, este tipo de modelos ecológicos basados en simulaciones son un punto de partida para establecer vínculos entre diferentes tipos de expertos (informáticos, matemáticos y/o ecólogos) (Duarte *et al*. 2019).

Por último, no se debe olvidar que las propiedades deseadas de este tipo de modelos matemáticos son el realismo, la precisión y la generalidad. Sin embargo, ningún modelo puede maximizar estas tres propiedades simultáneamente, por los propios trade-offs que existen entre ellas. Si desarrollamos un modelo muy realista será poco general, y si desarrollamos un modelo muy realista y muy general será un modelo muy impreciso. Por ello, hay que sacrificar alguna de estas propiedades dependiendo de nuestros objetivos: a) si queremos maximizar nuestro entendimiento del sistema es necesario potenciar la generalidad y sacrificar la precisión, b) si nuestro interés es generar un modelo lo más preciso posible debemos maximizar la precisión sin necesidad de ser muy general y realista y c) si el objetivo es tener un mayor control del modelo se necesita maximizar el realismo en detrimento de la precisión y la generalidad. De este modo podemos concluir que los ecólogos siempre deben estar al tanto de los peligros de la sobre-simplificación y hay que recordar que, aunque en ciencia se utiliza "la navaja de Occam" para escoger el modelo más simple capaz de explicar el fenómeno de estudio, la navaja tiene dos filos pues como decía Albert Einstein, "*un modelo tiene que ser tan simple como sea posible, pero tan complejo como sea necesario*" (Duarte *et al*. 2019).

1. Modelización en Ecología: Del ecosistema al individuo

En ecología los individuos se pueden considerar como la unidad básica de construcción de los sistemas ecológicos. Por ello, las propiedades y el comportamiento de los individuos determinan las propiedades del sistema que los compone. Los individuos crecen y se desarrollan, cambiando varios de sus rasgos a lo largo de su ciclo de vida. Los individuos también se reproducen y mueren, persistiendo mucho menos tiempo que los sistemas a los que pertenecen. Además, los individuos necesitan recursos para poder sobrevivir, y al utilizar estos recursos modifican el ambiente en el que viven. Difieren unos de otros incluso dentro de la misma especie y edad. Y quizás uno de los aspectos más importantes es que los individuos tienen un comportamiento flexible adaptativo que les permite sobrevivir, crecer y reproducirse ante cambios de su ambiente (DeAngelis & Grimm 2014, Grimm & Railsback 2005).

1.1. Modelos Basados en Individuos (IBMs)

Los Modelos Basados en Individuos (IBMs), también llamados Modelos Basados en Agentes (ABMs), son un tipo de modelos mecanicistas de resolución numérica que simulan poblaciones o comunidades compuestas de organismos individuales discretos. Cada individuo tiene un conjunto de variables de estado tales como la localización espacial, rasgos fisiológicos y comportamentales como

el crecimiento, reproducción, selección de hábitat, forrajeo o capacidad de dispersión, que varían entre individuos, inter- e intraespecíficamente, y también a lo largo del tiempo. En este tipo de modelos el comportamiento de las poblaciones emerge de las interacciones entre los individuos (factores bióticos) y de éstos con su propio ambiente (factores abióticos) (DeAngelis & Grimm 2014). Todo esto ha dado pie a desarrollar una nueva forma de aproximación para el estudio y modelización de los sistemas ecológicos caracterizado por ser una rama científica mucho más compleja e interdisciplinar que las aproximaciones de estudio y modelización en ecología tradicional. Esta nueva aproximación recibe el nombre de Ecología Basada en Individuos (IBE) y tienen siete grandes características: 1) los sistemas son modelizados y entendidos como colecciones de individuos únicos que interaccionan entre sí y con su ambiente; 2) los Modelos Basados en Individuos son la herramienta principal de esta nueva aproximación ya que permite estudiar la relación entre los comportamientos adaptativos y las propiedades emergentes; 3) los modelos están basados en la teoría, ya que suelen estar construidos en función de submodelos ya estudiados como el crecimiento, la reproducción o el comportamiento adaptativo; 4) los patrones observados son una de las principales fuentes de información utilizado para diseñar y testar los modelos; 5) el marco conceptual de los modelos es complejo ya que incluye: a) emergencia de patrones a nivel de sistema a partir de los rasgos de los individuos sin que originalmente el modelo se haya diseñado orientado a patrones, b) comportamiento adaptativo flexible, es decir los individuos puede mejorar su aptitud física, en respuesta a su ambiente (flexibilidad fenotípica) y c) eficacia biológica, el modelo está diseñado para que a lo largo de la simulación los individuos busquen y alcancen una condición física que sea la mejor posible dentro de las posibles restricciones (constraints); 6) este tipo de modelos se implementan mediante un código en el lenguaje de programación seleccionado y se resuelven mediante simulaciones por ordenador, y 7) los estudios de campo y de laboratorio son indispensables para implementar este tipo de modelos (Grimm & Railsback 2005).

Para esta nueva aproximación de la ecología, la modelización es un proceso iterativo (Haefner 1996, Thulke *et al*. 1999) en el cual existen una serie de pasos que se realizan una y otra vez, a este proceso se le conoce como "Ciclo de la Modelización" (Figura 1), y está compuesto de siete pasos fundamentales:

Paso 1: Formulación de la pregunta

Dependiendo del tipo de pregunta o problema que queramos resolver el modelo tendrá unas características u otras. En este paso se deciden qué aspectos del sistema real se quieren representar en el modelo.

Paso 2: Desarrollo de las hipótesis

Para poder construir un modelo con el que trabajar primero debemos desarrollar un modelo conceptual basado en la teoría y la experiencia (DeAngelis *et al*. 2003) que nos ayude a entender el

sistema que queremos estudiar. A partir de aquí podemos desarrollar nuestras hipótesis con las que empezar el Ciclo de la Modelización.

Paso 3: Elegir escalas, variables de estado, procesos y parámetros

Para construir el modelo necesitamos trasladar las hipótesis a una serie de ecuaciones y reglas que describan la dinámica de las entidades del modelo. Primero seleccionamos las variables que describen el estado del sistema y que definen la estructura del modelo, luego elegimos los procesos que provocan cambios en las variables de estado y establecemos los parámetros necesarios que se usan en los submodelos de los procesos seleccionados. Desde el punto de vista de los individuos el modelo tiene una serie de variables que describen el estado de los individuos, parámetros que describen el comportamiento de los individuos, y variables y parámetros que describen el ambiente en el que se encuentran los individuos. Por último, debemos elegir la escala espacial y temporal que tendrá nuestro modelo, considerando tanto el grano de la escala, que es la unidad más pequeña de espacio "tamaño de la celda" o de tiempo, por ejemplo, días, estaciones o años de cada "paso de tiempo o step", como la extensión, es decir, el área cubierta por el modelo y el horizonte de tiempo simulado.

Paso 4: Implementación del modelo

Este paso podemos dividirlo en tres subpasos aparentemente independientes, pero muy interrelacionados dado que cada uno de estos puede llevarnos irremediablemente al siguiente y *vicerversa*, en un bucle de retroalimentación:

> ***Paso 4.a: Parametrización del modelo***
>
> Para poder probar si el modelo funciona y conocer las consecuencias de las asunciones que hemos impuesto es necesario especificar e introducir el valor de todas la variables y parámetros mediante un proceso llamado parametrización que es realmente complejo en IBMs. Este proceso está basado en datos reales y puede ser realmente costoso hablando en términos de tiempo. No podemos probar el código programado sin datos de entrada o "inputs". Como dicen Grimm & Railsback 2005, muchos neófitos en este tipo de modelos se quedan atascados en este paso del Ciclo de la Modelización, por eso es particularmente importante utilizar la conocida "táctica del salami". No es más que comenzar a correr las primeras simulaciones no con el modelo completo, que puede ser muy complejo y si existe algún error es difícil de identificar o puede generar una cadena de errores; si no comenzar con un modelo nulo que es mucho más sencillo donde, por ejemplo, todos los individuos son iguales, el ambiente es homogéneo y constante y los individuos son denominados "estúpidos" o "dummy". A partir de aquí se pueden ir incorporando funcionalidades a medida que testamos los modelos, ya que tenemos la parametrización ya realizada. Desde mi punto de vista, consideraría la "táctica del salami" es la mejor forma de proceder con este tipo de modelos independientemente del nivel de experiencia del

programador, ecólogo o ambos. Para poder llevar a cabo este paso, el modelizador debe ser capaz de poder observar el comportamiento de los individuos, los patrones en el tiempo y el espacio y demás resultados, por lo tanto, el software donde está implementado el modelo debe ser también accesible y proveer esta información.

Paso 4.b: Debuggeo del modelo o depuración del programa

Una de las partes más importante de la revisión del programa implementado consiste en identificar y corregir errores de programación a lo largo del código fuente implementado. Este proceso puede llegar a ser más o menos tedioso y largo dependiendo de: a) la formación del investigador, por ejemplo, un ecólogo con conocimientos de programación puede tardar más que un desarrollador de software informático, y b) el lenguaje de programación elegido, los lenguajes de programación de nivel alto se caracterizan por expresar los algoritmos de una manera adecuada a la capacidad cognitiva humana, es decir, permiten una expresión casi oral de la escritura del programa (ej.: R, Java, PHP, Python o JavaScript), mientras que los lenguajes de nivel bajo o nivel máquina se expresan en código binario o textos de código fuente inteligibles a los humanos, que no necesitan una traducción entre el código y la máquina, siendo más potentes y ejerciendo un control directo sobre el hardware o sistema informático (ej.: Assembler x86, JMP o MULT). Los lenguajes C y C++ serían lenguajes de nivel intermedio, cuya programación es algo más compleja pero permiten controlar mucho mejor el uso de la memoria del ordenador durante la ejecución del programa. Los sistemas de depuración del código son más sencillos en lenguajes de nivel bajo que en los de nivel alto, cualquier error en la expresión escrita puede provocar un error o "bug", pero se necesita ser experto en programación para detectarlos. Por lo tanto, dependiendo del nivel de formación del creador del programa, de la complejidad del modelo y del nivel del lenguaje de programación será más o menos sencillo identificar el error.

Paso 4.c: Implementación del código fuente del modelo

Una vez decidido el lenguaje más adecuado para el modelo, se implementa este y acto seguido se lanzan las primeras simulaciones. En este momento podemos conocer las consecuencias de las asunciones de nuestro modelo, desarrollar nuevas asunciones, implementarlas, generar nuevas asunciones y así sucesivamente. Con lo cual realmente habremos entrado en el Ciclo de la Modelización.

Paso 5: Análisis, testado y revisión del modelo

Como ya hemos comentado en el Paso 4 una vez el modelo está implementado, es necesario analizar, testar y revisar el modelo de forma iterativa por si existen errores comparando diferentes versiones hasta que el modelo conteste a nuestra pregunta o preguntas iniciales de forma que se asemejen al sistema real. Una forma de realizar esta evaluación es mediante modelos orientados a patrones (Grimm *et al*. 1996, Grimm *et al*. 2005), conocido un patrón en el sistema real el Modelo

Basado en Individuos se diseña y se implementa orientado a reproducir este patrón que ha de encontrarse en el proceso de evaluación. Otra forma de evaluar los modelos es testando si se adaptan o no a las teorías que conocemos sin necesidad de diseñarlo orientando a patrones. Muchos ecólogos no modelizadores que diseñan un modelo piensan que la parte más difícil es la de programación, desarrollo e implementación. No obstante, el verdadero obstáculo se encuentra a la hora de analizar y revisar el modelo, de tal manera que modelizadores experimentados puede llegar a tardar 4 veces más en revisar el modelo que en programarlo. Una parte importante de este paso del Ciclo de la Modelización es determinar una regla que nos determine en qué punto paramos de revisar el modelo y lo consideramos bueno, a esto le llaman "stopping rule" (Haefner 1996). En ese momento entran en juego los recursos de los que disponemos. Por ejemplo, si sólo hay dos investigadores contratados durante dos años, no se puede implementar un modelo tan complejo que no pueda entrar en el Paso 6 (ver más abajo) antes de la finalización de los contratos de los investigadores, de no ser que haya algún investigador responsable que pueda seguir con el trabajo.

Paso 6: Comunicación al mundo o comunidad científica

¡Una vez finalizado el modelo, después de corroborar que tiene suficiente grado de veracidad y aporta respuestas a nuestras preguntas o problemas originales del Paso 1, aún no se ha terminado! Tenemos aún que comunicar a la comunidad científica nuestros hallazgos y novedades:

Paso 6.a: Comunicación del modelo y sus resultados

Todos los ciclos iterativos de implementación, debuggeo y análisis del modelo científicamente no sirven para nada a menos que comuniquemos tanto el modelo como sus resultados mediante publicaciones científicas. Este tipo de modelos tiene el inconveniente de que requiere un duro trabajo de construcción y análisis que no se puede describir con pocas ecuaciones, pero se ha de encontrar la forma de comunicar por completo nuestro modelo y nuestros resultados haciéndolo disponible para el resto de la comunidad científica.

Paso 6.b: Comunicación de estudios paralelos como consecuencia de la parametrización

En algunas ocasiones las revisiones bibliográficas o experimentos de laboratorio y/o campo que se utilizan para obtener datos durante el proceso de parametrización pueden dar lugar a nuevo conocimiento, y por ello, pueden ser comunicados y publicados como estudios independientes, derivados de las necesidades del propio Ciclo de la Modelización.

Paso 7: Retroalimentación

Una vez el modelo ha sido comunicado, podemos plantearnos nuevas preguntas y re-parametrizar el modelo con nueva información mediante un paso de retroalimentación que cerraría el Ciclo de la Modelización. Cuando se trata de datos reales obtenidos en experimentos diseñados para testar los modelos, dichos datos o resultados se utilizarían para retroalimentar y perfeccionar esos mismos

modelos que inspiraron la investigación, sobre todo si los resultados no corroboran el modelo. Este proceso de retroalimentación puede seguir hasta que el modelo y los datos reales se parezcan razonablemente, o seguir si se generan nuevas preguntas. A este proceso se le denomina Programa de Investigación Retroalimentada (PIR), y fue acuñado por primera vez por Moya-Laraño *et al*. 2012 y más tarde desarrollado en Moya-Laraño *et al*. 2014 (**Capítulo 1**). Aunque Grimm & Railsback 2005 lo contemplan implícitamente dentro del Paso 6, cuando hablan de la génesis de nuevas preguntas, así como la generación de experimentos, el PIR tiene una envergadura suficiente como para considerar este proceso un paso adicional que debe hacerse explícito.

Figura 1. Pasos del Ciclo de la Modelización. Los recuadros en blanco representan los 6 pasos originales descritos por Grimm & Railsback 2005 y los recuadros en amarillo son pasos intermedios considerados de gran importancia en el proceso de modelización. El recuadro en gris con borde negro dicontinuo agrupa pasos intermedios interrelacionados. Modificado de la Figura 2.1. de Grimm & Railsback 2005.

1.2. Programa de Investigación Retroalimentada (PIR)

Se puede considerar el PIR como un Ciclo de Investigación dentro del propio Ciclo de la Modelización en IBMs. La retroalimentación entre este tipo de Modelos Basados en Individuos y la realidad, usando una aproximación de biología de sistemas en ecología (Purdy *et al*. 2010), se puede utilizar para modificar los IBMs y acercarse lentamente la realidad con mayor detalle. Estos experimentos "in silico" y la extracción de todos los factores explicativos de la simulación es una de las principales ventajas de simular seres vivos en el ordenador, que han sido también llamados vidas sintéticas (Solé 2012). Además de los beneficios de utilizar este tipo de retroalimentación realizar estudios solo a nivel digital, puede proporcionar pistas e hipótesis importantes que deben probarse empíricamente en experimentos futuros de campo y/o de laboratorio.

Implemetar estos Programas de Investigación Retroalimentada (PIR) requeriría seguir un protocolo basado en tres pasos (Figura 2):

Paso 1: Obtención de datos, parametrización e implementación del modelo

Búsqueda u obtención de datos mediante revisión bibliográfica, experimentos de campo y/o laboratorio para parametrizar el ecosistema modelo. Estos datos de entrada o "inputs" puede provenir de ecosistemas iguales o muy similares al ecosistema modelo o de otros ecosistemas diferentes, extrapolando los parámetros a nuestro propio ecosistema.

Paso 2: Conocer el grado de realismo del modelo

Una vez parametrizado e implementado el Modelo Basado en Individuos lo ejecutamos de forma iterativa entre el Paso 1 y el Paso 2 con diferentes combinaciones de parámetros externos o "inputs", mientras que los parámetros internos, es decir aquellos que son estimados por el modelo internamente durante la simulación no se modifican. Las predicciones obtenidas de las distintas iteraciones se pueden comparar con observaciones empíricas, calculando la distancia entre los datos empíricos y simulados para cada combinación de parámetros externos (Grelaud *et al*. 2009; Sunnaker *et al*. 2013), y determinar el grado de realismo y robustez que tiene nuestro modelo.

Paso 3: Optimización del modelo

Una vez que los resultados de nuestro modelo sean estables, es decir, coincidan lo máximo posible con los datos empíricos observados, consideramos esta combinación de parámetros suficientemente adecuada para reproducir las observaciones empíricas (Melián *et al*. 2011, 2015), podemos incluir algunos de estos parámetros externos como parámetros internos del modelo o incluso modificar funcionalidades, y reducir el número de parámetros de entrada. En el caso contrario, en el que no conseguimos que los resultados del modelo se asemejen a la realidad y no podamos optimizar el modelo podemos volver al Paso 2 y realizar de nuevo el proceso iterativo de combinación de parámetros. Los nuevos datos obtenidos de testar el modelo deberán servir para mejorar nuestro modelo y acercarlo más a la realidad en un proceso continuo de retroalimentación.

Los Modelos Basados en Individuos pueden considerarse modelos con un gran conjunto de valores paramétricos *a priori* y mecanismos biológicos. Uno de los objetivos deseables de los IBMs sería determinar los valores de los parámetros de entrada factibles "inputs" para obtener los valores de salida "outputs" que mejor se aproximen a las observaciones empíricas. Sin embargo, los sistemas biológicos pueden contener parámetros que subyacen a los procesos biológicos, evolutivos y ecológicos. Dada esta complejidad, encontrar el número mínimo de parámetros y/o la combinación adecuada de los mismos que mejor predicen los datos empíricos es un gran desafío.

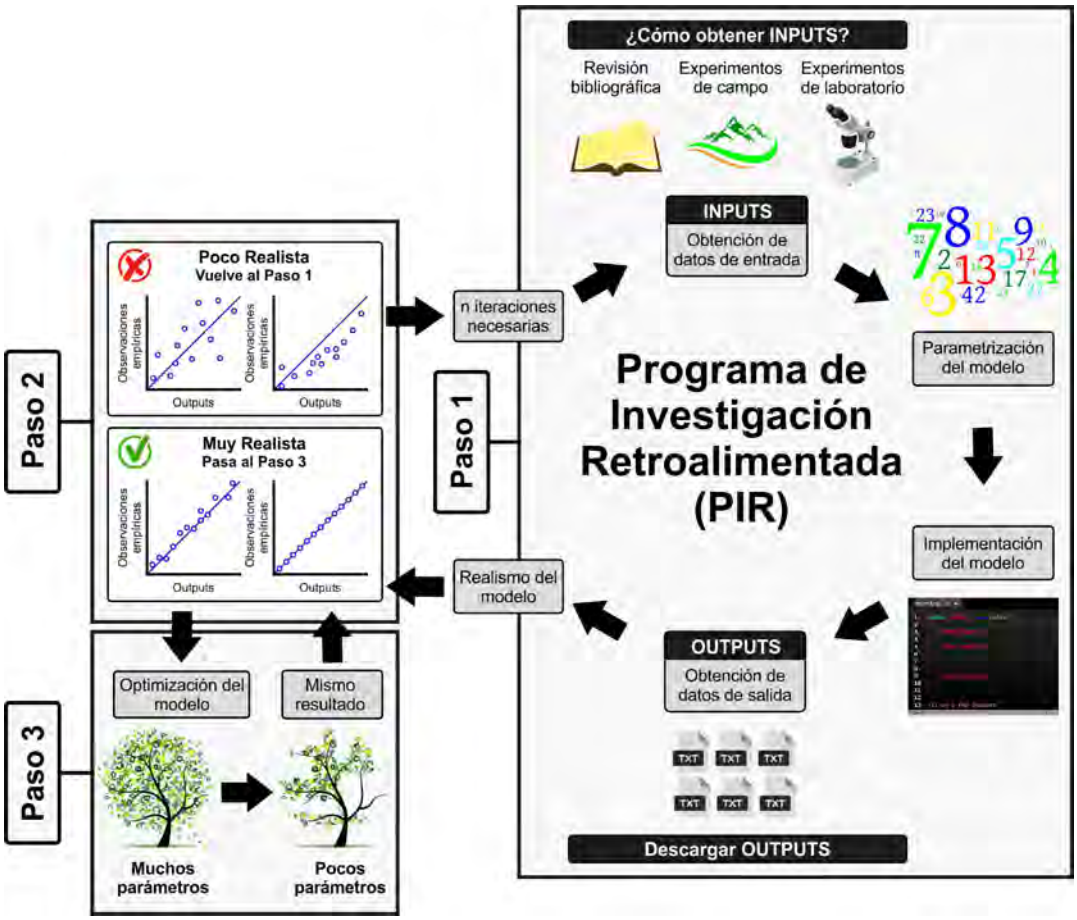

Figura 2. Pasos del Programa de Investigación Retroalimentada (PIR). Los recuadros en blanco representan los 3 pasos originales descritos por Moya-Laraño *et al*. 2012, 2014 y los recuadros en gris son pasos intermedios considerados de gran importancia en el Programa de Investigación Retroalimentada (PIR).

1.3. Precedentes e Historia de los Modelos Basados en Individuos en Ecología

Antes del gran salto a la modelización con IBMs los ecólogos trabajaban con modelos tradicionales de ecuaciones diferenciales a nivel de población, comunidad o ecosistema. En el ámbito en el que nos encontramos, los precedentes de los modernos IBMs están derivados del famoso Modelo Clásico Metapoblacional de Levins 1969, en el que se estudiaba la dinámica de poblaciones, en un hábitat

fragmentado en parches, de una única especie a lo largo del tiempo a través de la diferencia entre la tasa de colonización de parches vacíos y de extinción de parches ocupados. Este tipo de modelos pronto quedaron constreñidos por la dificultad que supone la resolución de gran cantidad de ecuaciones diferenciales. Destacamos el Modelo Metapoblacional de Nee & May 1992, una variante del Modelo Metapoblacional de Levins, en el cuál se incluía un nuevo parámetro que determinaba la fracción de parches destruidos (D) que no se podían colonizar. Cabe decir que este modelo era espacialmente implícito y fue diseñado para el estudio del efecto de la fragmentación de hábitat en dos especies que competían por los recursos, en este caso parches disponibles. Además, ambas especies se caracterizaban por un trade-off entre la capacidad de dispersión y la capacidad competitiva (Nee & May 1992). Como ya se había demostrado no era necesario destruir todos los parches para extinguir la metapoblacion por completo, el aislamiento inducía la propia extinción (Lande 1987). Programas de vacunación que erradicaban infecciones sin tener que llegar a vacunar a todos los huéspedes (cada huésped se consideraba un parche en la simulación) ya proporcionaban ilustraciones de este principio (Anderson & May 1985). No obstante, la revolución se produjo cuando empezaron a comparar los resultados obtenidos con ecuaciones diferenciales (Nee & May 1992) con los resultados obtenidos de un modelo espacialmente explícito basado en un Autómata Celular que simulaba un mundo de 50 x 50 celdas (Dytham 1994). Los Autómatas Celulares (AC) son modelos matemáticos para un sistema dinámico que evolucionan espacialmente en pasos de tiempo discretos o "steps". De ahí que sean muy adecuados para modelizar sistemas naturales dinámicos formados por un conjunto de objetos simples, en este caso poblaciones, que interactúan localmente unos con otros. A pesar de su gran aplicación a la biología, los Autómatas Celulares nacieron del campo de la física computacional (von Neumann 1966). Quizás uno de los Autómatas Celulares más conocidos sea el Juego de la Vida (Conway 1970), en el que cada celda tiene un valor: 0 para muerto y 1 para vivo; y el modelo evalúa el valor de las 8 celdas vecinas y contiguas a la celda diana (que es el Autómata Celular que toma decisiones). Dependiendo de los valores que tengan el Autómata Celular sigue cuatro reglas: a) muerte por soledad, b) estático o permaneciendo vivo en el siguiente paso , c) muerte por sobrepoblación y d) reproducción (enlace web: https://bitstorm.org/gameoflife/). A partir de estos trabajos se empezaron a desarrollar estudios que combinaban Modelos Metapoblacionales y Autómatas Celulares para estudiar el efecto de la fragmentación de hábitat sobre una especie (Bascompte & Solé 1996) o sobre cadenas tróficas depredador-presa (Bascompte & Solé 1998, Swihart *et al*. 2001). Posteriormente, incluso se desarrollaron Modelos Metapoblacionales de ecuaciones diferenciales con tres especies para estudiar la omnivoría, la competencia aparente y la depredación intragremial (Melián & Bascompte 2002) mediante ecuaciones diferenciales; o el efecto de la variabilidad genética de varios rasgos como crecimiento y la fenología sobre interacciones de una cadena tri-trófica (depredador-presa-recurso basal) embebida en en una red trófica compleja, así como sus consecuencias en la dinámica de meta-comunidades (Moya-Laraño 2011) mediante simulaciones por ordenador.

Los primeros Modelos Basados en Individuos empezaron a desarrollarse en el momento en el que los ordenadores tuvieron suficiente capacidad y potencia para poder llevar a cabo las simulaciones. Pasar de estudiar a nivel de ecosistema, comunidad o población a individuos y sus propiedades fue un gran paso pues tanto los modelos espacialmente implícitos basados en ecuaciones diferenciales como los modelos espacialmente explícitos basados en Autómatas Celulares, a pesar de sus aportaciones tanto en conocimiento de los sistemas formados por cadenas o redes tróficas sencillas como su aplicabilidad en el estudio de la fragmentación de hábitat (Nee & May 1992; Dytham 1994; Bascompte & Solé 1996, 1998), empezaron a quedarse obsoletos y el paso hacia modelizar el comportamiento de los individuos y testar si este comportamiento conduce a propiedades realistas a nivel de ecosistema fue una idea natural. Los Modelos Basados en Individuos permitían a los modelizadores en ecología investigar preguntas sobre sistemas ecológicos complejos que han sido difíciles o incluso imposibles de estudiar usando las aproximaciones clásicas de modelización o mediante experimentos de campo y/o laboratorio.

Dependiendo de los objetivos y motivaciones para desarrollar un Modelo Basado en Individuos en ecología existen dos categorías de IBMs: a) los modelos pragmáticos (Grimm 1999), donde la simulación de poblaciones, comunidades o ecosistemas se hace con un objetivo en mente donde representar explícitamente individuos es fundamental para responder a las preguntas y problemas planteadas que con otros modelos matemáticos más simples es imposible, y b) los modelos paradigmáticos (Lomnicki 1988; Uchmański 1985), que tienen como objetivo ayudarnos a tener una mejor compresión de las causas subyacentes de los fenómenos ecológicos porque se supone que se necesita un cambio de paradigma.

En las últimas cuatro décadas la evolución de los Modelos Basados en Individuos ha sido revolucionaria, pasando por tres grandes fases (DeAngelis & Grimm 2014). A continuación, vamos a centrarnos solamente en IBMs pragmáticos, dado que existe una preponderancia global a desarrollar este tipo de modelos (Grimm 1999):

Fase 1: Modelos Basados en Individuos de sucesión forestal

Uno de los primeros Modelos Basados en Individuos que fue muy influyente y además contribuyó significativamente al establecimiento de los IBMs fue un modelo de sucesión forestal llamado JABOWA (Botkin *et al*. 1972) en el que se describe el proceso de sucesión de comunidades de árboles en claros creados en bosques mixtos debido a la muerte de un área de dosel de árboles de 1000 m^2. La característica principal de este modelo era que cada árbol tenía una sola variable de estado, el diámetro del tronco. Mientras que el resto de variables se deducían del diámetro del tronco mediante relaciones alométricas ($Y = aX^b$). De esta forma diferentes especies tenían diferente crecimiento dentro del claro debido a los diferentes valores del factor de escala "a" y el factor alométrico "b", no por que se ajustasen a diferentes modelos. Era una forma sencilla de simular las

interacciones y dinámicas locales dentro del bosque, permitiendo tener el pedigree de todos los árboles y, además, debido a una sencilla parametrización, ser fácilmente testado. Cabe destacar que otro de los IBMs más importantes que sentó las bases de este tipo de modelos fue desarrollado por DeAngelis *et al*. 1979 y está basado en el mismo concepto que los modelos de sucesión forestal pero centrado en cohortes de peces, cuyo objetivo era predecir como el tamaño inicial de la distribución de la población provocaba cambios sustanciales en la distribución a lo largo del periodo de crecimiento.

No obstante, el éxito que tuvo el Modelo JABOWA en describir sucesiones forestales inspiró a muchos ecólogos a diseñar muchas variaciones de los llamados modelos forestales basados en gaps (Bugmann 2001), entre ellos, los modelos FORET (Sughart & West 1977), FORTNITE (Aber & Melillo 1982) y FORMIND (Köhler & Huth 1998).

Fase 2: Modelos Basados en Individuos de poblaciones animales

El paso de los Modelos Basados en Individuos de sucesión forestal hacia otros ámbitos de la ecología fue inicialmente lento, aunque empezaron a desarrollarse ya rápidamente a lo largo de los años 90 (DeAngelis & Gross 1992). La primera área en la que los IBMs empezaron a desarrollarse fue en el reclutamiento de poblaciones de peces, donde ya se incluía el impacto del ser humano en la mortalidad de los alevines, interacciones entre diferentes clases de edad, tasas de crecimiento, vulnerabilidad a la depredación y otras características que hacían que fueran más complejos pero que permitía modelizar y estudiar las interacciones entre individuos. De forma similar a lo que ocurrió con los modelos de sucesión forestal, estos modelos sentaron las bases para generar gran cantidad de submodelos en los ya se combinaban los IBMs con la bioenergética para determinar el crecimiento y supervivencia de los alevines (DeAngelis *et al*. 1993; Madenkian & Carpenter 1991; Rose & Cowan 1993; Scheffer *et al*. 1995). En una revisión de 2005 se cuantificó que ya existían aproximadamente 100 Modelos Basados en Individuos orientados a poblaciones de peces (DeAngelis & Mooij 2005). Gran cantidad de estos modelos estaban dedicados a peces de agua dulce, el salto hacia modelos de ecosistemas marinos permitió introducir el plancton y su ciclo de vida, así como otros factores físicos como temperatura, salinidad, flujos, turbulencia y luz (Parada *et al*. 2003; Werner *et al*. 1997; Werner *et al*. 2001).

Posteriormente empezaron a desarrollarse IBMs aplicados a otros tipos de poblaciones animales incluyendo funcionalidades que los hacían más realistas y donde se simulaban complejos comportamientos de los individuos y se incluía el paisaje. Surgen por primera vez los Modelos Basados en Individuos espacialmente explícitos para estudiar ungulados (Turner *et al*. 1993), cigüeñas (*Mycteria americana*) (Wolff 1994), osos pardos (*Ursus arctos*) (Wiegand *et al*. 1998), petirrojos (*Erithacus rubecula*) (Reuter & Brecking 1999), caracoleros comunes en Florida (*Rostrhamus sociabilis*) (Mooij *et al*. 2002); marmotas alpinas (*Marmota marmota*) (Stephens *et al*.

2002; Grimm *et al*. 2003) y gorriones costeros de Cabo Sable (*Ammodramus maritimus mirabilis*) - Modelo SIMSPAR (Elderd & Nott 2008).

Fase 3: Modelos Basados en Individuos de redes tróficas y epidemiología

Con el aumento de la potencia computacional empezaron a desarrollarse IBMs aún más realistas que permitían explorar conceptos básicos de la ecología y la biología evolutiva. En este momento los Modelos Basados en Individuos pueden simular comunidades de animales caracterizadas por su historia de vida e interacciones tróficas con múltiples trade-offs fisiológicos (Giacomini *et al*. 2013; Weiss *et al*. 2014), y por ello las redes tróficas empiezan a ser el centro de atención de los ecólogos modelizadores ya que pueden empezar a contestar preguntas que durante años eran imposibles de contestar usando los métodos clásicos de modelización, tales como las ecuaciones diferenciales (Schmitz & Booth 2014). Los tipos de regulación top-down y bottom-up de las poblaciones, así como, el estudio de cuáles son las causas que producen los ciclos poblacionales depredador-presa en las cadenas tróficas, ya conocidos por las ecuaciones diferenciales de Lotka-Volterra (Lotka 1925; Volterra 1926), son dos de las preguntas que más importancia adquieren con el desarrollo de estos IBMs.

Junto al estudio de las redes tróficas, otra de las ramas en la que empiezan a desarrollarse IBMs es en la modelización epidemiológica, donde no sólo vemos el modelo desde un punto de vista ecológico si no también social y público. Los primeros modelos en este ámbito están centrados en el estudio de la propagación de la rabia en mamíferos, concretamente en zorros (*Vulpes vulpes*) (Jeltsch *et al*. 1997; Eisinger & Thulke 2008).

Tenemos que destacar esta última fase por el boom que produjo los avances computacionales, ya que permitió que en el periodo entre el 2000 y el 2006 surgieran el mayor número de Modelos Basados en Individuos que se ha dado hasta la fecha. En tan solo 6 años se crearon, se validaron y dieron resultados, publicándose en algunos casos junto a su código fuente más de 70 IBMs (Jørgensen 2008).

1.4. Estandarización para describir los Modelos Basados en Individuos publicados: Protocolo ODD

Una de las grandes críticas de los Modelos Basados en Individuos era el hecho de la inexistencia de una estructura formal y métodos de análisis disponibles para los modelos matemáticos. Los modelos de simulación que describen organismos individuales han sido ampliamente utilizados no solo en ecología (DeAngelis & Gross 1992; DeAngelis & Mooij 2005; Grimm 1999; Grimm & Railsback 2005; Huse *et al*. 2002; Shugart *et al*. 1992; Van Winkle *et al*. 1993) si no también en ciencias sociales (Epstein & Axtell 1996; Gilbert & Troitzsch 2005), economía (Tesfatsion 2002), demografía (Billari & Prskawetz 2003), geografía (Parker *et al*. 2003) y ciencias políticas (Axelrod 1997; Huckfeldt *et al*. 2004). Estos IBMs son mucho más difíciles de analizar, entender y comunicar, y su descripción a

menudo es incompleta, ambigüa y menos accesible que los modelos analíticos tradicionales (Grimm *et al*. 1999). Esto supone que los resultados obtenidos con un IBM sean difíciles de reproducir, justo lo contrario a la base de la ciencia, en la que todas las observaciones deben ser reproducibles. Esto se debe a que no existe un protocolo estándar para describirlos, y en el caso de los que se describen las ecuaciones y reglas son explicadas verbalmente. Un protocolo estándar debe primero describir la estructura general del IBM independientemente de su estructura específica, propuesta y forma de implementación (Grimm 2002) y el lenguaje matemático debe estar separado de las consideraciones verbales.

Las ideas básicas de este protocolo fueron propuestas por Grimm & Railsback 2005 tras un workshop de Modelos Basados en Individuos en Bergen, Noruega en el año 2004 y que está descrito con el nombre de Protocolo PSPC + 3. Sin embargo, no fue hasta el año 2006 cuando se publicó un protocolo estandarizado dividido en tres bloques: 1) visión general, 2) conceptos del diseño y 3) detalles (Grimm *et al*. 2006), renombrado como Protocolo ODD. Este protocolo consiste en que la estructura e información sobre el IBM sea descrita siempre en la misma secuencia, formada por siete elementos agrupados en los tres bloques nombrados anteriormente (Tabla 1). El bloque 1 de visión general contiene tres elementos: 1) propuesta, 2) variables de estado y escalas, y 3) resumen del proceso y programación. Los lectores con solo leer este bloque se hacen una idea del objetivo, resolución y complejidad del modelo. El bloque 2 sólo contiene un elemento donde se describen los conceptos generales del modelo. Por último, el bloque 3 contiene tres elementos: 1) inicialización, 2) entradas, y 3) submodelos implementados. Esta estructura permite tener un primer acercamiento al modelo, para más tarde conocer otras consideraciones más específicas y finalmente entrar en los detalles técnicos del mismo (Tabla 1).

Tabla 1. Estructura del Protocolo ODD. Los siete elementos están agrupados en tres bloques: Visión General, Conceptos del diseño y Detalles junto a una descripción general. Modificado de la Figura 1 de Grimm *et al*. 2006.

Bloques	Elementos	Descripción
1 Visión General	**1 Propuesta**	¿Por qué el modelo contiene algunos aspectos de la realidad y otros han sido excluidos?
	2 Variables de estado y escalas	Conjunto completo de variables de estado o variables de bajo nivel que caracterizan a los individuos y el hábitat. No confundir con variables auxiliares o agregadas como el tamaño de la población o la estructura de edades que pueden obtenerse de las variables de estado. Conjunto de variables de alto nivel, el modelo simula poblaciones de individuos, una comunidad formada por poblaciones o un paisaje. Escalas: unidad de tiempo de cada "step", duración de las simulaciones, unidad de espacio (celda), tamaño del mundo.
	3 Resumen del proceso y programación	Descripción verbal de los procesos ambientales y de los individuos como producción de comida, alimentación, crecimiento, movimiento, mortalidad o reproducción.

(Continuación)

2	**Conceptos del diseño**	**4**	**Conceptos del diseño**	Lista de las características de diseño del modelo: • **Emergencia:** ¿Cómo emergen los fenómenos o patrones a nivel de sistema a partir de los rasgos de los individuos? • **Adaptación**: ¿Los individuos tienen un comportamiento adaptativo que les permite sobrevivir, crecer y reproducirse ante cambios de su ambiente? • **Eficacia biológica o fitness:** ¿Está modelizada explícita o implícitamente? • **Predicción:** ¿Los individuos adquieren experiencia en la simulación? • **Sensibilidad:** ¿Los individuos son capaces de captar los cambios en el ambiente y tomar decisiones de forma adaptativa? • **Interacción:** ¿Qué tipo de interacciones se producen? • **Estocasticidad:** ¿El modelo es estocástico? • **Colectivos:** ¿Los individuos se agrupan en grupos sociales? • **Observación:** ¿Cómo se obtienen, testan, entienden y analizan los datos procedentes del modelo?
3	**Detalles**	**5**	**Inicialización**	¿Cómo se crea el ambiente y los individuos al principio de la simulación?
		6	**Entradas**	Todas las entradas que se le proporcionan al modelo como las condiciones ambientales que cambian en el tiempo y en el espacio, así como las semillas de los números aleatorios para que la simlación sea reproducible.
		7	**Submodelos**	Explicación detallada y parametrización de todos los procesos descritos en el Elemento 3, mediante diagramas de flujo.

Cuatro años después de la publicación del Protocolo ODD, Grimm *et al*. 2010 realizaron una revisión con el fin de conocer el alcance de su protocolo de estandarización. Durante el proceso de revisión buscaron en "Web of Science" todas las publicaciones que hicieran referencia al Protocolo ODD, en ellas chequearon si el formato ODD se había seguido completamente siguiendo los tres bloques y los siete elementos, si habían seguido más o menos las premisas descritas por Grimm *et al.* 2006 o si habían hecho un uso incorrecto del Protocolo ODD (Figura 3). Hasta diciembre de 2009, habían encontrado 54 publicaciones que seguían el Protocolo ODD, de las cuales sólo 33 habían seguido la metodología propuesta por Grimm *et al*. 2006 y 11 no lo seguían completamente. La mayoría de las publicaciones eran de ecología (38 publicaciones o 70%), el resto eran de ciencias del comportamiento (6), epidemiología, ciencias forestales, microbiología, investigación biomédica y oceanografía (1 publicación en cada área).

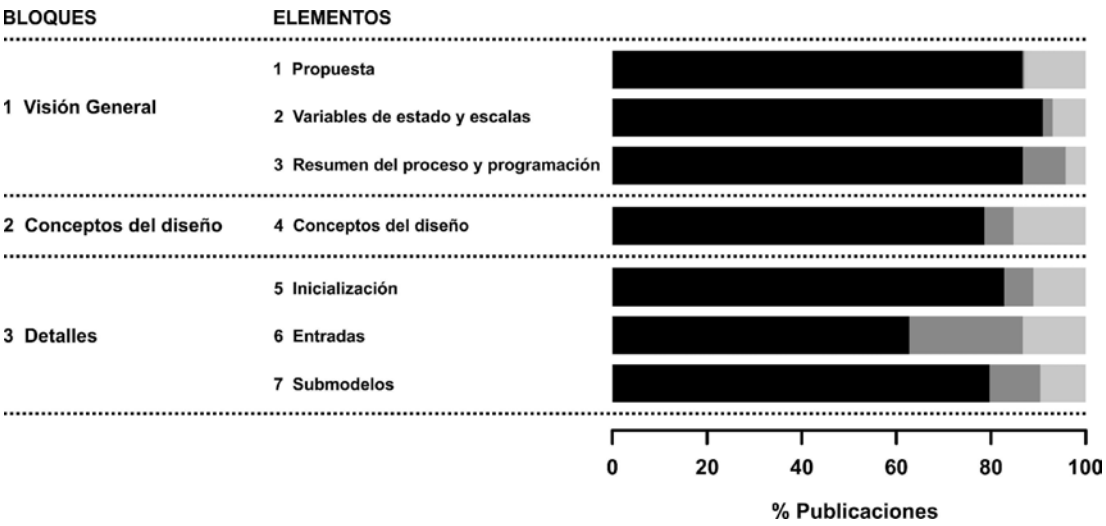

Figura 3. Porcentaje de publicaciones que utilizan el Protocolo ODD (n = 54) para describir Modelos Basados en Individuos (IBMs) o Agentes (AGMs) publicadas entre 2006 y 2009. El Protocolo ODD incluye los tres bloques y los siete elementos descritos en Grimm *et al*. 2006. En negro los elementos que han sido nombrados y utilizados como se describen en Grimm *et al*. 2006; en gris oscuro los elementos incluidos y nombrados pero que se han malinterpretado y en gris claro los elementos que han sido omitidos o nombrados incorrectamente. Modificado de la Figura 1 de Grimm *et al*. 2010.

Tras esta revisión decidieron hacer algunos cambios en el Protocolo ODD, cambiaron el nombre del elemento 3 de variables de estado y escalas a entidades, variables de estado y escalas, donde una entidad es un objeto que se comporta como una unidad que interactúa con otras unidades y con los factores ambientales, es decir, en la mayoría de casos los individuos. Además, decidieron incluir tres nuevos conceptos de diseño: 1) principios básicos, es decir, ¿cuáles son los conceptos, teorías, hipótesis o aproximaciones utilizadas para entender el diseño del modelo?, 2) objetivos, por ejemplo, si los rasgos adaptativos actúan sobre alguna medida aumentando el éxito del individuo (eficacia biológica o fitness) y qué objetivo tiene ese rasgo adaptativo, y 3) aprendizaje, ¿los individuos son capaces de modificar su comportamiento de forma adaptativa a lo largo del tiempo como consecuencia de la experiencia? Por último, decidieron quitar el concepto de eficacia biológica o fitness (Tabla 2).

Tabla 2. Comparación entre el Protocolo ODD original y el revisado. En negrita los conceptos añadidos en el elemento 2 y 4, y en gris claro los elementos eliminados. Modificado de la Tabla 1 de Grimm *et al*. 2010.

Bloques		**Elementos del Original Protocolo ODD Grimm *et al*. 2006**	**Elementos del Revisado Protocolo ODD Grimm *et al*. 2010**
1	Visión General	1 Propuesta	1 Propuesta
		2 Variables de estado y escalas	**2 Entidades**, variables de estado y escalas
		3 Resumen del proceso y programación	3 Resumen del proceso y programación

(*Continucación)*

2	Conceptos del diseño	4	Conceptos del diseño: • Emergencia • Adaptación • Eficacia biológica o fitness • Predicción • Sensibilidad • Interacción • Estocasticidad • Colectivos • Observación	4	Conceptos del diseño: • **Principios Básicos** • Emergencia • Adaptación • Eficacia biológica o fitness • **Objetivos** • **Aprendizaje** • Predicción • Sensibilidad • Interacción • Estocasticidad • Colectivos • Observación
3	Detalles	5	Inicialización	5	Inicialización
		6	Entradas	6	Entradas
		7	Submodelos	7	Submodelos

A pesar de la gran aceptación que tuvo el Protocolo ODD, hoy en día muchos autores no incluyen en sus publicaciones de IBMs todos los elementos descritos completos. Sin embargo, la revisión de Grimm *et al*. 2010 y el mejorado protocolo lo desarrollaron como estimulación a que los investigadores intentaran incorporarlo y ofrecieran una retroalimentación para poder ir mejorándolo.

2. Modelos Basados en Individuos de Nueva Generación en Ecología

La modelización ecológica hoy en día ha alcanzo un nivel de madurez suficiente para desarrollar lo que Grimm & Berger 2016a llama modelización de nueva generación que se caracteriza por tres elementos esenciales (Figura 4):

1) Realismo del modelo:

Se necesitan indicadores de realismo en los modelos y una nueva cultura para comunicarlos, tanto al mundo científico como al resto de la sociedad, así como que dichos modelos contesten a preguntas como: ¿hasta qué punto los modelos capturan la organización real del sistema? ¿Cuáles son los detalles clave de los modelos para entender su funcionamiento? (Grimm & Berger 2016b).

2) Emergencia de fenómenos ecológicos:

Para permitir que los modelos realicen predicciones sólidas ante condiciones ambientales cambiantes, los procesos clave a nivel de población, comunidad o ecosistema, así como los patrones deben surgir o emerger de los procesos de nivel inferior (individuos), por ejemplo, de los rasgos fisiológicos, los comportamientos de búsqueda de aptitud física o las reacciones entre organismos y su entorno abiótico. De esa manera, quedan vinculados dos o más niveles jerárquicos de los

ecosistemas y quedan demostradas las interconexiones entre los mecanismos, las estructuras y las restricciones generales (Roughgarden 2012).

3) Predicciones:

Las salidas o "outputs" que proporciona el modelo deben ser consideradas como predicciones sólidas, de manera que si se introducen nuevas condiciones de entrada o "inputs" los resultados obtenidos se puedan considerar como una buena predicción de respuesta ante condiciones iniciales cambiantes de las que no existen datos previos sobre sus consecuencias. Por lo tanto, el modelo debe estar bien calibrado y permitir una buena extrapolación, pronóstico y predición de nuevas preguntas.

Bajo el amparo de estos tres elementos descritos por Grimm & Berger 2016a, los autores aportan una guía de características esenciales que deben tener los modelos para ser considerados de nueva generación. De manera que los ecólogos, independientemente del sistema que estudien, puedan seguir una serie de pautas a la hora de diseñar y describir sus modelos. Las características que deben incluir en esta nueva generación de modelos en ecología son las siguientes (Figura 4):

a) Principios básicos

Las tasas demográficas o vitales (ej.: mortalidad, colonización, extinción o fecundidad) son elementos clave del ciclo de vida de un individuo y deben emerger a lo largo de la simulación como consecuencia de la interacción entre los individuos con las condiciones bióticas y abióticas del ambiente que les rodea. Estas tasas surgen de los llamados principios básicos del modelo que pueden proceder de características físicas o químicas del ambiente, y de la fisiología de los individuos (Fischer *et al*. 2016; van der Vaart *et al*. 2016), de la teoría evolutiva (Ayllón *et al*. 2016; Belarde & Railsback 2016; Eliassen *et al*. 2016; Stillman et al. 2015, 2016), tanques energéticos llamados "energy budgets" (Martin *et al*. 2012, 2013; Sibly *et al*. 2013; van der Vaart *et al*. 2016), de la estequiometría ecológica, que estudia el balance de energía y elementos químicos en las interacciones ecológicas (Kaiser *et al*. 2014; Smith *et al*. 2014) o de la fotosíntesis y competencia por la luz (Köhler & Huth 1998; Fischer *et al*. 2016).

b) Condiciones abióticas dinámicas y heterogéneas del ambiente

En los modelos espacialmente explícitos basados en celdas debe existir una interacción entre los individuos y su comportamiento adaptativo ante dinámicas heterogéneas de las condiciones ambientales. Los factores abióticos determinan las elecciones de los individuos y su eficacia biológica, además los individuos pueden modifican las condiciones abióticas, y éstas a su vez de vuelta a los individuos del modelo. En este nuevo tipo de modelos emergen dinámicas eco-evolutivas de manera que los agentes de selección (condiciones ambientales) pueden inducir cambios en la

arquitectura genética y a la inversa (Ayllón *et al*. 2016; Belarde & Railsback 2016; DeAngelis *et al*. 1980; Tietjen 2016). Este tipo de modelización requiere años de desarrollo, revisión y testado pudiéndose considerar la creación de modelos de nueva generación con estas características "big science" (Stillman *et al*. 2015), en el sentido que pueden implicar la participación cooperativa de un gran número de personas de diferentes nacionalidades y centros de investigación.

c) Desarrollo teórico: Vinculando comportamiento y fisiología con ecología

A la hora de diseñar un modelo hay que identificar los principios generales y teorías más allá del individuo (poblaciones, comunidades, ecosistemas e incluso paisajes) identificando y unificando la teoría ecológica (Houston *et al*. 1988) no focalizando el modelo en un sistema concreto si no flexible para estudiar cualquier sistema ecológico: animales, plantas, microbiota en el ámbito terrestre, marino o sistemas de agua dulce. De esta forma los factores bióticos y procesos asumidos durante el desarrollo teórico permiten que el modelo se pueda utilizar como un laboratorio virtual para testar modelos alternativos comparando las salidas que proporcionan. Este tipo de modelos se consideran "just working fine", que podríamos traducir en castellano desde mi punto de vista como "trabajando bien e hilando fino", por ser realistas y proporcionar predicciones robustas (Grimm & Berger 2016b).

d) Vinculando Modelos Basados en Individuos con Modelos Basados en Rasgos

Los Modelos Basados en Individuos de Nueva Generación deben romper la barrera del individuo y vincular la aproximación genérica de especies y con la aproximación basada en un pool de rasgos y combinaciones de rasgos para múltiples especies (McGill *et al*. 2006). Las aproximaciones basadas en rasgos y no en individuos se han hecho recientemetne muy populares en ecología (Lichtman & Klausmeier 2008; Suding *et al*. 2008) debido al incremento de las bases de datos de rasgos que correlacionaban las características del hábitat con los valores de los rasgos (Kattge *et al*. 2011).

e) Microevolución

En los modelos ecológicos, la evolución ha sido tradicionalmente totalmente ignorada ya que se creía que simularla era imposible por la escala temporal. Sin embargo, hoy en día sabemos que se producen procesos de microevolución en tiempo ecológico, ya no hablamos en términos de tiempo histórico donde pueden producirse procesos de especiación (Hairston *et al*. 2005), sobre todo si estudiamos taxones que pueden tener gran cantidad de generaciones en poco tiempo. Incluir algoritmos genéticos en los Modelos Basados en Individuos permite hacer que los rasgos evolucionen a lo largo de la simulación, incluyendo la evolución de la plasticidad fenotípica. Esto permite simular las dinámicas eco-evolutivas de una forma más realista y robusta a pesar de ser aún un campo joven dentro del mundo de la modelización (Pelletier *et al*. 2009).

f) Submodelos estandarizados

Los futuros modelos de nueva generación deben diferenciarse del tipo de modelización anterior por su coherencia, efectividad y fácil manejo desarrollando e implementando submodelos estandarizados que incluyen, por ejemplo, teorías de comportamiento o de interacciones de los individuos. Al ser submodelos estandarizados, el Modelo Basado en Individuos puede utilizarse para un amplio rango de especies, sistemas y ambientes simplemente con una nueva parametrización sencilla, dejando atrás los llamados "big models" iniciales imposibles de extrapolar a sistemas ecológicos que no sean para el que fueron creados (Grimm & Berger 2016a).

g) Resiliencia del sistema y múltiples estresores

Una de las principales cuestiones en ecología es poder predecir que ocurrirá es un sistema determinado si incluimos un factor de estrés, como podría ser por ejemplo ambiental como la temperatura o la sequía, sobre todo en estos últimos años con el creciente estudio de los efectos futuros del Cambio Climático (IPCC Special Report; Leahy 2018). Los IBMs son excelentes modelos para estudiar como un cambio en las condiciones ambientales bióticas o abióticas puede afectar al sistema, por ejemplo, colapsándolo o manteniendo su resiliencia (Grimm et al. 1999). Entendiendo la resiliencia de un ecosistema como la capacidad de estos de absorber perturbaciones, sin alterar significativamente sus características de estructura y funcionalidad; pudiendo regresar a su estado original una vez que la perturbación ha terminado (Holling 1973). Los modelos de nueva generación deben tener en cuenta la teoría de la resiliencia (Gunderson *et al*. 2009; Cumming 2011) y permitir estudiar qué propiedades estabilizan el sistema ante una perturbación.

h) Análisis del modelo y parametrización

Como se ha dicho anteriormente, este tipo de modelos sean o no de nueva generación requieren de un nivel de complejidad para ser útiles (Duarte *et al*. 2019) independientemente del objetivo de su creación, pero sobre todo si son creados para desarrollar soluciones teóricas o prácticas a problemas ambientales. Una de las características más importantes de los modelos de nueva generación es que el proceso de parametrización (Figura 1) debe ser independiente para cada submodelo estandarizado, basándose en observaciones y experimentos con individuos. Además, el análisis de modelos tan complejos de nueva generación es quizás una de las partes más importantes pues el volumen de datos proporcionados por las simulaciones puede ser inmenso. Por ello, la utilización de supercomputadoras con cientos o miles de CPUs y el acceso a diferentes clústers computacionales son un requisito básico para estos modelos (van der Vaart *et al*. 2016), lo que implica tener que afrontarse a "big data" o macrodatos, conjuntos de datos o combinaciones de conjuntos de datos cuyo tamaño (volumen), complejidad (variabilidad) y velocidad de crecimiento (velocidad) dificultan su captura, gestión, procesamiento o análisis mediante tecnologías y herramientas convencionales. Esta gran cantidad de datos no nos asusta, pues lo que hace que sea tan útil este tipo de simulación

es el hecho de que proporciona respuestas a muchas preguntas (Laney 2001; Hilbert & López 2011; Goes 2014; Marr 2014; Breur 2016).

i) Vinculando modelos de distribución de especies y mecanismos

Una de las aproximaciones de tipo correlativo que más se tienen en cuenta es la implementación de modelos de distribución de especies que incluyen objetivos mecanicistas; es decir, descripciones basadas en procesos como historia vital, fisiología e interacciones bióticas (Singer *et al*. 2016) y que puedan ser parametrizados con relativa facilidad (García-Callejas & Araújo 2016). Para llevar a cabo esto Singer *et al*. 2016 propusieron un protocolo estándar que incluye cinco grandes pasos: 1) un conocimiento basado en una preselección de los procesos ecológicos que queremos incluir en el modelo, 2) una buena y directa parametrización y calibración, 3) una prueba exhaustiva de la incertidumbre del modelo, 4) una retroalimentación entre las simulaciones y la investigación empírica y 5) una estrategia estandarizada de la comunicación del modelo que aporte transparencia y fiabilidad de las predicciones. Muchos elementos de este protocolo ya se encuentran entre las recomendaciones de otros protocolos de buenas prácticas de modelización (Schmolke *et al*. 2010; Grimm *et al*. 2014; Grimm & Railsback 2005).

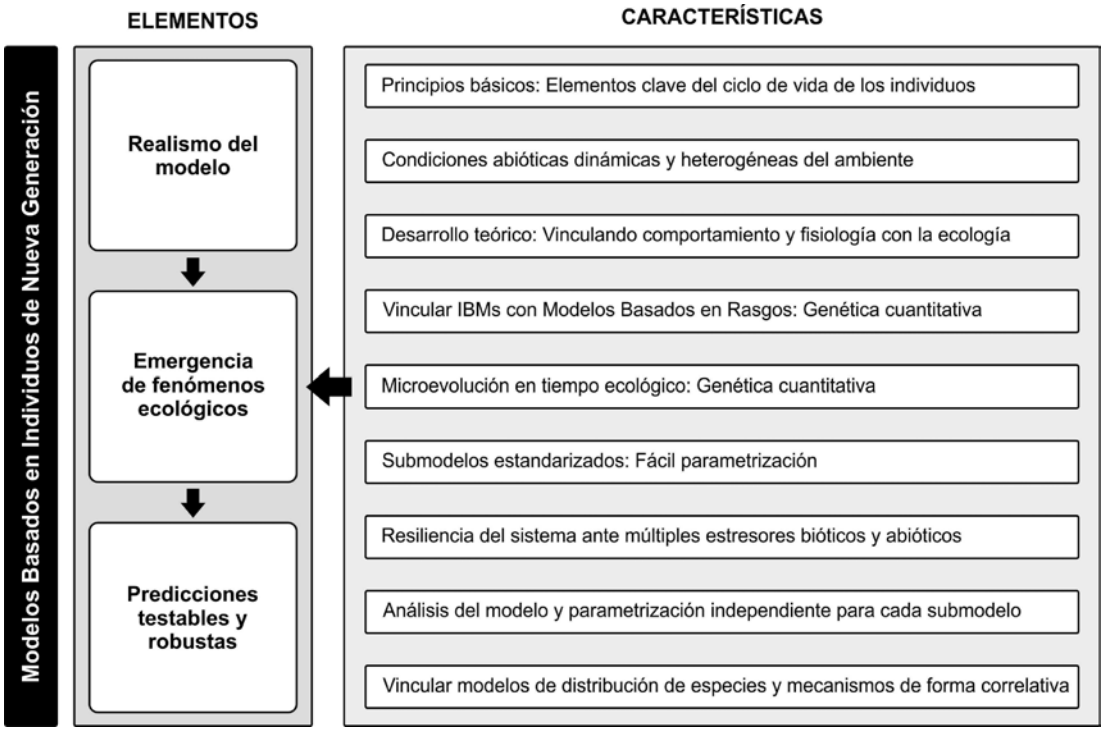

Figura 4. Elementos y características de los Modelos Basados en Individuos de Nueva Generación. Para más detalles sobre los elementos y características, leer el texto. Modificado de la Figura 1 de Grimm & Berger 2016a.

La creación y utilización de los Modelos Basados en Individuos de Nueva Generación deben dirigirse hacia grandes preguntas de la Ecología como, por ejemplo, la estabilidad y resiliencia de los ecosistemas, entendimiento de mecanismos, el papel de la biodiversidad, el papel de la variabilidad genética en las dinámicas eco-evolutivas, cómo los servicios ecosistémicos se pueden ver afectados ante el Cambio Climático, etc; sin olvidar que estamos hablando de "big science" donde poner todos los aspectos citados en común, crear, analizar, revisar y testar el modelo requiere largos periodos de tiempo y colaboraciones entre grupos de investigación interdisciplinares (Grimm *et al*. 2017). No obstante, bajo ciertas circunstancias esto no es posible, aunque es lo ideal, y en su lugar se puede formar un grupo de investigación de sistemas multidisciplinar dedicado a ecología computacional constituido por ecólogos con formación y conocimientos de programación, y técnicos informáticos con conocimientos en ecología. Podemos destacar dos Modelos Basados en Individuos de Nueva Generación en Ecología de los más completos que se han desarrollado hasta el momento, que siguen las características y elementos propuestos por Grimm & Berger 2016a:

InSTREAM-Gen (Ayllón *et al*. 2016):

Es un IBM espacialmente explícito basado en celdas desarrollado para simular dinámicas eco-evolutivas de poblaciones de truchas en ríos sometidas a cambios antrópicos del medio en el que viven. Los efectos a nivel de población emergen como consecuencia del comportamientos de los individuos y de las interacciones. La profundidad del río, la velocidad del flujo de agua, la temperatura, la turbidez, el riesgo de depredación y la competencia son los factores que determinan las dinámicas eco-evolutivas incluyendo la microevolución y la selección de hábitat. De todas las características propuestas por Grimm & Berger 2016a, este IBM incluye comportamientos adaptativos, tanques energéticos, genética cuantitativa, submodelos estandarizados, persistencia del sistema (teoría de la resiliencia) y un ambiente heterogéneo.

FORMIND (Fisher *et al*. 2016):

También es un IBM espacialmente explícito basado en celdas diseñado para estudiar las dinámicas del carbono mediante diferentes tipos funcionales de plantas, constituidas por cierta combinación de rasgos, en bosques tropicales húmedos. Los IBMs basados en celdas que simulan plantas normalmente no simulan individuos si no unidades espaciales, es decir, porcentaje de celdas con cubierta vegetal o recursos (Jiang *et al*. 2016; Tietjen 2016). FORMIND funciona de esta manera, considerando las interacciones entre celdas vecinas dependiendo de la distancia entre las plantas y su tamaño, también incorpora una aproximación estándar de competencia por la luz, incluyendo submodelos de fotosíntesis, de una forma parecida a los modelos basados en individuos de sucesión forestal mediante "gap models". De todas las características propuestas por Grimm & Berger 2016a, este IBM incluye flujos de carbono, submodelos estandarizados, características eco-fisiológicas de las plantas y vincula el modelo basado en individuos con un modelo basado en rasgos.

3. ¿Cómo encaja toda esta base teórica en la presente Tesis Doctoral?

Esta Tesis Doctoral está enmarcada dentro del contexto del estudio de las dinámicas eco-evolutivas de una red trófica de la hojarasca de los hayedos (*Fasgus sylvatica* L.) mediante simulación. Veremos que los Modelos Basados en Individuos o IBMs, el Ciclo de la Modelización descrito por Grimm & Railsback 2005 y el Programa de Investigación Retroalimentada acuñado y desarrollado por Moya-Laraño *et al*. 2012 copan un lugar primordial para llevar a cabo dichos estudios.

3.1. Modelo Basado en Individuos mini-AKIRA

mini-AKIRA es un Modelo Basado en Individuos (IBM) implementado en lenguaje R (R Development Core Team 2012) cuyo objetivo principal y para el que fue creado era simular y estudiar dinámicas eco-evolutivas en redes tróficas, más concretamente de una cadena trófica de la hojarasca de los hayedos (*Fagus sylvatica* L.) formada por un sistema depredador-presa-recurso basal (hongo). No obstante, actualmente esta versión está totalmente obsoleta y no se utiliza (Moya-Laraño *et al*. 2012). El programa tardaba aproximadamente 48h en correr una simulación y utilizábamos una Estación de trabajo llamada ARALE, localizada en la Estación Experimental de Zonas Áridas (EEZA-CSIC) formada por un ordenador Intel Core con un procesador i7 990 Extreme Edition y 24 GB DDR3 de memoria RAM, que podía soportar correr en continuo 10 réplicas de la misma simulación. Esta estación de trabajo aún existe en las instalaciones de la EEZA y sigue siendo utilizado por los diferentes grupos de investigación. Una copia del código fuente original la podéis encontrar en: http://www.eeza.csic.es/eeza/documentos/mini-Akira_1.01.zip

3.1.1. ¿Por qué se seleccionaron los hayedos (*Fagus sylvatica* L.) como sistema de estudio?

Los hayedos son bosques atlánticos típicos del piso montano de la Región Eurosiberiana de la Península Ibérica situados entre los 800 y 1000 m de altura por encima del nivel del mar (Blanco-Castro *et al*. 1997). La precipitación media anual en su rango de distribución oscila entre los 500 y 1500 mm dependiendo del ombroclima (subhúmedo, húmedo o hiperhúmedo) y la temperatura media anual se encuentra entre 7°C y los 10°C. El haya es un árbol caducifolio que da lugar a formaciones muy tupidas donde en algunos casos quedan excluidas otras especies leñosas e incluso herbáceas. La hoja del haya cae en otoño y produce una acumulación continua de hojarasca que se descompone. Esto proporciona condiciones ambientales más o menos estables que favorecen la actividad de la meso- y macrofauna del suelo (Melguizo-Ruiz *et al*. 2012; Melguizo-Ruiz 2016). Las características descritas anteriormente hacen que los hayedos sean sistemas idóneos para simular redes tróficas de invertebrados de la hojarasca por las siguientes razones:

1) Estructuración del hábitat e importantes dinámicas de metacomunidades:

El agua en estos ambientes está a menudo heterogéneamente distribuido a nivel de micro-escala (micro-topografía) (Herbst & Dikekkruger 2003; Jost *et al*. 2004; Melguizo-Ruiz *et al*. 2012; Schume *et al*. 2003). Esto se debe a la tasa diferencial de desecación del suelo que produce la existencia de

parches secos entremezclados con parches húmedos localizados debajo de las copas de las plantas, en la base de las rocas, debajo de troncos caídos, en vaguadas donde la pendiente del hayedo desaparece y en la parte baja de los hayedos donde la hojarasca y los nutrientes se acumulan (Famiglietti *et al*. 1998; Melguizo-Ruiz *et al*. 2012). Esta heterogeneidad espacial de bolsas de agua en el suelo ricas en recursos es muy importante para las dinámicas, estructura y persistencia de las redes tróficas en el tiempo (Levins 1969). Durante los periodos secos, cuando la distribución de estos bolsillos es más heterogénea, los invertebrados del suelo son atraídos por estos parches húmedos para disminuir la pérdida de agua (Verdeny-Vilalta & Moya-Laraño 2014). Esto provoca la aparición de grandes densidades de invertebrados en estas zonas respecto a otras partes del bosque, de manera que en un 1 m^2 de hojarasca no muy profunda podemos llegar a tener una densidad de entre 400 y 800 individuos considerando los siguientes grupos taxonómicos de meso- (considerada esta sólo la de gran tamaño > 0.5 mm) y macrofauna de la hojarasca: Acari, Annelida (Enchytraeidae y Lumbricidae), Araneane, Coleoptera (Carabidae y Staphylinidae), Collembola, Chilopoda (Geophilomorpha, Lithobiomorpha y Scolopendromorpha), Diplopoda (Julida y Pselaphognata) e Isopoda; y lo que hace que el número e intesidad de las interacciones aumente (Verdeny-Vilalta 2013).

2) Fácil experimentación mediante mesocosmos de campo:

Debido a la humedad de este suelo durante todo el año, permite con cierta facilidad instalar experimentos de mesocosmos de campo basados en aislar parte del ecosistema mediante parcelas cerradas. Estas parcelas de acero galvanizdo de de 50 x 50 cm^2 se entierran a 10 cm de profundidad en el suelo para minimizar las migraciones horizontales de los animales, para evitar las migraciones verticales se cubren superior e inferiormente con una malla de fibra de vidrio de 1.2 mm de luz de malla. Durante la primavera de 2012, entre mayo y julio, se instalaron 80 parcelas experimentales en 8 bosques de hayas (*Fagus sylvatica* L.) a lo largo de un gradiente pluviométrico en la Cordillera Cantábrica (Asturias). En este experimento de mesocosmos, se estudió entre otras cosas el efecto de la eliminación de los grandes depredadores sobre la red trófica. Demostraron que la ausencia de grandes depredadores en las redes tróficas del suelo puede causar una fuerte reducción de las poblaciones de invertebrados, desde depredadores pequeños hasta descomponedores primarios y secundarios, e incluso retrasar los procesos de los ecosistemas asociados, como la descomposición de la hojarasca (Melguizo-Ruiz, datos sin publicar). No existe una explicación clara de los procesos que llevaron a los patrones encontrados. La utilización de un IBM sería muy adecuada.

3) Fácil mantenimiento de la hojarasca en condiciones de laboratorio:

Por último, hay que destacar el fácil mantenimiento de la hojarasca de los hayedos (*Fagus sylvatica* L.) en condiciones de laboratorio durante largos periodos de tiempo, con el fin de realizar experimentos de mesocosmos de laboratorio de meso- y macrofauna de la hojarasca. Con éxito se han recolectado muestras de hojarasca en contenedores de plástico en diversos hayedos de la

Cordillera Cantábrica (Asturias), transportadas y mantenidas en una cámara climática a 20°C, entre el 60% y el 80% de humedad relativa y un fotoperiodo de 24 h de oscuridad (0h:24h) durante más de 12 meses en la Estación Experimental de Zonas Áridas (EEZA-CSIC) en Almería. La hojarasca es colocada en recipientes plásctcos de 50 x 40 x 25 cm^3 y cubiertos en la parte superior con organza de 0.2 mm de luz de malla para evitar la pérdida de individuos (Figura 5a). Solamente requiere la aportación 140 ml de agua en spray y 0.4 g de levadura de cerveza (*Saccharomyces cerevisiae* Meyen ex E.C. Hansen) a la semana para su mantenimiento. Este fácil mantenimiento permite llevar a cabo la medición de rasgos que luego puedan ser utilizados en simulaciones, tales como la capacidad de desecación o la capacidad de movimiento (velocidad y actividad) mediante filmaciones (Figura 5b, 5c, 5d).

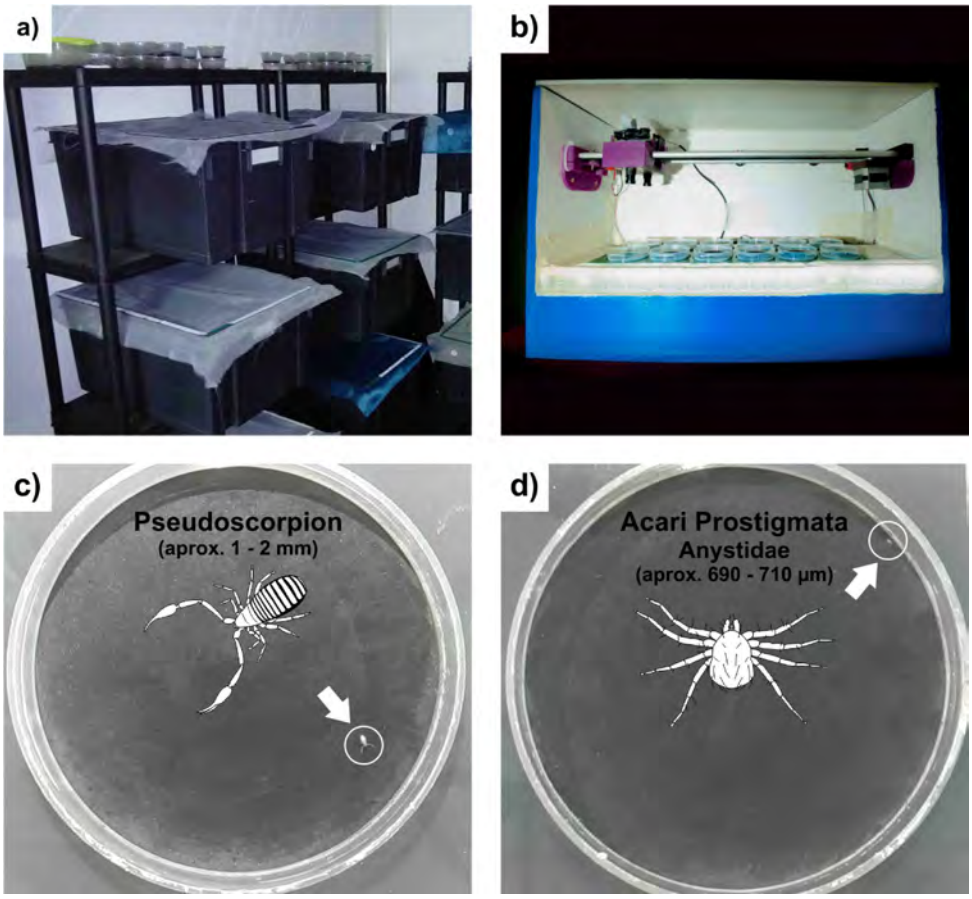

Figura 5. Mantenimineto de la hojarasca en laboratorio y sistema de filmación por infrarrojos. a) Sistema de mantenimiento de la hojarasca de los hayedos (*Fagus sylvatica* L.) en condiciones de laboratorio, b) sistema de filmación por infrarrojos diseñado por Alberto Ruiz y Ramón Ordiales de la Estación Experimental de Zonas Áridas (EEZA-CSIC), c) filmación de un pseudoscorpión (aprox. 1 - 2 mm de longitud corporal sin apéndices) y d) filmación de un ácaro de la familia Anystidae, el grupo animal más rápido del mundo para su tamaño corporal (apox. 690 - 710 µm de longitud corporal sin apéndices) (fotos cedidas por Eva de Mas y Dolores Ruiz-Lupión).

3.1.2. Características del Modelo Basado en Individuos mini-AKIRA

Este IBM en su momento fue novedoso por utilizar una aproximación que vinculaba genes a cascadas tróficas y consideraba explícitamente la Teoría Metabólica en Ecología (Brown *et al*. 2004), lo que lo hacía muy útil para estudiar dinámicas tróficas bajo diferentes condiciones de temperatura y, por ende, diferentes escenarios de Cambio Climático, así como demostrar como la genética afecta a las dinámicas eco-evolutivas en redes tróficas. A continuación, mostramos un resumen de las características básicas del modelo (Ruiz-Lupión 2013, Trabajo Fin de Máster disponible en el enlace web: http://hdl.handle.net/10261/180397), para más información consultar (Moya-Laraño *et al*. 2012):

1) Espacio y recursos basales:

mini-AKIRA es un modelo semi-espacialmente explícito, pues no está formado por un mundo virtual basado en celdas formando una cuadrícula, si no que está compuesto por 100 celdas localizadas en un círculo cerrado (toro), en el cual los animales sólo tienen dos direcciones alternativas para moverse (izquierda o derecha). Así, cuando los individuos se encuentran en la celda 1 pueden desplazarse hacia la celda 100 y *viceversa*. Además, la productividad de cada celda puede estar o no espacialmente autocorrelacionada, al inicio de las simulaciones la celda central (50) contenía el pico de productividad máxima dependiendo de la capacidad de carga (K) y disminuía linealmente hacia las celdas de los bordes (1 y 100) (Figura 6).

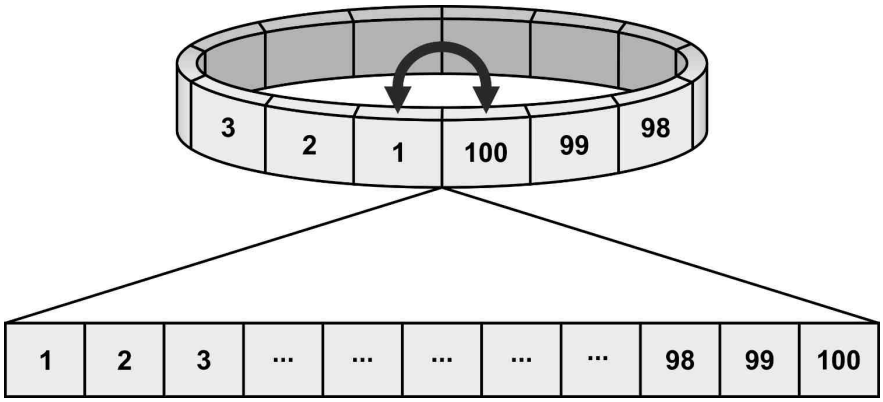

Figura 6. Estructura semi-espacialmente explícita implementada en el IBM mini-AKIRA. La doble flecha negra indica que los individuos pueden pasar de la primera (1) a la última celda (100) del espacio virtual y *viceversa*.

2) Cadena trófica de la hojarasca de los hayedos (*Fagus sylvatica* L.):

En mini-AKIRA la cadena trófica está compuesta por tres especies de niveles tróficos diferentes, incluye una única especie de recurso basal (hongo) que crece según una función logística dependiente de la temperatura, haciéndolo crecer como máximo hasta alcanzar la capacidad de carga (K) dentro de cada parche rico en recursos simulado o celda (ver más abajo), una única especie de presa fungívora o consumidor primario (Orden Collembola) y una única especie de depredador

(ácaro, Suborden Mesostigmata) que además es caníbal, con lo cual realmente está formada por cuatro niveles tróficos. Tanto las presas como los depredadores simulados siempre pesan < 1 mg. Las simulaciones comienzan con el 99% de K para el hongo en la celda 50, 500 presas y 50 depredadores los cuales constituyen la Generación 0 Parental, que se distribuyen inicialmente en celdas al azar. Cada simulación dura 120 días de tiempo simulado o "steps", durante el cual los individuos nacen, se mueven, se alimentan, crecen, se reproducen y mueren (Figura 2 en Moya-Laraño *et al*. 2012)

3) Reglas de movimiento:

El modelo incorpora un conjunto de reglas adaptativas de movimiento, los depredadores y las presas se mueven de una celda a otra según experiencias previas de cada individuo y el estrés que inducen los depredadores, tanto sobre individuos de su propia especie como de las presas afectando a la tasa metabólica y a la eficiencia de asimilación (Hawlena *et al*. 2010). Las tasas metabólicas de campo son calculadas a través de un algoritmo que incluye el estrés ambiental producido por el número de encuentros con depredadores (Hawlena & Schmitz 2010).

Ejemplos:

- **Movimiento de una presa en ausencia de depredadores:** Cada individuo evalúa la disponibilidad de recurso (hongo) en las tres celdas disponibles (en la que se encuentra actualmente, la de la izquierda y la de la derecha) y después decide moverse a la celda con mayor biomasa de hongo.

- **Movimiento de una presa en presencia de depredadores:** Cada individuo evalúa la disponibilidad de recurso (hongo) y el número de depredadores en las tres celdas disponibles (en la que se encuentra actualmente, y las que tiene a izquierda y derecha) y después decide moverse hacia la celda con el valor más bajo del ratio (P/B_f). Donde P es el número de depredadores de la celda y B_f en la biomasa de hongo.

- **Movimiento de los depredadores:** Cada individuo evalúa el número de presas y el número de depredadores en las tres celdas disponibles (en la que se encuentra actualmente, la de la izquierda y la de la derecha) y después decide moverse hacia la celda con el valor más bajo del ratio (P_d/P_Y). Donde P_d es el número de depredadores de la celda y P_Y es el número de presas.

En todos los casos, si los recursos se han extinguido ya sea biomasa de hongo o número de presas más depredadores, los individuos saltan hacia otra celda en una dirección aleatoria y la longitud del salto es igual al número de parches determinados por el rasgo área de búsqueda o de campeo de cada especie más 2.

4) Base genética cuantitativa multidimensional

Tanto los depredadores como las presas tienen asociados 13 rasgos heredables basados en genética cuantitativa (muchos genes de efecto pequeño determinan el valor fenotípico de los rasgos y puede haber correlaciones genéticas por pleiotropía), algunos de los cuales (Tabla 1 Moya-Laraño *et al*. 2012), siguiendo la Teoría Metabólica en Ecología (Brown *et al*. 2004) se encuentran afectados por la temperatura ambiental. Cada rasgo está formado por un par de cromosomas y determinado por 20 loci con 10 posibles alelos. Estos 13 rasgos fueron agrupados en 4 módulos con tres rasgos cada uno y un quinto módulo con un solo rasgo. Cada módulo puede definirse como un conjunto de rasgos interrelacionados que son independientes de otro conjunto de rasgos interrelacionado de otro módulo (Figura 7; Figura 1 Moya-Laraño *et al*. 2012). La modularidad explica como los rasgos cuantitativos están interrelacionados positiva o negativamente (trade-offs genéticos) entre sí a través de los individuos de una población (Magwene 2001; Pigliucci 2003). El nivel de correlación genética entre los rasgos está definido por un parámetro ρ (rango -1,1) que fija el número de loci de efectos pleiotrópicos (es decir, aquellos loci que afectan a más de un carácter a la vez) de entre los que determinan el valor fenotípico de los rasgos (integración fenotípica). Para ρ = 0.9 la correlación entre los rasgos es muy fuerte (alta integración fenotípica) y para ρ = 0 cada rasgo está completamente desacoplado de otro (baja integración fenotípica) y la correlación es 0.

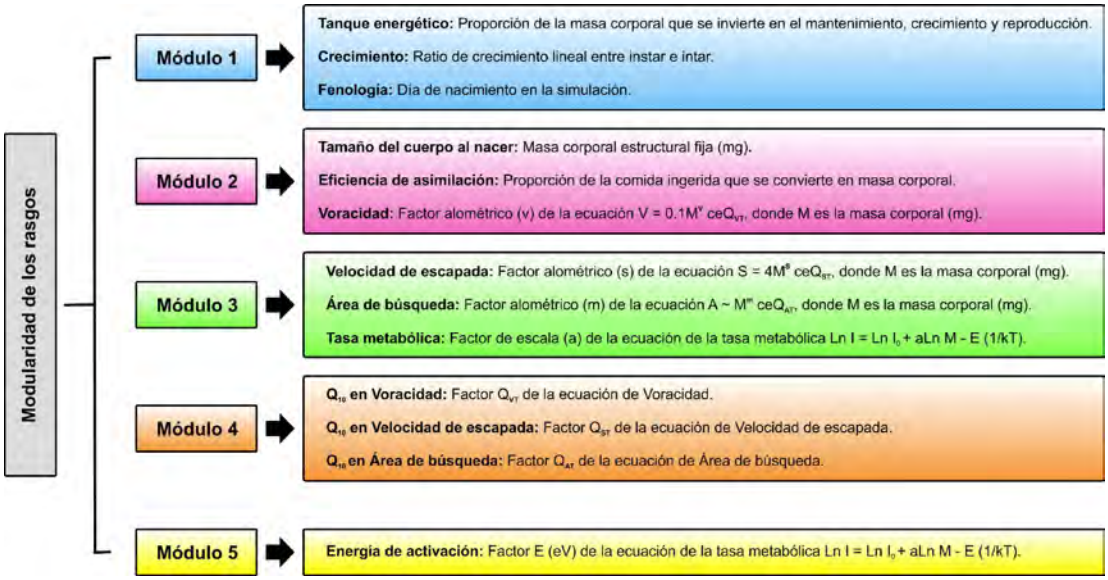

Figura 7. Modularidad de los rasgos basado en genética cuantitativa multidimensional. Los rasgos están agrupados en cinco módulos que son genéticamente independientes unos de otros, aunque los genes pueden interactuar epistáticamente (como los valores de Q_{10} y Energía de activación). Dentro de cada módulo los rasgos están correlacionados entre sí, y su grado de correlación determina el grado de integración fenotípica.

Cada rasgo además tiene un rango de variación asociado con un a base genética heredable (l_x, u_x). El parámetro φ (rango 0-1) controla qué parte de la variación genética dentro de un rango

disponible (L_x, U_x que se hallan siempre dentro de unos límites evolutivos impuestos por restricciones físicas y fisiológicas) será explicada por la genética cuantitativa y por tanto utilizada y heredable en la simulación.

$$l_x = L_x + \varphi \left(\frac{U_x - L_x}{2}\right) \quad (1)$$

$$u_x = U_x + \varphi \left(\frac{U_x - L_x}{2}\right) \quad (2)$$

Estos criterios aseguran que la variabilidad sea suficientemente grande como para que se desarrollen nuevos fenotipos determinados por variación genética, y sobre los que pueda actuar la selección natural, pero que nunca se alcanzacen fenotipos evolutivamente imposibles (ej.: valores negativos).

5) Teoría Metabólica en Ecología (MTE):

La temperatura está incluida en el modelo siguiendo la Teoría Metabólica en Ecología (Brown *et al*. 2004) y modifica los siguientes rasgos dependiendo de las condiciones ambientales:

- **Tasa metabólica:** La tasa metabólica está implementada siguiendo la MTE y estima el efecto de la temperatura en la tasa metabólica, energía de activación y masa corporal (Ehnes *et al*. 2011).

$$\text{Ln } I = \text{Ln } I_0 + a\text{Ln } M - E\left(\frac{1}{kT}\right) \quad (3)$$

  donde I es la tasa metabólica (J/h), I_0 es una constante de normalización, a es un coeficiente que relaciona el tamaño estructural con la tasa metabólica (Rasgo Tasa Metabólica, Módulo 3 Figura 7), E es la energía de activación (eV) (Rasgo Energía de activación para la tasa metabólica, Módulo 5 Figura 7), k es la constante de Boltzmann ($8.62 \cdot 10^{-5}$ eV/K) y T es la temperatura ambiental (K).

- **Movilidad, área de búsqueda o de campeo, voracidad y velocidad de escapada:** Todos estos rasgos son sensibles a la temperatura, y para evaluar el efecto de la misma sobre estos rasgos se han incorporado los Q_{10}, para cada uno de ellos. Es decir, si la temperatura aumenta 10°C cuanto aumenta o disminuye el rasgo. A partir de ahí se realiza una interpolación lineal de Q dependiendo de cuanto aumenta o disminuye la temperatura respecto al valor original de Q_{10} calculado a 25°C. Además, los Q_{10} para área de búsqueda, voracidad y velocidad de escapada se incluyen como rasgos con base genética cuantitativa, de forma que no solo se incluyó el efecto de la temperatura sobre dichos rasgos si no también la plasticidad fenotípica de los mismos y cómo afectan por epistasis a los rasgos área de búsqueda, voracidad y velocidad de escapada. De manera que la expresión de estos rasgos depende a su vez de la expresión de los rasgos Q_{10} en

área de búsqueda, Q_{10} en voracidad y Q_{10} en velocidad de escapada (Módulo 4 Figura 7). Lo mismo ocurre para la energía de activación sobre la tasa metabólica (Módulo 5 Figura 7).

- **Tiempo de desarrollo del huevo:** Tiempo que transcurre desde el comienzo de la simulación y el día de la ovoposición. También es un rasgo sensible a la temperatura, por ello, se incluyeron las ecuaciones de tasas de desarrollo ya publicadas (Gillooly *et al*. 2002) y se calcularon los Q_{10} de la misma forma que para los rasgos anteriores (ver más arriba).

- **Tiempo de digestión:** Cuando una presa es capturada por un depredador y ésta es de mayor tamaño el depredador necesita un tiempo para digerirla que puede ser mayor al "step" establecido en el modelo, en este caso en días. Este rasgo también es sensible a la temperatura y se siguió el mismo procedimiento que en los rasgos anteriores calculando el Q_{10} (ver más arriba), sin embargo, el valor original de Q_{10} sobre el que se interpola no es a 25°C si no a 15°C de temperatura.

6) Algoritmo de muda:

El rasgo crecimiento es un valor fijo para cada individuo y un conjunto de aumento lineales fijos del tamaño estructural para cada muda. Es decir, el crecimiento es el ratio entre el tamaño estructural después de la muda y el tamaño estructural en el instar anterior. En el modelo se asume que 90% de la energía y los nutrientes están disponibles en cada proceso de muda mientras que el 10% restante se pierde. Cuando un individuo acumula suficiente energía entre crecimiento (tamaño estructural) más el almacenamiento de energía (tanque energético) se produce el evento de muda.

7) Algoritmo de reproducción:

Todos los individuos, presas y depredadores alcanzan la madurez en el instar 4, una vez se produce esto los requerimientos de energía para poder reproducirse son similares al algoritmo de muda. Los individuos son hermafroditas recíprocos y en la simulación se asume que la posición espacial no importa para encontrar pareja, de esta manera no hay gasto energético asociado a la búsqueda de pareja. Los gametos se forman induciendo la formación de un quiasma en cada cromosoma en una posición aleatoria, así cada nuevo individuo recibe un cromosoma de cada progenitor.

A pesar de los grandes avances que incorporaba este IBM en su época que, y aunque parece relativamente reciente, la evolución de los trabajos con modelos de simulación ha crecido y se ha desarrollado tan rápidamente que está actualmente obsoleto (ver más arriba). Como dijo Robert D. Holt 1990: "*No hay ninguna especie de la que sepamos los suficiente sobre su ecología, fisiología y genética como para predecir su respuesta evolutiva al cambio climático*". Con esta cita podemos concluir, que la respuesta evolutiva hacia numerosos estresores ambientales es difícil de predecir y

por ello, hemos seguido elaborando IBMs más complejos, pero mucho más realistas. Este tema lo abordaremos a lo largo del **Capítulo 1** y el **Capítulo 4** de la presente Tesis Doctoral.

3.2. ¿mini-AKIRA sigue el Protocolo ODD desarrollado por Grimm *et al*. 2006?

La descripción y publicación del modelo mini-AKIRA cumple con todos los elementos descritos en el Protocolo ODD desarrollado por Grimm *et al*. 2006, salvo uno, tal como se muestran en la Tabla 3.

Tabla 3. Conjunto de características del Protocolo ODD que sigue el IBM mini-AKIRA. Los ticks en verde reflejan los elementos incorporados en la descripción del modelo, las cruces rojas reflejan los no incorporados.

Bloques		Elementos		mini-AKIRA	Descripción
1	Visión General	1	Propuesta	√	¿Por qué el modelo contiene algunos aspectos de la realidad y otros han sido excluidos?
		2	Variables de estado y escalas	√	Conjunto completo de variables de estado
				√	Conjunto de variables de alto nivel, el modelo simula poblaciones de individuos
				√	Escalas: unidad de tiempo de cada "step", duración de las simulaciones, unidad de espacio (celda), tamaño del mundo.
		3	Resumen del proceso y programación	√	Descripción verbal de los procesos ambientales y de los individuos como producción de comida, alimentación, crecimiento, movimiento, mortalidad o reproducción.
2	Conceptos del diseño	4	Conceptos del diseño	√	Lista de las características de diseño del modelo: • **Emergencia:** ¿Cómo emergen los fenómenos o patrones a nivel de sistema a partir de los rasgos de los individuos?
				√	• **Adaptación**: ¿Los individuos tienen un comportamiento adaptativo que les permite sobrevivir, crecer y reproducirse ante cambios de su ambiente?
				√	• **Eficacia biológica o fitness:** ¿Está modelizada explícita o implícitamente?
				√	• **Predicción:** ¿Los individuos adquieren experiencia en la simulación?
				√	• **Sensibilidad:** ¿Los individuos son capaces de captar los cambios en el ambiente y tomar decisiones de forma adaptativa?
				√	• **Interacción:** ¿Qué tipo de interacciones se producen?
				√	• **Estocasticidad:** ¿El modelo es estocástico?
				X	• **Colectivos:** ¿Los individuos se agrupan en grupos sociales?
				√	• **Observación:** ¿Cómo se obtiene, testan, entienden y analizan los datos procedentes del modelo?

(Continuación)

Detalles	**5**	**Inicialización**	√	¿Cómo se crea el ambiente y los individuos al principio de la simulación?
	6	**Entradas**	√	Todas las entradas que se le proporcionan al modelo.
	7	**Submodelos**	√	Explicación detallada y parametrización de todos los procesos descritos en el Elemento 3, mediante diagramas de flujo.

3.3. ¿Se puede considerar mini-AKIRA como un IBM de Nueva Generación?

Teniendo en cuenta los elementos y características descritas por Grimm & Berger 2016a que deben contener los Modelos Basados en Individuos de Nueva Generación no podemos considerar mini-AKIRA como uno de ellos pues de las 7 características principales le faltan dos consideradas fundamentales (Figura 8).

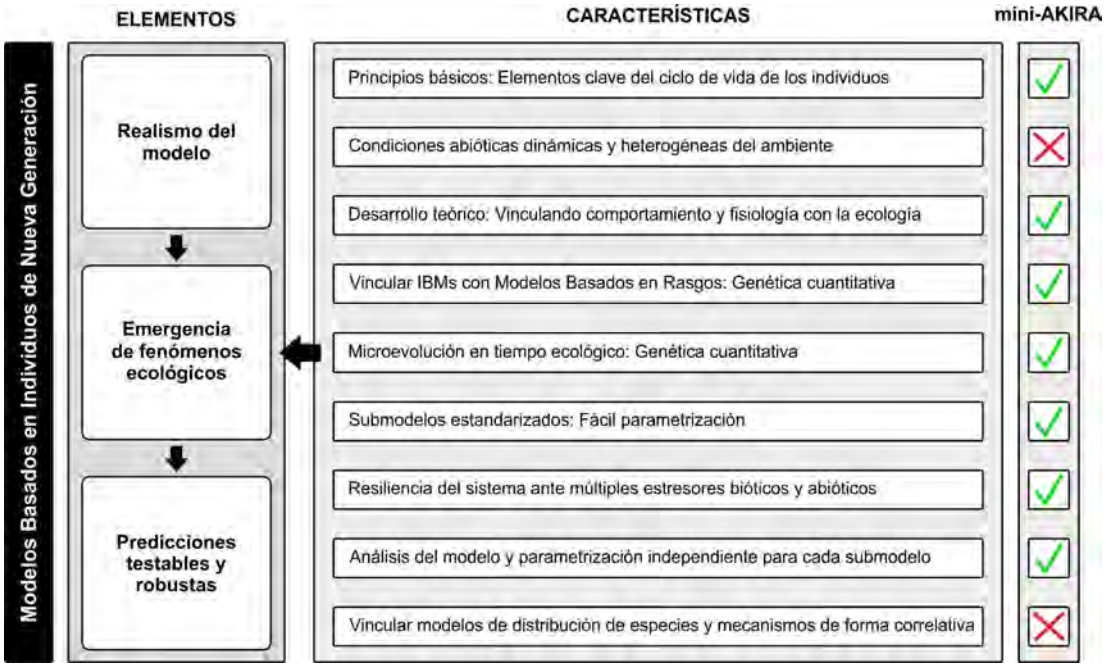

Figura 8. Elementos y características de los Modelos Basados en Individuos de Nueva Generación según Grimm & Berger 2016a. Los ticks en verde reflejan los elementos que cumple el IBM mini-AKIRA, las cruces rojas reflejan los que no cumple.

3.4. Estudios derivados de la utilización del IBM mini-AKIRA

La creación, desarrollo, implementación y parametrización de mini-AKIRA permitió llevar a cabo los siguientes tres grandes estudios que enumeramos y explicamos de manera cronológica:

1) Estudios de las cascadas tróficas en una cadena trófica depredador-presa-hongo:

mini-AKIRA fue creado para estudiar dinámicas eco-evolutivas en redes tróficas, concretamente de una red trófica de la hojarasca de los hayedos (ver más arriba). Uno de los resultados principales de Moya-Laraño *et al*. 2012 fue simular exitosamente el control top-down en una cadena trófica formada por una especie de recurso basal (hongo), una especie de presa fungívora (colémbolo) y una especie de depredador (ácaro). Los depredadores ejercieron un control sobre la abundancia de presas favoreciendo el crecimiento del hongo y evitando su extinción, mediante un efecto en cascada en todas las simulaciones realizadas a tres temperaturas 16°C, 20°C, 25°C. En ausencia de los depredadores, las poblaciones de presas crecían muy rápidamente y como consecuencia consumían el hongo a un ritmo más rápido de lo que el hongo crecía, lo que daba lugar a su extinción en pocos días en todas las simulaciones, siendo esta extinción más rápida a mayores temperaturas. Esto se estudió para dos grados de correlación genética entre los rasgos (baja $\rho = 0.1$ y alta $\rho = 0.9$ correlación genética) y se pudieron observar los mismos resultados siendo la fuerza de la cascada trófica mayor a altas temperaturas y alta correlación genética (Figura 3 Moya-Laraño *et al*. 2012). Además, se pudo verificar que la tasa de encuentros aumentaba con la temperatura, independientemente del grado de correlación entre los rasgos tanto para las presas como para los depredadores (Figura 4, Figura 5 Moya-Laraño *et al*. 2012).

2) Posibles efectos del cambio climático sobre la selección natural en redes tróficas:

Utilizando la misma cadena trófica que en el trabajo anterior se desarrolló un estudio cuyo objetivo era, partiendo de múltiples rasgos con variación multidimensional, determinar la fuerza y dirección de la selección actuando sobre las presas en un contexto de red trófica a diferentes temperaturas, calculando los gradientes de selección (Ruiz-Lupión 2013, Trabajo Fin de Máster disponible en el enlace web: http://hdl.handle.net/10261/180397). Se evaluó: 1) si la temperatura actuaba como agente de selección (direccional, estabilizadora o disruptiva) sobre las presas, 2) si los depredadores actuaban como agente de selección sobre las presas y si esta selección cambiaba con la temperatura, 3) si se produce una selección correlativa o indirecta entre los rasgos estudiados, debido a la correlación existente entre este rasgo y otro que si está siendo seleccionado, y si cambiaba con la temperatura y presencia/ausencia de depredadores y 4) bajo qué condiciones ambientales la fuerza de la selección era de mayor intensidad.

De este trabajo se desprenden los siguientes resultados: 1) la temperatura es un componente ambiental determinante que ejerce una importante presión de selección sobre las presas, 2) los depredadores tienen un papel fundamental pues sí actúan como presión de selección sobre las presas tanto de forma directa por depredación como indirecta por efectos no consuntivos, es decir, por los costes energéticos que les inducen como consecuencia de las diferentes estrategias defensivas que adoptan en respuesta al mayor riesgo de depredación, 3) la combinación de ambos agentes de selección, temperatura y presencia/ausencia de depredadores induce procesos de selección lineal y no lineal que dependen a su vez de la arquitectura genética de las presas y los

depredadores, 4) los patrones de selección correlacional permiten que diferentes combinaciones de rasgos sean seleccionados en diferentes ambientes y 5) la selección es de mayor intensidad cuando los rasgos de las presas están fuertemente correlacionados, lo que permite identificar patrones de selección correlacional. Sólo si se rompe dicha correlación genética gracias a la selección correlacional (Delph *et al*. 2010), puede entonces haber una respuesta evolutiva a la selección natural.

3) Efectos de la variabilidad en 13 rasgos en depredadores y presas sobre las dinámicas eco-evolutivas en redes tróficas:

Siguiendo con el mismo sistema de estudio pero incluyendo algunas mejoras de programación para poder cambiar la variabilidad de los rasgos (parámetro φ, ver más arriba) dentro de cada módulo de forma independiente y no global, se quiso estudiar el efecto de la variabilidad genética de los rasgos implementados sobre las dinámicas eco-evolutivas de ambas especies, para ello se siguió la siguiente metodología: 1) se mantuvo un valor medio de la correlación genética de los rasgos (parámetro ρ, ver más arriba) dentro de cada módulo igual para presas y depredadores (ρ = 0.5) en todas las simulaciones, 2) se mantuvo la variabilidad genética de todos los rasgos constante y centrada en la media para todos los depredadores (φ = 0.9, baja variabilidad genética), 3) se estableció una simulación control en la variabilidad de los rasgos de los cinco módulos era muy amplia (φ = 0.1, alta variabilidad genética) y 3) se realizaron simulaciones para evaluar el efecto de una alta variabilidad genética en cada módulo, en la dinámicas eco-evolutivas de presas y depredadores (ej.: Módulo 1 (φ = 0.1), Módulo 2 (φ = 0.9) , Módulo 3 (φ = 0.9) , Módulo 4 (φ = 0.9) y Módulo 5 (φ = 0.9)). Todo ello se evaluó a tres temperaturas 16°C, 20°C y 25°C, en presencia y ausencia de depredadores.

Tras las simulaciones se pudo concluir globalmente que: 1) para el módulo focal de estudio el hecho de que haya o no variabilidad genética en el resto de los rasgos produce que tanto las dinámicas poblacionales depredador-presa-hongo sean como los patrones de selección natural sean diferentes. Actuando la variabilidad genética en el resto de los rasgos como agente de selección sobre los rasgos de los del módulo focal (módulos 1, 2 y 3 y, 2) el módulo 4 de plasticidad y el módulo 5 no afectan a las dinámicas poblacionales (Ruiz-Lupión, datos sin publicar).

4) Estudio dinámicas eco-evolutivas de arañas con dos tipos de depredación diferente

Las arañas embebidas en una red trófica compleja con depredación sit-and-wait, es decir, aquellas capaces de tejer una telaraña y esperar a que las presas caigan en la red persisten y aportan estabilidad por medio de cascadas tróficas respecto a las arañas active-hunting que son típicamente de suelo y depredan activamente. Esta implementación se hizo en mini-AKIRA posteriormente a su publicación (Moya-Laraño *et al*. 2012) y se caracterizaba porque las presas no eran conscientes en la simulación de la presencia de las arañas sit-and-wait imitando así el carácter críptico de estas arañas en la naturaleza (Moya-Laraño *et al*. 2013).

A partir de ese momento se decidió dar un salto significativo y llevar mini-AKIRA al siguiente nivel, traduciendo el código fuente a un lenguaje de programación más eficiente que el lenguaje R, creado, desarrollodado y orientado principalmente para llevar a cabo una variada gama de análisis estadísticos. Además, se incluiran nuevas características y funcionalidades que abordaremos en el **Capítulo 1** de la presente Tesis Doctoral.

3.5. ¿Qué pasos del Ciclo de la Modelización cumplió el IBM mini-AKIRA?

Según el Ciclo de la Modelización propuesto por Grimm & Railsback 2005, se ha completado una vuelta del ciclo completa antes de pasar al **Capítulo 1** de la presente Tesis Doctoral (Figura 9).

Figura 9. Pasos del Ciclo de la Modelización cumplidos por el IBM mini-AKIRA. Los recuadros en blanco representan los 6 pasos originales descritos por Grimm & Railsback 2005 y los recuadros en amarillo son pasos intermedios considerados de gran importancia en el proceso de modelización. El recuadro en gris con borde negro dicontinuo agrupa pasos intermedios interrelacionados. El paso en gris 6.b no fue necesario porque no hubo suficientes estudios paralelos.

4. Justificación de la tesis doctoral: La Integración de investigación teórica y empírica en IBMs

Como ya hemos citado anteriormente los Modelos Basados en Individuos deben integrar la investigación teórica y empírica, mediante estudios de revisión bibliográfica o experimentos de campo y laboratorio que permitan parametrizar el modelo haciéndolo más realista (Grimm & Railsback 2005, Moya-Laraño *et al*. 2012). Con el modelo mini-AKIRA se completó una vuelta del Ciclo de la Modelización, durante el **Capítulo 1** veremos las nuevas funcionalidades y estudios derivados de la mejorada versión del modelo, al que se le cambia de nombre a WEAVER 1.0, un manual de usuario junto a los archivos de entrada podéis encontrarlo en Barrionuevo-Rosales 2014, Proyecto Fin de Carrera disponible en el enlace web: http://repositorio.ual.es/handle/10835/3240. Con este nuevo modelo abordaremos otro Ciclo completo de la Modelización y estudiaremos dos aspectos muy importantes que dieron lugar a publicaciones paralelas al modelo **(Capítulo 2 y Capítulo 3)**, y a una revisión y extensión de su implementación **(Capítulo 4)**.

4.1. El debate de la diversidad-estabilidad o complejidad-estabilidad

En ecología existe una gran amplitud de definiciones sobre estabilidad, no obstante, la teoría ecológica ha tendido tradicionalmente a definir un sistema estable si, y solo si, está gobernado por una dinámica de equilibrio estable, en el que tras una perturbación el sistema retorna a esta situación de equilibrio y asume que cuando el sistema es estable no existe variabilidad (McCann 2000). La relación entre diversidad (número de especies de la comunidad) y estabilidad ha fascinado a los ecólogos durante generaciones, entender cómo efecta la diversidad a la estabilidad de los ecosistemas ha dado lugar a un debate que se remonta a antes de los años 70. En un principio los ecólogos creían que una mayor diversidad de las comunidades daba lugar a una mayor estabilidad de los ecosistemas, debido a que tras observaciones repetidas de comunidades terrestres muy simplificadas se caracterizaban por fluctuaciones más violentas en la densidad de población que las comunidades terrestres más diversas (Odum 1953; MacArthur 1955; Elton 1958). Además de la diversidad, los ecosistemas pueden ser más o menos complejos y en una red ecológica la complejidad puede medirse tanto por el número de especies presente, como por el número de enlaces entre pares de especies (o las dos cosas en conjunto), siendo las redes más conectadas consideradas más complejas. Los primeros modelos matemáticos que intentaron relacionar la complejidad con la estabilidad encontraron resultados contrarios a la "sabiduría popular" ("common wisdom"), y mostraron que las redes más complejas (producto de riqueza por número de enlaces) eran menos estables (May 1973). Años después se produjo un cambio de perspectiva, los ecólogos empezaron a pensar que como las poblaciones reales fluctúan en números, es posible que la persistencia de comunidades complejas dependa en cierta medida de las fluctuaciones de la población (aumento y disminución de la densidad de la población), de manera que diferentes especies pueden responder de manera diferente a cambios en su entorno. Los resultados indican que, dentro de un ecosistema, la diversidad tiende a correlacionarse positivamente con la estabilidad del ecosistema, pero esta correlación no se extiende a la estabilidad a nivel de la

población. La estabilidad a nivel de la comunidad depende de la respuesta diferencial de las especies o grupos funcionales a las condiciones variables, así como de la redundancia funcional de las especies que tienen importantes funciones estabilizadoras (DeAngelis & Waterhouse 1987; Hastings & Higgins 1994; Law & Morton 1996; Huisman & Weissing 1999; Michalski & Arditi 1999).

Desde un punto de vista de las redes tróficas, el debate se ha centrado además en algunos aspectos de la red, tales como el grado de omnivoría (Pimm 1982; Polis 1991; McCann & Hastings 1997), la distribución de las fuerzas de interacción (McCann 2000) y la presencia de bucles más o menos largos de depredación recíproca entre especies (Neutel *et al*. 2007; Mitchell & Neutel 2012). Las interaciones depredador-presa, así como la variabilidad genética intraespecífica de ambos y cómo esta afecta a dichas interacciones determinan la estructura y dinámicas y son muy importantes para entender cómo esto mejora la robustez y estabilidad de la red trófica. Con un simple ejercicio de simulación se demostró que una mayor variabilidad genética intraespecífica podría contribuir a la estabilidad de la red trófica al aumentar la conectancia y la variabilidad en las fuerzas de interacción, con muchas interacciones débiles y pocas fuertes (Moya-Larano 2011). Esto es particularmente relevante en sistemas de meta-comunidades multi-tróficas en el que las especies se encuentran dispersas en un espacio heterogéneo, en el que las interacciones locales determinarán el resultado de cada subpoblación. La heterogeneidad espacial juega un papel importante en la estructuración de las redes tróficas, ya que la alta movilidad de los depredadores puede acoplar diferentes canales de energía a través del espacio y contribuir a la estabilidad de la red trófica (McCann *et al*. 2005; Rooney *et al*. 2006, 2008). Además, la dispersión de omnívoros puede contribuir a la robustez de la metacomunidad, mejorando así la complejidad de la red alimentaria y la diversidad de especies (Pillai *et al*. 2011). Por lo tanto, la variabilidad genética puede promover la estabilidad de la red trófica a través de sus efectos en la evolución contemporánea o por dar lugar a una alta diversidad de interacciones en las especies embebidas en redes tróficas complejas, aumentando así la conectancia ponderada (fracción de posibles enlaces en la red trófica teniendo en cuenta los flujos o tasas de alimentación), la omnivoría y una distribución variable de las fuerzas de interacción (Moya-Laraño 2011; van Altena 2016) Abordaremos estos concepto a lo largo del **Capítulo 1**, utilizando diferentes conjuntos de simulaciones con WEAVER 1.0.

4.2. Dinámicas eco-evolutivas y redes tróficas

La evolución está obviamente dirigida por diferencias ecológicas (ej.: radiación adaptativa de los pinzones de Darwin), lo que es menos obvio es que los procesos ecológicos se vean influidos por la evolución (ej.: los ecosistemas dependen del oxígeno producido después de la evolución de la fotosíntesis). Además, este efecto recíproco entre ecología y evolución en las interacciones biológicas se puede producir a escalas de tiempo ecológico, lo que fue reconocido por primera vez por Pimentel 1961, 1968 hace más de 50 años quien destacó que la variabilidad genética era un factor importante que regulaba la estabilidad de la dinámica de poblaciones de especies que

interaccionaban unas con otras. Muchos autores han confirmado que la variación genética y los procesos evolutivos dan forma a las comunidades ecológicas y que el contexto ecológico en el que se encuentran las poblaciones puede influir en su evolución posterior (Wade & Kalisz 1990; Odling-Smee et al. 2003; Thompson 2005; Whitham *et al*. 2006; Johnson & Stinchcombe 2007; Johnson *et al.* 2009; Pelletier *et al.* 2009; Ellers 2010; Genung *et al.* 2011; MacColl 2011; Schoener 2011; Smith *et al.* 2011). Por ejemplo, en una sistema depredador-presa al producirse cambios ecológicos (ej.: cambios en la temperatura por cambio climático, presencia de depredadores o distinto nivel de correlación genética entre los rasgos de los depredadores) causan cambios fenotípicos en las poblaciones naturales de presas, como resultado de cambios genéticos y no por plasticidad fenotípica (eco a evo) y esta evolución influye en las variables ecológicas (ej.: dinámicas ecológicas de las presa que hacen que actúen como agente de selección sobre los depredadores) modificando las dinámicas ecológicas de los depredadores (evo a eco) dando lugar a las retroalimentaciones eco-evolutivas que constituyen la base de las dinámicas eco-evolutivas en redes tróficas (Figura 10) que estudiaremos en el **Capítulo 1**.

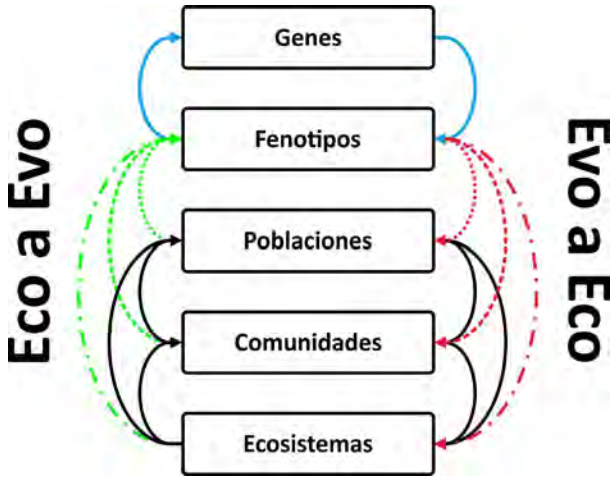

Figura 10. Dinámicas eco-evolutivas. Las características de las poblaciones, las comunidades y los ecosistemas influyen en los fenotipos a través de la selección natural y la plasticidad (flechas verdes). La selección natural se traduce en un cambio evolutivo a través de la herencia genética (flechas azules). Los fenotipos resultantes pueden influir en las características de las poblaciones, comunidades y ecosistemas (flechas rojas). Estos efectos pueden caer en cascada entre los niveles de organización ecológica a través de efectos ecológicos, como las interacciones tróficas (flechas negras). Las retroalimentaciones eco-evolutivas describen los efectos de la "evolución contemporánea" en la dinámica ecológica y los efectos recíprocos de la ecología en la trayectoria de la evolución (bucles representados por diferentes líneas discontinuas). Modificado de la Figura 1 de Palkovacs & Hendry 2010.

4.3. Estudios teóricos de revisión bibliográfica

Mediante una revisión bibliográfica completa desde 1967 hasta la actualidad pudimos obtener datos de la literatura de ecuaciones alométricas longitud-peso $M = aL^b$, donde M es la masa (mg) y L la longitud (mm); cuyos parámetros "a" y "b" son muy importantes para el funcionamiento de las versiones WEAVER 1.0 **(Capítulo 1)** y WEAVER 2.0 **(Capítulo 4)** pues los rasgos con base genética cuantitativa y los parámetros dependientes de la temperatura (según la Teoría Metabólica en Ecología de Brown *et al*. 2004) implementados en mini-AKIRA, y por tanto en todas sus posteriores versiones, como la voracidad, la velocidad de escapa, el área de búsqueda o de campeo, la tasa metabólica, así como el tiempo de desarrollo del huevo y el tiempo de digestión están escalados con la masa corporal (mg). Además, el algoritmo de muda (crecimiento) depende de que el individuo durante la simulación acumule un umbral de energía para mudar, considerando esta energía como la suma de la masa estructural (mg) más la energía del tanque energético disponible para el crecimiento. En base al valor del ratio fijo de crecimiento entre el tamaño estructural después de la muda y el tamaño estructural en el instar anterior, y teniendo en cuenta que los datos de entrada en el modelo están expresados en longitud total sin apéndices (mm), durante toda la simulación se produce una conversión constante entre longitud total (mm) y masa corporal (mg), que es fácilmente convertible a energía considerando que 1 g de peso equivale a 7 J de energía (Peters 1983), lo que nos permite convertir el peso del animal en tasa metabólica (gasto energético). Si a esto le incluimos las nuevas implementaciones incluidas en la versión WEAVER 2.0 **(Capítulo 4)**, donde se suprime el ratio de crecimiento y se implementan curvas de crecimiento reales con target en longitud total (mm) que los individuos deben alcanzar para mudar, en base a la masa corporal que van adquiriendo, estudiar bien las posibles fuentes de variación que afectan a la alometría longitud-masa era necesario. Por ello, desarrollamos un estudio para evaluar cómo variaban los parámetros alométricos (de ahora en adelante factor de escala "a" y factor alométric "b") a escala global dependiendo de la productividad primaria del ecosistema (NDVI), el bauplan morfológico de los grupos taxonómicos implicados, así como la filogenia, o a falta de poder crearla, utilizar el menor nivel taxonómico como control en los análisis, las variables geográficas (latitud, longitud y altitud) y climáticas (temperatura y pluviometría).

Finalmente, la base de datos recopilada dispone de 292 ecuaciones de 63 familias de artrópodos del suelo de 45 localizaciones a escala global. Para cada ecuación se ha obtenido información sobre 7 tipos de variables: 1) Clasificación Taxonómica, 2) Bauplan morfológico utilizando Morfometría Geométrica, 3) Datos asociados a la ecuación (valores de a y b), 4) Variables Climáticas, obtenidas de WorldClim, 5) Índice de vegetación de diferencia normalizada (NDVI) y 7) Variables espaciales (Latitud, Longitud y Altitud). Con todo ello, hemos llevado a cabo un estudio comparativo del efecto de la productividad primaria del ecosistema, el gradiente geográfico y el gradiente ambiental en la evolución de las alometrías longitud-peso, concretamente en la capacidad de evolución de los parámetros "a" y "b" de las ecuaciones **(Capítulo 2)**.

4.4. Estudios empíricos de campo y laboratorio

Con el objetivo de obtener datos reales mediante experimentos de mesocosmos en hayedos (*Fagus sylvatica* L.) en Asturias (España) para la parametrización e implementación de una nueva red trófica de la hojarasca de los hayedos mucho más realista para la versión WEAVER 2.0 **(Capítulo 4)**. Se realizó un estudio que conlleva la comparación entre la idoneidad de las trampas de caída (pitfalls) frente a dos nuevos tipos de trampas (basket y cul-de-sac) para la medida de la actividad de meso- y macrofauna de la hojarasca. Este tipo de estudios no solo es importante por la adquisición de datos reales de abundancia de los principales grupos de artrópodos del suelo, si no también de actividad de los mismos. Entendiendo la actividad, como la cantidad de tiempo al día que un individuo está en movimiento. Por ejemplo, hemos observado en el laboratorio que los pseudoscorpiones tienen una gran actividad, permanecen en movimiento durante largos periodos de tiempo a una velocidad de crucero mientras que otros taxonones como grandes depredadores del grupo de los cienpiés (Lithobiomorpha y Geophilomorpha), a pesar de poder tener un área de campeo mucho mayor, por ser más grande que un pseudoscorpion permanecen menos tiempo en movimiento al día. Actualmente, este tipo de información se está obteniendo en laboratorio con el sistema de filmaciones (ver más arriba). No obstante, es necesario obtener esta información también de experimentos de mesosocosmos en campo y optimizar los métodos de muestreo para obtener este tipo de información, no sólo en la hojarasca de los hayedos si no también en otros sistemas ecológicos. Para estudiar la eficiencia de dichas trampas midiendo la actividad de la fauna del suelo se llevó a cabo un experimento de mesocosmos de campo en 4 hayedos (*Fagus sylvatica* L.) de Asturias a lo largo de la Cordillera Cantábrica, uno en la Reserva Integral de Muniellos, dos en el Parque Natural Las Ubiñas-La Mes cerca de los pueblos de Ricabo y Páramo y otro en el Parque Natural de Ponga cerca del pueblo Juan de Beleño. Se establecieron en cada sitio de estudio dos bloques constituidos cada uno por dos parcelas de 1 x 1 m^2 a las que se le excluyó la lluvia y se les homogeneizo el contenido de agua de la hojarasca antes del inicio del experimento de mesocosmos.

En cada parcela se recogieron 2 litros de hojarasca y se determinó la abundancia de diferentes grupos taxonómicos (arañas, escarabajos tanto adultos como larvas, ciempiés y milpiés). Posteriormente en cada parcela se instalaron 4 trampas de caída (pitfalls traps), 2 trampas de cesta (basket traps) y 2 trampas de calcetín (cul-de-sac traps). Se recogieron las trampas y el contenido se llevó al laboratorio para determinar las capturas de individuos vivos de los taxones mencionados por cada tipo de trampa. Se analizó el contenido de agua (porcentaje) de la hojarasca de cada trampa en el momento de la recogida, se evaluó la capacidad de captura de cada trampa corrigiendo por la abundancia real que había en cada micro-hábitat (parcela) y se estudió un índice de actividad para cada tipo de trampa **(Capítulo 3)**.

5. Objetivos

Dentro del contexto de los Modelos Basados en Individuos (IBMs), nuestro interés se centra en el estudio de las dinámicas eco-evolutivas en redes tróficas de la hojarasca de los hayedos (*Fagus sylvatica* L.) mediante simulaciones utilizando un nuevo IBM modificado y mejorado del modelo mini-AKIRA, así como, hacerlo más realista y robusto basando la parametrización en datos reales obtenidos de revisiones bibliográficas y de estudios de mesocosmos de campo y laboratorio, contribuyendo así a un Programa de Investigación Retroalimentada que ya está en marcha. Los objetivos específicos que nos planteamos son los siguientes:

1) Estudiar cómo afecta la conectancia en una red trófica de la hojarasca de los hayedos, es decir, qué efecto tiene una baja, media o alta fracción de posibles conexiones entre las especies implementadas en WEAVER 1.0. Así como, variabilidad genética de los rasgos de los individuos y la distancia entre islas ricas en recursos basales en la persistencia en el tiempo de dicha red trófica mediante el estudio de las dinámicas ecológicas o poblacionales a lo largo de 200 días de simulación **(Capítulo 1)**.

2) Explorar las dinámicas evolutivas, cómo cambia el valor de los 14 rasgos con base genética cuantitativa en WEAVER 1.0, en una red trófica de la hojarasca de los hayedos persistente en el tiempo a lo largo de 500 días de simulación, y el efecto que tiene la presencia/ausencia de depredadores en dichas dinámicas evolutivas de un grupo de anélidos (Familia Enchytraeidae) **(Capítulo 1)**.

3) Realizar un estudio comparativo con datos reales para conocer el efecto de la productividad primaria del ecosistema, el gradiente geográfico y el gradiente ambiental en la evolución de las alometrías longitud-peso $M = aL^b$, donde M es la masa (mg) y L es la longitud (mm), concretamente en la capacidad de evolución de los factores “a” y “b” de las ecuaciones en artrópodos del suelo. Esto es importante porque ayudará a entender mejor la conversión constante de longitud total (mm) a masa corporal (mg) y *viceversa* a lo largo de simulaciones futuras, y permitirá hacer los ajustes que sean necesarios **(Capítulo 2)**.

4) Evaluar la idoneidad de las trampas de caída (pitfalls) frente a dos nuevos tipos de trampas (basket y cul-de-sac) para la medida de la actividad de meso- y macrofauna de la hojarasca de los hayedos; con el fin de mejorar la capacidad de obtener datos reales de actividad de los principales grupos de artrópodos del suelo para parametrizar de forma más realista el modelo WEAVER 1.0 y sus versiones posteriores **(Capítulo 3)**.

5) Mostrar las nuevas funcionalidades, implementaciones, recopilación de estudios para la parametrización e implementación de una nueva red trófica de la hojarasca de los hayedos únicamente de artrópodos, y futuras preguntas e hipótesis a llevar a cabo con la última versión de WEAVER 1.0, el modelo WEAVER 2.0 **(Capítulo 4)**.

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Capítulo 1

Eco-Evolutionary Spatial Dynamics: Rapid Evolution and Isolation Explain Food Web Persistence

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Eco-Evolutionary Spatial Dynamics: Rapid Evolution and Isolation Explain Food Web Persistence

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Abstract

One of the current challenges in evolutionary ecology is understanding the long-term persistence of contemporary-evolving predator–prey interactions across space and time. To address this, we developed an extension of a multi-locus, multi-trait ecoevolutionary individual-based model that incorporates several interacting species in explicit landscapes. We simulated eco-evolutionary dynamics of multiple species food webs with different degrees of connectance across soil-moisture islands. A broad set of parameter combinations led to the local extinction of species, but some species persisted, and this was associated with (1) high connectance and omnivory and (2) ongoing evolution, due to multi-trait genetic variability of the embedded species. Furthermore, persistence was highest at intermediate island distances, likely because of a balance between predation-induced extinction (strongest at short island distances) and the coupling of island diversity by top predators, which by travelling among islands exert global top-down control of biodiversity. In the simulations with high genetic variation, we also found widespread trait evolutionary changes indicative of eco-evolutionary dynamics. We discuss how the ever-increasing computing power and high-resolution data availability will soon allow researchers to start bridging the "in vivo" - "in silico" gap.

Keywords

Food webs, rapid evolution, eco-evolutionary dynamics, multi-trophic metacommunities, animal personalities, genetic variation, Food Web Engineering, food web stability.

The more ambitious plan may have more chances of success…This sounds paradoxical…[but] the paradox disappears if we look closely at a few examples…provided [these are] not based on a mere pretension but on some vision of the things beyond those immediately present.

György Pólya 1957

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1. Introduction

1.1. Food webs and eco-evolutionary dynamics

Although the notion that ecology and evolution operate at similar timescales has been put forward nearly 50 years ago (Pimentel 1968), the first use of the term eco-evolutionary dynamics dates to Savill *et al*. (1997). At the very origin of the concept and the term lies the reciprocal effect of ecology and evolution on biological interactions, and eco-evolutionary dynamics have mainly been studied in this context. This is illustrated by the fact that the most prominent reviews (e.g., Carroll 2007, Schoener 2011) and the seminal studies on eco-evolutionary dynamics (Reznick *et al.* 1990; Yoshida 2003) concern species interactions. At least two main factors may account for this predominance of biological interactions in the eco-evolutionary dynamics literature. First, the selection pressure posed by (mainly) antagonistic interactions is very strong (Benkman 2013). Thus, evolutionary responses resulting from such interactions are expected to be rapid, a pre-requisite for the merging of ecological and evolutionary timescales. Indeed, several studies have documented fast responses to the selection pressure posed by predators (e.g., Reznick *et al.* 1990; Orsini *et al.* 2012) or parasites (e.g., Kraaieveld and Godfray 1997, Martins *et al.* 2013). Second, ecological dynamics are best described for species interactions thus providing a solid ground to incorporate predictions of evolutionary feed-backs into ecology.

Most eco-evolutionary studies have addressed antagonistic interactions among two species (Losos 2004, Palcovacs & Post 2009, Terhorst 2010). Beginning with Darwin's tangled bank (Darwin 1859), however, ecologists have long been aware of the complex web of interactions in which individuals are embedded (Elton 1927; Winemiller & Polis 1996). Hence, incorporating ecological networks in the framework of eco-evolutionary dynamics seems like a natural step. This has been highlighted in a series of reviews and opinions (Thompson 1998; Agrawal, Lau & Hambäck 2006; Fussmann, Loreau & Abrams 2007; Olesen *et al.* 2010; Bolnick 2011, Fontaine *et al.* 2011, Stewart *et al.* 2013).

Most available experimental studies of eco-evolutionary dynamics in food webs have tested how individuals with different evolutionary histories differentially affect an ecological community (Urban, 2013; Farkas *et al.* 2013; Bassar *et al.* 2012; Lau 2012, Walsh *et al.* 2012, Palkovacs & Post 2009,

Harmon *et al.* 2009, Ingram *et al.* 2011, Chislock 2013). For example, Bassar *et al.* (2012, this volume) showed that guppies that had evolved in ponds with or without predators affected differentially the invertebrate community that they fed on. These examples show how the product of a rapid evolutionary process (i.e., organisms that have evolved in one environment or another) affect ecosystems, yet the strength and sign of prey selection (i.e., positive or negative frequency-dependent selection) remain to be tested in experiments also accounting for prey abundance (see Melian et al this volume)

Another possible way by which evolution may affect ecology on a contemporary timescale is if the evolution of the genetic composition of populations affects ecological dynamics (Becks 2010, Yoshida 2003, Rowntree *et al.* 2011, Johnson *et al.* 2009). For the predator-prey dynamics observed in prey genetically-homogeneous populations changed dramatically when the prey population included two clones with different resistance properties (Yoshida *et al.* 2003). This led to rapid evolution of the prey population, affecting the ecological dynamics of predator-prey cycles. The same methodology was used in host-parasite webs by Lennon & Martiny (2008) in which the introduction of viruses in a community of algae resulted in rapid evolution of resistance in the algal host, ensuing a dampening of the initial effect of viruses on nutrient cycling. Similarly, Johnson *et al.* (2009) showed rapid evolution of plant traits, and used a model to predict the impact of such changes in the arthropod community inhabiting the plants. Such an approach requires either populations with different standing genetic variation at the outset, in order to have a control for the evolutionary rate, or a strong modelling approach to generate testable predictions on the relative role of ecology and evolution in the dynamics of preys and predators.

In summary, standing genetic variation and the strength and sign of selection may impact population dynamics of species in ways that may be difficult to anticipate. Thus, one question that remains to be addressed is how genetic variation at the outset of dynamics and the strength and sign of selection may affect food web structure and dynamics. Earlier results, using a modelling approach, suggested that higher genetic variability for traits contribute to food web stability by increasing food web connectance and variability in interaction strengths (Moya-Laraño 2011, see also Melián 2011). This issue is particularly relevant in food webs that are scattered around a heterogeneous space, in which local interactions will shape the outcome of each subpopulation.

1.2. Space, the next frontier

Although the literature on eco-evolutionary dynamics has been growing at an extraordinary pace, the incorporation of space has somehow been lagging behind (Urban et al 2008). This is at odds with the fact that space has, traditionally, been a major component of both ecological and evolutionary studies (Levins 1968). Moreover, early attempts at combining ecological changes in population densities with evolutionary changes in gene frequencies were done in the context of spatially-

heterogeneous environments (Levene 1953), and some researchers have even produced spatial ecological and evolutionary data in the same study system (e.g., Singer & Thomas 1996, Thomas *et al.* 1996).

Dispersal is a very powerful trait to establish a direct link between ecology and evolution. Indeed, migration among patches changes both the density and the allele frequency of populations. In turn, both the connectivity among patches and their genetic composition can affect the sign and strength of selection for dispersal. For example, traits from rare migrants can become dominant (i.e., the advantage of the rare or negative-frequency dependent selection) or go quickly to extinction in a new patch (i.e., the advantage of the common or positive-frequency dependent selection). In spite of this, the role of spatial heterogeneity in eco-evolutionary dynamics has only been addressed in few experimental systems (Farkas 2013, Kerr 2006, Singer & McBride 2012, Hanski 2011). A particularly well-documented example is that of the Glanville fritillary butterfly, where the allele frequency in the pgi dispersing gene is driven by spatial heterogeneity (Hanski 2011).

Given the links between dispersal, and the dynamics of interacting populations and allele frequencies, several avenues of research remain to be undertaken to understand how systems occurring in spatially heterogeneous landscapes are shaped by eco-evolutionary dynamics.

1.3. Merging space, food webs and evolution

Recently, researchers (mainly ecologists) have focused on the study of multi-trophic metacommunities (i.e., communities linked by dispersal and trophic interactions– Wilson 1992; Holyoak *et al.* 2005; Pillai et al 2011; Haegeman & Loreau, 2014; Melian *et al.* in press). The composition of such multi-trohic metacommunities reflects that of simple communities, in which species may be linked by a linear food chain or embedded in a complex food web (Winnemiller & Polis 1996).

Spatial heterogeneity plays an important role in structuring food webs. Indeed, McCann *et al.* (2005) and Rooney *et al.* (2006) showed that the high mobility of predators can couple different food web energy channels across space and contribute to global food web stability (the “bird feeder effect”) (McCann *et al.* 2005; Rooney *et al.* 2006). Moreover, dispersal of omnivores may contribute to the robustness of the metacommunity, thereby enhancing food web complexity and species diversity (Pillai *et al.* 2011). None of these examples, however, considers the evolution of any of the players involved in the food web.

In a subsequent study, a mathematical model predicted that local extinction patterns in a predator-prey metacommunity affected differently the evolution of dispersal in predators and in prey (Pillai *et al.* 2012). This promising result suggests that emergent properties stem from the

combination of ecology and evolution in metacommunities of two species. Hence, eco-evolutionary dynamics in metacommunities composed of more complex food webs may be a propitious ground from which emergent patterns are generated. Still, both empirical and theoretical studies on this topic are conspicuously lacking (Thuiller 2013, Urban *et al.* 2008): we aim to merge empirical observations and theory by extending food webs in heterogeneous space using invertebrate soil food webs as a model system (Moya-Laraño *et al.* 2012).

1.4. Soil food webs as a model system

Soil food webs are formidably diverse systems that are responsible for the decomposition of organic material and nutrient recycling in terrestrial ecosystems (Swift *et al.* 1979; André *et al.* 2002; Hättenschwiler *et al.* 2005; Wardle 2006; Decaëns 2010). In recent years both laboratory (Brose *et al.* 2008; Schneider *et al.* 2012) and field experiments (Scheu & Schaefer 1998; Wise & Chen 1999; Chen & Wise 1999; Moya-Laraño & Wise 2007; McLaughlin *et al.* 2010) have been conducted to address relevant ecological questions related to food web theory, including how water affects decomposition processes indirectly via its effects on the food web (Lensing & Wise 2006). Soils are highly heterogeneous ecosystems (Moore *et al.* 2004), with strong spatial heterogeneity in water content (Schume *et al.* 2003). This can drive the spatial structuring of leaf-litter food webs at micro, local and regional scales (Melguizo-Ruiz *et al.* 2012). At the micro-environmental scale, water availability can accumulate in water pockets (i.e., soil patches were moisture accumulates) due to the micro-topography of the area in which the leaf litter sits (e.g., the base of slopes) or to other landmarks which affect the micro-environment (e.g., underneath shrubs at the base of tree trunks). Since soil moisture affects soil fauna, by attracting them to moist areas during dry conditions (Verdeny-Vilalta & Moya-Laraño 2014), these moisture pockets may work as islands of productivity during drought conditions. This sets the perfect scenario to study metacommunity dynamics, understood as micro-environmental patches connected by migration.

1.5. Aims: a few examples of hypothesis testing using WEAVER 1.0

Here, we present WEAVER 1.0, an Individual-Based Modelling computer program that aim to fill the gap between empirical observations of individual based food webs in heterogeneous space with the theoretical predictions coming from eco-evolutionary multi-trophic metacommunity dynamics. This programme is an extension of a former simpler platform (mini-AKIRA, Moya-Laraño *et al.* 2012) which by having increased computing performance to a great extent allows the exploration of individual based eco-evolutionary dynamics in multi-species food webs across space. This framework successfully links genes to ecosystems through space, reaching an unprecedented level of comprehensiveness which helps to understanding both ecological and evolutionary dynamics at the gene, individual, population, community and spatial levels. In addition, all of these can be linked to ecosystem processes, such as top-down control of predators inducing trophic cascades affecting basal resources at different temperatures (Moya-Laraño *et al.* 2012), or the role of predators for

maintaining biodiversity across space under different food web, island and genetic configurations (this paper). In addition, rather than being a "black box", the present framework, and as in empirical studies, produces several detailed outputs (including gene spatio-temporal dynamics) that can be used to understanding all the mechanisms behind eco-evolutionary dynamics. Actually, if needed, the researcher can know everything that each gene and each individual have done in the simulation. As far as we know no other framework that exists to date is able of such detail. However, although we recreate some hypotheses in the Discussion, in this paper we were not interested in understanding all the mechanisms for the patterns found but rather in exploring food web persistence and trait evolution under different genetic and ecological scenarios. We note that one of the great advantages is that one can perform any additional simulation experiments (e.g., eliminating particular species or knocking down variability in a particular trait) to uncover the mechanisms responsible for the patterns emerging from simulations.

The overall purpose of the simulations presented in this article is to illustrate the usefulness of our IBM framework through a few examples, addressing some of the main open questions in the field of eco-evolutionary dynamics and ecological networks in space. We ask six questions 1) Does connectance affect food web persistence?, 2) Does standing intraspecific genetic variation alter food web persistence by triggering rapid evolution?, 3) In a multi-trophic metacommunity context, how does the spatial structure (i.e., degree of spatial isolation) alter persistence and rapid evolution in food webs?, 4) In all of the above scenarios, do predators inhibit prey populations in rapid evolving predator-prey systems? and if so do predators contribute to maintain prey diversity? 5) How does standing genetic variation alter the evolutionary rate and the persistence of predator-prey systems? and 6) do traits evolve differently in prey under purely competitive environments (without predators) than when both predation and competition are at play?

We note that any results derived from this approach need to be looked as what they are: digital approximations of nature. To take full advantage of this simulation platform the results must be contrasted with real systems and continuously feedback on each other. We propose how to integrate simulations with real systems to link, step by step, the "in vivo" - "in silico" gap, this having the potential of generating an unprecedented level of understanding about how real ecosystems work. For instance, if one output is produced in nature which simulations are not reproducing, one must use the new estimates and parameters found in the experiment and include them in further simulations. We have included a section in the Discussion to explain how to implement this Feedback Research Program. However, we stress that performing studies at the digital level only, as we do here, can provide important clues and hypotheses to be empirically tested in future experiments.

2. Materials and Methods

Unless stated otherwise, we here use the same approach as in the former paper (Moya-Laraño *et al.* 2012), in which we provided a level of detail that is out of reach in the current article. We therefore refer to the reader who wants to fully grasp all the underpinnings and details of this modeling framework to the above reference. However, we have made an effort to explain the most relevant parameters to follow the approach and make this article as self-explanatory as possible. When necessary, we have actually replicated some of the information in Moya-Laraño *et al.* 2012.

We modelled 20-species beech forest soil food webs (Melguizo-Ruiz *et al.* 2012) with differing degrees of connectivity and genetic variation in the same 13 traits as in Moya-Laraño *et al.* 2012 (Appendix), namely fixed body size at birth, amount of energy for maintenance and growth at birth, growth ratio, phenology (or genetically-determined development time determining birth date beyond environmental constraints such as changes in temperature), searching area, voracity, sprint speed, metabolic rate, temperature plasticity for speed, voracity and searching area, and activation energy for metabolic rate. Estimates of ecological ranges for temperature-dependent traits were obtained from the literature (Dell *et al.* 2011, Ehnes *et al.* 2011). The amount of genetic trait variability is governed by the parameter φ (Moya-Laraño *et al.* 2012) which can be thought of as a genetic restriction parameter ranging between 0 and 1 (Appendix). Values of φ close to 0 indicate that the trait has the highest possible genetic variation (i.e., across the entire phenotypic range, Table 1) and a value of 1 means that all animals are genetically identical for that particular trait. For simplicity we used the same value for all traits and did not play for different amounts of genetic variation in different traits. φ = 0.99 means that animals are genetically identical, hence adaptation cannot occur from standing genetic variation. In absence of genetic correlation among traits (Moya-Laraño *et al.* 2012), φ = 0.01 means that genetic constrains are minimal, hence evolution can occur at rapid pace and in any direction. To narrow down the questions to be answered, we ran all simulations without genetic correlation among traits (Moya-Laraño *et al.* 2012). We therefore compared scenarios in which all species had maximum genetic variation in all traits (φ = 0.01) against others in which genetic variability was restricted to a minimum (φ = 0.99; Appendix).

One important feature of WEAVER 1.0 is that it can restrict which species are able to feed on each other by including a vector of edible species allowing initializing simulations with particular food web structures. To manipulate connectance and to simulate realistic food webs, we asked the program Network3D to build two random 20-species webs restricted to the niche model (Williams and Martinez 2000), one with relatively low connectance (0.1) and another with relatively high connectance (0.3). To fit in the animals from the beech forest food web, top predators were assigned to the largest species (harvestmen, spiders and centipedes), intermediate size predators to predators of the smallest size (Mesostigmata and Prostigmata mites) and the smallest sizes were alloted to fungivores, namely springtails (Collembola), oribatid mites (Oribatida) and enchytraeid

worms (Clitellata). Within each taxon, we chose a diversity of offspring and adult body sizes to generate across-species diversity. The ranges of the other traits were similar among species, with the exception of that of enchytraeids. Indeed, due to their high starvation resistance, likely coming from their low activation energies for metabolic rates (Ehnes *et al.* 2011; see Appendix), this group grew to disproportionately large numbers in our simulations as compared to other fungivore species. We believe that some additional constraints, such as their low desiccation resistance (Lindberg *et al.* 2002; Maraldo *et al.* 2008), which is not yet incorporated in our framework, may make populations of these worms growing at lower rates in the wild despite their relatively low energy expenditure to activate metabolism. We thus decided to compensate this by decreasing their assimilation efficiencies relative to other taxa (Table 1). In addition, to further test the effect of connectivity on food web persistence, we simulated a hypergeneralist food web, in which all predators were able to feed on all the species, including themselves (connectance = 0.55, Figure 1). Food webs with connecntance 0.1 and 0.55 had the exact same species, 11 species of predators and 9 species of fungivores. To allow its fitting to the niche model, the food web with intermediate connectance (0.3) necessarily included a different number of predators (16) and fungivores (4, Figure 1, Table 1). Hence, we created our hypergeneralist web by allowing all predators in the original niche model food web with connectance 0.1 to feed on all other prey and predators, therefore manipulating the latter to have a connectance of 0.55. Food web structure was built taken into account animals only. For simplicity we included in all webs a single fungus species upon which all fungivores fed. As highly connected webs were the most persistent, the remaining simulations were performed using these hypergeneralist webs.

To incorporate a spatial component, we simulated a 4-micro-island scenario mimicking water (moisture) pockets in the forest floor (e.g., Melguizo-Ruiz *et al.* 2012) in which fungi were able to grow (Figure 1). The space surrounding these islands was drier (initialized at 0% RH), thus not allowing fungi to grow. Since animals did not sense water, nor water did directly affect them, this 0% RH had only effect on fungi (i.e., it could have been any number below that that allowed fungus growth in this scenario, < 85% see Appendix). These micro-islands were spheres of 5-cell (patch) units of radius (see Supplementary Material) and were either close to each other (distance among centers 10 cells, distance among borders 0 cells) or at a distance (10 or 40-cell distance among borders). Therefore, the four micro-islands had equal basal productivity. The dimensions of the Worlds containing these islands were (depth x width x length) 10 x 20 x 20, 10 x 50 x 50 or 10 x 80 x 80 cells respectively. For the two last scenarios, in which islands were far apart, we minimized edge effects by allowing a 10-cell space around islands. Since so far migration in WEAVER 1.0 depends merely on an animal's mobility which in turn depends on several state variables (e.g., fungi or prey availability, predatory threat, internal stage -condition, *c*-, and the trait searching area), here we did not consider long-distant dispersal (e.g., aerial dispersal in springtails and spiders).

Table 1. Species and trait ranges included in simulations.

					Trait Ranges	
Species ID	**Class**	**Common name**	**Taxon[a]**	**Feeding guild**	**Energy tank (%)[b]**	**Growth ratio**
(a) Webs with connectance 0.1 or 0.55						
aca1	Arachnida	mite	Mesostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca2	Arachnida	mite	Prostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca3	Arachnida	mite	Mesostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca4	Arachnida	mite	Prostigmata	predator	0.25 - 0.50	1.35 - 1.45
spd1	Arachnida	spider	Agelenidae	predator	0.25 - 0.50	1.20 - 1.30
spd2	Arachnida	spider	Erigoninae	predator	0.25 - 0.50	1.25 - 1.35
spd3	Arachnida	spider	Dysderidae	predator	0.25 - 0.50	1.15 - 1.25
spd4	Arachnida	spider	Theridiidae	predator	0.25 - 0.50	1.15 - 1.25
geo1	Chilopoda	centipede	Geophilomorpha	predator	0.25 - 0.50	1.15 - 1.25
lit1	Chilopoda	centipede	Lithobimorpha	predator	0.25 - 0.50	1.15 - 1.25
opi1	Arachnida	hartvestmen	Opilionida	predator	0.25 - 0.50	1.15 - 1.25
col1	Insecta	springtail	Collembola	fungivore	0.25 - 0.50	1.25 - 1.35
col2	Insecta	springtail	Collembola	fungivore	0.25 - 0.50	1.35 - 1.45
col3	Insecta	springtail	Collembola	fungivore	0.25 - 0.50	1.15 - 1.25
enc1	Oligochaeta	potworm	Enchytraeidae	Fungivore	0.25 - 0.50	1.35 - 1.45
enc2	Oligochaeta	potworm	Enchytraeidae	fungivore	0.25 - 0.50	1.25 - 1.35
enc3	Oligochaeta	potworm	Enchytraeidae	fungivore	0.25 - 0.50	1.25 - 1.35
ori1	Arachnida	mite	Oribatida	fungivore	0.25 - 0.50	1.35 - 1.45
ori2	Arachnida	mite	Oribatida	fungivore	0.25 - 0.50	1.15 - 1.25
ori3	Arachnida	mite	Oribatida	fungivore	0.25 - 0.50	1.25 - 1.35

Table 1. Species and trait ranges included in simulations (cont'd).

	Trait Ranges					
Species ID	**Phenology (days)**	**Body size at birth (mg)**	**Assimilation efficiency**	**Voracity**	**Speed**	**Search area**
aca1	3 - 11	0.0010 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca2	3 - 11	0.0020 - 0.0040	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca3	3 - 11	0.0030 - 0.0050	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca4	3 - 11	0.0040 - 0.0060	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd1	3 - 11	0.0130 - 0.0330	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd2	3 - 11	0.0080 - 0.0100	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd3	3 - 11	0.0409 - 0.0690	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd4	3 - 11	0.0090 - 0.0290	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
geo1	3 - 11	0.0900 - 0.1000	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
lit1	3 - 11	0.0450 - 0.0650	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
opi1	3 - 11	0.0040 - 0.0260	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
col1	3 - 11	0.0010 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
col2	3 - 11	0.0040 - 0.0240	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
col3	3 - 11	0.0020 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
enc1	3 - 11	0.0001 - 0.0020	0.5 - 0.7	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
enc2	3 - 11	0.0001 - 0.0020	0.5 - 0.7	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
enc3	3 - 11	0.0010 - 0.0030	0.5 - 0.7	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
ori1	3 - 11	0.0030 - 0.0050	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
ori2	3 - 11	0.0001 - 0.0020	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
ori3	3 - 11	0.0010 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3

Table 1. Species and trait ranges included in simulations (cont'd).

	Trait Ranges				
Species ID	**met_rate**	**Q_{10} voracity**	**Q_{10} speed**	**Q_{10} search area**	**Activation E (eV)**
aca1	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.33 - 0.42
aca2	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.36 - 0.46
aca3	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.33 - 0.42
aca4	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.36 - 0.46
spd1	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.65 - 0.75
spd2	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.65 - 0.75
spd3	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.65 - 0.75
spd4	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.65 - 0.75
geo1	0.46 - 0.66	3 - 4	1.5 - 2.5	2.0 - 2.5	0.75 - 0.85
lit1	0.45 - 0.65	3 - 4	1.5 - 2.5	2.0 - 2.5	0.75 - 0.85
opi1	0.46 - 0.76	3 - 4	1.5 - 2.5	2.0 - 2.5	0.65 - 0.75
col1	0.65 - 0.85	2 - 4	1.5 - 2.5	1.5 - 2.5	0.61 - 0.70
col2	0.65 - 0.85	2 - 4	1.5 - 2.5	1.5 - 2.5	0.61 - 0.70
col3	0.55 - 0.85	2 - 4	1.5 - 2.5	1.5 - 2.5	0.61 - 0.70
enc1	0.70 - 0.90	2 - 4	1.5 - 2.5	1.5 - 2.5	0.39 - 0.49
enc2	0.70 - 0.90	2 - 4	1.5 - 2.5	1.5 - 2.5	0.39 - 0.49
enc3	0.70 - 0.90	2 - 4	1.5 - 2.5	1.5 - 2.5	0.39 - 0.49
ori1	0.57 - 0.77	2 - 4	1.5 - 2.5	1.5 - 2.5	0.66 - 0.76
ori2	0.57 - 0.77	2 - 4	1.5 - 2.5	1.5 - 2.5	0.66 - 0.76
ori3	0.57 - 0.77	2 - 4	1.5 - 2.5	1.5 - 2.5	0.66 - 0.76

Table 1. Species and trait ranges included in simulations (cont'd).

					Trait Ranges	
Species ID	**Class**	**Common name**	**Taxon[a]**	**Feeding guild**	**Energy tank (%)[b]**	**Growth ratio**
(b) Webs with connectance 0.3						
aca1	Arachnida	mite	Mesostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca2	Arachnida	mite	Prostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca3	Arachnida	mite	Mesostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca4	Arachnida	mite	Prostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca5	Arachnida	mite	Mesostigmata	predator	0.25 - 0.50	1.35 - 1.45
aca6	Arachnida	mite	Prostigmata	predator	0.25 - 0.50	1.35 - 1.45
spd1	Arachnida	spider	Agelenidae	predator	0.25 - 0.50	1.20 - 1.30
spd2	Arachnida	spider	Erigoninae	predator	0.25 - 0.50	1.25 - 1.35
spd3	Arachnida	spider	Dysderidae	predator	0.25 - 0.50	1.15 - 1.25
spd4	Arachnida	spider	Theridiidae	predator	0.25 - 0.50	1.15 - 1.25
spd5	Arachnida	spider	Dysderidae	predator	0.25 - 0.50	1.15 - 1.25
spd6	Arachnida	spider	Erigoninae	predator	0.25 - 0.50	1.15 - 1.25
geo1	Chilopoda	centipede	Geophilomorpha	predator	0.25 - 0.50	1.15 - 1.25
geo2	Chilopoda	centipede	Geophilomorpha	predator	0.25 - 0.50	1.15 - 1.25
lit1	Chilopoda	centipede	Lithobiomorpha	predator	0.25 - 0.50	1.15 - 1.25
lit2	Chilopoda	centipede	Lithobiomorpha	predator	0.25 - 0.50	1.15 - 1.25
col1	Insecta	springtail	Collembola	fungivore	0.25 - 0.50	1.25 - 1.35
col2	Insecta	springtail	Collembola	fungivore	0.25 - 0.50	1.35 - 1.45
enc1	Oligochaeta	potworm	Enchytraeidae	fungivore	0.25 - 0.50	1.35 - 1.45
ori1	Arachnida	mite	Oribatida	fungivore	0.25 - 0.50	1.35 - 1.45

Table 1. Species and trait ranges included in simulations (cont'd).

	Trait Ranges					
Species ID	**Phenology (days)**	**Body size at birth (mg)**	**Assimilation efficiency**	**Voracity**	**Speed**	**Search area**
aca1	3 - 11	0.0010 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca2	3 - 11	0.0020 - 0.0040	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca3	3 - 11	0.0030 - 0.0050	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca4	3 - 11	0.0040 - 0.0035	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca5	3 - 11	0.0028 - 0.0035	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
aca6	3 - 11	0.0200 - 0.0300	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd1	3 - 11	0.0130 - 0.0330	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd2	3 - 11	0.0080 - 0.0100	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd3	3 - 11	0.0490 - 0.0690	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd4	3 - 11	0.0090 - 0.0290	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd5	3 - 11	0.0600 - 0.0800	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
spd6	3 - 11	0.0035 - 0.0045	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
geo1	3 - 11	0.0900 - 0.1000	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
geo2	3 - 11	0.0500 - 0.0700	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
lit1	3 - 11	0.0450 - 0.0650	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
lit2	3 - 11	0.0400 - 0.0500	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.4
col1	3 - 11	0.0010 - 0.0030	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
col2	3 - 11	0.0040 - 0.0240	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
enc1	3 - 11	0.0001 - 0.0020	0.5 - 0.7	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3
ori1	3 - 11	0.0030 - 0.0050	0.7 - 0.9	0.55 - 0.75	0.1 - 0.3	0.1 - 0.3

Table 1. Species and trait ranges included in simulations (cont'd).

	Trait Ranges				
Species ID	**met_rate**	**Q_{10} voracity**	**Q_{10} speed**	**Q_{10} search area**	**Activation E (eV)**
aca1	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.33 - 0.42
aca2	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.36 - 0.46
aca3	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.33 - 0.42
aca4	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.36 - 0.46
aca5	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.33 - 0.42
aca6	0.60 - 0.80	3 - 4	1.5 - 2.5	2.0 - 2.5	0.36 - 0.46
spd1	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
spd2	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
spd3	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
spd4	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
spd5	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
spd6	0.50 - 0.70	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
geo1	0.46 - 0.66	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
geo2	0.46 - 0.66	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
lit1	0.45 - 0.65	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
lit2	0.45 - 0.65	3 - 4	1.5 - 2.5	2.0 - 2.5	0.45 - 0.55
col1	0.65 - 0.85	2 - 4	1.5 - 2.5	1.5 - 2.5	0.61 - 0.70
col2	0.65 - 0.85	2 - 4	1.5 - 2.5	1.5 - 2.5	0.61 - 0.70
enc1	0.70 - 0.90	2 - 4	1.5 - 2.5	1.5 - 2.5	0.39 - 0.49
ori1	0.57 - 0.77	2 - 4	1.5 - 2.5	1.5 - 2.5	0.66 - 0.76

[a]Taxonomic level specification differs depending on the group.

[b]Trait definitions: energy tank, percentage of body size devoted to maintenance and growth at birth; growth ratio, ratio between two instar body lengths; phenology, time between egg laying and birth; body size at birth, mass of the tructural body size; assimilation efficiency, percentage of ingested food converted to own mass; voracity, sprint speed, search rea, and metabolic rates are mass scaling coefficients for ingested mass, maximum speed, number of cells travelled per day, nd metabolic rates, respectively; Q10s and activation energy for metabolic rate denote genetic variability in temperature plasticity for the same four traits (further information can be found in Moya-Laraño *et al.*, 2012 and in Appendix).

To further include realism in the simulations, we initialized the density of each species and instar following mass-abundance allometric constraints (Reuman *et al.* 2009), for which we used the equation $N = 74.8M^{-0.75}$ as in Schneider *et al.* (2012). As in other equations involving Mass (see Appendix), we assumed 70% of water body content to calculate the number of individuals of each instar and species. To accommodate the output coming from the above allometric equation to our simulation, we applied the above equation to all instars and species and the absolute resulting number was then divided by the total number of individuals, therefore obtaining a fraction for each species and instar. To calculate the absolute number of each species and instar in the simulation we then multiplied this fraction by the total number of individuals at initialization (i.e., the community size, which was set at 20,000) and rounded the resulting number. We tested the effect of predators on prey density and diversity (like in keystone predation – Paine 1966) by running simulations with all species in the food web and comparing these with simulations in which redators were excluded i.e., with fungivores only.

Because these simulations have a strong stochastic component, to assess the consistency of the results we ran 5 replicates of each simulation. However, as the main patterns are sumarized in the statistical analyses, we only display a few of the dynamics as examples. All statistical analyses were performed in R (R development core team 2014). The main hypotheses stated above were tested using general linear models (GLM) on all replicates, with proportion of prey, predators and of all species remaining at the end as dependent variables. When necessary, we ran log-likelihood ratio tests to unravel potential differences among groups and post-hoc Tukey tests to compare pairs of groups (package “multcomp”). All simulations were ran for 200 days. For one of the parameter combinations that showed the strongest signs of stability we additionally ran one simulation for 500 days with a twofold purpose 1) to determine how many and which species would remain (long-term persistence) and to draw the final (persistent) web with species-to-species interaction strengths and 2) to explore trait evolutionary dynamics, for which we measured the change in constitutive traits through time by fitting splines in a glm model (R library “splines”) in which time (day) was the independent variable and the constitutive trait value the dependent variable. The results of the simulations were then plotted with 95% confidence bands using the library “effects” (Fox 2003) in R. We further explored trait evolution in one of the fungivore species that persisted until the end in one of the webs (predators present), as well as in simulations that involved competition only. The purpose of this analysis was to explore whether trait evolution differed in a purely competitive environment as compared to an environment in which both predation and competition occurred. We predicted that traits associated with competition or anti-predatory behaviour would evolve differently.

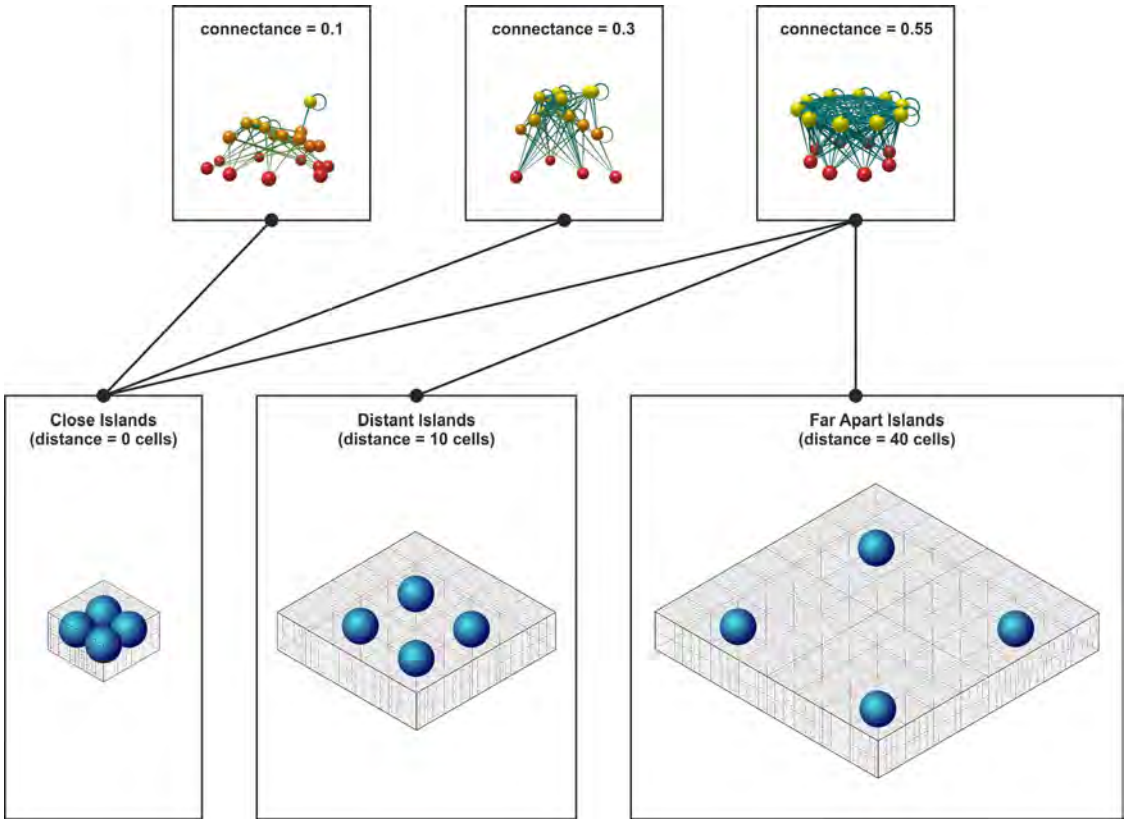

Figure 1. Food web and metacommunity structures included in the simulations. The joining segments indicate which food web structures were tested under which metacommunity spatial structures. The spheres in the lower panel correspond to micro-islands of moisture (moisture pockets) in the forest floor.

3. Results

3.1. Connectance and food web persistence

An example of the dynamics can be found in Figure 2. Connectance increased the proportion of species remaining at the end of the simulation by 1.7x. An example of the dynamics can be found in Figure 2. (GLM, b = 0.34, t_{14} = 2.66, p = 0.0197, Figure 3). This effect was stronger and highly significant for predators (GLM, b = 1.02, t_{14} = 6.79, p < 0.0001, Figure 3). However, increasing connectance increased the extinction rate for prey (GLM, b = -0.46, t_{14} = -3.32, p = 0.006, Figure 3). Note however that the trends are not linear, as the webs with connectance 0.1 and 0.3 are similar to each other (post-hoc "Tukey" test, p > 0.13 for both comparisons) and they both significantly differ from the web with connectance 0.55 (both p < 0.025).

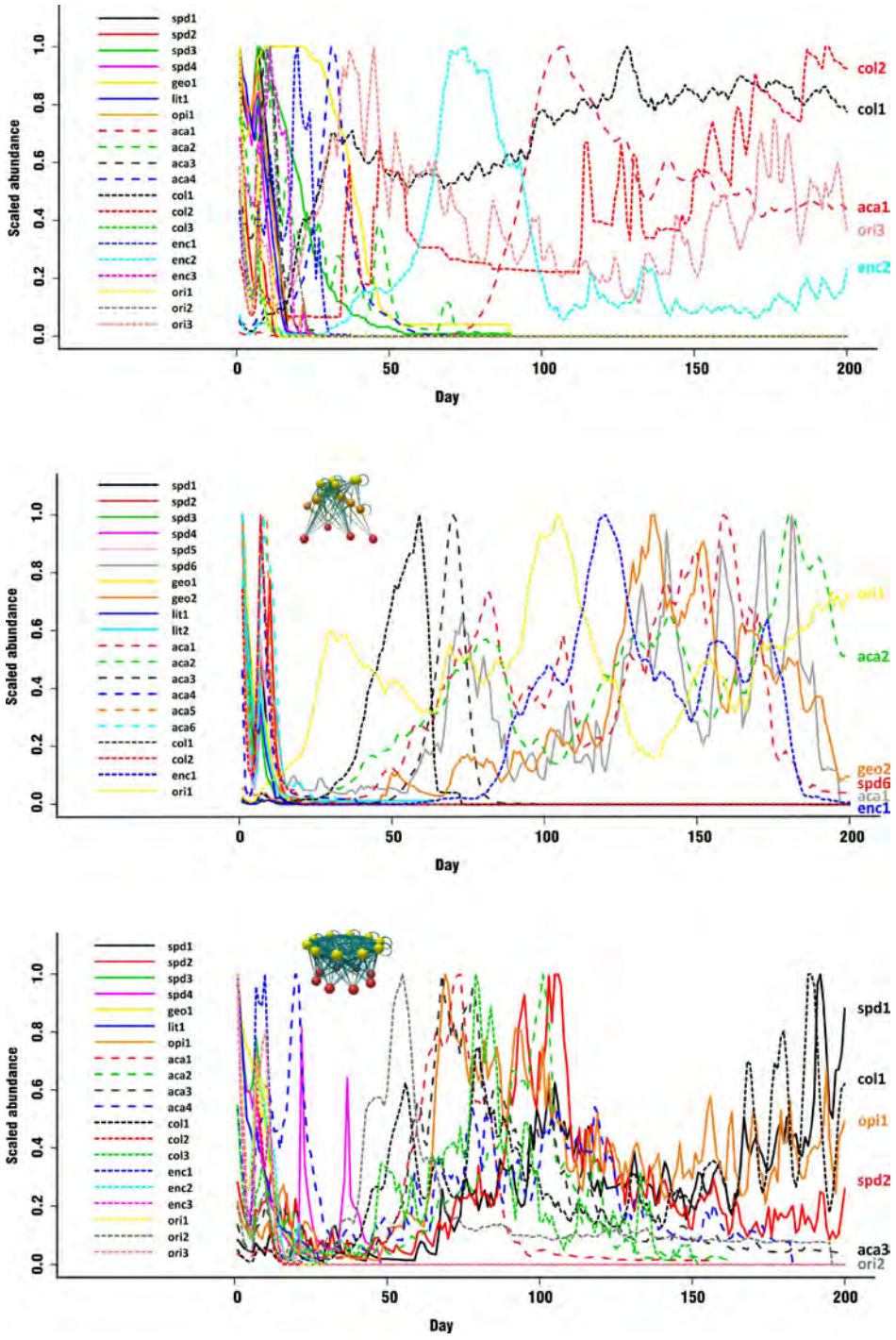

Figure 2. Effect of connectance in ecological dynamics. Dynamics of the population of each species (starting with 20 species) during 200 days, when the connectance of the food web was low (0.1, upper panel), relatively high (0.3, middle panel) or very high (0.55, lower panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (y-axis) are shown scaled at 0-1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines to small predators (predatory mites) and solid lines to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species. Names in the legend correspond to those in Table 1.

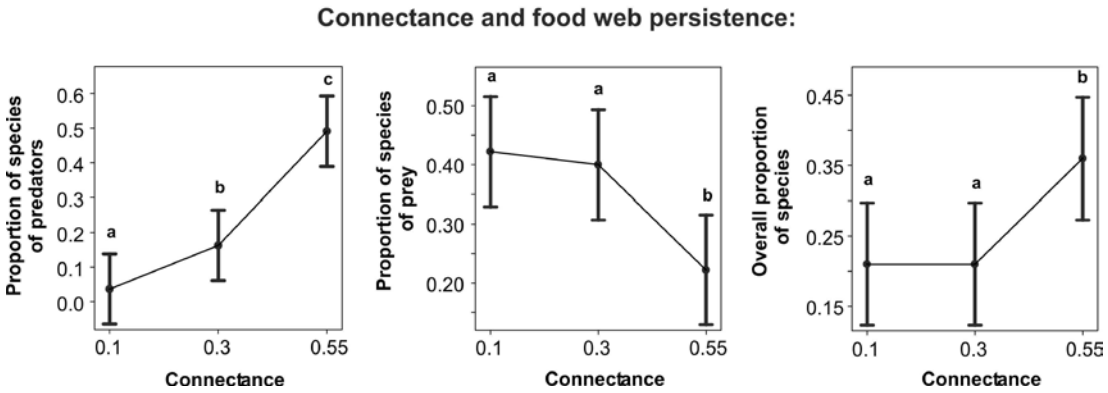

Figure 3. Effect of connectance. However, increasing connectance increased the extinction rate for prey (GLM, b = -0.46, t_{14} = -3.32, p = 0.006). Note however that the trends are not linear, as the webs with connectance 0.1 and 0.3 are similar to each other (post hoc "Tukey" test, p > 0.13 for both comparisons) and they both significantly differ from the web with connectance 0.55 (both p < 0.025).

3.2. Genetic variation and food web persistence

High genetic variation allowed the persistence of 3.6x more species than either no genetic variation at all, or an intermediate level. An example of the dynamics can be found in Figure 4 (prey, GLM, b = 0.06, t_{14} = 3.17, p = 0.007; predators, GLM, b = 0.23, t_{14} = 5.54, p < 0.0001; overall, GLM, b = 0.15, t_{14} = 5.3, p = 0.0001, Figure 5). However, some patterns are clearly non-linear, and allowing the highest variability was only significantly different for prey between the two extremes (highest vs. lowest, post-hoc "Tukey" test, p = 0.006, remaining comparisons p > 15), being the two lowest levels of genetic variation not significantly different for the proportion of predators that persisted (p = 0.662) and both significantly lower than the scenario with high genetic variation (both p's < 0.0001). The pattern for overall diversity was similar to that of the predators (comparison between the two lowest levels, p = 0.443; comparison between each of the two lowest levels *vs*. high genetic variation, both p < 0.0001).

3.3. Island distance and food web persistence

The overall proportion of species was between 2.6x and 3.5x more persistent in islands that were contiguous to each other or at relatively shorter distances (minimum distance 20 cells) respectively, than when they were farther apart (50 cells). An example of the dynamics can be found in Figure 6. In addition, the proportion of prey species was 2x - 2.5x more persistent at intermediate distances. The three models differed significantly from each other (all p < 0.0001; Figure 7). Post-hoc comparisons revealed no differences between the shortest and longest distances in the proportion of prey species that remained (Tukey test, p = 0.750). However, the proportion of species remaining was significantly higher at intermediate distances when compared with the shortest (p < 0.0001) or longest (p < 0.0001) distances. Predator species, on the other hand, persisted equally well at the

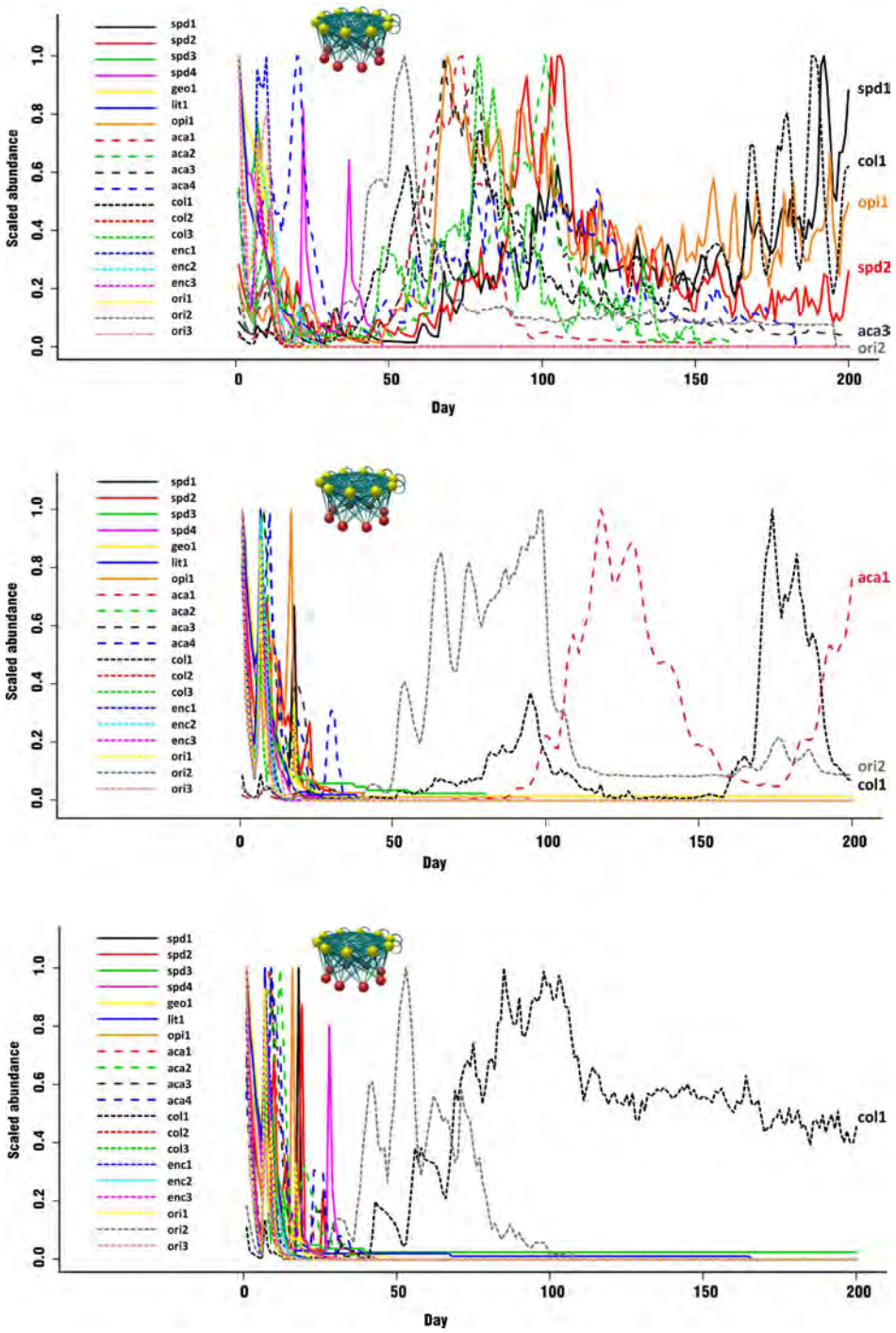

Figure 4. Effect of genetic variation in ecológica dynamics. Dynamics of the population of each species during 200 days when the connectance of the food web was very high (0.55), and trait genetic variation was either high (φ = 0.01, superior panel), medium (φ = 0.49, middle panel) or almost zero (φ = 0.99, inferior panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (y-axis) are shown scaled at 0-1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines to small predators (predatory mites) and solid lines to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species. Names in the legend correspond to those in Table 1.

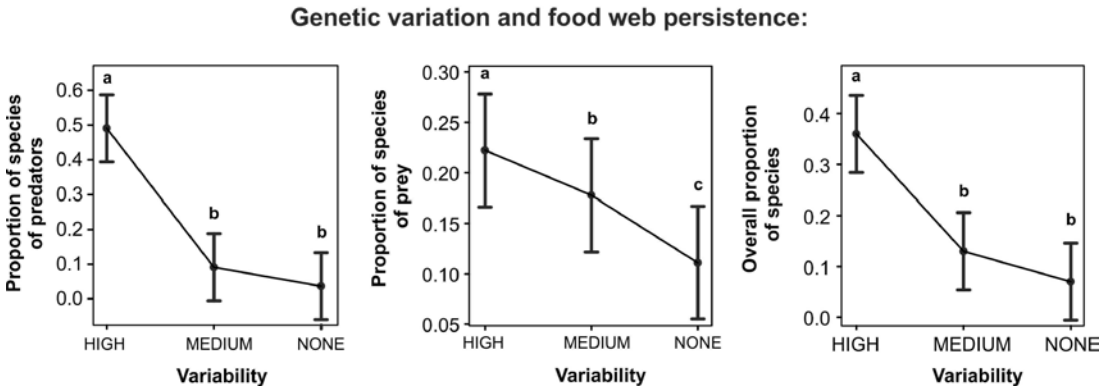

Figure 5. Effect of genetic variation. Proportion of predator (left panel), prey (central panel) and overall (right panel) species remaining at the end of the simulations (N = 5) when genetic variation in the species embedded in the food web was high (φ = 0.01), intermediate (φ = 0.49), or almost zero (φ = 0.99). Values are least-squares means ± SE. Letters on top of bars denote significant differences among groups (< 0.05).

shortest and intermediate distances (p = 0.969) and a 4.5x higher proportion of predators persisted at these two distances relatively to the longest distances (both p's < 0.0001). The pattern of overall diversity also showed the highest persistence of species at intermediate distances, with only the comparison between shortest and intermediate distances being marginally significant (p = 0.065), with the other two comparisons highly significant (both p's < 0.0001). A total 50% of species remained at the end of the simulation at intermediate distances.

3.4. Predator top down control on prey diversity

Overall, the presence of predators resulted in high extinction rates on prey. An example of the dynamics (Figure 8) reveals that, in presence of predators results in the extinction of two species of potworms (upper panel) that would make it to the end in a competitive environment (lower panel). Conversely, in the presence of predators a species of springtail (col1) and another of oribatid mite (ori2) persisted, a pattern that never occurred in absence of predators (not shown). In the islands located at the shortest distances (i.e., contiguous to each other), predators had a strong negative effect on prey species, diminishing the proportion of species that remained at the end of the simulation by 40% (Figure 9, 0 distance), especially after longer periods, when only two species of echytraeids persisted in the presence of predators (lower panel of Figure 8). In addition, comparing the effect according to island distance reveals that, at intermediate distances, the proportion of prey species that is maintained does not differ between environments with or without predators (GLM, distance*predator presence, $\chi_2^2 = 21.6$; $p < 0.0001$; Figure 9 see also Figure 7 Tukey test on predator effect at intermediate distances, p = 1). Therefore, predators had a strong effect on the extinction rate of prey species, but this was contingent upon the spatial composition of the food web. In particular, predators showed a strong stabilizing effect at intermediate island distances, in which half the prey species remained until the end of the simulation. Moreover, more importantly, predators affected the identity of the species that remained.

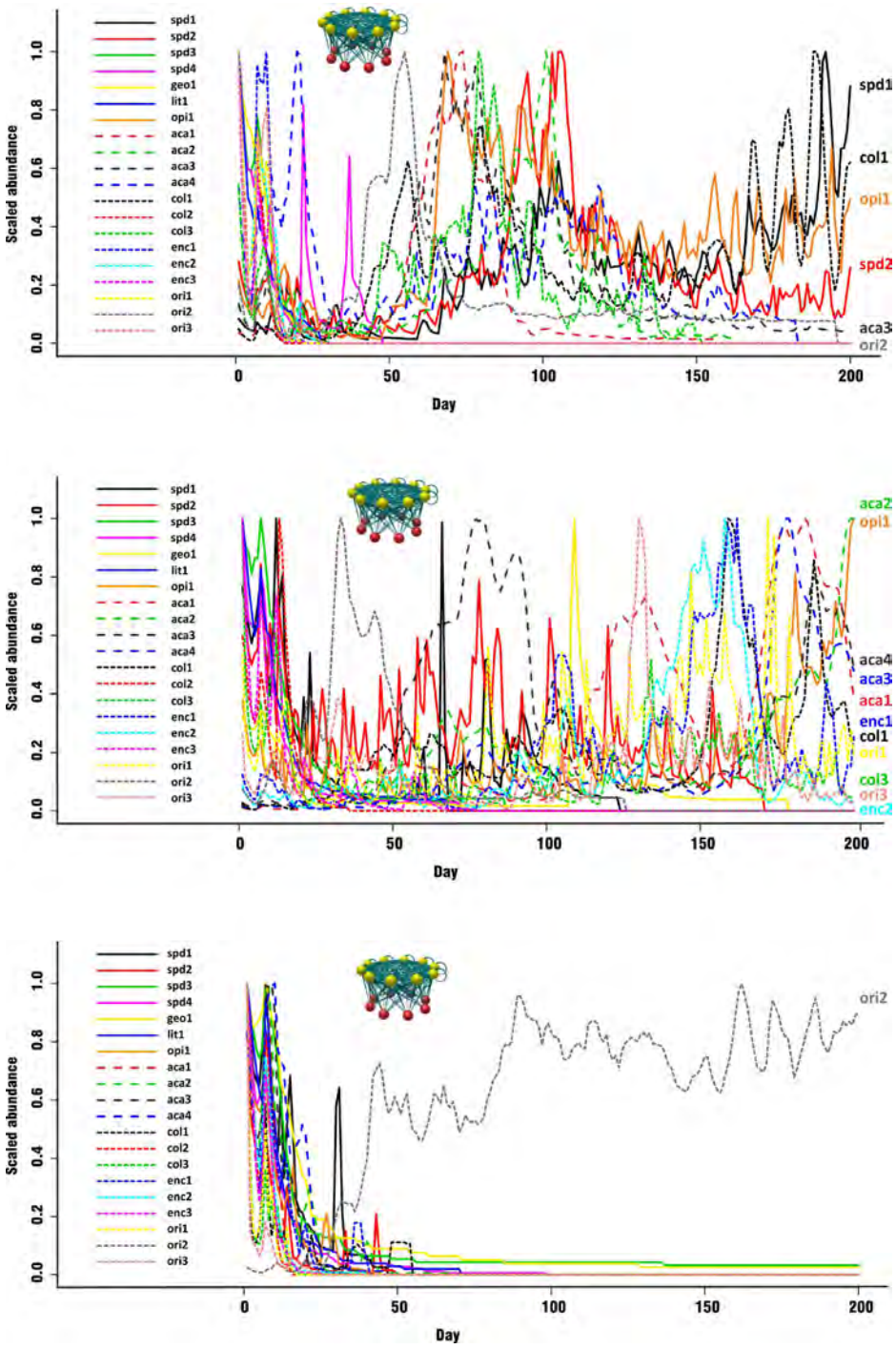

Figure 6. Effect of distance between islands in ecological dynamics. Dynamics of the population of each species (starting with 20 species) during 200 days when the connectance of the food web was very high (0.55), but islands were at different distances from each other (0 cells-superior panel; 10 cells-middle; or 40 cells-inferior panel). Figures depict one replicate out of the five ran per simulation. Abundances of each species (Y-axis) are shown scaled at 0-1. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines correspond to small predators (predatory mites) and solid lines correspond to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant. Names in the legend correspond to those in Table 1.

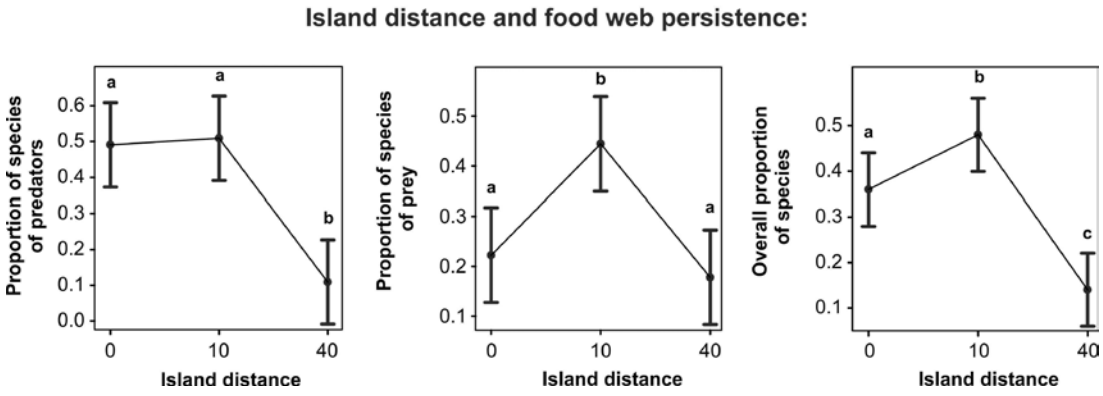

Figure 7. Effect of distances between islands. Proportion of predator (left panel), prey (central panel) and overall (right panel) species remaining at the end of the simulations (N = 5) when islands were contiguous to each other (distance = 0) or when they were separated by a minimum distance of either 10 or 40 cells. Values are least-squares means ± SE. Letters on top of bars denote significant differences among groups (< 0.05).

3.5. Multi-trophic spatio-temporal dynamics during a 500-day simulation

We ran one of the most stable scenarios (highly connected web, high genetic variability islands at intermediate distances) for a longer period of time (500 days) and found that out of 20 species, 5 persisted (4 species of predators and 1 prey, Figure 10), and there was a steady increase in abundance of the top predator (the centipede lit1). The spatial dynamics for these five species were highly complex and showed some emergent patterns. First, large predators (centipedes and opilionids) were highly mobile relative to fungivores and small predators. Second, the first snapshot (day 58) showed an emerging spatial segregation among the two species of predatory mites, which occupied different islands, and also for the shared prey (springtail), which was mostly in one island only. Third, at day 256 prey populations had gone extinct in three of the islands, and almost all individuals (predators and prey) were concentrated in the one island in which numbers of shared prey were still large. In subsequent days the peak of prey populations occurred in different islands and then went extinct in the originally highly populated island: thus spatial dynamics had a very strong influence on the patterns of extinction and persistence.

During the above simulation, we also recorded all the foraging interactions and built the persistent subweb with interaction strengths, defined in two ways: a) the proportion of individuals of each species eaten by each predator species (predator perspective, red arrows), and b) the proportion of individuals of each species that is eaten by each predator species (prey perspective, blue arrows). This subweb (Figure 11) was fairly independent of the remaining web (i.e. that including all of the extinct species) as the interaction strengths both within (cannibalism) and among these 5 species were much higher. The centipede was the top predator, as it interacted more strongly by feeding on all other species than *vice-versa*. Most predators fed heavily on the shared prey. Cannibalism among predator populations was in general very strong and the smaller predator

species (mites) interacted much less strongly among each other than with themselves: in general intraguild predation (IGP) was weaker than cannibalism.

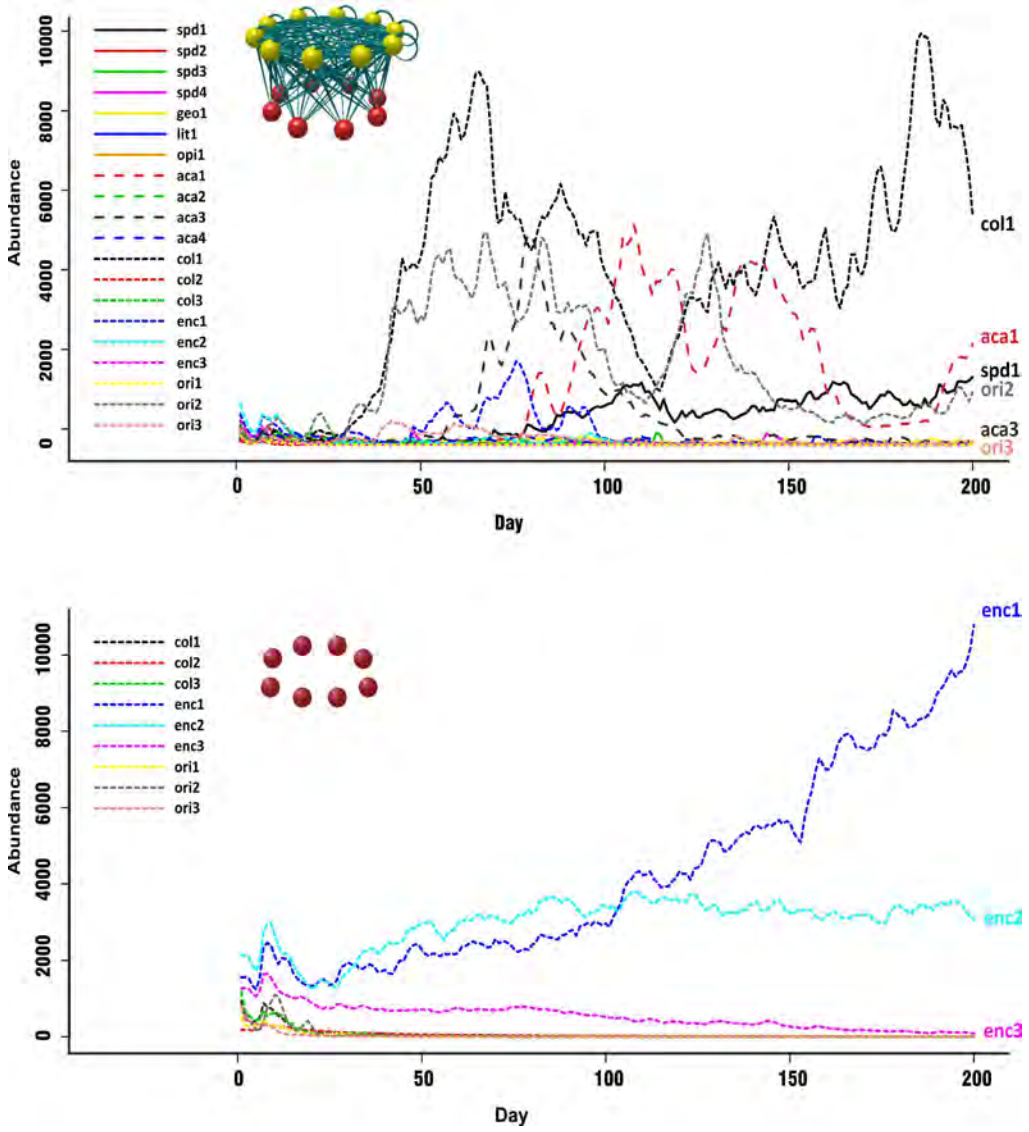

Figure 8. Effect of presence/ausence of predators in ecological dynamics. Dynamics of the population of each species during 200 days when the connectance of the food web was very high (0.55), in the presence (upper panel) or absence (lower panel) of predators. Figures depict one replicate out of the five ran per simulation. Dotted lines correspond to fungivores (oribatid mites, springtails and potworms), dashed lines correspond to small predators (predatory mites), and solid lines correspond to large predators (spiders, opilionids and centipedes). The codes on the right facilitate the identification of extant species. Names in the legend correspond to those in Table 1.

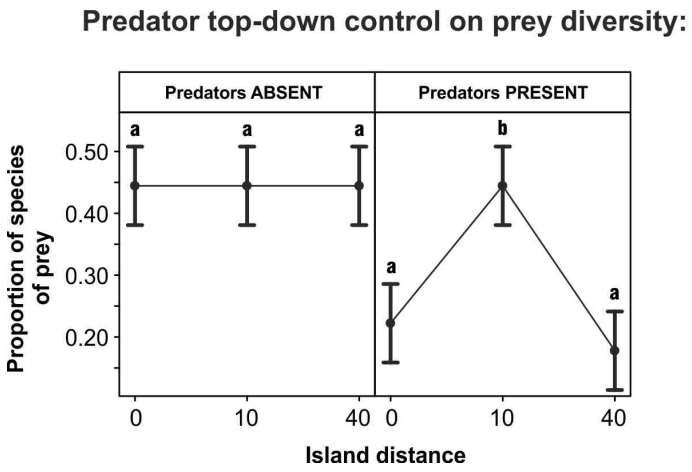

Figure 9. Effect of presence/ausence of predators. Proportion of prey species remaining at the end of the simulations (N = 5) at three different distances between islands, and in the absence (left panel) or presence (right panel) of predators. Values are least-squares means ± SE. Letters on top of bars denote significant differences among groups (< 0.05).

3.6. Relatively long-term micro-evolution (500 days) in a persistent web

Figure 12 shows the evolutionary dynamics for 14 traits associated to the 5-species food web, which persisted for 500 days (Figure 10). Unless their biological relationships were established otherwise, the traits displayed in Figure 12 will be discussed in turn, from top to bottom. Evolution was widespread across species and traits, with some of the latter showing clear oscillation through the course of the ecological dynamics. The first apparent outcome is that the evolution of offspring mass is largely driven by the evolution of mass allocated to maintenance, growth and reproduction and not by the fixed (structural) body size of offspring (compare three top panels in Figure 12). Evolution of offspring mass also differed across taxa, with some evolving larger offspring, others smaller offspring, and the mesostigmata mite (aca1) showing significant oscillations but without a significant change at the endpoint. In addition, fixed body size evolved to a smaller size in the smallest animals (mites and springtails) and showed either no changes (opi1) or oscillation of trait values (lit1) without evolution chain both cases.

The growth rates of the two small predatory mites showed opposite patterns, with one (mesostigmata) increasing and the other (prostigmata) decreasing. Springtails (the only fungivore) decreased in growth ratio. In the large predators, one did not evolve in growth ratio whereas the other increased (lit1). Phenology, or egg developmental time, showed the opposite pattern in a mite species (aca1) and the shared prey (the springtail col1), and either oscillated or did not evolve at all in the remaining three predators. As expected, assimilation efficiency generally increased over time.

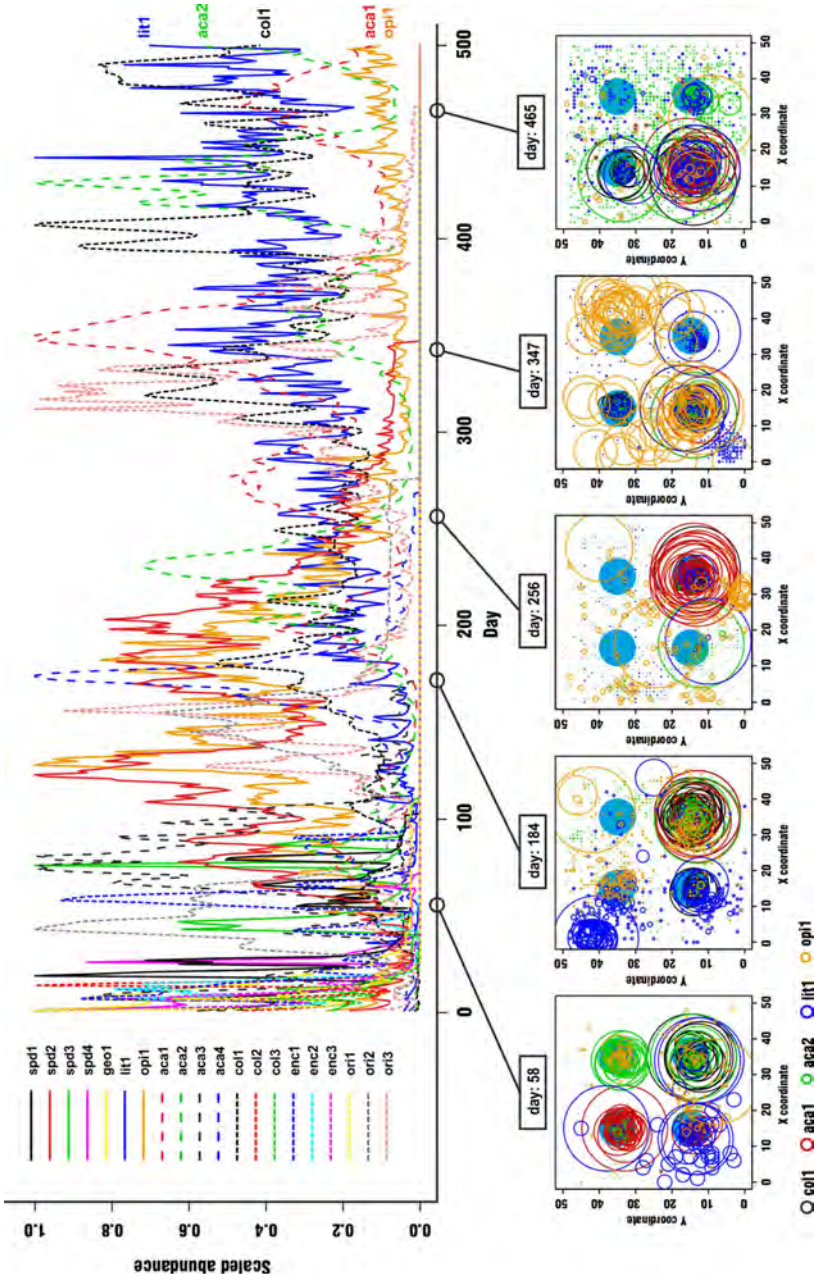

Figure 10. Dynamics of the most stable scenario (i.e., highly connected web, with high genetic variability and with islands at intermediate distances along 500 days. Solid blue circles in the bottom panels represent resource islands, when five species (four species of predators and 1 prey) persisted until the end of the simulation (superior panel). The inferior panel shows the snapshots of the spatial dynamics occurring for these five species during these 500 days. The size of the circles of equal colour correspond to the abundance of one species in that particular patch, relative to the abundance of that same species in other patches. In total, this simulation experiment included 8.891.887 individuals. The codes on the right facilitate the identification of extant species. Names in the legend correspond to those in Table 1.

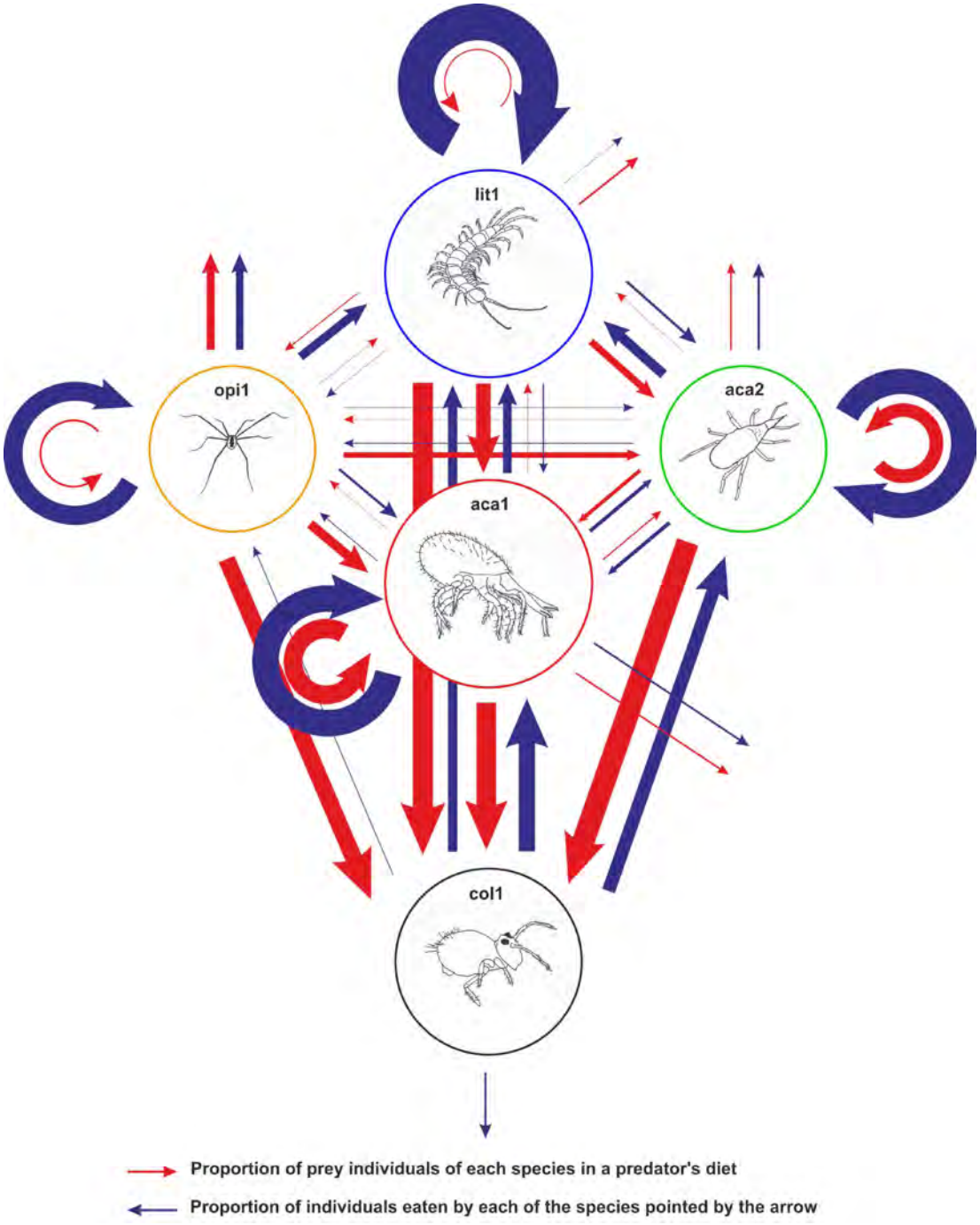

Figure 11. Interaction strengths of a persistent web after 500 days of simulation (population and spatial dynamics in Figure 10). The red arrows departing from a species denote the proportion of individuals of each species killed and consumed by that particular species. The blue arrows departing from a species denote the proportion of individuals of that particular species that have been killed and consumed by the species to which the arrow is pointing. Therefore, red arrows denote the direction of predation (who eats whom) and blue arrows the direction of the energy flux.

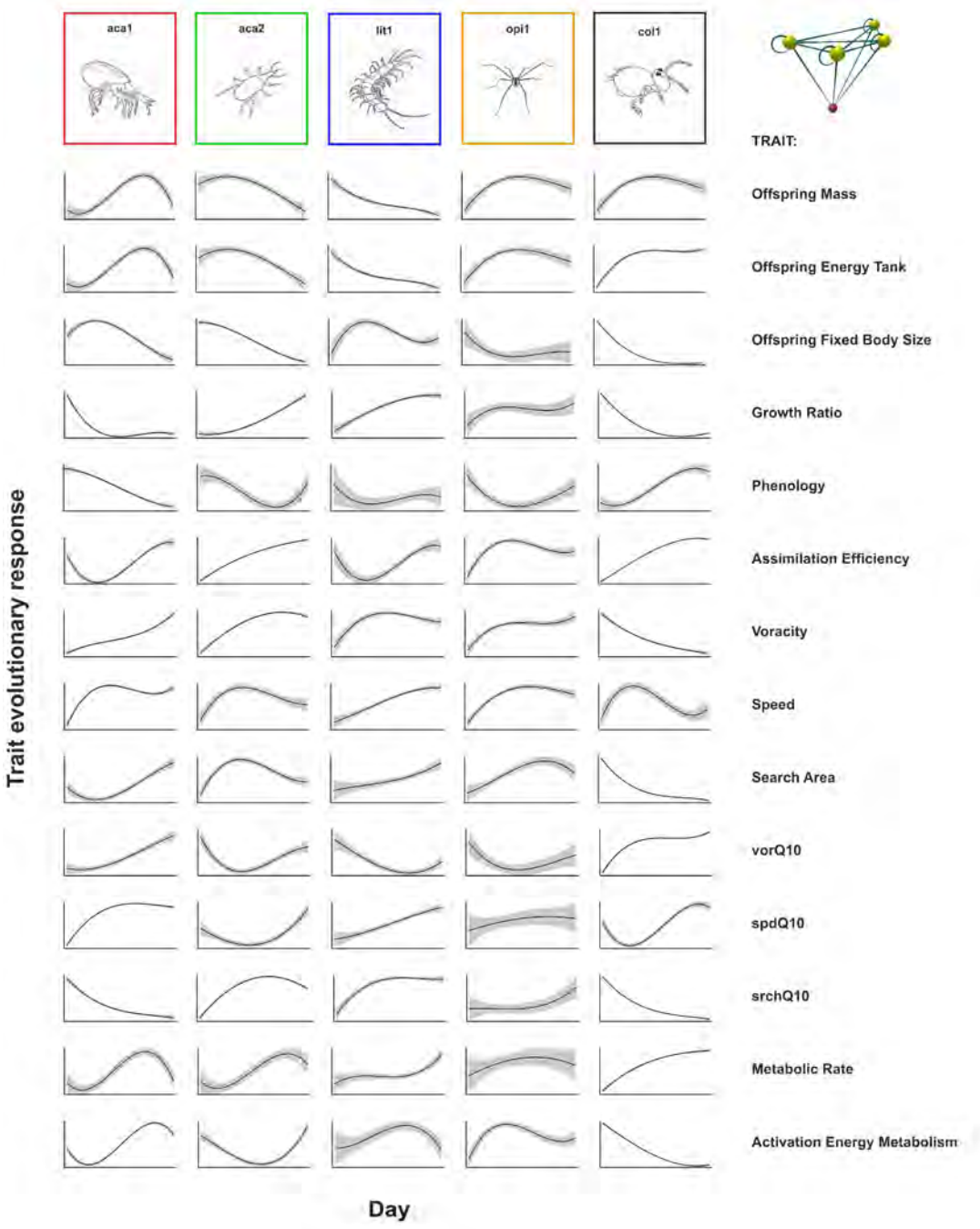

Figure 12. Evolution of 14 traits in the 5 species that remained in the food web after 500 days. From left to right: a mesostigmatid mite (aca1), a prostigmatid mite (aca2), a lithobiomorph centipede (lit1), an opilionid (opi1) and a collembolan (col1). The diagram in the upper right corner depicts the structure of the food web (but see Figure 11). In all panels, the x-axis represents time, whereas the y-axis represents trait values. Areas in grey correspond to 95% confidence bands, calculated across individuals. Trait definitions can be found in Table 1, the Appendix and in Moya-Laraño *et al*. (2012). The maximum number of generations attained by each population was aca1 = 58; aca2 = 39; col1 =52; lit1 = 12; and opi1 = 14.

Some traits have both a purely additive effect as well as an epistatic component (phenotypic plasticity; Appendix); the latter consisting of genes of additive effect that tune the trait value according to environmental temperature (Q_{10}, Moya-Laraño *et al*. 2012). Since both the purely additive and the epistatic component have effects on the final trait, we discuss them together. Voracity, which determines animal foraging activity within a patch, increased consistently (both the additive and the epistatic component) in only the mesostigmatid mite (aca1). In the other three species either the two components evolved in opposite directions or only one of the components evolved. Sprint speed evolved to a higher value in all animals and for both the additive and the epistatic component. However, the evolutionary response was lowest for the shared prey.

Search area, which determines animal foraging activity among patches, evolved consistently in both components (additive and epistatic) only for the shared prey (decrease) and for the top predator (increase). The other three species of predators showed opposite patterns of evolution for the additive and epistatic effects (aca1) or very weak oscillatory evolution in one of them (aca2) or no evolution at all (opi1). Finally, although there was significant evolution and oscillations on metabolic rates, the only strong response was for the shared prey in which the two components of metabolic rate, the scaling coefficient and the activation energy, evolved in opposite directions.

3.7. Evolutionary dynamics of potworms in presence and absence of predators

In the simulations with high connectance (i.e., 0.55), that the potworm enc2 was only species that consistently persisted until day 200, both with and without predators. Moreover, in a purely competitive environment it became the co-dominant species together with another potworm (Figure 13). We took advantage of this persistence in both environments to test for differences in the response to selection in enc2 between the two ecological scenarios. In a purely competitive environment, selection favoured the investment in offspring with higher energy budgets (energy tanks) and smaller fixed size, whereas these traits did not significantly evolve in presence of predators (Figure 13). Surprisingly, in the absence of predators voracity evolved to a lower value and metabolic rate to a higher value. Also, temperature-dependent plasticity of sprint speed, which is only functional under the threat of predation, evolved to a higher value. Finally, activation energy for metabolic rate evolved to a lower value. In contrast, only traits directly related to predatory avoidance (i.e., speed and temperature-dependent plasticity for speed) clearly evolved to a higher value in presence of predators. The other traits showed either no significant response (e.g., activation energy for metabolic rate) or an oscillating response, ending up in a trait value that did not differ from the initial one (e.g., voracity and search area).

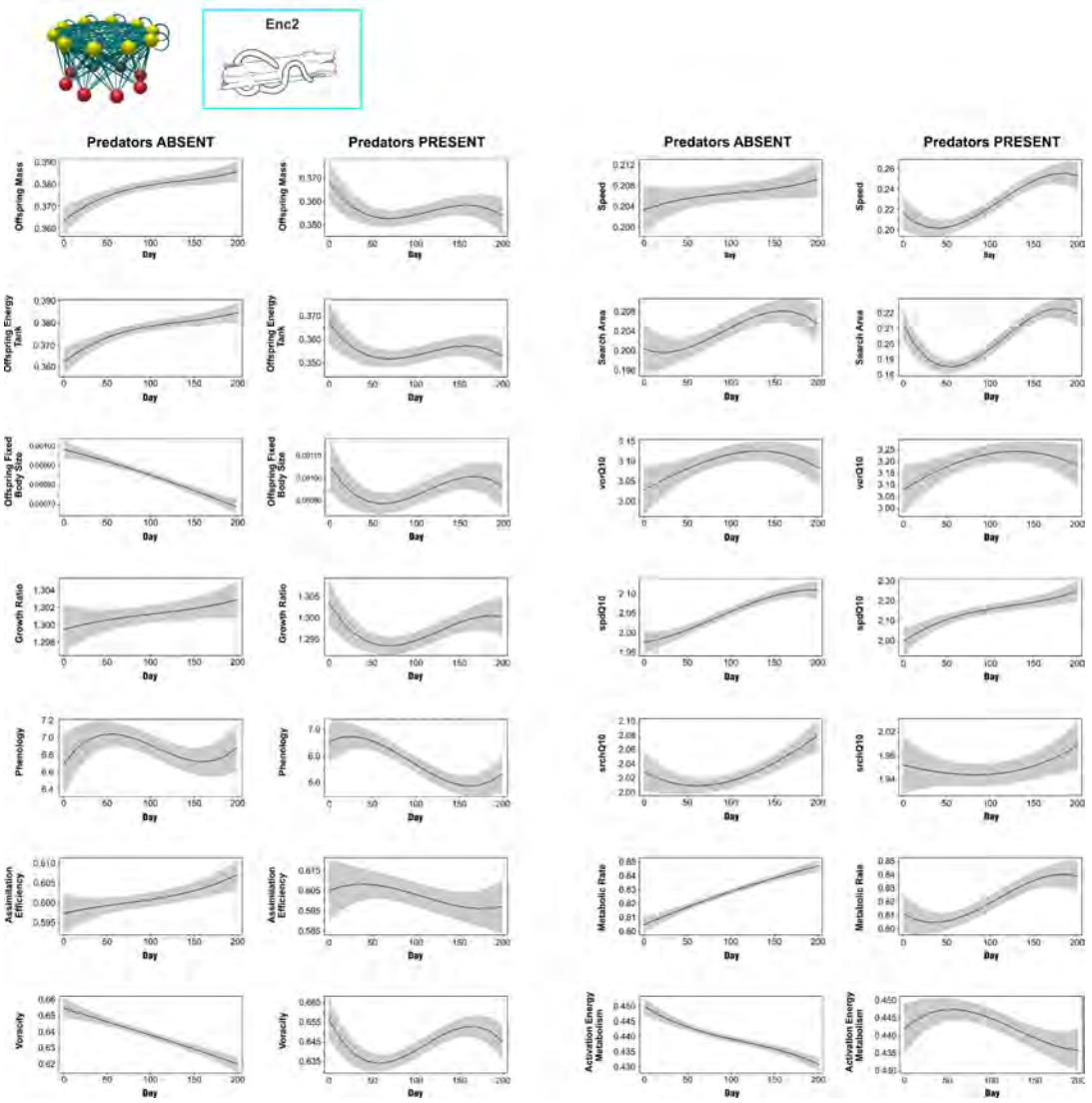

Figure 13. Evolution of traits in a fungivorous potworm species under two ecological scenarios: "predators absent", in which only competitive interactions are present and "predators present" in which species engage in both competition and predation. In all panels, the x-axis represents time, whereas the y-axis represents trait values. Areas in grey correspond to 95% confidence bands, calculated across individuals.

3.8. Results summary

Our simulations showed some relevant patterns that will hopefully entail a step-change in our understanding of eco-evolutionary dynamics in complex systems. We found that highly connected webs, with widespread trophic omnivory, suffered far less from extinction than less-connected webs. Nevertheless, this effect differed between predators and prey, with fewer prey and more predators remaining in connected webs. Moreover, decreasing genetic variability reduced the proportion of surviving species by 72%. However, while the effect on prey was a reduction to 50%, predators suffered a much dramatic reduction, decreasing by 87% when genetic variation was reduced by half.

Furthermore, we found relevant patterns of metacommunity dynamics as the distance among 4 islands of identical basal productivity also explained species persistence in a highly connected food web. At intermediate distances, the proportion of prey species that persisted until the end were 2x to 2.5x higher than when islands were either close to each other or farther apart. For predators, both when islands were close to each other and at intermediate distance, the proportion of species that remained was 4.5x higher than when the islands were further apart. Overallwe found the highest diversity at intermediate distances, slightly less when islands were close to each other and much lower diversity (higher rate of extinction) when islands were further apart.

We also found that in highly connected webs with widespread omnivory and high trait genetic variation, predators had a strong top-down effect on prey diversity, tending to increase the extinction rates of prey when islands were either close to each other or at the longest distances, and greatly increasing prey diversity at intermediate distances. In addition, when the amount of prey that remained in a purely competitive environment was similar to that remaining in an environment in which both competition and predation were at play, the identity of the species tended to be different, indicating that predators modified community composition.

The 500-days simulations revealed strong spatial patterns, with clear migration-extinction dynamics typical of metacommunities and spatio-temporal segregation of species, all of which could have contributed to the overall stability of this 5-species food web.

Finally, we found evidence for widespread trait evolution when high genetic variation was involved. Trait evolution differed between top predators and the rest of other predators, and also between predators and fungivores. In addition, trait evolution also differed for fungivores in a purely competitive environment when compared with the same species in an environment involving predation plus competition. Remarkably, depending on the trophic level, some traits were selected up, others down, and others oscillated.

4. Discussion

4.1. Ecological dynamics

Our findings that (a) highly connected webs with widespread omnivory were less prone to extinction and (b) the simulation in the long run (500 days) ended up with 5 species that were only weakly dependent on the extinct species, agree with the view that higher connectance and intermediately strong omnivory is stabilizing (McCann & Hastings 1997, McCann 2000, Solé & Montoya 2002). It is intriguing, however, that interactions were fairly strong, while stable food webs usually have many weak and a few strong interactions (McCann *et al*. 1998). This apparent paradox could be explained

by the high cannibalistic rates, as like in some natural food webs (e.g., Woodward and Hilldrew 2002), our persistent web was maintained with a strong degree of cannibalism (Figure 11). Recent findings show that both cannibalism and anti-predatory behaviour directed towards conspecifics contribute to stabilize food webs (Rudolf 2007a, b): the highly cannibalistic web depicted in Figure 11 are in line with these predictions.

A previous very simple simulation exercise (Moya-Laraño 2011) suggested that higher trait variability would lead to higher connectance and higher variability in interaction strengths, with many weak and a few strong interactions, all of which could lead to food web stability (see above). However, the latter study did not consider the fact that higher genetic trait variability could also promote rapid or contemporary evolution with ecological time (i.e., during population dynamics). Here, genetic variation on 13 traits strongly promoted food web persistence, as the most persistent webs were those in which populations had genetic variation. Moreover, rapid trait evolution in the five species embedded in the food web persisted for the longest time. Therefore, we can tentatively conclude that genetic variation, through its effects on contemporary evolution, is also an important factor contributing to the food web stability debate.

Genetic variability may promote stability by a) enhancing contemporary evolution as shown here, or b) leading to a high diversity of interactions in the species embedded in the food webs, therefore increasing connectance, omnivory and a variable distribution of interaction strengths (Moya-Laraño 2011, see also Steiner & Masse 2013). Distinguishing among these two drivers of stability is important and we propose that this is feasible in a platform such as WEAVER 1.0.

Our finding that at intermediate micro-island distances food webs are more persistent can be explained by a strong top down extinction effect of IGP predators on prey and on each other at the closest distances (i.e., spatially compressed food webs, McCann *et al*. 2005), predator coupling of the 4 islands at intermediate distances and lack of coupling of the global dynamics at longer distances, leading to strong extinction rates in each of the 4 islands. These results are consistent with the predictions of recent models (McCann *et al*. 2005, Rooney *et al*. 2006, Rooney *et al*. 2008) in which adaptive search and rapid responses arising from highly mobile (top) predators moving towards patches where prey are available help to stabilize the system. The high mobility displayed by top predator populations during the long-term 500-day dynamics supports this view (Figure 10). Our findings confirm these models and add to other models of spatial dynamics in metacommunities involving more than one trophic level (Abrams 1997, Koelle & Vandermeer 2005, Amarasekare 2008a, 2010). Note however that the effect found was only detected in highly connected webs with high genetic variation, meaning that other previously unexplored relevant ecological variables may interact with predator coupling to stabilize metacommunities.

Predators changed the identity of the dominant prey species, driving the strongest competitors to extinction and in islands located at intermediate distances, they actually enhanced prey diversity. Therefore, our heuristic approach adds novel information for the link between keystone predation and metacommunity dynamics (Paine 1966, Amarasekare 2008b), in more complex systems.

4.2. Evolutionary dynamics: Relatively long-term micro-evolution (500 days) in a persistent webb

Our simulations revealed that allocation of energy into offspring (offspring energy storage) had a stronger impact on the evolution of offspring mass than did structural body size at birth. This is very relevant because, given a fundamental egg-number/egg-size trade-off (Fox & Czesak 2000), female energy allocation in offspring with materials providing starvation resistance (e.g., energy tanks) may be more important than allocation in structural body size, even though the latter provides an advantage during predator-prey interactions. This could be translated into an egg-number/ starvation resistance trade-off. We found that evolution resulted in lighter offspring in 2 predator species and in heavier offspring in another predator species and in the shared prey (springtail). However, in another predator species, no evolutionary changes occurred in this trait. Hence, very different strategies evolved, with no clear taxonomic or trophic-level pattern. Given the egg-number/egg-size trade-off, the evolution of heavier offspring was necessarily accompanied by the concomitant evolution of lower fecundities. Therefore, selection could be targeting fecundity or egg mass in each case: further simulations and experiments could be conducted to distinguish between these two possibilities.

Despite their disadvantage in predator-prey encounters with most predators, the smaller animals (springtails and mites) evolved toward smaller offspring sizes. Possibly, in structurally smaller offspring the overall amount of energy necessary to reach adulthood is lower and faster to accrue, and therefore viability selection (selection to reach the adult stage and reproduce) may favour smaller fixed body sizes. However, this explanation was not supported by our results, as for each of the three small species, the individuals with structurally smaller offspring matured later: no explanation for this pattern is immediately obvious, however, and further simulations and output analyses are needed.

Much variation was also found in the evolution of growth ratio. Clearly, the evolution of shorter growth ratios can be favoured again by faster egg-to-adult developmental times, increasing viability selection, as it occurred in the fungivore (springtail) and in the mesostigmatid mite. The prostigmatid mite and the top predator (a lithobiomorph centipede) evolved higher growth ratios, which should provide an advantage during predator-prey encounters. Moreover, larger adult sizes are associated with higher reproductive investments, and therefore increased fecundity. This is consistent with the fact that these two species evolved lighter offspring, suggesting that, for these two predator species, investing in offspring number rather than survival is a better strategy.

Phenology (or egg developmental time) evolved in opposite directions in the shared prey (longer) and in one of its predators (shorter), which largely uncoupled their phenologies, allowing prey to diminish predation from at least this species. As no constraint was imposed on assimilation efficiency, all animals evolved towards higher values for this trait.

Remarkably, traits associated with animal "personalities" (Wolf *et al*. 2007, Carter *et al*. 2013), e.g., voracity (related to aggression and within patch activity) and search area (related to boldness and activity among patches) showed patterns consistent with the balance between the need to find food and the level of predation risk affecting each species. The shared prey (springtails) was the only species that most consistently evolved lower searching areas and voracities with only one of the four activity-related traits (Q_{10} on voracity) evolving to higher values. Given the amount of predation threat upon this species (Figure 11), the evolution of a cautious personality might be expected. On the other hand, predators tended to evolve at least two activity-related traits to a higher value, consistent with their lower predation risk.

Searching area is also a dispersal trait, and our results are consistent with those of Pillai *et al*. (2012) who found that in a metacommunity under strong predation extinction pressure during predator-prey dynamics predators evolved higher dispersal rates, and their prey evolved to lower dispersal rates. This similarity of results, stemming from two very different modelling approaches, provides some degree of robustness and increases confidence in our simulation approach. The intermediate degrees in the evolution of dispersal of the remaining predators can thus be understood by the differing degrees of predation risk and extinction.

The evolution of higher sprint speed was most consistent in the four predator species than in the shared prey, for which only the Q_{10} for speed evolved. In predators engaged in IGP, sprint speed is subject to two selection pressures: catching prey and escaping from predators. In contrast, in the shared prey, selection on this trait stems from predation avoidance only. Hence, selection pressure for sprint speed may be lower in prey than in IG prey. This hypothesis can be tested in real food webs. The prediction would be that after controlling for phylogenetic effects (Harvey & Pagel 1991), the degree to which predators are involved in interactions with other predators (e.g., cannibalism or IGP either as predators or as prey) should correlate positively with their sprint speeds relatively to their body sizes and to prey of similar size.

The evolution of traits related to metabolic rates (scaling mass coefficient and activation energies) showed either oscillations or no consistent pattern between the scaling coefficient and activation energies. In other words, if higher energy expenditures would have evolved, both the scaling coefficient and activation energies should have been higher (see the Appendix for an explanation). However, in none of the species did both coefficients evolve consistently. Therefore, deriving any mechanistic explanations for these patterns is not possible at this moment. These

results, however, are consistent with previous findings that showed that activation energies for metabolic rates can evolve (Moya-Laraño *et al*. 2012).

The fact that a few traits oscillated during the time period of our simulations is consistent with the idea that during population dynamics, selective pressures change, probably due to changes in population numbers of the different species embedded in the food web, and to patterns of space use, which also show their own emerging dynamics (Figure 10).

4.3. Evolutionary dynamics of potworms in the presence and absence of predators

In general, responses to selection were more linear in the competitive environment than in the predation environment, reflecting the higher complexity of selective pressures in the latter environment. In a purely competitive environment, potworms (enc2) evolved to produce smaller offspring (structural size) with a high energy storage (energy tank). The latter may provide a competitive advantage by preventing death from starvation, and smaller structural offspring sizes will result in smaller adult sizes (given a fixed growth ratio and amount of energy) and shorter developmental times. Therefore, the overall effect arising from the opposing evolution of the two size traits could be to increase offspring viability. However, when predation is present, investing in a higher number of larger (e.g. larger fixed size) offspring may decrease predation risk (a size refugia - Wilson 1975, Paine 1976). Also, given the fundamental trade-off between offspring mass and number (Fox & Czesak 2000), which is implicit in the model (as offspring mass and number are allocated according to the energy available for reproduction in the mother), investing in more offspring also means investing in lower energy budgets. Therefore, the counterbalancing selective pressures of competition and predation might explain why neither fixed offspring size nor the offspring energy budget evolved in the environment in which predators were present.

The fact that a competitive environment selected for lower voracity is puzzling. One possible explanation is that genetic drift, rather than selection, produced these evolutionary patterns. We have not yet incorporated non-functional traits in the simulations, which will allow controlling for random genetic drift. However, it is unlikely that the robust evolutionary patterns that we found, such as that for metabolic rates, arose from drift alone in so few (< 7) generations and in a pattern that was consistent across replicated simulations (not shown). Thus, these results must be seen as emerging patterns of responses to selection coming from a complex system, which are difficult to grasp from a reductionist viewpoint. For instance, we know that in WEAVER 1.0 - and likely in the real world - voracity and basal metabolic rates feedback on one another: animals that genetically spend more energy (higher basal metabolic rates) will as a consequence have lower energy storages, which will prompt them to be more active and voracious regardless of their constitutive (i.e., genetically-determined) activity and voracity traits, leading to higher energy intake which may or may not translate into higher competitive ability depending on other traits, such as assimilation

efficiencies. Similarly, animals with lower voracities will maintain lower energy tanks, which will make them more active searching for suitable patches.

Curiously, temperature-dependent sprint speeds evolved to higher values in the competitive environment, in the absence of predation. The evolution of body mass (at all stages) largely depends on how body mass constraints other traits (e.g., voracity, search area, metabolic rates or speed). Hence, selection targeting one of these traits can indirectly affect others, via the covarying effect on body mass, even in the absence of genetic correlations, as was the case here. Nevertheless, the only two traits that showed a positive response to selection were fixed body size at birth and activation energy for metabolic rate, which cannot directly explain the evolution on sprint speed.

In general, when predators were present, trait evolution was weaker and oscillating, likely explained by the higher complexity of selective pressures in the presence of predators. These oscillatory evolutionary trait dynamics in more complex environments could be the result of fluctuating selection due to fluctuating selective pressures during ecological dynamics (e.g., numbers of the different species of predators changing through time) or even co-evolution (e.g., rapid evolution in predator traits acting as dynamical selective pressures on prey traits). Future simulation experiments including different food web structures and diversity of predators should reveal if there is a positive association between trait oscillations and the diversity of selective pressures. Moreover, more simulations are needed to identify consistent evolutionary patterns in webs with or without predators. One way to test this is by playing with the dimensionality of selective agents; that is, the O matrix (MacColl 2011, Moya-Laraño 2012).

4.4. Future directions

We found exceptionally fast dynamics, with all animals growing and reproducing at rates that are much higher than in natural soil food webs (Coleman *et al*. 2004). *Lithobiomorpha* centipedes, for instance usually take more than one year to mature (Lewis 1981), which would have yielded only 1.5 generations instead of the documented 12 generations. Our models are therefore still very far from reproducing the pace of soil interactions. There are various ways that the WEAVER 1.0 platform could be altered in subsequent incarnations to make its constituent animals more realistic. First, we need to add periods of inactivity before moulting or during egg guarding (e.g., Geophilomorpha, Lewis 1981. Second, the standard metabolic rates as documented by Ehnes *et al*. (2011) need to be accompanied by the possibility of decreasing metabolic rates to survive starvation periods, a pattern that is widespread, for instance, in spiders (Anderson 1970, 1974, Schmalhofer 2011) and could be linked to discontinuous gas exchange occuring during resource shortage (Chown 2011). Allowing for a decrease in metabolic rates during starvation will allow having more realistic foraging patterns and slow down the dynamics.

Although we have simulated food webs across space, we have not included many of the typical drivers of coexistence in metacommunities, such as colonization-competition and competition-predation trade-offs, which can be parameterized by manipulating trait range values (e.g., assimilation efficiencies and searching areas, for instance). In addition, WEAVER 1.0 allows the inclusion of multiple genetic correlations and genetic trade-offs (antagonistic pleiotropy), which we have not exploited in the present paper (but see Moya-Laraño *et al*. 2012, 2013). Exploring food web persistence across space in the presence of multiple trade-offs, both ecological and evolutionary, will open new avenues of research to help us understand the eco-evolutionary stability of these complex systems. However, the problem remains of determining how realistic are the results produced *in silico*. Next, we describe how to validate this framework by continuous feedback with real systems.

4.4.1. The quest for eco-evolutionary patterns: An FRP using global optimization algorithms and approximate Bayesian computation

Ideally, to test the reliability of models one has to always confront the model results with real data (e.g., Boit *et al*. 2012, Hudson & Reuman 2014). In order to ensure that WEAVER 1.0 is simulating realistic scenarios, our outputs should include eco-evolutionary patterns that reproduce the empirical observations of real food webs, including patterns of stability. For example, given ecological and evolutionary empirical data, what can we tell about the mechanisms that best reproduce those data? In the previous sections and in the Appendix, we have described the different components and parameters of the simulations, as well as some relevant results. Here, we briefly describe some advanced methods to compare our model predictions with the empirical data using approximate Bayesian computation (ABC), and also global optimization algorithms to produce digitally-stable webs that can be then compared with real data.

Our preliminary simulations, showed that some species persisted more than others and that some traits changed monotonically (evolved) through the entire simulation, while others oscillated. Indeed, stability of the entire system (i.e., 20 species interacting with each other following a niche model food web structure) was not reached in any of the simulations: neither ecological (population dynamics) nor evolutionary (trait dynamics) dynamics showed signs of stability. Instead, a variable number of species went to extinction before the end of each simulation. Stability could be reached given the large number of parameters involved, but here we just used a small combination of them. Actually, each simulation included 20 animal species*13 parameters + 20 animal species*13 trait ranges + 1 World configuration*4 parameters + 1 fungus species*3 parameters, which gives 268 parameters and 260 trait ranges one could work with in order to search for more realistic eco-evolutionary food webs. Exploring in full all these parameter combinations would be extremely labour-intensive, and many of them would be likely to be meaningless anyway (e.g., too far apart a combination of values from the real World to begin with): so, we need a more efficient way to refine the approach.

With the aim to address several main research questions, e.g., what drives stability, distinguish neutral from non-neutral scenarios, how does the evolution of adaptive traits affects food web structure, how does evolution affect food-web associated ecosystem process, etc., we propose a working protocol, which consists in a three-step iterative strategy or Feedback Research Program (FRP):

1) Identify the data used to parameterize the model ecosystem as either internal (e.g., data coming for the same or very similar ecosystems) or external to the system (data or parameters extrapolated from other systems). In absence of internal and external data to parametrize the model for some specific parameter values, in the Bayesian framework our *a priori* data would be drawn from a uniform distribution (Grelaud *et al*. 2009, Beamount 2010).

2) Search for eco-evolutionary patterns by iteratively running models with different combinations of parameters. In this iterative process, set the internal parameters to the real (estimated) values and manipulate the external parameters. The predictions can then be compared with empirical observations. This is done by computing the distance between the empirical and simulated data for each parameter combination (Grelaud *et al*. 2009, Sunnaker *et al*. 2013).

3) Once a stable eco-evolutionary web has been reached, pick some of the parameter values and outputs found by the system and check if they apply to your system (e.g., check if animal fecundities in the outputs are within those measured in some of the animals of your food web). If this is not the case, either feed the newly-measured parameters to WEAVER 1.0 setting them as internal or implement new algorithms (e.g., criteria for reproducing or different coefficients in the deterministic encounter probabilities – Eq. A6) and repeat step (2). In summary, this last step requires selecting the parameter combination that best matches the empirical observations. This can be done by setting a threshold to generate *a posterior* distribution, with all the parameter combinations being sufficiently similar to the empirical observations (i.e., those that are far from reality are discarded; Melián *et al*. 2011, 2014).

As an example of what type of data would be considered internal or external, animal body lengths that came from accurate measures in field experiments would be clearly internal. However, as these length data were then transformed to body masses using equations from other systems and assuming 70% of water body content as estimated in a different system (see the Appendix), the latter would then be considered external parameters. As another example, basal metabolic rates came from published data on animals coming from similar soil systems (Ehnes *et al*. 2011) and were

therefore considered as internal. Given the body lengths and metabolic rates as internal and external data, respectively, additionals assumptions to include in the model are, for instance, the fitness consequences of body length and metabolic rate for each individual. In the neutral scenario, each individual would have the same fitness irrespective to its body length and metabolic rate. But, how can one meet the neutrality assumptions when these traits are actually functional and lead to different fitnesses across individuals? We propose that neutral eco-evolutionary dynamics, which could be used as null models to contrast the occurrence of niche-oriented dynamics and adaptive evolutionary dynamics, can be reproduced by randomizing reproductive events not only across individuals, but also across species. This would require running two simulations in parallel, starting with the exact same individuals, one randomizing reproductive events (neutral) and another letting the traits drive the dynamics (functional).

Importantly, the above protocol can be applied to model assumptions and parameters. For instance, Moya-Laraño *et al*. 2013 simulated situations in which prey were able to assess predator threat before entering a patch and others in which predator threat could not be assessed by prey. They found that system stability involving sit-and-wait predators could only be achieved if prey were not aware about predator presence when entering a new patch. Many other biological assumptions could be tested by generating predictions and comparing them with empirical observations.

Combining parameters and algorithms in an iterative process would not be done completely at random, as this would be also almost unfeasible even for highly optimized parallel code running in High Performance Computers. Instead, Global Optimization Algorithms (Floudas & Pardalos 2009) should be used. Next we review these algorithms and discuss which ones would be more appropriate to accomplish step (2).

Biological systems may contain several parameters that underlie biological, evolutionary and ecological processes. Given such complexity, finding the minimal number of mechanisms (or parameters) that best predict the empirical data is challenging. Global optimization algorithms, the most popular of which in ecology and evolution are "genetic algorithms" (Hamblin 2013) fit this purpose. The first problem we face is to explore efficiently the highly dimensional parameter space in our model. In general terms, we have to optimize the search by giving a nonempty closed (searching domain) set S and a function f , to find the minimal value f^* and all the points $x^* \in S$ such that $f^* = f(x^*) \leq f(x)$ for all $x \in S$, or show that no such a point exists. The problem to solve can be written as

$$\min f(x) \qquad [1]$$
$$\text{s.t. } x \in S.$$

The purpose of global optimization is to find the global minimum value f^* and the set of global minimizer points $X^* = \{x^* \in S \mid f(x^*) = f^*\}$. The conversion of a maximization problem to a minimization one is straightforward ($\max\{f(x) \mid x \in S\} = -\min\{-f(x) \mid x \in S\}$).

Problem (1) can be classified depending on the dimension of x (e.g., number of parameters and rules), its type (discrete, continuous or mixed), the type of f (linear, quadratic or nonlinear) and how the search domain S is defined (constrained or unconstrained).

When any local minimum of problem (1) is also a global minimum (e.g., in linear - Linear programming FAQ- or convex programming; Boyd & Vandenbherge 2004), local optimization methods can find the optimum easily. However, in many problems this is not the case (Nonlinear programming FAQ). The field of global optimization and ABC are devoted to the latter; i.e., those problems of type (1) which can have several local optima apart from the global optimum (Beamount 2010).

The algorithms to solve these problems can be classified in different ways. A typical classification distinguishes between deterministic or stochastic methods. Stochastic methods (for instance, tabu search, genetic algorithms or simulated annealing; Talbi 2009) apply some random factors in the local phase to converge to a solution and in the global phase to avoid getting trapped in local optima. Although these methods can find the global optimum, they can only guarantee it when the number of iterations tends to infinity. In deterministic methods (such as outer approximation, Lipschitzian optimization or Branch and Bound; Scholz 2012) no random factors are included. Some of them converge to the global optimum under certain conditions, but when the algorithm is stopped after a finite number of iterations the accuracy of the solution may not be known with exactness.

A better classification of the algorithms, based on the degree of rigour with which they find the global optimum, is the following (Markót *et al*. 2006): *incomplete methods*, which may become stuck in a local optimum; *asymptotically complete methods*, which reach a global optimizer with probability one if allowed to run infinitely long, but have no means of knowing when a global minimizer has been found; *complete methods*, which reach a global optimizer with certainty (assuming exact computations and infinitely long run), but knowing after a finite time that an approximate global optimizer has been found; and finally *rigorous methods*, which reach the global optimizers with certainty within a given tolerance even in the presence of rounding errors.

According to the previous classification rigorous methods, like the *interval branch-and-bound* algorithm (Markót *et al*. 2006), are desirable. However, although, they reach the global solution with the desired precision, execution time increases exponentially with the dimension of the problem.

Additionally, they usually need the formulation of the objective function. In summary, regardless of the methods used, the global optimum may be extremely costly to find for highly dimensional ecosystems. Thus, obtaining a Bayesian posterior distribution with the parameter values that best approximate to the empirical observations may be a useful way to decrease the number of parameter candidates to infer the mechanisms explaining the observed patterns step (3). For example we may obtain the number of parameters and their values to characterize the distribution of trait values or phenotypes and predation coefficients that best approximate to the empirical observations.

The WEAVER 1.0 algorithm can be considered a model with a large set of *a priori* parameter values and biological mechanisms. One of the desirable goals of WEAVER would be to determine the feasible input parameter values to obtain the output values that best approximate to the empirical observations. Depending on the research question, output values to optimize could be the distribution of traits or phenotypes, species richness and diversity or ecosystem productivity through time.

Given the high dimensionality involved in WEAVER, the optimization approach, together with approximate Bayesian computation methods, are candidates in this FRP protocol for inferring with higher accuracy the mechanisms that shape diversity patterns in ecological and evolutionary systems.

4.4.2. Engineering food webs for pest control

The present eco-evolutionary framework could be used successfully to help engineering food webs for effective pest control (Moya-Laraño *et al*. 2012). The increasing social demand for pesticide residue-free agricultural products and recent transgovernmental policies that explicitly demand sustainability in agriculture, is pushing the productive sector worldwide to put agricultural methods for improving pest control while avoiding environmental impacts (Bale *et al*. 2008, OJEU 2009). As a consequence, over the last 10 years the percentage of the World's cultivated land using biological control to fight pests has increased, and the identity of the species of natural enemies involved has suffered an ecologically rational switch, as more indigenous than exotic species are being used as biocontrol agents (van Lenteren 2012). This tendency is expected to continue in the future because biological control will be a key feature of sustainable crop production.

When untreated with chemicals, agricultural systems typically hold multiple plant-inhabiting species, which interact with each other forming complex food webs. For example, in a typical Mediterranean greenhouse different herbivore species listed as pest organisms (aphids, spider mites, trips, caterpillars) and several species of natural enemies (phytoseiid mites, predatory bugs, lady beetles, parasitoid wasps) can coexist, all interacting directly (i.e., predation) and indirectly (competition, apparent competition) mechanisms (Messelink *et al*. 2012). Furthermore, the

landscape in which agriculture takes place is commonly surrounded by margins and natural and semi-natural habitats that can provide source populations of natural enemies, as well as act as a reservoir for pest species (Winkler 2005), expanding the network of agricultural interacting species beyond the actual space occupied by crops. Finally, biotic (predation, competition) and abiotic (e.g. heat stress) selective pressures acting simultaneously on whole agricultural communities may induce rapid evolutionary responses that can be key drivers in the dynamics of populations (i.e., eco-evolutionary dynamics; Fussmann *et al*. 2007, Pelletier *et al*. 2009). Hence, to develop a sustainable agriculture with robust predictive power, pest management will need to take into account both the effects of complex interactive networks and complex architectural landscapes (Bohan *et al*. 2013), and rapid evolutionary responses (Loeuille *et al*. 2013), on the dynamics and structure of agricultural communities.

Moya-Laraño *et al*. (2012) coined the concept of Food Web Engineering (FWE, hereafter) as an extension of biological pest control that integrates community ecology and evolutionary biology into the management of agricultural systems. The idea is to unravel how specific community modules in agricultural systems can be manipulated, so that top-down pest control is maximised. The approach implicitly requires prior knowledge on which species form the community, how they interact, and which traits are relevant for interactions within and among species and with the environment, and the IBM platform presented here (WEAVER 1.0) is a suitable tool to address this. Through simulations of the dynamics of specific communities by using different ranges (variability) and assumptions on the genetic determination of traits (number of loci, allele values, pleiotropic effects), different scenarios of pest control, as well as optimal solutions and conditions for stability, can be determined. Using a systems biology approach to connect the IBM and the real world could help to uncover those traits that should be selected in natural enemies to maximize trophic cascades.

The potential of WEAVER 1.0 in FWE is illustrated in the results presented here, which provide useful general guidelines of potential relevance to the development of more sustainable agriculture. On the one hand, simulations show that the higher the connectance in the food web the higher the persistence of predators, hence herbivore top-down control, will be. Moreover, generalist predators are those that persist more often in our food web, thereby ensuring long-term prey control. These results support the idea that the presence of multiple generalist predators can effectively control pest populations (Faria *et al*. 2008, Messelink *et al*. 2012), contradicting the traditional view that they are less effective than specialist predators (Sydmonson *et al*. 2002), (van Lenteren and Woets 1988). However, our results also show that persistence of generalist predators in intermediate-highly connected food webs is strongly dependent on genetic trait variability. This implies that increasing predator diversity by releasing several species that are commercially available might not be appropriate. Mass-reared populations are expected to have low genetic variability because they originally started from a relatively small number of individuals, and because populations may have

experienced several bottlenecks caused by the rearing methods. Instead, conservation strategies aimed at promoting naturally occurring populations of natural enemies (e.g., manipulation and recreation of the habitats they live in, adding alternative food sources to the habitat, etc), may be a more appropriate approach.

The IBM platform WEAVER 1.0 also offers the possibility to mimic dynamics at a meta-community level by increasing the distance between patches (islands). A key result of the simulations is that increasing such distance reduces the persistence of predators, and decreases the stability of the systems. Therefore, persistence of generalist predators could be increased by introducing islands of diversity, i.e., non-crop plant species harbouring alternative food/prey, amidst the cropping area. There is evidence that densities of herbivorous pests and natural enemies within agricultural fields are influenced by the features of the surrounding landscape (Nicholls & Altieri 2001), enlightening the importance of considering the spatial layout when designing future agro-ecosystems.

In conclusion, we have shown how our heuristic IBM approach is useful to test eco-evolutionary hypotheses “in silico”. We found that connectance, rapid evolution occurring contemporarily to the ecological dynamics, as well as island distance, affected food web persistence. Moreover, depending on which of these scenarios is at play, we show that predators can exert a strong effect on prey diversity. In addition, we documented diverse evolutionary responses across the different trophic levels of the food web and for up to 14 functional traits. Although these *in silico* systems may still be far from fully realistic, we propose a Feedback Research Program (FRP) protocol by which we hope to fill the “in silico” - “in vivo gap”. We also envisage that this research protocol can also be successfully incorporated in Food Web Engineering (FWE) to improve biological pest control in a changing and increasingly spatially fragmented world.

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APPENDIX

A.1. WEAVER 1.0: an IBM platform to simulate eco-evolutionary dynamics in food webs

WEAVER 1.0 is the C++ porting of the former R code mini-Akira (Moya-Laraño *et al*. 2012), which has been additionally extended to 2D and 3D space. This porting means a great improvement in computer performance, in part due to algorithm optimization, and in part due to the higher performance of C++ relative to R. For instance, each simulation set in Moya-Laraño *et al*. 2013 took about 48h of execution in mini-Akira, which became 10s for Weaver run in the exact same machine (17,280 times faster!). This improvement in speed has allowed us to increase the number of species and to work with more complex food webs (20 species and 20,000 individuals at initialization). Access to the executable programme as well as an explanation of the input and output files can be found here (www.eeza.csic.es/foodweb). In addition, some other changes in the former R code, as well as a different application, can be found in the material of Moya-Laraño *et al*. (2013), also available in the above site. Updates on the code and potential encountered bugs will also be reported there.

A.2. Space and basal resources – 2D and 3D and a chemostat

WEAVER 1.0's spatio-temporal domain is currently conceived as a portion of soil where animal interactions will occur and in which many parameters can be manipulated. Currently this includes soil moisture and temperature. A future version will include Carbon, Nitrogen and Phosphorous, mimicking decomposing leaf litter. Computationally, space has been modelled as a set of discrete, squared, contiguous, spatial cells or voxels. Cell size can be arbitrarily chosen by the user which yields high flexibility and adaptability for different animal sizes and movement characteristics. Reducing voxel size while increasing their number will lead to much higher spatio-temporal resolution while reducing computational performance as the amount of processing needs increase consistently. Each voxel has its own values for different parameters like moisture, fungus content, etc., and based on macro- and micro-climatic conditions and resource consumption, these values will fluctuate as the simulation proceeds.

WEAVER 1.0 initializes the cells (voxels) that will form the simulation domain as a 3D array with width, depth and height dimensions. This creates a data structure that will hold the living individuals and basal resources. Each individual, whether a fungus oran animal (and even plants in future releases), is initialized based on user-provided parameters: genetic trait variability, genetic correlation among traits, species identity and a series of parameters that aim at both providing realism as well as allowing simulation functionality. As such parameters are commonly defined as a range of possible values, each individual is initialized following a random initialization process and can be considered unique. Upon initialization, each individual is randomly located into one of the

existing cells. Once soil, fungi and animals are initialized, simulation starts until one or more of the stopping conditions are satisfied (e.g., number of days).

Spatial patchiness is of extreme importance to mimic meta-population and meta-community dynamics, as well as divergent evolution within distant islands. Related to this, the user has major control over some aspects of soil initialization such as moisture and fungus geometric distribution. For instance, one can set a homogeneous moisture value that will be the same for all cells in the world or set fungus availability at random among cells. More complex initialization can also be carried out. The user can instruct the program to create as many patches (spheric or gaussian shaped) as needed and to select or to randomize the different parameters that define them, such as relative humidity, fungus biomass, radius of the patch (spheric patches), sigma of the gaussian distribution (gaussian patches). Finally, these structures can be mixed, to create very complex basal resource spatial distributions. In the case that many structures affect the same voxel, the highest value (e.g., moisture) is retained for that particular voxel.

In the present version, fungi grow within the cell based on the level of relative humidity present in that cell (C-N-P will be implemented in future releases). In the absence of fungivores, fungus growth is governed by the same equations as in the former version of the framework (equations A1 and A2 in Moya-Laraño *et al*. 2012). Water availability affects only fungi thus far. In future versions of WEAVER 1.0, animals will also have water tanks as state variables and water availability will change dynamically through space and time. All simulations presented here were ran at constant 87.5% relative humidity and with a single basal resource (fungus species) that grew optimally at this humidity with a species-specific rate (i.e., r_T in eq A1 of Moya-Laraño *et al*. 2012 is maximum at 87.5% RH; r_T = 0.017, growth range, RH= 85 - 90%, r_T = 0 - 0.017). In the future, other fungus species differing in optimal RHs will be incorporated. However, in the current version this possibility was not included because water availability does not change with time yet.

A.2.1. Chemostat

Preliminary behaviour of a set of simulations (11 species of predators, 9 species of prey and 4 of fungi, see main text) showed that basal resources would always go to extinction within less than 40 days. Since we were primarily interested in investigating eco-evolutionary dynamics of predator-prey interactions, and since pulses of basal resources have been shown to strongly contribute to community stability (Roelke *et al*. 2003), we incorporated in the simulator a chemostat that provided pulses of basal resources either at a certain (constant) frequency ($days^{-1}$) or when resources were close to depletion within a pre-established threshold. The former type of pulse mimics, for instance, rainy days allowing bursts of fungi growth, being by far the most realistic case. The second type can be used to allow predator-prey dynamics to go on for longer periods of time when one is interested in exploring the evolution of certain traits. In the present paper, we only present results using the

most realistic frequency-based pulsing chemostat. However, to enhance the duration of the simulation, we set the chemostat at a refilling rate of 100%/day.

A.3. Phenotypic ranges with quantitative genetic variation

The following is a simplified description of how genetics are implemented in our approach (further details in Moya-Laraño *et al*. 2012). Each trait is determined by a couple of vectors which include an arrangement of loci with values varying between 0 and 1. To establish the trait value for each individual the values across loci are added and the result interpolated between the phenotypic ranges of the trait (Table 1). For each trait, we established evolutionary limits, beyond which the population can not evolve (assuming physical and physiological constraints), and therefore the genetically-based trait variability is determined within these limits. Thus, for each trait *X* we describe the limits and the phenotypic range used as follows:

$$l_X = L_X + \varphi\left(\frac{U_X - L_X}{2}\right) \quad [A1]$$

$$u_X = U_X - \varphi\left(\frac{U_X - L_X}{2}\right) \quad [A2]$$

where l_x and u_x define respectively the lower and upper limits of the range used for trait *X* in the simulation, L_x and U_x define standard lower and upper limits for the trait (Table 1) and φ is a coefficient (range 0-1) which determines what proportion of the distance from the standard limits to the mid-point between them is used to calculate the final trait range (l_x, u_x). Thus, a higher φ involves lower trait variability. We forced $U_X < K_X$ and $L_X > \Pi_X$, where K_X and Π_X are the uppermost and lowermost evolutionary limits for trait *X*, respectively. The above criteria ensures that variability was sufficiently large for new phenotypes to evolve (determined by standing genetic variation), but with thresholds far enough (L_X *and* U_X) from the evolutionary limits (Π_X and K_X). We used φ=0.01 or 0.99 for simulations with high or low genetic variability respectively.

A.4. Animal traits

We refer to the reader to our repository (www.eeza.csic.es/foodweb) to learn about all the input parameters and evolutionary limits used for each trait and species. The 13 traits (or 14 if consider total body size; e.g., B + $\boldsymbol{\varepsilon_0}$ below) included in the present simulations were the following (see ranges on Table 1):

body size at birth (size_ini, B_0): structural body mass at birth.

energy tank at birth and after molting (tank_ini, ε_o): percentage of mass devoted to maintenance and future growth and reproduction. Individual body mass (*M*) is thus the sum of body size and the energy tank, both of which are also state variables.

voracity (*v*): maximal consumption rate per day (implemented as a scaling coefficient *v* which makes voracity to scale with body mass as $0.1M^v$). Source: Yodzis & Innes 1992, DeRoos *unpublished notes*, which provide a fixed maximal consumption rate coefficient of 0.75; see also Englund *et al*. 2011 for variation around this value). This trait does not just constrain how much food an animal can consume per day, but also affects predation risk, as the more voracious animals expend more time foraging. Thus, the probability of encounter with predators (P_p in Eq. A10 below) depends, among other things, on this trait. Hence, animals that are genetically highly voracious are more exposed to predation risk, which is consistent with what we know from animal personalities and behavioural syndromes (Sih *et al*. 2004), and does therefore include them explicitly in the framework.

speed (*s*): sprint speed (cm/s) when a predator (in the case of prey) or a prey (in the case of predators) is encountered and the prey tries to escape from the predator and the predator tries to catch the prey. Implemented as a scaling coefficient *s* which makes speed to scale with body mass as $\propto M^s$. This coefficient has been documented to vary across studies: 0.17 - 0.25 (Peters 1983, Schmidt-Nielsen 1984). Taking 4 as the normalisation constant ($4M^s$) we obtain sprint speeds which fall within the observed ranges from the tiniest mites to the largest wandering spiders, covering a mass range of 0.03 - 465 mg.

metabolic rate (met_rate, *a*): Energy losses from metabolism follow the Metabolic Theory of Ecology (MTE, Brown *et al*. 2004) and recent estimates in soil fauna for the separate effects on metabolic rate of temperature, activation energy and body mass (Ehnes *et al*. 2011):

$$\ln I = \ln I_0 + a \ln M - E\left(\frac{1}{kT}\right) \qquad \text{[A3]}$$

where *I* is metabolic rate (J/h), I_0 a normalisation constant, *a* a coefficient which relates body size to metabolic rate, *E* is the activation energy (in electron-volts eV), *k* the Bolzmann's constant (8.62×10^{-5} eV/K), and *T* the environmental temperature in Kelvin. All parameters are included as reported for each animal soil group (Ehnes *et al*. 2011). Genetic variability was included and modelled around the coefficient "a".

In addition, we also included field metabolic rates, which were calculated in an algorithm that includes environmental stress from encounters with predators (Hawlena & Schmitz 2010) as well as on the state of voracity and amount of movement of each individual (Eq. A7 below).

growth (*g*): Growth is a trait that determines how much an individual grows in each moulting event. Note that we are simulating invertebrates which grow by moulting. Thus, this trait is not truly growth rate but growth ratio at moulting independently of the rate (t^{-1}) at which moulting occurs. Therefore, this trait determines how much of the available energy storage is allocated to fixed body parts in the next developmental stage (instar). Since a fraction of the energy tank at moulting should be also allocated to the post-moulting energy tank, these two traits basically decide when an individual will moult. Growth is merely included as a ratio of the linear dimension of fixed (structural) body parts of the new (target) instar relative to the previous instar. In Section A.7 we describe how the algorithm for growth has been improved in WEAVER 1.0.

search area (search_area, *m*): Importantly, we distinguish between speed and mobility. Speed reflects sprint speed when trying to escape from a predator or trying to catch a prey. However, we consider mobility (search area) as how much one individual is able to move to search for resources or for safe patches. Lacking better information, the entire area covered in one day (*m*), scales with body size in a similar way as sprint speed: M^m. Differently than in mini-AKIRA (Moya-Laraño *et al.* 2012), for translating mobility into actual search area in the simulation we have derived scaling constants for WEAVER 1.0 (see Section A6 below).

assimilation efficiency (assim): Assimilation efficiency is merely the amount of ingested food which is converted in own body mass. Following previous work on soil fauna, we can assume to be around 0.85 (85%) (Rall *et al*. 2010 and references therein).

phenology (pheno): Day of birth since either the beginning of the season (simulation) or since the date of oviposition. This trait can be also called egg developmental time, as the date of birth will depend on how fast eggs develop beyond what is dictated by temperature and other environmental constraints. Thus, for calculating the final phenological date, which will vary depending on temperature, we further included temperature-dependent developmental rates by using published equations (Gillooly *et al*. 2002) and calculating the average Q_{10} values across the range of body masses for our propagule sizes in the simulation, which gave $Q_{10} = 2.84$).

activation energy for metabolic rate (E_{met}, *E* in Eq. A3): To further control for the effecto fo temperature on eco-evolutionary dynamics, we also included, in addition to simulations at different temperatures, variability around *E*, which will serve to study adaptive evolution around

thermal sensitivity of metabolic rate, a form of thermal adaptation. Ranges in Table 1 were set around published coefficients in Ehnes *et al*. 2011.

We further included three additional traits that represented variability in plasticity to temperature (Q_{10}) for three activity traits: voracity, speed and search area ($vorQ_{10}$, $spdQ_{10}$ and $srchQ_{10}$, respectively). We used recent published accounts from a thorough review on temperature-dependent ecological traits in predator-prey interactions (Dell *et al*. 2011). For activity traits, we used Q_{10} (i.e., how many times a given trait increases for a 10°C increase in temperature) instead of *E*, because we lacked information for how *E* and *M* combine to determine trait values, as it is the case for metabolic rate (*I*) in Eq. A3 (Ehnes *et al*. 2011). In addition, Q_{10} values are more easily interpretable and converted to reaction norms. Jointly, these three traits represents thermal plastic adaptation for mobility. For simplicity we ran all simulations at 18°C.

Q_{10} on voracity ($vorQ_{10}$): Based on data on consumption rates (Dell *et al*. 2011).
Q_{10} on speed ($spdQ_{10}$): Based on data on escaping speeds (Dell *et al*. 2011).
Q_{10} on search area ($srchQ_{10}$): *Based on data on voluntary body speed (Dell et* al. 2011).

To estimate the effect of Q_{10} values in the simulation for all traits that involved temperature sensitivity, we used linear interpolation between the minimum and maximum temperatures used for all simulations (15 - 25°C). Thus, real Q_{10} would be used if a simulation was performed at 25°C, and for simulations at intermediate temperatures we estimated the value of Q (e.g., Q_3 at 18°C) by interpolation between the two temperatures, which assumes linearity of Q across temperatures. Since Q_{10} have a quantitative genetic basis and modify other genetically-driven traits, Q_{10} genes are epistatic in nature (i.e., the action of one gene on the phenotype is affected by the expression of Q_{10} genes). This is an epistatic view of phenotypic plasticity (Scheiner 1993, Roff 1997), as the phenotypic effect of Q_{10} genes as the environment changes (i.e., increase in temperature) is to modify the expression of other genes. Thus, this fourth module includes genes for trait plasticity to temperature variation.

A.5. Predator and prey quantitative genetics with more realistic recombination rates

In the former version of this IBM framework (Moya-Laraño *et al*. 2012) the authors successfully induced genetic correlations from pleiotropic effects by including all loci that affected the same traits in arrays which were called chromosomes. This was unrealistic because genetic correlations occur by both pleiotropic effects of quantitative genes and from linkage disequilibrium (Roff 1997), and we only considered the former. In linkage disequilibrium, loci that are close to each other in the chromosome tend to stay together for several generations (linkage), the number of which depends on their relative distance in the chromosome and on the recombination rate. Since linkage

disequilibrium has its own evolutionary importance (e.g., in genetic drift) and can be driven by many mechanisms, such as selection and non-random mating (Falconer & Mackey 1996) we decided to improve our modelling of quantitative genetics by better mimicking true recombination. The formerly described loci vectors (Moya-Laraño *et al*. 2012), which are useful to induce the desired degrees of genetic correlations among traits, we now term "correlosomes". In the current version of the algorithm, we include more realistic recombination rates by randomly permuting the position of each locus across the genome before cross-over. These random positions are established at the beginning of each simulation and are kept constant throughout for all animals. After cross-over, and before the new egg is built, the position of the loci are returned back to the correlosome position, which will allow assigning phenotypes to the newborns by keeping the original degree of genetic correlation (ρ parameter in Moya-Laraño *et al*. 2012). Note that the previous claim (Moya-Laraño 2012) that non-expressing alleles in correlosomes could be taken as microsatellite markers depending on the distance to expressing alleles still holds. However, now these alleles, as functional alleles do, will recombine in random positions and their position to functional alleles will be also random, a much more realistic situation.

A.6. New adjustments in all mass-dependent equations and plastic traits

A.6.1. Water body content

In the former version of this framework the authors did not explicitly model water body content (Moya-Laraño *et al*. 2012). Although water content is still static in the present version, as a prelude of a future version in which water loss will drive individual behaviour as well (e.g., Verdeny-Vilalta & Moya-Laraño 2014), here we modelled all animals as having 70% of their body mass in water form (following Sabo *et al*. 2002).

A.6.2. Adjustment of scaling constants in mass- and temperature-dependent equations

In Moya-Laraño *et al*. (2012) the authors modelled animals that were smaller than 1mg at maturation, which allowed all non-linear equations to behave consistently (e.g., larger animals had always higher speeds than smaller animals). In order to accommodate larger animals and to be sure that scaling was realistic, we used here linear interpolation to predict scaling constants (intercepts) from scaling coefficients (slopes). To estimate voracity, speed and search area of each animal (V, A and S in equations A6, A7 and A8 of Moya-Laraño *et al*. 2012 respectively), we estimated the intercepts (note that former equation A7 –Eq. A5 below- now includes an scaling constant) by linear interpolation in which each constitutive trait assigned to each animal (the scaling coefficients v, m and s to obtain V, A and S respectively) was linearly interpolated from the scale of the evolutionary limits (Π_x and K_x) to a final scale. This ensured that, for the smallest and for the largest animals, V, A and S were always higher for larger animals. We observed a high rate of starvation and a low rate of mobility depending on the coefficients of body condition (c) and rates of encounters with predators (e) in the former equations A6 and A7 (Moya-Laraño *et al*. 2012). To enhance survival and mobility,

in what are now Eq. A4 and Eq. A5 below, the term *c·e* has been changed to (*c+e*)/2. This gives equal weight to condition and anti-predator behaviour in determining animal voracity and mobility and does not penalize voracity and mobility as strongly when animals are well fed and have encountered many predators (e.g., low *c* and *e* values). Future data across a few animal taxa should determine how the internal state of the animal (*c*) and anti-predatory behaviour (*e*) interact to determine the levels of animal activity. Therefore, the new equations are:

$$V = f_V M^v [(c+e)/2] Q_{VT} \quad [A4]$$

$$A = f_A M^m [(c+e)/2] Q_{AT} \quad [A5]$$

$$S = f_S M^s c Q_{ST} \quad [A6]$$

where the *f's* are the interpolated scaling constants (ranges f_V: 0.05 - 0.15, f_A: 1 - 12.85, f_S: 1 - 7). All other terms discussed in Moya-Laraño *et al*. 2012.To improve basal metabolic rate estimates, we took advantage of the strong correlation occurring between lnI_0 and *E* across 9 taxa of soil organisms in the data of Ehnes *et al*. (2011; equation A3) and used linear regression (lnI_0 = -7.29 + 43.97 *E;* R^2 = 0.99*; P* < 0.0001*;* N = 9) to predict basal metabolic losses for individuals genetically differing in the scaling coefficient (*a*) and activation energies for metabolic rates (*E*). This approach ensured that animals with higher *E* expended more energy for a given environmental temperature (more energy was needed to activate their metabolism) and greatly improved survival from starvation in the simulations.

A.6.3. Field metabolic rates

Field metabolic rates can be obtained by multiplying basal metabolic rates by a value of 2.5 - 3 (Yodzis & Innes 1992, Brose *et al*. 2008). In order to make sense of individual variation, we used a more dynamic approach of assigning the multiplying coefficient of field metabolic rates (3) only to the fraction of time (P_t) that animals were really active (Moya-Laraño 2012):

$$P_t = w_A \cdot \left(\frac{W}{A_{\max}} \right) + (1 - w_A) \cdot \left(\frac{V}{V_{\max}} \right) \quad [A7]$$

were w_A determines how much weight is given to activity among patches (*W*) or within patches (*V*), and A_{max} and V_{max} are maximum searching area and voracities in the community (i.e., for the largest animals with lowest condition, lowest previous encounter rates with predators and at the highest temperature T = 25°C), respectively. In the current version an A_{max} and V_{max} values have been

calculated for each species. This implies that the offspring of the largest species has a survival bonus, as they will spend relatively much lower energy from moving around than the offspring of the smallest species, which will be closer to their maximum. We decided to pursue this strategy for now because, due to the initialization following allometric mass-abundance scaling, too few of the large predators were included in the simulations, which were therefore highly subjected to stochasticity and went rapidly extinct. This procedure ensured that large predators persisted more. In a future parallelized code, which will allow initializations with > 100.000 individuals, each individual will have its own A_{max} and V_{max}, which will in turn depend on its own traits, a much more realistic situation.

A.7. Moulting algorithm

An improvement relative to the former moulting algorithm is that now the shape of the animals, and thus the length-mass allometric relationship is taken into account to decide when the next instar should be achieved:

$$M=aL^b \qquad [A8]$$

We obtained most of the *a* anb *b* coefficients from published accounts (Hódar 1996, Edwards & Gabriel 1998, & Gruner 2003), and for enchytraeids (Clitellata) we used unpublished estimates (a = 0.0039, b= 2.53; O. Verdeny-Vilalta, N. Melguizo-Ruiz & J. Moya-Laraño, unpublished data). In all equations body length is measured in mm and mass in mg. Now, the mass available for moulting (i.e., 90% of the state variable energy tank, ε) is transformed into the length of the animal (by rearranging Eq. A5) in order to allow for length growth to be governed by the trait growth ratio. Once an individual molts the original equation A5 is applied to estimate the body mass of the instar. The mass allocated to ε is a fixed proportion of the fixed body mass (i.e., the *B* trait) which is the same proportion as that given at birth (i.e., the ε_o trait).

In the current version, the number of instars was species-specific and was calculated by first estimating egg mass for each species by fitting the following adult-offspring allometric relationship: offspring mass = 0.03 · adult mass$^{0.5}$, which was calculated by visually fitting the intercept for the invertebrate relationship presented in Figure 3.3 of Hendriks and Moulder (2008). We then obtained adult masses from a unpublished data set on individual lengths across 4 beech forests (J. Moya-Laraño, E. De Mas, J. Pato, G. Giménez-Navarro & Melguizo-Ruiz, unpublished data) to which we applied equation A5 and the same coefficients as in our simulations. Finally, we applied the moulting algorithm described above to the offspring of each species, for which we included the same growth ratio (mid-point of the range) used in our simulations. By iteration of this algorithm we calculated the number of instars which matched the targeted adult body size and this result was used as the total number of instars for each simulated species.

Since growth curves are not ruled by a single ratio parameter, as they usually have a sigmoid shape, we allowed animals to also plastically moult by including time as an alternative for moulting. We included a couple of state variables which were time elapsed in the prior instar and time elapsed in the present instar. The ratio between time in present and time in past instars was established as a second rule of thumb to moult with whatever amount of resources the animal could have accumulated to that point, forcing a moulting event which does not follow the growth ratio. This provides some realism to growth curves as arthropods are generally phenotypically plastic in developmental time (Nylin & Gotthard 1998). If an individual has not moulted due to its growth ratio trait by the time determined by this ratio, the animal proceeds to moult. Ratios used in simulations were 0.8, 0.9 and 1.5 for large predators, small predators and fungivores respectively. This difference was necessary to enhance maturation in predators, which were larger on average than prey.

A.8. Reproductive algorithm

In addition to the changes in recombination explained above, we simplified the criterion for reproduction. Now we calculated the biomass available for reproduction as 90% of the energy tank (ε) and when this value was twice as large as the weight of the fixed body mass of the adult individual, the animal was able to lay an egg batch. In future versions, this criterion should be changed to a species-specific mode of reproduction criterion, allowing for continuous egg laying (as many mites do) and also laying large batches at once (as spiders). Note that this is not merely a distinction between iteroparity or semelparity, as iteroparous animals can still lay either one egg at each reproductive event or an entire clutch. What is relevant for the dynamics is how much energy an individual needs to accrue before a reproductive event occurs. Continuing with this simple criterion for reproduction, and as in the former version, each prey individual was allowed to lay up to 2 batches before dying and predators up to 5. The number of batches and the number of eggs per batch, which are closely associated to the mode for reproduction, should be adjusted in the future in a species-specific basis.

In the former version of this IBM mate search was not necessary because we assumed that animals would encounter a mate with 100% probability as long as there was one present in the population. Since space is now relatively much larger (albeit still in arbitrary units; i.e., 4000 *vs.* 100 cells), we have implemented a momentary solution in which once an individual enters the reproductive state it starts searching for patches with mates (moving preferentially to patches with more reproductive individuals of their own species) and will be allowed to move up to 1000 steps per day. These individuals are both invulnerable to predation and do not expend energy during searching. This simplification had to be added to enhance mating encounters and improve ecological dynamics. However, once mates attractants are successfully implemented, future versions should also include the cost of mate search (e.g., predation risk and energy expenditure).

A.9. Restricting and controlling attack rates

Within a given patch (or cell) the probability that a predator finds a prey and *vice versa*, as well as the probability that predation occurs upon an encounter depend on probabilities drawn at random from a uniform distribution which are contrasted with deterministic probabilities that come from the animal traits involved (equations A13 and A14 in Moya-Laraño *et al*. 2012 respectively). The logistic relationship between the traits of the two animals involved in a potential encounter or predation event and the deterministic probability dependent on a set of coefficients ($\alpha...\eta$ for encounters and $\alpha...\delta$ for predation..δ) which determined the relative importance of each predator and prey trait would take in either encounters or predation. These coefficients were called naïve coefficients because they are not based on real data. In the future, they should either be estimated from real data or be the subject of sensitivity analysis, in particular if we want to make strong inferences about the evolution of certain traits. To facilitate the task of simulating the effects of different values for these coefficients, we estimated by simulation means and standard deviations for all traits and trait combinations (e.g. predator by prey mass interaction) which allowed standardizing these traits and their combinations as if following a standard normal distribution. This ensured that all traits and combinations had identical units in the equations, which allowed the naïve coefficients to have identical weight on the final probabilities regardless of the units of measurement of the traits involved. The final equations are thus:

$$P_e = \frac{1}{\left[1+e^{-\left(\alpha+\beta V'_{P_d}+\gamma V'_{P_y}+\delta\left(V_{P_d}V_{P_y}\right)'+\varepsilon B'_{P_d}+\xi B'_{P_y}+\eta\left(B_{P_d}B_{P_y}\right)'\right)}\right]} \qquad [A9]$$

$$P_p = \frac{1}{\left[1+e^{-\left(\alpha+\beta V'_{P_d}+\gamma R'_B+\delta R'_S\right)}\right]} \qquad [A10]$$

where the ‘s refer to the fact that the variables (or their products) were standardized. Traits are voracities (V) of the predator or attacking individual in IGP and cannibalism (P_d) or prey or attacked individual (P_y), B is structural body mass and R_B and R_S are structural body size and speed ratios respectively. More details can be found in Moya-Laraño *et al*. 2012. The naïve coefficients used in the present simulation were for encounter probabilities ($\alpha...\eta$): 1, 0.1, 0.1, 0.1, 0.1, 0.1., 0.1; and for predation probabilities given an encounter ($\alpha...\delta$): 1, 0.1, 0.1, 0.1. Therefore, we assumed that all variables (and thus all traits) had equal weight in deciding an interaction outcome.

One of the problems of the above equations is that predator-prey interactions are ruled by traits and naïve coefficients and therefore attack rates could be overlay too high or excessively low to ensure any ecological dynamics. We added an additional control, which could be used for controlling

attack rates upon each species. This was accomplished by restricting the range of those p-values randomly obtained from a uniform distribution which were to be contrasted against P_e and P_p to decide the outcome of interactions (i.e.; an encouter occurs if P_e > random p-value). We first obtained the distribution of values by running a simulation and then established the following ranges of random p-values for large and small predators, and prey respectively (webs with connectance 0.1 or 0.55): *encounters*, 0.337 - 0.342, 0.337 - 0.340, 0.337 - 0.3394; *predation*, 0.606 - 0.623, 0.606 - 0.617, 0.606 - 0.6149. For the web with connectance 0.3 (which had different species), the values were respectively: *encounters*, 0.337 - 0.3375, 0.337 - 0.338, 0.337 - 0.339; *predation*, 0.607 - 0.612, 0.607 - 0.614, 0.607 - 0.617. This ensured that large predators (and especially the juvenile stages) suffered less from IGP. Again, this simulation strategy allowed large predators to stay longer in the simulations, as otherwise extinction occurred too rapidly. For the same reason (improving large predator survival), and since small predators already had a predation pressure coming from higher trophic levels, all background mortalities (Moya-Laraño *et al*. 2012) were set to zero. Although we do not know what defensive traits allow the offspring of large predators to reach maturation, it is obvious that without these improvements we were not able to mimic the survival of juveniles in large predatory species. This in itself opens an interesting question to investigate a) whether the offspring of large predators have improved survival over other predators of the same size, and b) which traits may be involved in this differential survival.

To further control attack rates and make them more realistic, we allowed encounters and predation events only within the following range of log body mass ratios: -1.21 - 6.68, as data on 800 induced predator-prey encounters among individuals of a beech forest food web has shown that predation never occurs beyond these thresholds (J. Moya-Laraño, E. De Mas, J. Pato, G. Giménez-Navarro & Melguizo-Ruiz, unpublished data).

In addition, we relaxed the one-day one-prey criterion to allow larger predators to feed in a more realistic way. Now all predators can search and feed on several prey per day as long as the ingested body mass does not surpass that of their voracity (*V*) or as long as the number of visited patches in one day does not surpass that of the individual trait area searched (*A*). Since now food ingestion is at is maximum (*V*) we assumed that all food could be handled and digested in one day and set all digestion times (regardless of temperature) to zero. Therefore, all predators that rested alive were ready to hunt again the following day regardless of how much they had ingested the day before. Once we improve the capabilities of our framework we will be able to establish simulations with time steps of hours or minutes, when real handling and digestion times will be appropriately included.

A.10. Adaptive animal movement

Animals move adaptively in 3D space similarly as they did in 1D mini-AKIRA (Moya-Laraño *et al*. 2012) with the plus that they now remember the cells they visited within the same day as not to repeat the same cell in a given day. This was implemented as to make predators to move more naturally, as once interactions (encounters plus predation) have been unsuccessfully attempted with all individuals in a patch the predator should assess the patch as unsuitable for hunting prey. Although WEAVER 1.0 now implements the possibility of animals assessing cells farther away from neighbouring cells, all simulations in this paper assume that animals can only assess the 26 cells that immediate surround the cell in which the animal is located in a given time. At each move, fungivores will move to cells with the lowest ratio between predation threat and fungus biomass with the additional improvement that fungivores assess only the species to which they are linked according to the food web structure established at the beginning of the simulation (see main text) and within the predatory threshold imposed by the limits of log mass ratios (-1.21 to 6.68). Predators behave in a similar way: they assess predator threat and prey availability (both fungivores and IGP-prey) considering only those species with which they are linked according to food web structure and following the log mass ratio criterion.

In addition, as in mini-AKIRA, both prey and predators can perform jumps so as to clear out from the areas in which edible items have been depleted. To accommodate these jumps to a 3D environment, when food availability within the 27 neighbouring cells (26 surrounding cells plus the cell where the animal is currently located) is zero, the animal will perform a jump at a distance which is established by drawing a random number from a uniform distribution which ranges between 2 and its search area trait (*A*). This animal then evaluates the new area and can either perform another jump or just stay put if food is available. At each jump the animal evaluates how many cells are within its jump value (in the 3D directions) and if an edge (wall) of the world is at a shorter distance than the projected jump, the direction pointing towards that edge is immediately discarded from the universe of possible directions towards which a jump can be performed. This same edge procedure takes place at normal moves (e.g., when only one step is performed at a time).

To prevent animals from getting stuck in an area, they track the cells they have visited each day and they do not go back to those cells within the same day. Therefore, each cell is assessed by each predator only once per day and if after having attempted to catch prey in a cell, additional prey need to be caught that day to meet the voracity demands (see above), these will be sought in a different cell. This process applies also when the animals jump, so they do not jump back to an already visited cell in the very same day, encouraging them to move through new areas. As in Moya-Laraño *et al*. (2012) the number of maximum steps an animal can attempt each day equals its search area trait (*A*). However, now each displacement (either a simple step or a jump) adds only a single step unit to *W* for estimating field metabolic rates in Eq. A7 above (equation A10 in Moya-Laraño *et al.* 2012).

A.11. Computational demand and requirements

Computationally, WEAVER 1.0 can be highly demanding both in terms of memory and of CPU needs. Memory will be impacted by the number of individuals living in the world at a given time and cells comprising the soil structure. This should be taken into account by the user when running potentially large simulations. For example, a simulation running for 200 days with 9 species or fungivores and 11 species of predators (community size = 20,000 individuals), such as that presented here, may take only about 1 hour but more than 18GB of memory and store more than 100GB of information, including the genetics of all organisms, the predator-prey interactions at the species level, the daily reports on trait and state variable values for each alive animal (including spatial location), the constitutive traits to document evolutionary dynamics and the number of animals for each state and instar for each day. Therefore, the program outputs will require vast amounts of hard disk to store all the information needed (which is also customizable), especially if binary snapshots are stored at each simulation step to graphically visualize water and fungus levels, animal population densities, etc.

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Capítulo 2

Mass-Length allometry covaries with ecosystem productivity at global scale

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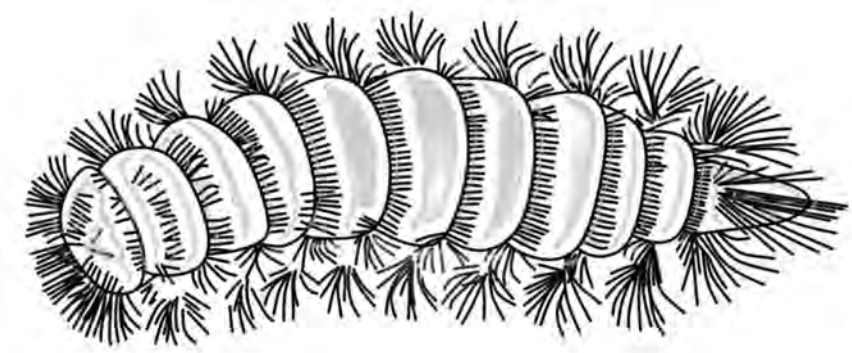

Mass-Length allometry covaries with ecosystem productivity at global scale

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Segunda Revisión: Global Ecology and Biogeography

Abstract

Aim: It is still hotly debated whether allometry, the relationship of body size with body parts, entails merely an evolutionary constraint or can itself evolve. Recently, a hypothesis has been proposed which states that static allometry (allometry measured across individuals at the same developmental stage) can evolve from differences in the developmental pathways between pairs of traits under different nutritional environments. A macroecological prediction stemming from this hypothesis is that allometric coefficients (scaling and allometric factors) should covary with ecosystem productivity. Here, we tested this prediction using a worldwide database of mass-length allometric equations.

Location: worldwide, data distributed across the entire globe.

Time period: 1967-2017.

Major taxa studied: soil arthropods.

Methods: We fitted general linear models with the allometric coefficients (the scaling *a* and allometric *b* factors) as the dependent variables. The target independent variable was NDVI, as a proxy of ecosystem productivity. Longitude, absolute latitude and altitude, as well as mean annual temperature and mean annual precipitation were included as both covariates and additional variables of interest. We also included body bauplan (obtained from geometric morphometrics), taxonomic affiliation (a proxy of phylogenetic relationships) and the reciprocal allometric coefficient as covariates in the model.

Results: We found a strong negative association between both allometric factors and the productivity of the ecosystems, and the effect for the allometric factor *b* was stronger at lower trophic levels. We also detected strikingly similar effects of geographic and climatic predictors on both allometric factors, suggesting the occurrence of similar selective regimes.

Main conclusions: The fact that productivity, geography and climate affect the value of mass-length allometric coefficients has important consequences not only to understand the evolution of allometries, but also how energy is processed in soil ecosystems across the globe.

Keywords: Allometry evolvability, body energy storage, climatic gradient, ecosystem productivity, mass-length allometry, soil arthropods, space gradient.

Introduction

Allometry refers to the scaling relationship between two body parts across either taxa within the same developmental stage, typically adults (static allometry), or developmental stages within the same individual (ontogenetic allometry). This relationship is described by a power function with form $y=ax^b$ relating the trait *x*, usually body size, with the trait *y* through the scaling factor *a* and the allometric factor *b* (Huxley, 1932; Cock, 1966; Gould, 1966) (see Appendix S1 in Supporting Information). Whether static allometries remain more or less fixed and constrain the evolution of phenotypic diversity has been hotly debated in evolutionary biology (Huxley, 1932; Gould, 1977; Lande, 1979; Maynard-Smith *et al.*, 1985). However, recently the constraint hypothesis has been dismissed to some extent, as several empirical studies have concluded that there is evolvability in static allometry by showing that allometry coefficients respond to natural selection (Shingleton *et al.*, 2007; Voje & Hansen, 2012; Pélabon *et al.,* 2014; Craig Stillwell *et al.,* 2016). Actually, because scaling and allometric factors differ across taxa, this may entail evidence that static allometry may evolve. At microevolutionary time scales, on the other hand, the evolution of allometry can only occur in the absence of develomental constraints (Frankino *et al.,* 2005). Indeed, microevolutionary studies suggest that the evolvability of the allometric factor (i.e.: evolution of the allometry *sensu stricto*) is much lower and less efficient relative to the evolvability of the scaling factor (i.e.: evolution *sensu lato*) (Owen & Harder, 1995; Tobler & Nijhout, 2010; Egset *et al.,* 2012).

A recent theoretical approach has linked the proximate mechanisms leading to static allometric to the evolution of allometry (Shingleton *et al.,* 2007). This approach shows how the differences in the developmental reaction norms of body size and any other trait covarying with it can explain whether static allometries are isometric or deviate from isometry. This mechanism then will constrain the shape of evolutionary allometries and thus the evolution of allometry itself. In arthropods, nutrition and the regulation of the insuling/IGF signaling pathway has been shown as one of the most important mechanisms to shape body size and related trait reaction norms (Shingleton *et al.,* 2007; Emlen *et al.,* 2012).

Given the above tenets, we predict that the amount of energy available in ecosystems will influence the magnitude of allometry (the scaling and allometric factors) through affecting the nutritional status of organisms during development. Furthermore, long-term (i.e.: at evolutionary timescales) persistent differences in energy availability across ecosystems should promote the evolution of static or evolutionary allometries in a manner consistent with the idea that differences

in nutritional reaction norms between body size and other traits have become constitutive over evolutionary time.

Here, we test the above hypothesis by deciphering if mass-length allometric relationships in soil arthropods covary with the energy available in the ecosystem. This test is based on the assumption that higher primary productivity is linked to higher rates of litter accumulation in soils and that there is an indirect bottom-up effect of primary productivity on soil productivity (Capellesso *et al.,* 2016). In particular, we predicted that in highly productive environments selection should favor length over mass (lower allometric coefficients) because growth should be favored over energy storage. To evaluate this hypothesis, we analyzed the relationship between productivity and the scaling and allometric factors of the mass-length allometric equations built for soil arthropods in many localities all over the World. The information was retrieved both from allometries estimated by the authors as well as from a comprehensive bibliographic review. Because the data were heterogeneous, we controlled for possible confounding effects by including in all analyses not only the allometric variables but also the geographical location, as well as the major climate variables (mean annual temperature and precipitation) of each study site. These variables could influence allometry independently on ecosystem productivity. We here assume that a smaller value in the allometric factors may be a sign of selection favoring faster development (or growth rate in length), instead of favoring energy storage or investment in other body structures (Dmtriew, 2011). This even applies to the scaling factor *a*, as this coefficient is an estimate of the body mass of animals that are 1 mm in length (White & Gould, 1965) (see Appendix S1). Since most animals in our database are adults at a body length > 1 mm (see Table S1), a low value of *a* may be a sign that the next instar (i.e.: growing above 1 mm in length) could be attained relatively fast after accumulating relatively less energy.

In addition, we included the type of allometry (static *vs* ontogenetic *vs* evolutionary) (see Appendix S1), the taxonomic affiliation, the morphological body bauplan and the feeding habit or trophic level (low trophic level: decomposers plus herbivores; higher trophic level: omnivores plus predators) of the arthropods for which each equation was estimated. As predicted, we found a significant and negative relationship between the primary productivity of each locality and the allometric factors, and the effect on the allometric factor *b* was stronger at higher trophic levels. Moreover, differences in body shape had relevant effects on the allometric coefficients. We also found relevant negative relationships between the scaling and allometric factors and some of the geographic and climatic predictors, indicative of selection favoring faster development. These findings have important ecological consequences, as these documented differences in allometry may be an indication of how energy is processed differently by the soil fauna in different parts of the globe and different climates, with possible implications for abundance-body mass relationships and the energetic equivalence rule (Damuth, 1981).

Material and Methods

Database

We compiled a database containing information on the relationships between mass and length of individuals from six main groups of soil invertebrate arthropods: arachnida, chilopoda, diplopoda, entognatha, insecta and isopoda (see Table S1). This information was obtained both from the literature and from our own field sampling (see Appendix S2, Table S2). All studies included in the database estimated length as the total body length of the arthropods without appendages, which according to how it is measured, it is a homologous trait across all the studied taxa (Fig. 1). In total, the database included 283 mass-length relationships (equations hereafter) from 45 georeferenced sites located all over the world, from the Equator to high latitudes, and from many disparate biomes (Fig. 2, see Table S3). The most intensely sampled arthropods were arachnida (112 equations) and insecta (102 equations) (see Table S2). Because sample size usually affects the accuracy of the estimates, we included in the database only those equations that included information on sample size, of which only 66% contained information on the standard errors of the *a* and *b* estimates.

Handling the scaling factor *a* and allometric factor *b*

Because of the high heterogeneity in how different works presented the equations, we retrieved the scaling factor *a* and allometric factor *b* from each of these 283 equations differently. Therefore, when necessary we transformed the original equations to convert all of them to power functions (see Appendix S3). In particular, no transformation was performed when the original equations were already power functions, whereas back-transformation was performed when the original equations were log-log functions (see Table S4). Despite the fact that Model II regression would be desirable for the purpose of our study (LaBarbera, 1989), in order to make the database as homogeneous as possible, and consistently across studies, in the cases in which we had the original datasets we also estimated the allometric exponents by means of Model I OLS regressions (see Appendix S4). Transformations that are more sophisticated were necessary when equations were provided as semi-logarithm functions, polynomial functions or square-root functions (see Table S4). We tested the accuracy of the transformations by comparing the original equations to the transformed ones. We only needed to transform the equations in a very small proportion of the cases (3.5%), and the proportion of variances explained by the newly constructed equations on the older ones ranged between 93-100%, indicating very low error (see Fig. S1, Table S5). The scaling factor *a* was also transformed appropriately to allow comparisons across equations (see Appendix S3).

Estimation of primary productivity

We estimated primary productivity for each of the sites by means of the normalized difference vegetation index (NDVI) (Verdin *et al*., 2003). We obtained the values of NDVI for each georeferenced site from the web of Global Agricultural Monitoring of the NASA (GIMMS). To ensure that the data were comparable among sites, we downloaded a NDVI temporal series for each 0.25°

cell from the MODIS sensor in the Terra satellite, and calculated the average NDVI among years for each site (time window: 2000-2016) (Weier & Herring, 2000).

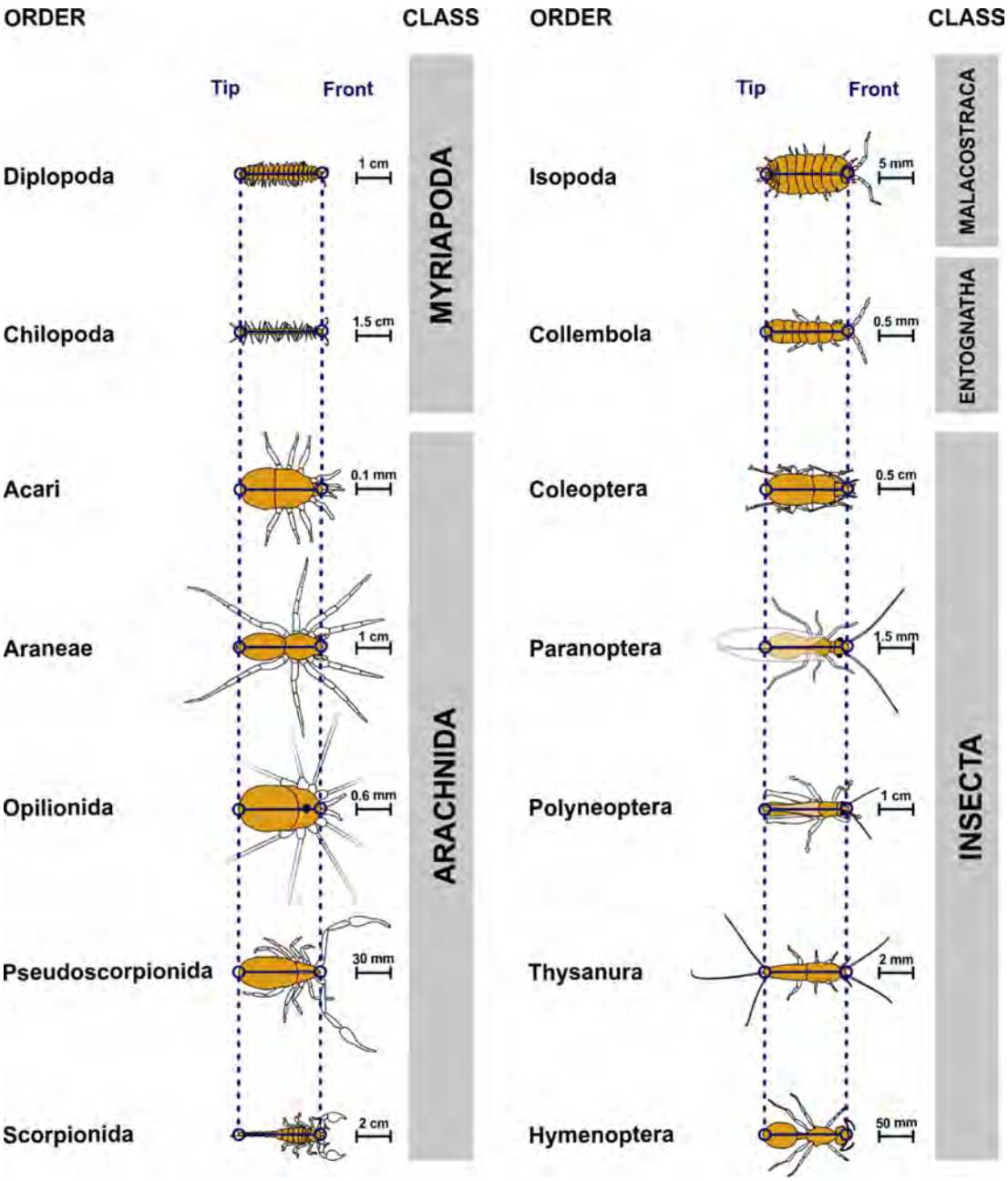

Fig. 1. Schematic representation of how body length was measured for each arthropod group included in this study. Homologous traits are represented by dark blue points. Total body length was estimated as the length of the dark blue lines connecting these homologous traits and excluding appendages.

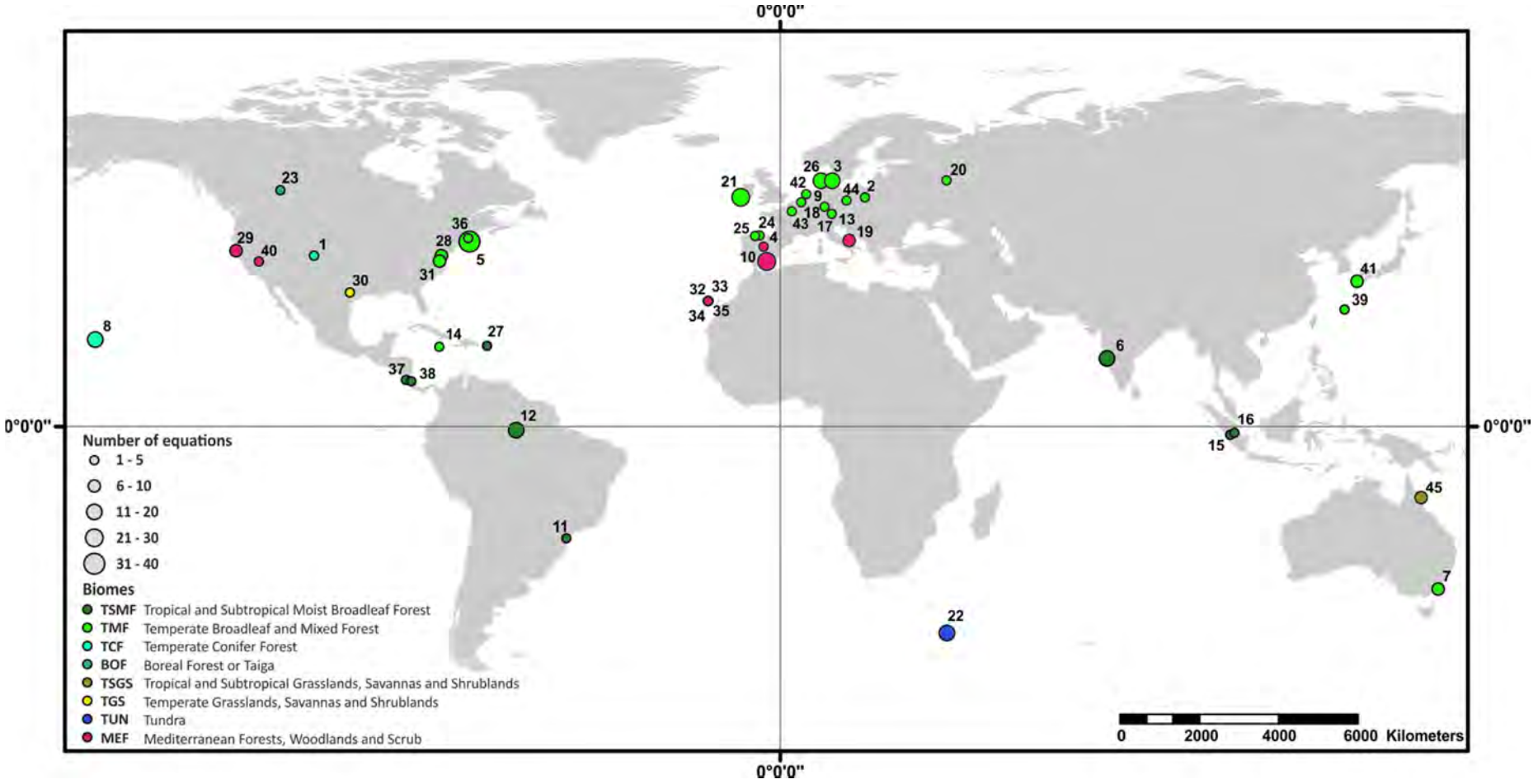

Fig. 2. Global distribution of the mass-length allometry dataset. The number on each dot denotes the site/study as coded in the dataset (see Table S3). Each color represents the type of environment according to the ecological classification system developed by the World Wildlife Fund (WWF) in which the major habitat types, similar to biomes, were identified. The size of the dot indicates the number of equations in each locality.

Climate variables

The relationship between the allometric factors and productivity can be masked by the same climate variables that influence the NDVI (e.g.: water availability, temperature). For this reason, we controlled for the climate of each location in all the models. The climate of each location was described by two widely used variables, the mean annual temperature (MAT) and the mean annual precipitation (MAP). Climate data were downloaded from WorldClim-Global Climate Data, a free accessible climate database for ecological modeling. We used the GIS Version 1.4 for current conditions (~1950-2000) with a 30 arc-seconds (1 Km^2) resolution. This database contains 19 bioclimatic variables (codes BIO_1 to BIO_{19}) derived from the monthly mean, minimum and maximum temperature and monthly precipitation values that are transformed into biologically meaningful variables. The altitude of each locality was also obtained from the above database. The data layers were generated through interpolation of average monthly climate data obtained from those weather stations for which there were records for at least 10 years (max 30 years: 1960-1990). In some cases, the time period extended to the range 1950-2000 (Hijmans *et al.,* 2005). The extraction of data was accomplished by the use of the SRTM elevation database and the ANUSPLIN software, a program which interpolates multivariate data using plate smoothing splines (latitude, longitude and altitude as independent variables).

Phylogenetic relationships among the arthropods included in the study

Allometry may also depend on the phylogenetic relationships among the taxa included in the study (i.e.: phylogenetic signal). Due to the idiosyncrasy of each study, and the variability in the level of taxonomic accuracy for which equations were built, no phylogeny was available to account for phylogenetic distances. Thus, in order to partially control for this potential source of pseudoreplication, the common taxonomic group to all studies, class, was considered an accurate proxy of the phylogenetic relationships of the studied arthropods. A similar approach has been previously used in other comparative studies in macroecology (Clutton-Brock & Harvey, 1977; Hadfield & Nakagawa, 2010; Ehnes *et al.,* 2011).

Body bauplan of the arthropods included in the study

Our equations were built for many different groups of arthropods having very different body bauplans. Since the value of the mass-length allometric relationship probably depends on the bauplan of the different arthropod taxa, which is an important factor of shape variation (Outomuro & Johansson, 2017), we used geometric morphometrics to describe body shape as a proxy of the bauplan for each arthropod group considered in this study, and used the Principal Components obtained from the analyses as covariates (PCGMs) to control for shape in the regression models. Geometric morphometrics is a tool to summarize the shape of organisms by the use of landmark points, which we assigned following the arthropod homologies on their tagmosis. A Procrustes fit one can standardize all the information about size, position and orientation, resulting in variables

that explain different aspects of the shape of the animal, and which can then be further subjected to interpretation and analysis (Zelditch *et al.,* 2012) (see Appendix S5, Fig. S2, Fig. S3). In addition to landmarks, pseudo-landmarks were considered as to increase the chances to grasp the shape of body condition across all taxa (e.g.: abdomen expanding with food acquisition in spiders) (Jakob *et al.,* 1966) (see Appendix S5, Fig. S4). This procedure of shape analysis was performed using pictures for the 51 families and 13 orders of arthropods included in our dataset (see Appendix S5, Fig. S5). Using a Principal Component Analysis, we obtained the first three components which explained together 96.2% of the variance in shape. The first component (PCGM1) was interpreted as body slenderness with reduction of cephalic area (a high value represented by the myriapoda), the second (PCGM2) was associated to a change in body thickness (e.g.: opilionida). The third (PCGM3) was associated to a change in relative abdomen volume (e.g.: pseudoscorpionida) (see Appendix S5, Fig. S6).

Feeding habits of the arthropods

Different trophic habits (decomposer, herbivore, omnivore or predator) (see Appendix S6, Fig. S7a) entail different stoichiometry compositions (Jakob *et al.,* 1966; Fagan & Denno, 2004; Raubenheimer *et al.,* 2009), with predators having lower C:N than herbivores (Fagan *et al.,* 2002; Fagan & Denno, 2004; Rubenheimer *et al.,* 2009). Since different body compositions may lead to different body masses and even densities (Moya-Laraño *et al.,* 2008), and this in turn could affect the relationship between the environmental variables and allometry, we also considered a variation of the final model which included the interaction between feeding habits and NDVI. In that respect, we anticipated that the effect of productivity on allometry could dampen or disproportionally increase from lower (herbivores, decomposers) to higher trophic levels (predators, omnivores) (see Fig. S7b).

Types of mass-length allometry equations

The database included a mixture of static (19 studies), ontogenetic (49 studies) and evolutionary allometries (215 studies) (see Appendices S1 and S7, Fig. S8a, S8b), which may be subject to different evolutionary constraints (Reiss, 1989; Klingenberg, 1998; Voje *et al.,* 2014). In order to test if NDVI could differently affect each of these types of allometries, we included the type of allometry (static, ontogenetic or evolutionary) as a categorical variable for analysis and its interaction with NDVI. If, as suggested by Voje *et al*. (2014), different types of allometry could follow similar trajectories, then, we could expect no interaction between the type of allometry and the environmental factor. If an interaction was found, we then re-run the models including only the data for evolutionary allometries, as this was the only one with sufficient sample size (n = 215) to allow fitting all the parameters to finally testing NDVI. Some more details are provided in the next section.

Statistical analysis

We ran four nested general linear models for each of the two allometric factors after checking that there are no significant correlations between the target variables (see above), except as we expected between MAT and MAP with latitude (r = 0.85 and r = 0.59) (see Table S6):

1. The first model, or Base model, included the reciprocal factors (*a* for testing *b*, and *b* for testing *a*), the class of the arthropods and the target variable NDVI (see Table S7, Table S8). The reciprocal factors were included because the factors *a* and *b* can be strongly negatively correlated with each other by geometric constraints alone (White & Gould, 1965), and indeed they were in our database (see Appendix S8, Fig. S9). Class was considered as a fixed factor because it had less than 10 categories (Zuur *et al.,* 2009). To test for spatial autocorrelation, we added random variation to the Longitude and Latitude of each data point by adding a random number drawn from a normal (mean = 0, standard deviation = 1) distribution, which allowed testing for autocorrelation of the residuals even due to the equations obtained from the same locations. When autocorrelation was detected, we corrected it by adding an extra variable obtained from the residuals of the model lagged one position as proposed by Bivand *et al*. (2013) (see Appendix S8).

2. In the second model, or Shape model, we additionally included the shape of the arthropods estimated by the three major geometric morphometric components.

3. In the third model, or Geographic model, we additionally included the geographic variables longitude, absolute latitude and altitude. We included them as independent variables because regardless of controlling for spatial autocorrelation we wanted to test the geographic effects *per se*, even beyond the correlation with climatic variables (see Table S6). The idea behind this approach is that geographic variables can act as proxies of unknown environmental selective factors affecting the evolution of allometries. For instance, absolute latitude could be affecting allometric values because it can be a proxy of the strength, frequency and diversity of biotic interactions (Dobzhansky, 1950; Schemske *et al.,* 2009; Schemske, 2009; Moya-Laraño, 2010). Furthermore, if these variables explained a relevant amount of the variance in the model, their inclusion would increase the accuracy of the remaining estimates (e.g.: NDVI).

4. In the fourth model, or Full model, we additionally added the two climatic variables mean annual temperature (MAT) and mean annual precipitation (MAP). Both temperature and water availability could directly affect growth beyond ecosystem productivity as well as productivity itself. To test whether the results concerning NDVI were robust across trophic levels or type of allometry, we also compared the Full models with models that included the interactions between type of allometry and NDVI and feeding habits (or their grouping by trophic level) and NDVI.

All analyses were performed with the function "lm" (R 3.4.1 development core team 2016) and the main figures of partial effects produced by means of the R package "effects" (Fox, 2003). Models were compared via AIC (Burnham & Anderson, 2002). Both the dependent variable and all explanatory variables were standardized (mean = 0, standard deviation = 1) to make the magnitude of the effects among the different environmental variables comparable in terms of standard deviation units. To ensure normality of the residuals, we first transformed the *a* and the *b* values via optimality by the iterative use of the function "MLE_LambertW" within the R library "LambertW" (Goerg, 2016), and then we additionally normalized the residuals of the models by the same procedure. Also, since sample size could have affected the accuracy in the estimates of the allometric parameters in each of the fitted equations, we ran all the analyses by weighting by sample size, which allowed a 50% larger sample size than weighting by the SE of the estimates. As a sensitivity analysis, we ran the full models using robust regression in the function "rlm" of the R library "MASS".

Results

Comparisons of Base, Shape, Geographic and Full models suggested that shape PCs, geographic and climatic variables should be included in the models explaining both the scaling (*a*) and the allometric (*b*) factors (Table 1).

Table 1. Summary of AIC and R^2 values of the models for both allometric factors.

Factor	Model	AIC	R^2
Scaling *a*	Base model	761	0.613
	Shape model	722	0.671
	Geographic model	672	0.730
	Full model	650	0.754
Allometric *b*	Base model	1019	0.450
	Shape model	942	0.586
	Geographic model	905	0.644
	Full model	848	0.716

Both the scaling (*a*) and allometric (*b*) factors were strongly and negatively affected by the target variable NDVI in all the base, shape, geographic and full models (Fig. 3a, 3b, Table 2, see Table S7, Table S8). Both the scaling (*a*) and allometric (*b*) factors were negatively affected by the absolute latitude and altitude (Fig. 3c, 3d, 3e, 3f, Table 2, see Table S7, see Table S8). Regarding the climatic variables MAT and MAP, both the scaling factor *a* and the allometric factor *b* were negatively affected by MAT (Fig. 3g, 3h) and only allometric factor *b* was negatively affected by MAP (Fig. 3i, 3j).

For the scaling factor *a*, the variables ordered from strongest to weakest negative effects according to their standardized partial regression coefficients were absolute latitude, NDVI, altitude and MAT. Geometric morphometric variables had positive and relatively weaker effects with PCGM1, PCGM2 and PCGM3 showing effects from strongest to weakest (Table 2). Overall, the full model for *a* explained around 75% of the variance ($R^2 = 0.754$) (Table 1). For the allometric factor *b*, the variables ordered from strongest to weakest negative effects were absolute latitude, MAT, altitude, NDVI and MAP. PCGM1 and PCGM3 had stronger and weaker positive effects respectively (Table 2). Overall, the full model for *b* explained around 71% of the variance ($R^2 = 0.716$) (Table 1). The spatial autocorrelation of the residuals was successfully corrected in all models as shown in the correlograms (see Fig. S10, Fig. S11). Actually, the additional lagged term was no longer significant in the full models and barely significant for *a* and not significant for *b* in the geographic model. However, we left this variable in the final models for consistency. Taxonomic class was highly significant in both full models (a: $F_{5,265} = 31.369$, $p < 0.001$ and b: $F_{5,265} = 18.723$, $p < 0.001$) and post-hoc test revealed strong differences among some of the taxonomic classes (see Fig. S12). The results of the robust linear regression for full models were qualitatively the same, with all significant terms matching those of the general linear model with normalized residuals. However, the relative effects detected for the predictors were 2-3 times weaker, likely because the lack of normality in the residuals (see Table S9).

Table 2. Summary of the results of the Full model analyzing the predictors on the alometric factors *a* and *b*.

Factor	Variables included	Estimate	SE	F	d.f.	p (F)
Scaling *a*	(intercept)	0.5347	0.0785			
	b	-0.4048	0.0362	125.021	1, 265	***< 0.001***
	Class			31.369	5, 265	***< 0.001***
	PCGM1	0.2714	0.0736	13.592	1, 265	***< 0.001***
	PCGM2	0.1054	0.0398	6.993	1, 265	**0.0087**
	PCGM3	0.0988	0.0466	4.491	1, 265	*0.0350*
	Altitude	-0.4711	0.0734	41.189	1, 265	***< 0.001***
	Absolute latitude	-0.7813	0.1428	29.944	1, 265	***< 0.001***
	Longitude	0.0587	0.0456	1.654	1, 265	0.1996
	MAT	-0.4480	0.1246	12.920	1, 265	***< 0.001***
	MAP	0.0547	0.0579	0.892	1, 265	0.3458
	NDVI	-0.5408	0.0548	97.321	1, 265	***< 0.001***
	lag1	0.0418	0.0572	0.535	1, 265	0.4653
Allometric *b*	(intercept)	0.1987	0.1173			
	a	-0.7401	0.0710	108.607	1, 265	***< 0.001***
	Class			18.723	5, 265	***< 0.001***
	PCGM1	0.3649	0.1046	12.175	1, 265	***< 0.001***
	PCGM2	0.0650	0.0574	1.281	1, 265	0.2587
	PCGM3	0.2763	0.0650	18.082	1, 265	***< 0.001***
	Altitude	-0.7943	0.0982	65.380	1, 265	***< 0.001***
	Absolute latitude	-1.7736	0.1891	87.959	1, 265	***< 0.001***
	Longitude	0.2231	0.0640	12.167	1, 265	***< 0.001***
	MAT	-1.3434	0.1664	65.209	1, 265	***< 0.001***
	MAP	-0.2622	0.0803	10.658	1, 265	*0.0012*
	NDVI	-0.3911	0.0829	22.277	1, 265	***< 0.001***
	lag1	0.0794	0.0464	2.926	1, 265	0.0883

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

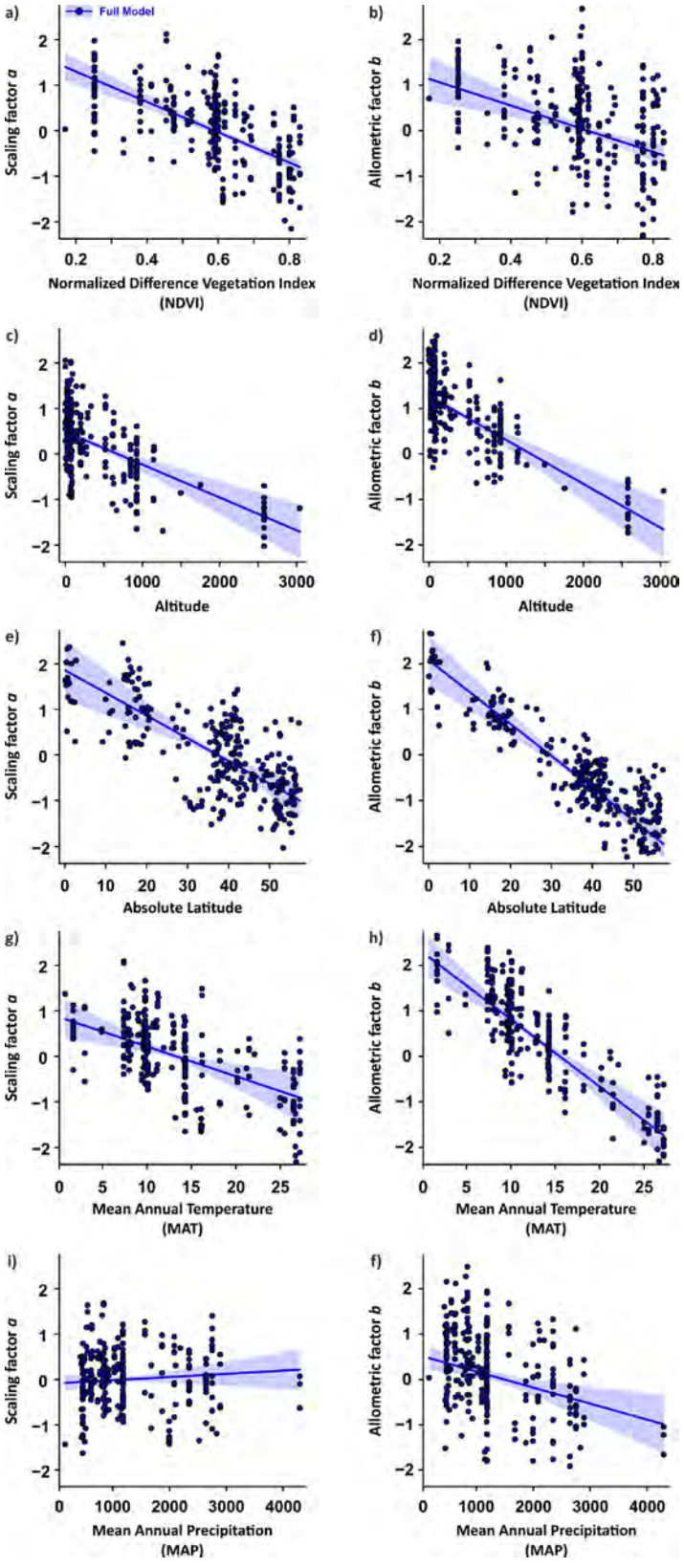

Fig. 3. Relationship between the allometric factors (*a* and *b*) and the NDVI, geographic and climatic variables according to the full model. We show partial effects on the scaling factor *a* of a) NDVI, c) altitude, e) absolute latitude, g) MAT and i) MAP, and on the allometric factor *b* of b) NDVI, d) altitude, f) absolute latitude, h) MAT and f) MAP. Blue areas represent 95% confidence bands.

However, the type of allometry showed a strong significant interaction with NDVI for both the scale factor a ($F_{2,263}$ = 8.612, p = 0.0002) and the allometric factor b ($F_{2,263}$ = 5.041, p = 0.0071). The plot to check for the nature of the interaction shows a negative relationship for both evolutionary and ontogenetic allometries (see Fig. S13a, S13b), with perhaps a less step relationship for the allometric factor *b* in ontogenetic allometry. Static allometries tend to have a positive relationship, however, the sample size is too small and precludes us from reaching any firm conclusions. We had enough sample size to run the full model only for evolutionary allometries, and the results were qualitatively identical to those using the entire data set (see Table S10). For the ontogenetic model we did not have enough sample size to run the full model, but with the shape model alone (with much fewer parameters), the negative relationship between both of the allometric factors and NDVI prevailed (see Table S11). Thus, our results were robust and consistent for evolutionary allometries, and likely for ontogenetic allometries.

After removing 28 data points for which it was not possible to assign the feeding habits (undefined, see Fig. S7) of the arthropods involved, we found no interaction between feeding habits and NDVI for the scaling factor *a* ($F_{3,233}$ = 0.784, p = 0.504) but did find a significant interaction for allometric factor *b* ($F_{3,233}$ = 5.145, p = 0.0018) (see Fig. S14). When grouping the feeding habits by trophic level (high: predators and omnivores and low: decomposers and herbivores;) we found a strong significant interaction which showed how the relationship between allometric factor *b* and NDVI was substantially steeper for lower trophic levels ($F_{1,237}$ = 15.854, p < 0.001) (Fig. 4).

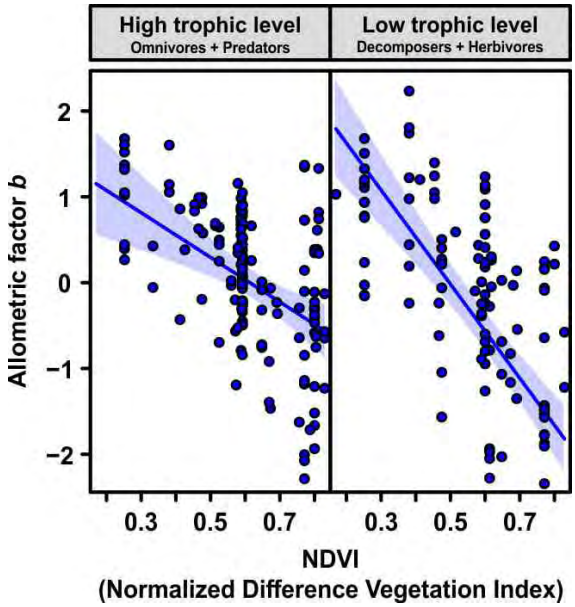

Fig. 4. Interaction between trophic level and NDVI for the allometric factor *b*, according to the full model. Blue areas represent 95% confidence bands.

Discussion

Our results are consistent with the notion that a developmental mechanism can explain the evolution of allometry (Shingleton *et al.,* 2007). Assuming that nutrition can differently shape the reaction norms of body length and mass, this leads to nutrition-dependent static allometries that set the raw material for natural selection. If the above mechanism is plausible, we predicted that globally NDVI should have an effect on both the scaling (*a*) and allometric (*b*) factors. After controlling for a great deal of potentially confounding factors, we indeed found a negative, strong and significant relationship between NDVI and both *a* and *b*. Interpretation of the results are made easier if we assume that lower values for the allometric factors are a sign of faster development entailing lower storage. Thus, the negative relationship between productivity and the allometric factors can be explained because in ecosystems with higher productivity animals would develop faster without acquiring more mass for storage or building other body structures. The ultimate cause could be differences in selection for energy storage across ecosystems differing in productivity. Understanding how the energy available in ecosystems translates into mass-length allometric relationships is equivalent to understanding how food acquisition is stored in the form of body condition. Indeed, a recent body condition index, the Scaled Mass Index (SMI) (Peig & Green, 2009) takes into account the allometric factor of the mass-length relationship, with animals coming from populations with higher allometric factors having relatively better body conditions as they grow in body size. Therefore, our results imply that animal populations in ecosystems with higher amounts of energy available grow with poorer body conditions. This could arise from weaker selection for energy storage in relatively rich environments, where shorter developmental times, and faster growth in length would be favored from natural selection instead. This also provides with an adaptive mechanism to explain why and how mass and length reaction norms would differ (Shingleton *et al.,* 2007), closing the eco-evo-devo loop. Remarkably, we found that for the allometric factor *b*, the effect was stronger for lower trophic levels, which suggests that energy storage is more important in higher trophic levels regardless of primary productivity. This is consistent with the fact that soil predators, such as spiders, are food limited (Wise 1993) and have developed structures for energy storage to overcome periods of food limitation (Grassé, 1949, Foelix 1996), and do even decrease their metabolic rates during periods of starvation (Anderson 1970). We found a significant interaction between the type of allometry and both the scaling and allometric factors. However, the similar visual pattern of the relationships for each type of allometry (see Fig. S13), the relatively small sample sizes for ontogenetic and static allometries, and the consistent pattern of the results between evolutionary allometries and the general pattern with the entire data set, precludes us from making any firm conclusions about whether different selective pressures differently affect each type of allometry.

As for the shape (bauplan) of the animals we have found that they have an influence on both the scaling and allometric factors. PCGM2 (body thickness) and PCGM3 (relative abdomen volume)

positively affect the scaling factor *a*, probably indicating that animals with higher capacity to store nutrients according to their shape do actually have larger storages and slower development. PCGM1 (slenderness with reduction of cephalic area) reflect animals with very elongated bodies and relatively small cephalic parts, such as myriapodes. This axis has a positive effect on both the scaling *a* and allometric factor *b*, probably indicating that for animals with very elongated bodies, growing in length entails a relatively higher investment in high density structures, such as muscle to move all the legs (Grassé, 1949). Finally, the fact that PCGM3 (relative abdomen volume) is positively associated to the allometric factor *b* may reflect again that a shape allowing a relatively larger storage capacity turns into actual larger storages. Similarly, the fact that Arachnida have both higher scaling and allometric factors relatively to all other taxa (see Fig. S12) may be due to their higher storage capacities from their expandable abdomens and storing *caeca* in their guts (Grassé, 1949).

We also found that the geographic and climatic variables contribute substantially to the variability of the scaling and allometric factors. Geographic variables can be considered as surrogates of some unknown environmental variables (Legendre, 1993) which could act as selective factors on the evolution of allometries. Since the main climatic and productivity variables covarian with altitude and latitude where accounted for in the analysis (i.e.: MAT, MAP and NDVI), any geographic pattern should reflect selective pressures other than average climate. Because the short duration of the growing season, arthropods inhabiting high altitudes and latitudes usually grow faster (Yamahira & Conover, 2002; Dmitriew, 2011; Laiolo & Obeso, 2017). Thus, the negative association between both of the allometric coefficients and altitude and absolute latitude could be a consequence of selection favoring faster development or growth in length. In addition, at high altitudes oxygen pressure (PO_2) is much lower (Hoback & Stanley, 2001; Greenlee & Harrison, 2004; Laiolo & Obeso, 2017), which entails a chronic exposure to relatively hypoxic environments affecting several life history traits (Woods & Hill, 2004). Hence, the negative relationship between altitude and both the scaling and allometric factors may be due to a decrease in body densities caused from the empty spaces of an improved respiratory system (e.g.; increase in number of tracheas) which could contribute to compensate the lack of oxygen (Dillon *et al.,* 2005). Lastly, altitudinal and latitudinal variation in the number, strength and diversity of biotic interactions (Dobzhansky, 1950; Pianka, 1966; Moya-Laraño, 2010; Laiolo & Obeso, 2017; Roslin *et al.,* 2017) could potentially explain the negative relationship that we found if biotic interactions would select for energy storage. On the one hand, one may think that this is unlikely because at least from competition and predation, usually faster growth (shorter developmental time) is favored (Dmitriew, 2011), which would have led to the opposite pattern than the one we found. On the other hand, higher predation rates may select for slower growth (extended developmental time) because this will decrease predation risk (Lima & Dill, 1990; reviewed in Dmitriew, 2011). Therefore, we cannot dismiss the possibility that biotic interactions are behind the negative relationships between absolute latitude and latitude and the allometric factors.

Among the climate variables, temperature (MAT) affects negatively both allometric coefficients. Higher temperatures entail higher metabolic rates (Brown *et al.,* 2004), and in general faster paces of life with shorter developmental times, which could explain the negative relationship found, provided that by using multiple regression this is an effect that has been evaluated orthogonally to altitude and absolute latitude. Another potential explanation is that animals in very hot environments can prevent overheating by having longer bodies relative to their mass (higher S/V), which could allow excessive heat to dissipate through the cuticle. This explanation assumes that mass is proportional to body volume and thus to L^3 (Gibbings, 2011), and that volume can still evolve beyond the constraint imposed by the bauplan. Indeed, we found the negative pattern once controlled for the geometric morphometrics PCs. Similarly, in colder environments heat will be retained more efficiently with lower S/V ratios, allowing animals to expand their daily activities.

Although precipitation may absorb in part the proportion of variance of the available energy (i.e.: more rain entails higher productivity), the negative pattern between MAP and the allometric factor *b* could also be indicative of a relaxation in selection for building up structures for desiccation resistance. Arthropods have different cuticle structures to protect themselves from the loss of water by transpiration, such as epicuticle lipids (Hadley, 1982). Also increasing the thickness of the integumental cuticle is a frequent defense against water loss (Vittori & Štruss 2014). Assuming that these structures add extra-weight to the animals, when water availability is high, selection would favor growing (faster) in length instead on investing in these structures. Actually, we used our own extended dataset on mass-length relationships to compare the mass-length ratios of adults vs last instar larvae in beetles measuring between 1 and 10 mm and found that the ratio of body masses between the non-sclerotized larvae and the adults of the same length is 2.5 - 4.5, indicating that at least for beetles, building a water-resistant cuticle can be extremely costly.

In addition to the evolutionary implications of our findings, the ecological consequences may be also important. Lower energy storage in the more productive ecosystems, and the suggested faster development in warmer and wetter environments, as well as at higher altitudes and latitudes, may be a sign that energy is processed differently by the soil fauna in different parts of the globe, and in locations of contrasting climates. The latter could affect studies in which it is assumed that mass-length relationships for the different animal groups are invariant, and that estimates coming from different localitites and climates can be used indistinctly (e.g.: Ehnes *et al*., 2014; Melguizo-Ruiz *et al*., 2016). In addition, these findings may have important consequences for the Energy Equivalence Rule (Damuth, 1981), which states that animal populations in communities use and equal amount of energy regardless of the individual body sizes (in terms of mass), which explains why larger animals have lower abundances and smaller animals have higher abundances. Our evidence that energy is processed differently in different parts of the globe and in different climates, may explain why this rule is far from universal (Ehnes *et al.,* 2014).

Overall, this study provides strong evidence that allometries can evolve. However, regardless of what it has been suggested by previous studies (Maynard-Smith *et al*., 1985; Frankino *et al*., 2005; Egset *et al*., 2012; Pélabon *et al*., 2014), the allometric factor *b* has similar evolutionary potential as the scaling factor *a*. One striking pattern that arises is the consistency of the predictors, which match very closely in significance and the direction of effects for both *a* and *b* factors, strongly suggesting than both allometric factors are subject to the same selective pressures.

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Data accessibility statement

We confirm that, should the manuscript be accepted, the data supporting the results will be archived in Ruiz-Lupión, Dolores; Gómez, José María; Moya-Laraño, Jordi "Mass-length allometry database" 2018. DIGITAL.CSIC http://hdl.handle.net/10261/170286.

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APPENDIX

Appendix S1. Mass-Length allometry

A mass-length or a weight-length allometric relationship is often expressed as a power law equation (Giuseppe *et al.* 2014),

$$M = aL^b \qquad [S1]$$

where M is the body dry weight, L is the body length without appendages, *a* is a scaling (or conversion) factor that moves the value of L^b up or down depending on the measurement units of M and L, and *b* is an exponent (power or allometric factor) which determines the rate of growth or decay of the function. For length measured in millimeters, the scaling factor corresponds to the mass of an animal that is 1mm in length (White & Gould 1965). This equation provides information about to what extent mass is increased or decreased during growth (Muller 2001). Although mass is an unconventional trait to use in allometry, one can see mass-length relationships as integrative allometries, as the scaling of mass with body length could rule the scaling of any other organ with body length, being therefore of central importance. The relationship is isometric if the body length increases at the same rate as body mass and there are no changes in mass per unit length with an increase of length. Because mass in proportional to L^3 and body length to L, isometry would be expected when b = 3. Dividing factor *b* by 3 gives the conventional situation for isometry (b = 1). Following this approach, positive allometry occurs when body mass increases disproportionately more than body length (b > 1) and negative allometry when body length increases disproportionately more than body mass (b < 1). However, b = 3 is expected during isometry only if animals would have a perfect sphere shape, where mass truly increases as L^3 with body length. The expectation for isometry should vary depending on the shape of the animals and this is another reason why we controlled for body shape in our models (see Appendix S5).

The power equation [S1] can be linearized by logarithmic transformation using either base *e* or base 10,

$\text{Ln } M = \text{Ln } a + b\text{Ln } L$ [S2]

$\log_{10} M = \log_{10} a + b\log_{10} L$ [S3]

There are two main reasons for logarithmic transformation. Biologically, log-log transformation places numbers into a geometric domain so that proportional deviations are represented consistently, independent on the scale and units of measurement (Kerkhoff & Enquist 2009). Statistically, it is convenient to transform both axes using logarithms in order to obtain a linear regression. This linearization normalizes the data set and usually reduces heteroscedasticity (O'Hara & Kotze 2010). There are three main types of allometries, ontogenetic, static and evolutionary (Cock 1966; Cheverud 1982; Klingenberg & Zimmermann 1992). Ontogenetic allometries study allocation of mass and length during post-embrionic development and can be studied by comparing different individuals of the same population varying in age or instar. Static allometry compares individuals within the same population and age and evolutionary allometry is when the allometry has been established through evolutionary time, and it is usually studied by comparing populations within species or by comparing different species. The database that we compiled is a mixture of these three types of allometries, being however more abundant the data points for species-based evolutionary allometry.

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Appendix S2. Database

The database contains information about 283 Mass-Length equations scattered across six main groups of soil invertebrate arthropods (Table S1): arachnida (112), chilopoda (14), diplopoda (8), entognatha (37), insecta (102) and isopoda (10). Most arachnida equations were araneae while most insecta equations were coleoptera (Table S2). Two main sources of information were included in our database: bibliographic and field sampling.

Bibliographic review

We searched Web of Science and Google Scholar for articles containing relevant information on ML equations. We used the following keywords: length, weight, length-weight, mass, growth, growth allometry and a diversity of names specific for each of the arthropod groups. The equations came from 45 locations around the world from the Equator to the North Pole and from a great diversity of biomes (Table S3).

Field sampling and laboratory measures

The database also includes 3 equations obtained from individuals captured on 5 beech forests from Asturias (Spain) in October 2011 and between April and October 2012. About 1 to 2 kg of litter was collected and transported in boxes to the laboratory for screening and removal of mesofauna and macrofauna by Berlese-Tullgren funnel (Berlese 1905; Tullgren 1918) for 48 hours, being the animals directly collected in vials containing 100% EtOH. In total 58 Entomobryomorpha springtails and 30 Lithobiomorpha centipedes were extracted from the Las Ubiñas-La Mesa Natural Park (43.0895°N, 6.0447°W and 43.0978°N, 5.9922°W), Ponga Natural Park (43.2037°N, 5.1390°W) and Integral Reserve of Muniellos (43.0376°N, 6.6767°W), and 60 Geophilomorpha centipedes from the Picos de Europa National Park (43.2366°N, 4.8230°W). For the larger taxa (Centipedes) a Mettler Toledo AB135-S/FACT electronic balance (precision of 0.01 mg) was used, and a Mettler Toledo XP26 Delta Range Excellence Plus electronic ultrabalance (precision of 0.1 µg) was used to weight the springtails. All specimens were individually dried in an oven at 60 °C for 48 hours and their dry mass individually estimated in the above balances. For the smaller Collembola, however, five individuals of approximate the same length were weighed together and the overall mass divided by 5 (with 3 repetitions per measurement). A mean body mass was then calculated for each length category (0.77 ± 0.05 mm - 17.0 ± 0.82 µg; 0.88 ± 0.03 mm - 13.7 ± 1.25 µg; 0.97 ± 0.03 mm - 19.7 ± 1.25 µg; 1.11 ± 0.01 mm - 44.3 ± 1.70 µg; 1.16 ± 0.03 - 52.7 ± 1.25 µg and 1.28 ± 0.04 mm - 35.3 ± 1.25 µg). Body length was measured from the apical part (head) to the end of the body (dismissing appendages), using either a Leica MZ 12.5 or Zeiss Stemi DV4 stereomicroscopes at a magnifying size of 8-32x depending on the group (minimum precission: nearest 0.1 mm).

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Appendix S3. Database standardization

In order to compare the estimates of *a* and *b* factors across studies, we standardized the data following a two-step process. In the first step we converted the equations into power functions and in the second we rescaled the scaling factor *a* to the corresponding value in a power function [S1] (Appendix S1).

Conversion into power function

Four types of equations were included in database (Table S4): I) Simple power functions, II) logarithmically linearized power functions, III) other more sophisticated models, IV) the raw data or the original model. To obtain the scaling and allometric factors, we performed different transformation for each of the four types of equations (Table S4). We checked the error (calculated by subtracting one from the coefficient of determination, $1\text{-}R^2$) of performing the transformations for the Type III equations and in all cases it proved to be very small (Fig. S1, Table S5).

Standardization of the scaling factor a

We rescaled *a* to common units by means of three sequential steps. First, we converted all length measures into mm. Second, we converted all mass measurements into mg. Third, we converted the equations that included wet (fresh) instead of wet mass into dry masses. To do this latter step, we assumed that the total body water of terrestrial arthropods was roughly 70%, as averaged among studies in Table 2.1 of Hadley (1994). Note that this approach also assumes that water body content proportions do not change with body mass (e.g.: perfect isometry) and thus that on average it does not affect Mass-Length allometric relationships.

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Appendix S4. Model I vs Model II regression

For fitting allometric equations of log-transformed data, if the X variable is assumed to be measured with as much error as Y, then Model II (e.g.: Major Axis or Standardized Major Axis) regression should be used instead of Model I (OLS), particularly if the aim of the study is to estimate the value of the functional relationship between X and Y. Otherwise the value of the allometric factor *b* is underestimated (LaBarbera 1989; Warton *et al*. 2006). However, when the purpose of fitting the equation is to predict Y from X, OLS should be used instead (Legendre & Legendre 1998). Since the purpose of the available Mass-Length equations is to estimate biomass from body lengths across arthropod groups, most authors have appropriately used OLS or non-linear regression to perform the fits. In order to test hypotheses around the allometric exponent, as it is our case here, we need

to consider the fact that these OLS estimates are likely underestimates of b. We therefore assumed that the magnitude of the underestimation from OLS was similar across taxa and localities, thus not affecting our results.

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Appendix S5. Shape analysis

Because allometric scaling could potentially differ among body bauplans, we included the shape of each taxonomic group in all analyses as obtained from geometric morphometrics. We downloaded 12 photographs in dorsal view for each of the 51 families and 13 orders of soil arthropods that were included in the equations retrieved from the original literature (Table S1). We used 24 photographs in the case of acari, because the level of taxonomic accuracy in the articles was usually low (the infraorder acari is what many studies provided as the level of taxonomical affiliation) and this group is morphologically highly variable. Because it was not possible to find 12 photographs in dorsal view for the springtail family tullbergiidae from the Southern Hemisphere, the set was completed with photographs of the family onychiuridae, since both belong to the same superfamily onychiuroidea. Another difficulty was to find photographs of elongated myriapods (geophilomorpha and scolopendromorpha) and scorpionida in dorsal view that were sufficiently straighten for geometric morphometrics. We therefore modified the photographs using the program CorelDRAW X7, for which each individual photograph was cut into segments, and each tergite or group of tergita were cut and pasted following the straight line delimiting the sagittal plane (Fig. S2).

Geometric morphometrics

Geometric morphometrics is a tool to summarize the shape of organisms by using landmarks points with which all the information about size, position and orientation is adjusted using a procrustes fit. As a result, one obtains useful information about the shape of the animal, which can then be further subjected to interpretation and analysis.

For shape analyses using geometric morphometrics by means of landmark points we used a four-step procedure. In the first step we took the photographs for each taxonomic group (Fig. S3a) and marked 4 landmark points following the arthropod tagmosis homologies described by Fusco & Minelli (2013) plus 2 pseudo-landmarks than did not necessarily follow tagmosis homologies but that we included during shape matching to be sure that we grasped most of the variance in shape (e.g.:

include the widest parts of all bauplans for analyses). For landmark labeling we used the package tpsDig2 2.25 (Rohlf 2010). We marked one point at the apical part of the body (without counting the appendages) in the tip of the "head", another two points, one on each side of the sagittal plane, in the homologous junction of what it would be the thorax-abdomen junction in insects as follows: for insecta other than ants the pronotum-abdomen junction, for ants the petiolo-gaster junction, for arachnida the prosoma-opisthosoma junction, and finally the head-trunk junction for chilopoda, diplopoda and isopoda. We also added two pseudo-landmarks (i.e.: which do not necessarily correspond to homologous anatomical parts) on each side of the widest part of the posterior part of the body: abdomen, gaster, opisthosoma or trunk. Finally, a last landmark was added to the posterior-most part of the body (Fig. S4). The two pseudo-landmarks were added to increase the probability of grasping the form of body condition typical of each taxonomic group, as some arthropod groups have non-hardened cuticles which expand with food acquisition and visibly change in shape as they increase in mass (Moya-Laraño *et al.* 2008) (Fig. S3b). Second, we performed a procrustes fit to obtain new shape coordinates for each photograph, consisting in traslation, rotation and scaling of the shapes to minimize the sum of squared deviations between landmarks with software MorphoJ 2.0 (Fig. S3.c). Third, we obtained the procustes coordinates for each taxon using a consensus figure and used these coordinates to perform a principal component analysis (done used the R package "geomorph") (Fig. S3d). Finally, since the first three components (PCGMs) explained 96.2% of the shape variance, the scores of these 3 were included in the database as shape covariates (Fig. S3e). The results show that the first component is associated with slenderness with reduction of cephalic area, the second represents the body thickness, and the last component explains the relative abdomen volume (Fig. S5). Note that the second axis will be a proxy of body condition, as the taxa with wider abdomens could be able to store higher amounts of nutrients (e.g.: spiders). Other differences in shape across taxa are also very patent: mites, spiders, beetles, collembola and myriapods. Finally, we obtained the PCGM scores for the 51 families and 13 orders. The database contains 308 equations resolved either at the taxonomic level of class, order or family. For the equations at a given taxonomic level we averaged the PCGM scores of the shapes beloging to photographs from their immediate lower taxonomic levels appearing in the database. In Fig. S6 we summarize the procedure followed to get the shape of our focal groups of arthropods from the photographs.

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Appendix S6. Feeding habits

We assigned feeding habits following the expertise criteria of JML for arachnida and JMG about coleoptera. The feeding habits for the rest of the taxa were searched in the literature for the lowest possible taxonomic level. We used Wikipedia as a baseline for searching and then checked for the literature sources cited therein. The study includes a substantial amount of variation in feeding habits among arthropods (Fig. S7). All spiders were predators, while the beetles included taxa with very different trophic habits (predators, omnivores, herbivores, decomposers or undefined if the details provided on the taxonomic level were poor and the group could include groups with different feeding habits).

Appendix S7. Type of mass-length allometric relationship

The data also included a categorization of the 5 main sources of data used for allometric fits, which correspond to either static, ontogenetic or evolutionary allometries (Klingenberg 1998; Reiss 1989). Static allometries are equations including only juveniles of the same species (intraspecific juvenile), only adults of the same species (intraspecific adult). Ontogenetic allometric are equations obtained from different instars of the same species (intraspecific multi-instar). and evolutionary allometries included equations from only adults or differente instars from different species (interspecific adult and interspecific multi-instar) (Fig. S8a, Fig. S8b).

References

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Appendix S8. Details on statistical analysis

Geometric relationship between the scaling factor a and the allometric factor b

As demonstrated by White & Gould (1965), depending on the scale of measurement, one may expect a negative relationship between the scaling factor *a* and the allometric factor *b* due to geometric reasons alone. If we consider two log-transformed (linearized) allometric equations, depending on where the point of intersection between these two lines occur, equal or above Ln length = 1 the relationship changes. If the intersection is equal to Ln length = 1 the value of allometric factor b_1 of line 1 is higher than the allometric factor b_2 of line 2 and the value of scaling factor *a* is the same for lines 1 and 2 (Fig. S9. Case 1). However, if the intersection is smaller or above Ln length = 1 this relationship is different. When the intersection is above Ln length = 1, there is an inverse relationship between the scaling factor *a* and the allometric factor *b* between the two lines (Fig. S9. Case 2). Finally, when the intersection is below Ln length = 1, there is a positive relationship between the scaling factor *a* and the allometric factor *b* of line 1 and line 2 (Fig. S9. Case 3). Since in our data there was a strong negative relationship between the two coefficients, we included them as reciprocal covariates. This allowed us testing for an effect on variables on *a* as if all equations had

identical *b* and *viceversa*, test for the effect of variables on *b* as if all equations had indentical elevations. Thus, this procedure allowed for testing the evolution of allometries *sensu stricto*.

Regression Models

To evaluate the relationship between allometry (*a* and *b* factors) and the Normalized Difference Vegetation Index (NDVI) we compared 4 general linear models including different types of covariates. We constructed a Base model, a Shape model, a Geographic model and a Full model. The Base models included the reciprocal factor *b,* when we analyzed the scaling factor *a* or *a,* when we analyzed the allometric factor *b* and the taxonomic affiliation (class). The Shape models included the previous variables plus shape PCs (PCGM1, PCGM2 and PCGM3). The Geographic models included additionally the previous variables plus the geographic factors (altitude, absolute latitude and longitude) (Table S7, Table S8), and the Full modesl included the previous variables and the climate factors (MAT and MAP) (Table 2). In order to test the better model, we compared the AIC values of Base model, Shape model, Geographic model and Full model for *a* and *b* (Table 1).

Dealing with spatial autocorrelation

In general, spatial autocorrelation was low and barely significant (Fig. S10, Fig. S11). The slight autocorrelation found for *a* and *b*, was corrected by including the residuals of the model lagged one position (Bivand *et al*. 2013) relative to longitude, which was sufficient to bring spatial autocorrelation down to negligible values (Fig. S10, Fig. S11). To that end, we sorted the dataset by longitude, ran the multiple regression model, obtained the residuals and lagged them one position down to the dataset. After removing the case that necessarily remained without a residual value after lagging, we used this new dataset to re-run the model with this new residual lagged variable as covariate. To test and plot spatial autocorrelation we used the function “spline.correlog” (Bjornstad & Falck 2001) within the R library “ncf” (Bjornstad 2018). The function “spline.correlog” computes and plots the index of autocorrelation (Moran’s I or Geary's) on distance classes from a set of spatial coordinates and corresponding z values to obtain spatial correlograms. To slide the dataset for one lag position we used the function “slide” in library “DataCombine” (Ganrud 2016).

References

Bivand, R.S., Pebesma, E.J., & Gómez-Rubio, V. (2013). *Applied Spatial Data Analysis with R*. Springer, 378 pp.

Bjonstad, O.N. (2018). ncf: Spatial Covariance Functions. R package versión 1.2-5. Available at: https://CRAN.R-project.org/package=ncf. Last accessed: 10/09/2018.

Bjornstad, O.N., & Falck, W. (2001). Nonparametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics*, 8, 53-70.

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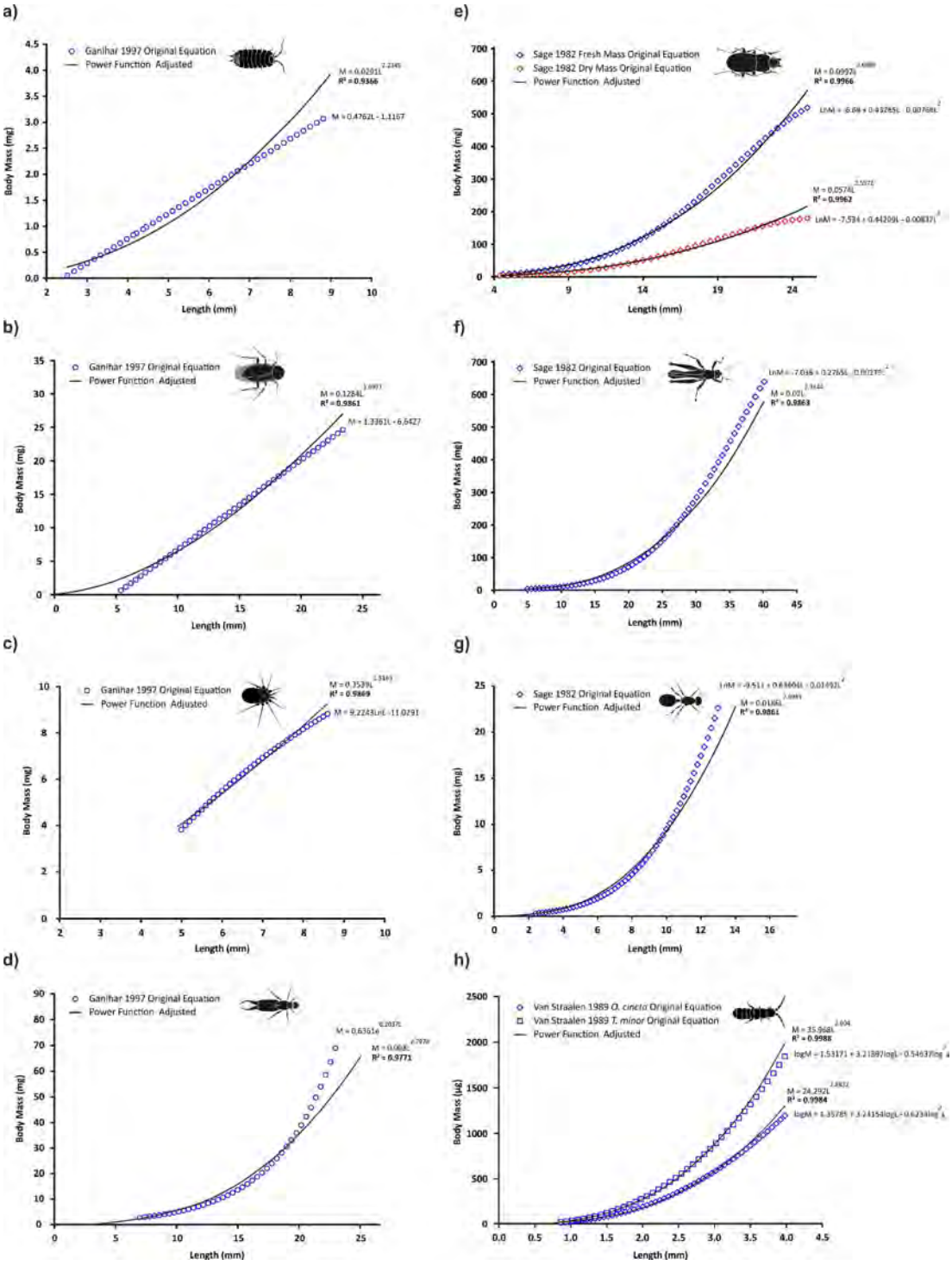


Fig. S1. Reconstructed potential equations from the different original equations adjusted by some authors (Table S4, Table S5). a) Ganihar 1997, equation type 4 for Isopoda, b) Ganihar 1997, equation type 4 for Dyctioptera (i.e.: Blattodea), c) Ganihar 1997, equation type 5 for Opilionida, d) Ganihar 1997, equation type 6 for Dermaptera, e) Sage 1982, equation type 7 for Coleoptera (dry and fresh mass), f) Sage 1982, equation type 7 for Orthoptera, g) Sage 1982, equation type 7 for Formicidae and h) Van Straalen 1989, equation type 9 for Collembola (*Orchesella cincta* and *Tomocerus minor*).

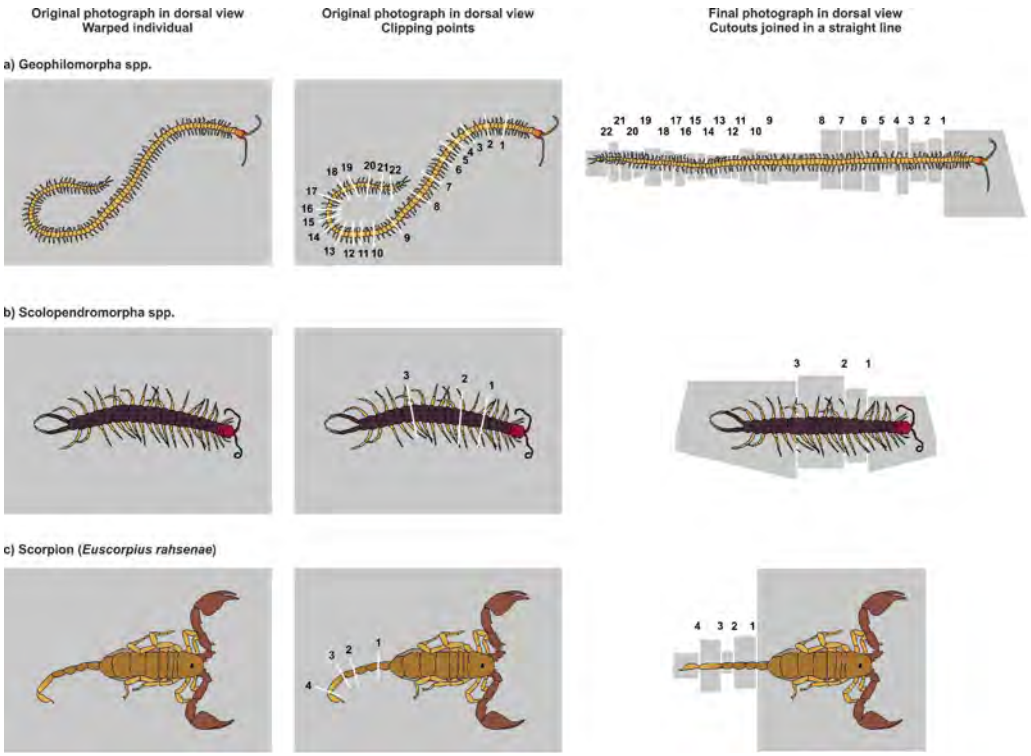
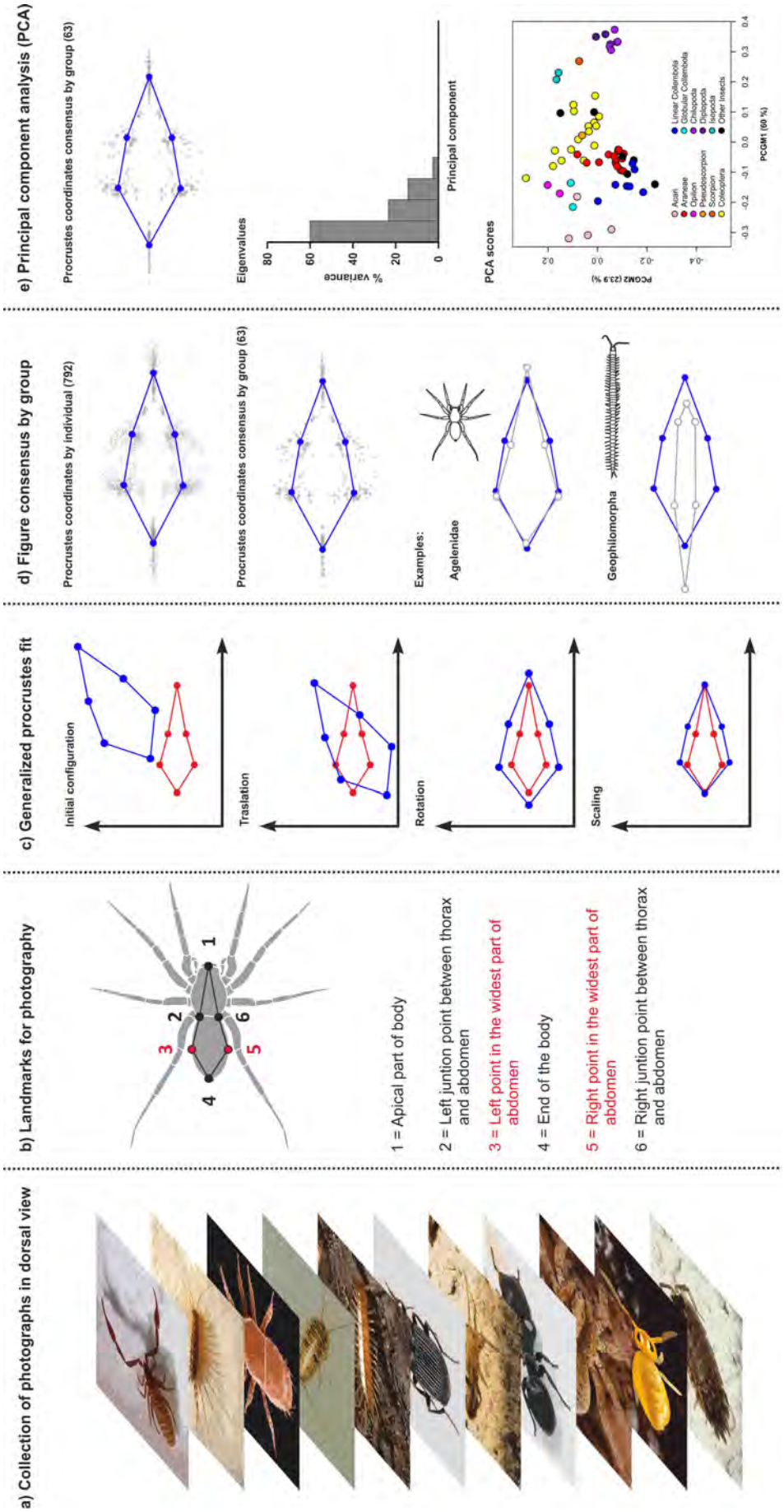


Fig. S2. Original photographs of warped specimens of myriapods (whole body) and scorpion (metasoma and telson) in dorsal view trimmed into segments (clipping points). Each segment corresponds to a tergite or group of tergita (each of the plates that cover the back of an arthropod); the segments were pasted following the straight line delimiting the sagittal plane in order to perform the shape analysis. a) Geophilomorpha (unidentified species), b) Scolopendromorpha (unidentified species), and c) Scorpion (*Euscorpius rahsenae*).

Fig. S3. Workflow (steps a-e) showing the shape analysis of soil arthropods using geometric morphometrics. a) Twelve photographs in dorsal view for each family or order used in the analyses were downloaded from the web, b) for each photograph we located four landmarks (black points 1, 2, 4 and 6) two pseudo-landmarks (red points 3 and 5), c) we performed a generalized procrustes fit to compare the shapes of different groups. We exemplified the procrustes analysis for two simple configurations, the red configuration represents the average shape of all evaluated shapes and the blue configuration is an example of the shape of an individual. To minimize the sum of the squared deviations between landmarks of red and blue configurations, the procrustes analysis follows three steps: 1) Translation: both configurations have a common centroid, 2) rotation: the blue configuration is rotated to match the position of the six landmarks and pseudo-landmarks between two configurations, and 3) scaling: the blue configuration are adjusted by reduction such that the error is minimized, d) after the procrustes analysis we obtained the procrustes coordinates of each group (we show the example for the spider family Agelenidae and the order Geophilomorpha). We averaged the individual procrustes coordinates within each group of arthropods in order to obtain their consensus shape, e) the consensus were included in a principal component analysis (PCA) to obtain the PC scores for each significant axis according to the eigenvalues (% variance explained).

Continued →


a) Collection of photographs in dorsal view
b) Landmarks for photography
1 = Apical part of body
2 = Left juntion point between thorax and abdomen
3 = Left point in the widest part of abdomen
4 = End of the body
5 = Right point in the widest part of abdomen
6 = Right juntion point between thorax and abdomen
c) Generalized procrustes fit
Initial configuration
Traslation
Rotation
Scaling
d) Figure consensus by group
Procrustes coordinates by individual (792)
Procrustes coordinates consensus by group (63)
Examples:
Agelenidae
Geophilomorpha
e) Principal component analysis (PCA)
Procrustes coordinates consensus by group (63)
Eigenvalues
% variance
Principal component
PCA scores
PCGM2 (23.9 %)
PCGM1 (69 %)
Linear Collembola
Globular Collembola
Chilopoda
Diplopoda
Isopoda
Other Insects
Acari
Araneae
Opilion
Pseudoscorpion
Blattodea
Coleoptera

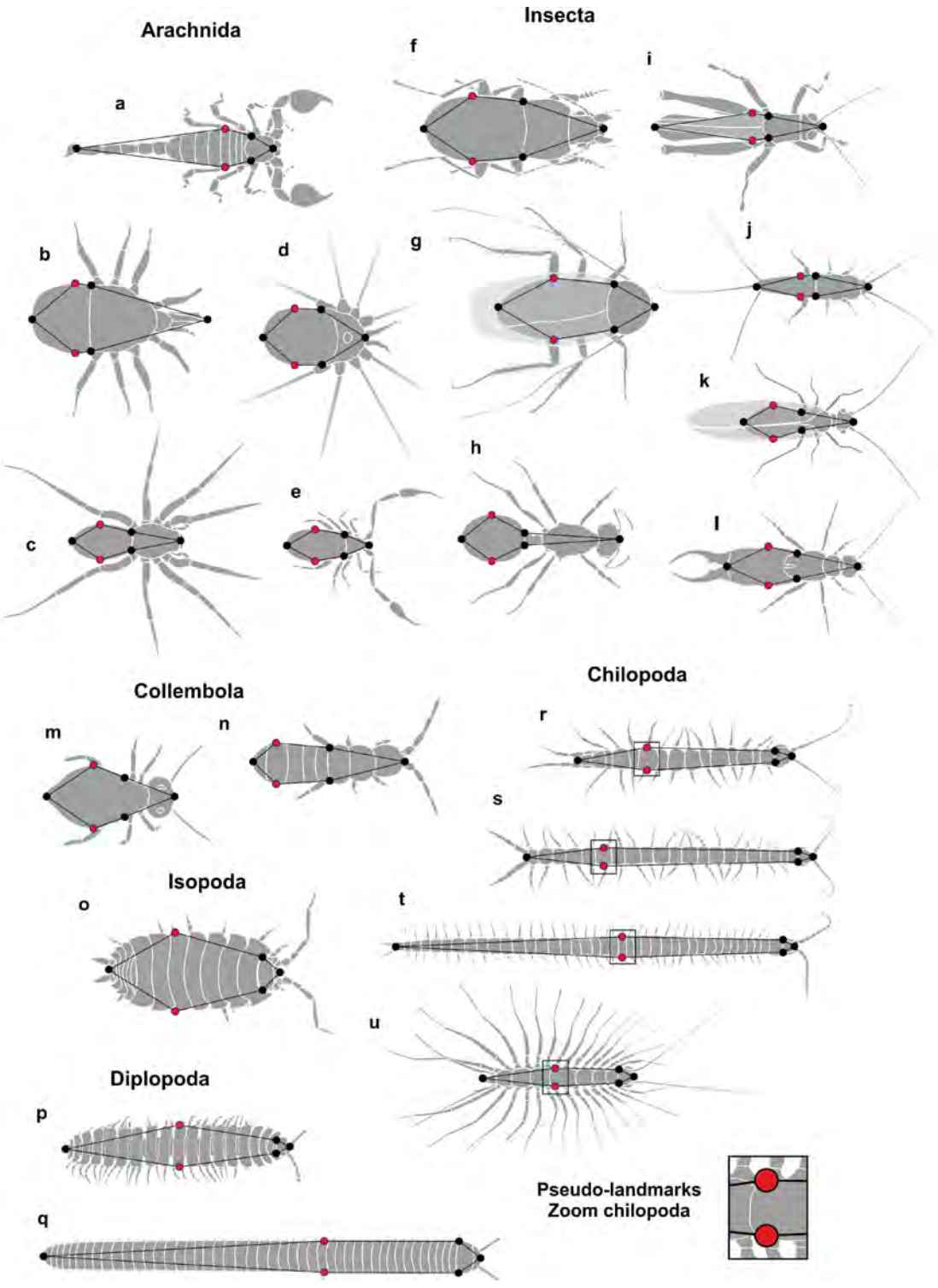


Fig. S4. Location of the landmarks (black) and pseudo-landmarks (red) for each taxonomic group. Arachnida: a) scorpionida, b) acari, c) araneae, d) opilionida and e) pseudoscorpionida; insecta: f) coleoptera, g) blattodea, h) hymenoptera fFormicidae), i) orthoptera, j) thysanura, k) psocoptera and l) dermaptera; collembola: m) globular collembola and n) lineal collembola; o) isopoda; diplopoda: p) polydesmida and q) julidae; chilopoda: r) lithobiomorpha, s) scolopendromorpha, t) geophilomorpha, and u) scutigeromorpha.

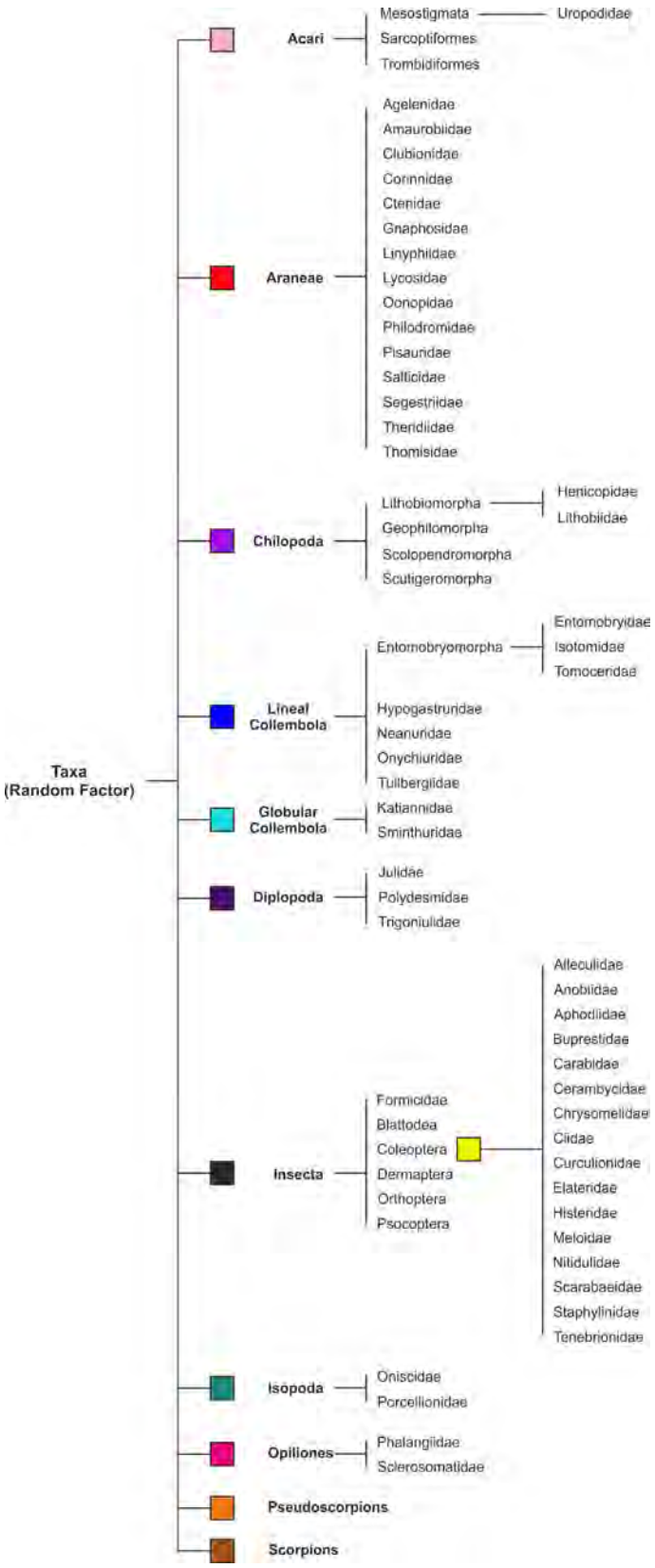


Fig. S5. Procedure of shape analysis for each of the 51 families and 13 orders of arthropods included in our set of equations. The PCGM scores were averaged at each taxonomic level appearing in bold using the data (photographs) from their lower taxonomic level. For example, we obtained the PCGM scores for each of the 16 families of coleoptera and we then obtained a mean value for coleoptera by averaging the family values.

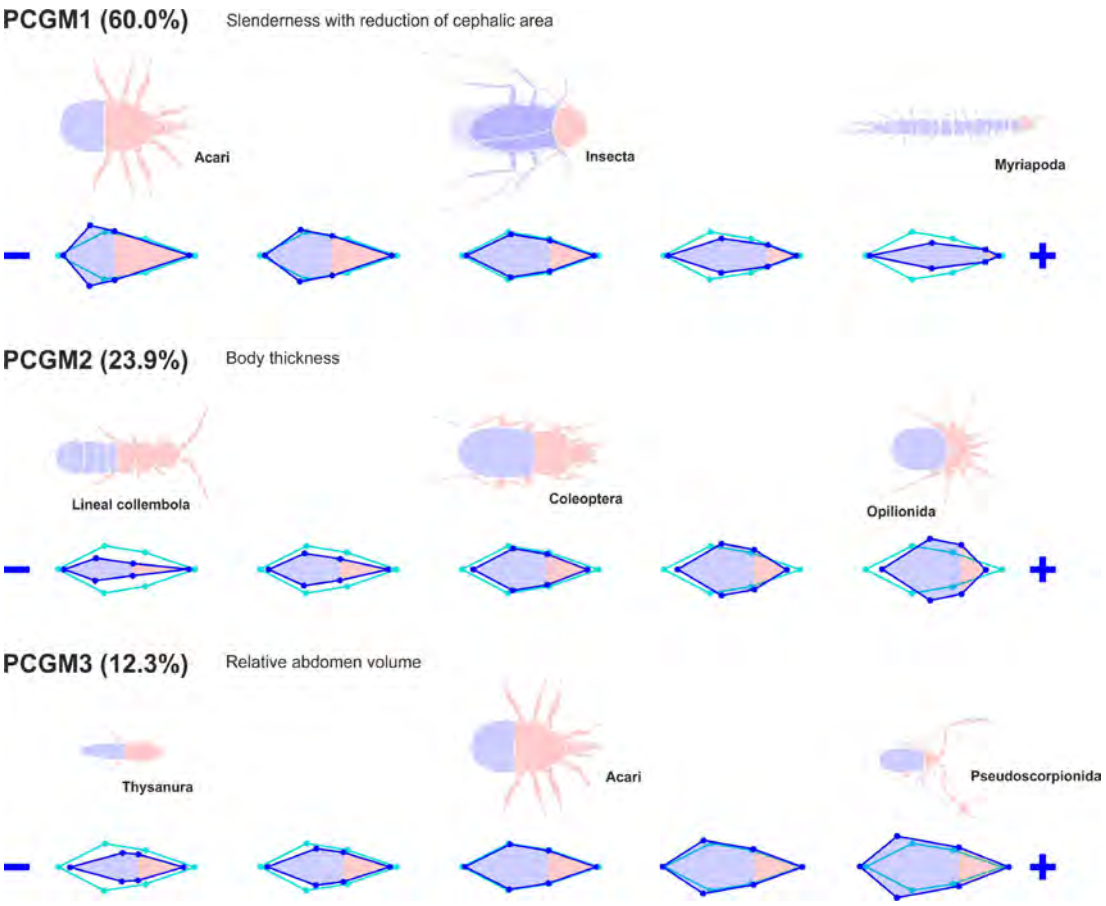


Fig. S6. Three major Principal Components obtained after the geometric morphometric analyses. The consensus shape is shown in light blue and the changes in shape caused by each axis in dark blue. Some representative arthropods for negative, intermediate and positive values of each axis are also shown. The first principal component (PCGM1) represents the slenderness with reduction of cephalic area. PCGM2 represents the body thickness. PCGM3 represents the relative abdomen volume.

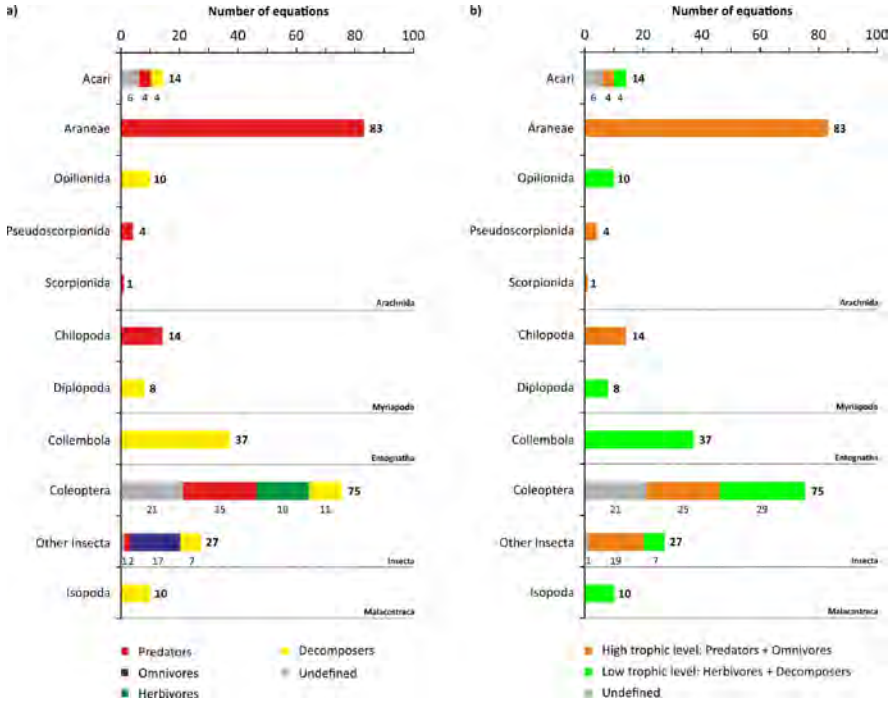


Fig. S7. Number of equations for each arthropod taxa and type of feeding habits. a) Classification depending on type of feeding habits, and b) classification depending on the trophic level to which they belong according to their feeding habits.

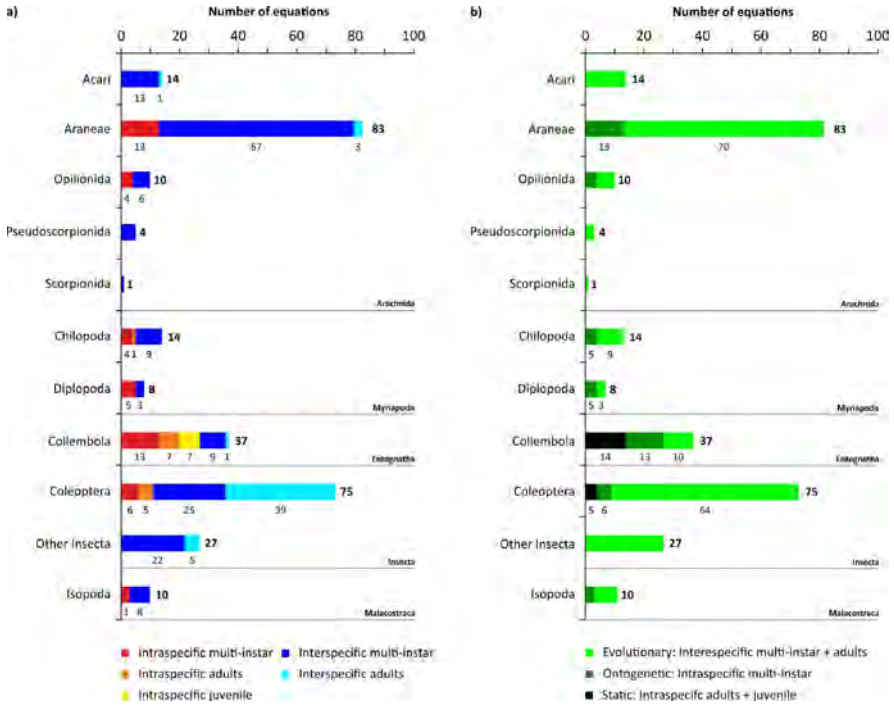


Fig. S8 Number of equations for each arthropod taxa and type of allometry. a) Classification depending on whether equations were fitted within *vs.* among species, or within *vs.* among instars, and b) classification depending on whether allometries were evolutionary, ontogenetic or static.

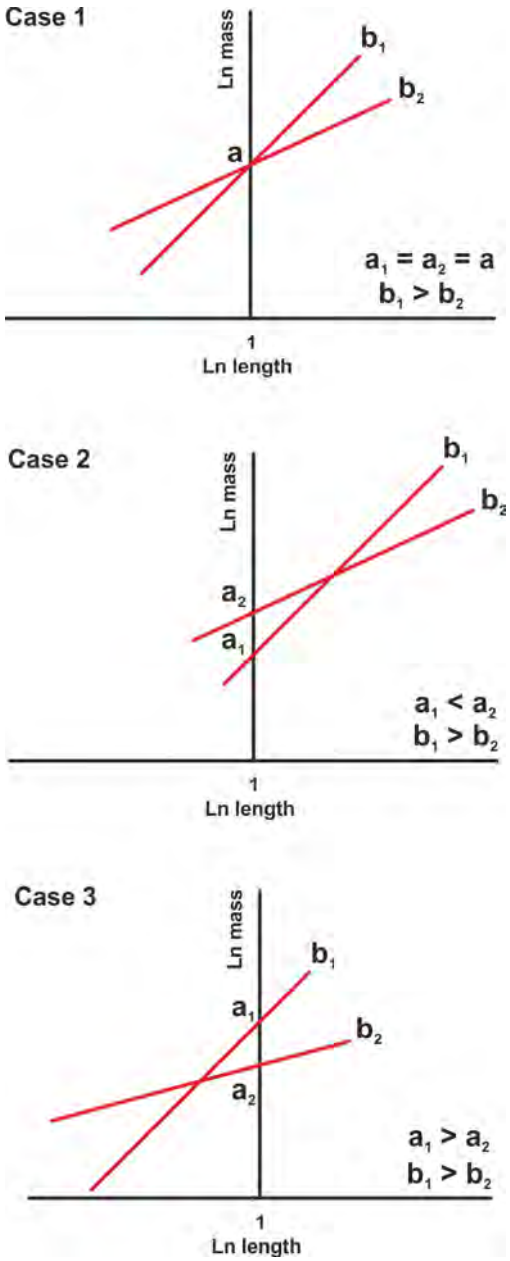


Fig. S9. Relationship between scaling and allometric factors as applied to mass-length equations. a) There is a relationship between scaling factor *a* and allometric factor *b* that depends on the cross-linking position of the allometric equations 1 and 2. Case 1: the equation 1 and 2 intersect when Ln length is equal to 1, the value of allometric factor b1 is higher than b2 and the value of a1 and a2 is the same. Case 2: the equation 1 and 2 intersect when Ln length is higher than 1, the value of allometric factor b1 is higher than b2 and the value of a1 is lower than a2 and a negative correlation between the factors arises. Case 3: the equation 1 and 2 intersect when Ln length is lower than 1, the value of allometric factor b1 is higher than b2 and the value of a1 is higher than a2 (positive correlation between the factors). Modified from Fig. 1 in White & Gould 1965.

References

White, J.F., & Gould, S.J. (1965). Interpretation of allometric equations. *American Naturalist*, 99 (904), 5-18.

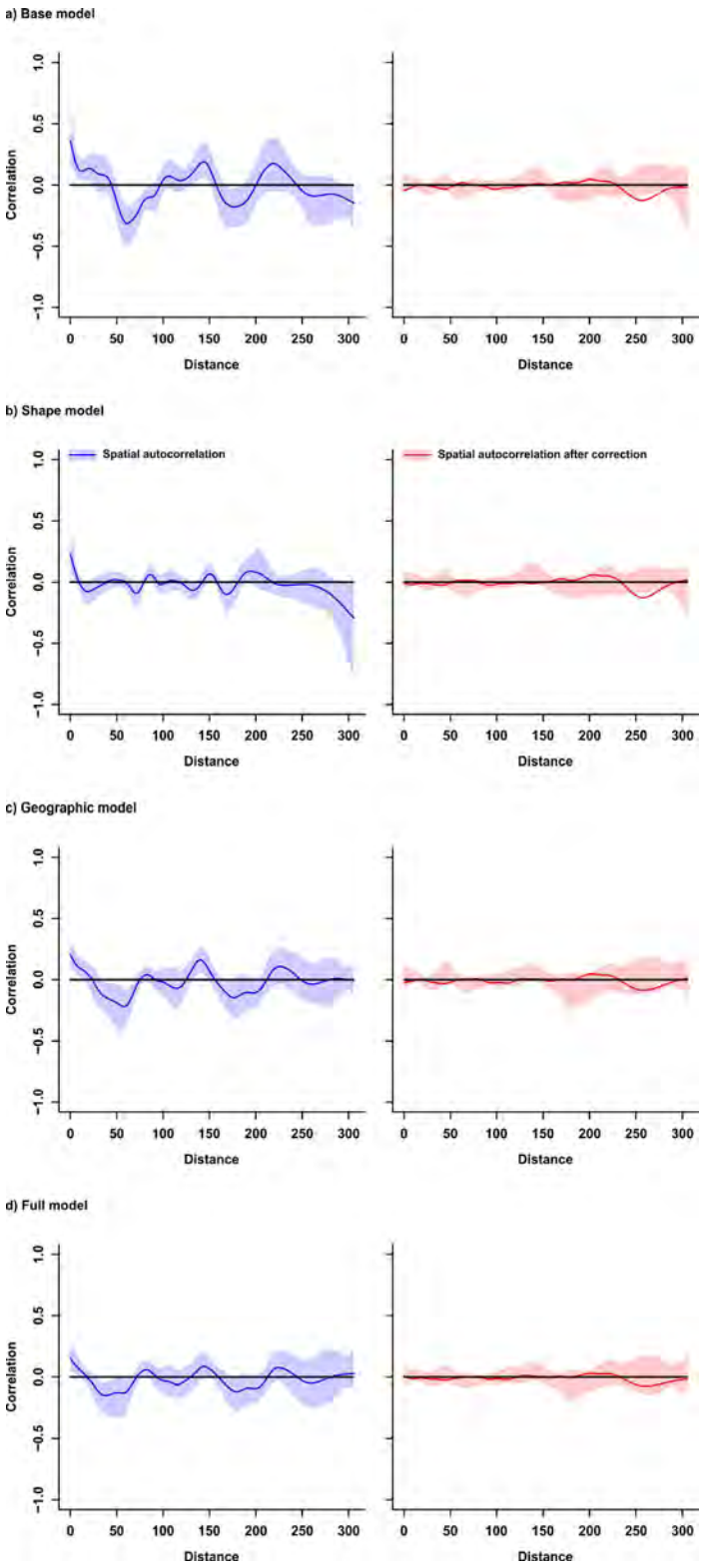


Fig. S10. Spatial autocorrelation for the models on the scaling factor *a*. Depicted are residuals of models before (blue, left) and after (red, right) correction. a) Base model including the reciprocal factor *b*, class and NDVI as covariates, b) Shape model including the previous covariates plus shape PCs (PCGM1, PCGM2 and PCGM3), c) Geographic model including the variables in the model b plus absolute latitude, longitude and altitude, and d) Full model including the variables in the model in c plus MAT and MAP. The red models include lag1 as a covariate. Blue and red areas represent 95% confidence bands.

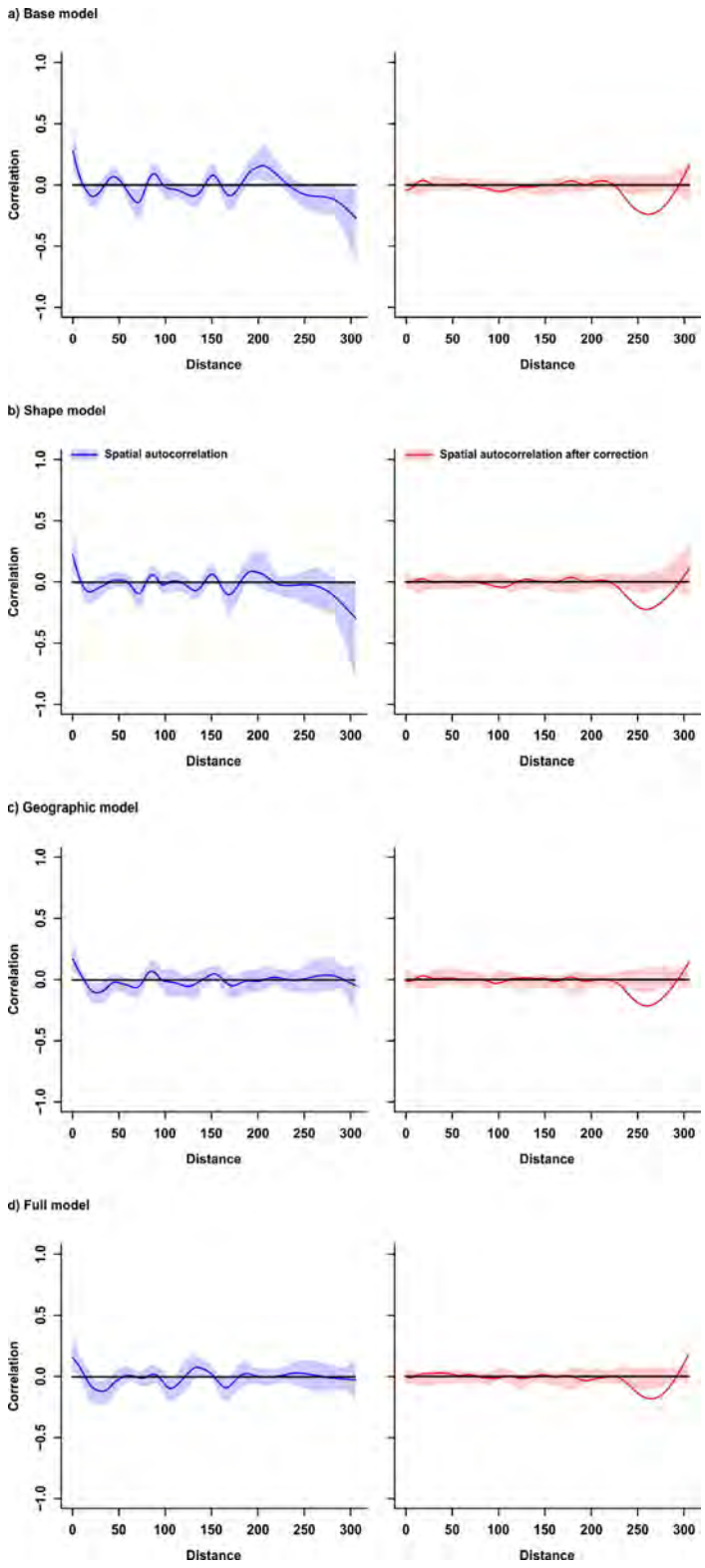


Fig. S11. Spatial autocorrelation for the models on the allometric factor *b*. Depicted are residuals of models before (blue, left) and after (red, right) correction. a) Base model including the reciprocal factor *a*, class and NDVI as covariates, b) Shape model including the previous covariates plus shape PCs (PCGM1, PCGM2 and PCGM3), c) Geographic model including the variables in the model b plus absolute latitude, longitude and altitude, and d) Full model including the variables in the model in c plus MAT and MAP. The red models include lag1 as a covariate. Blue and red areas represent 95% confidence bands.

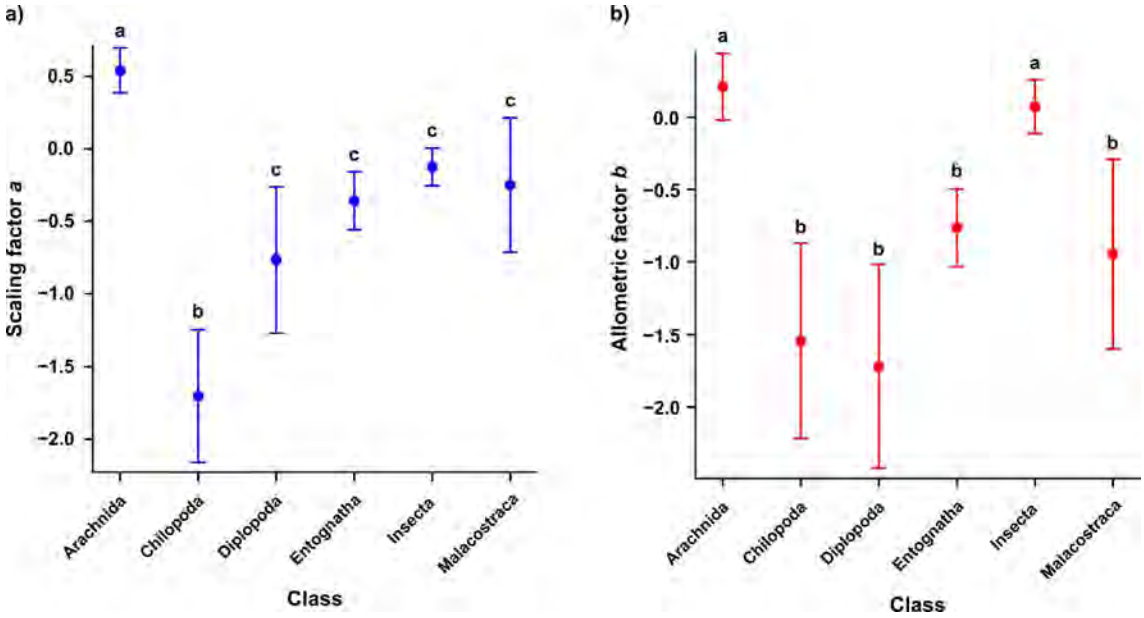


Fig. S12. Pairwise post-hoc analysis (Tukey tests in package "multcomp") among taxonomic classes. For a) the scaling factor *a,* and b) allometric factor *b*. Both analysis were performed with the Full model, which included the shape PCs.

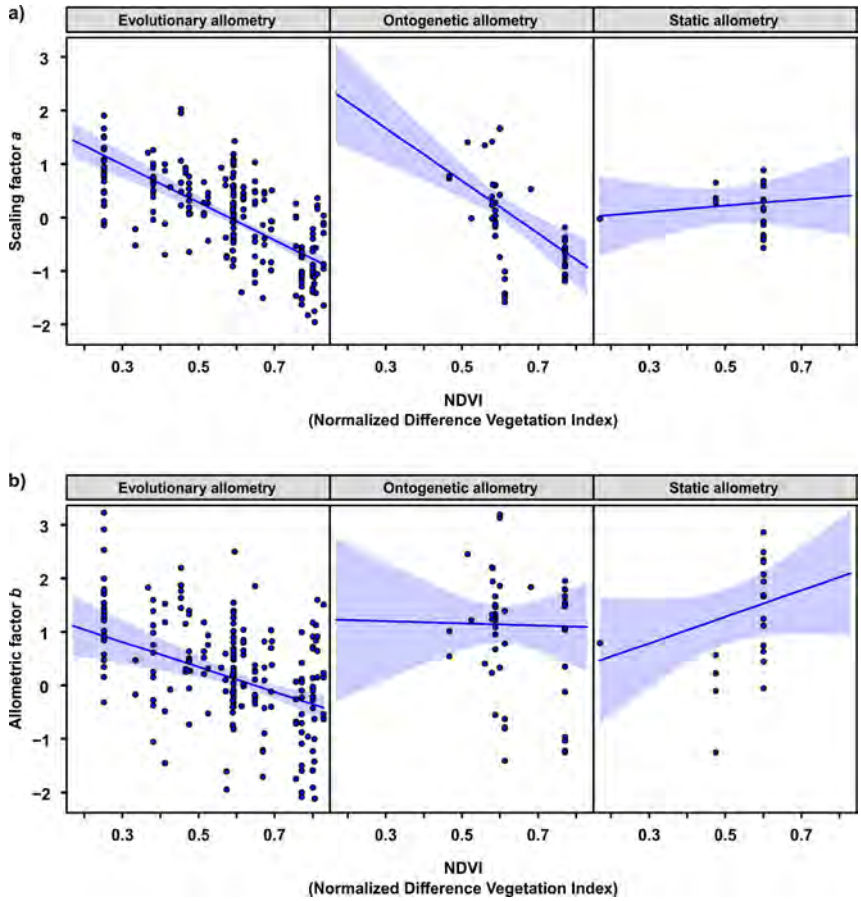


Fig. S13. Interaction between type of allometry and NDVI. For a) the scaling factor *a,* and b) allometric factor *b*. Both analysis were performed by expanding the Full model. Blue areas represent 95% confidence bands.

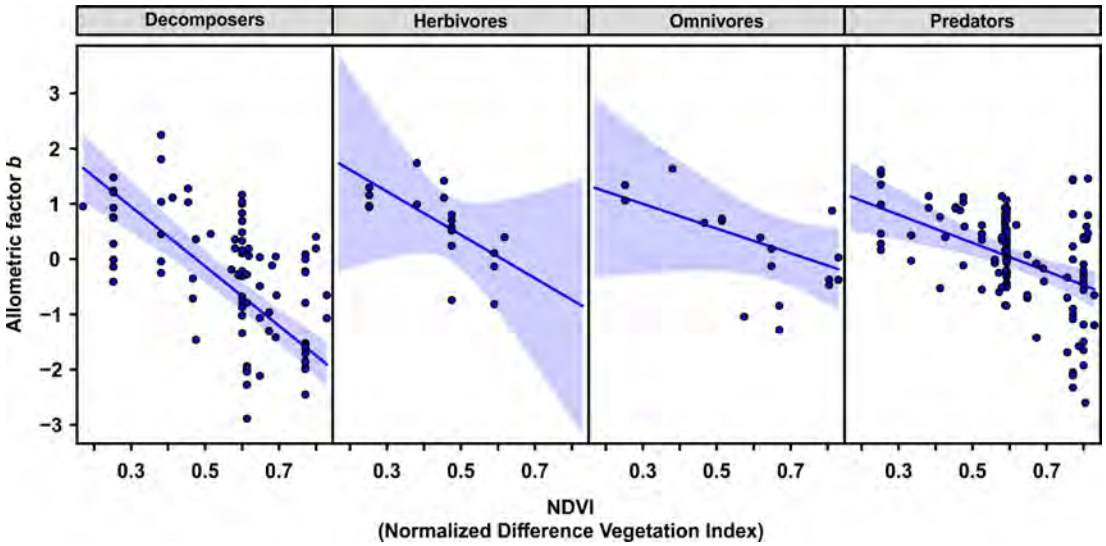


Fig. S14. Interaction between type of feeding habits and NDVI for allometric factor *b*. Interaction between four types: predators, omnivores, herbivores and detritivores. The analysis was performed by expanding the Full model. Blue areas represent 95% confidence bands.

Table S1: Database used to evaluate scaling factor *a* and allometric factor *b*.

Code	Class	a	b	SE a	SE b	NLS a	NLS b	OLS a	OLS b	Normal a	Normal b	Normal a2	Normal b2	Original equation	Site	Reference
1	Arachnida	0.0530	2.4940	0.2560	0.2970	0.0530	2.4940	0.0530	2.4940	0.0438	2.4997	0.7786	-0.5265	2	11	Hódar 1996
2	Arachnida	0.1423	3.0930	---	---	0.1522	3.4517	0.1423	3.0930	0.0694	3.0794	0.7778	-0.1341	9	20	LeBrun 1971
3	Arachnida	0.0146	2.3300	---	---	0.0146	2.3300	0.0146	2.3300	0.0125	2.3538	-0.3667	-0.8727	2	23	McLaughlin *et al.* 2010
4	Arachnida	0.0393	2.7110	0.0104	0.0333	0.0393	2.7110	0.0393	2.7110	0.0362	2.7110	0.4999	-0.0280	3	24	Mercer *et al.* 2001
5	Arachnida	0.0177	2.2180	---	---	0.1267	5.7245	0.0104	1.9092	0.0053	2.0517	-0.3178	-1.3061	9	25	Newton & Proctor 2013
6	Arachnida	0.0397	2.7610	0.1710	0.3090	0.0397	2.7610	0.0397	2.7610	0.0364	2.7610	0.4850	0.0512	2	30	Rogers *et al.* 1977
7	Arachnida	0.0348	2.8570	0.0198	0.1067	0.0348	2.8570	0.0348	2.8570	0.0331	2.8566	0.3847	0.2793	3	24	Mercer *et al.* 2001
8	Arachnida	0.0353	2.7400	---	---	0.0340	2.5697	0.0353	2.7400	0.0335	2.7400	0.3947	0.0120	9	25	Newton & Proctor 2013
9	Arachnida	0.0137	1.7000	---	---	0.0137	1.7000	0.0137	1.7000	0.0111	1.9356	-0.3951	-1.7927	2	23	McLaughlin *et al.* 2010
10	Arachnida	0.0420	2.7700	0.0103	0.0357	0.0420	2.7700	0.0420	2.7700	0.0378	2.7700	0.5623	0.1097	3	24	Mercer *et al.* 2001
11	Arachnida	0.0432	3.0220	---	---	0.0548	3.7810	0.0432	3.0223	0.0386	3.0153	0.5740	0.6338	9	25	Newton & Proctor 2013
12	Arachnida	0.0516	2.7900	0.1030	0.2070	0.0516	2.7900	0.0516	2.7900	0.0431	2.7900	0.7239	0.1444	2	30	Rogers *et al.* 1977
13	Arachnida	0.0399	2.8080	0.0467	0.1107	0.0399	2.8080	0.0399	2.8080	0.0365	2.8080	0.4972	0.1699	3	24	Mercer *et al.* 2001
14	Arachnida	0.0104	1.9090	---	---	0.0352	2.8763	0.0177	2.2175	0.0168	2.2629	-0.1628	-1.0575	9	25	Newton & Proctor 2013
15	Arachnida	0.0572	2.5530	0.3260	0.3080	0.0572	2.5530	0.0572	2.5530	0.0457	2.5556	0.8492	-0.3988	2	6	Edwards & Gabriel 1998
16	Arachnida	0.0111	3.1840	0.3260	0.3080	0.0111	3.1840	0.0111	3.1840	0.0066	3.1578	-0.5137	1.0247	2	6	Edwards & Gabriel 1998
17	Arachnida	0.1312	2.6600	0.2350	0.0970	0.1312	2.6600	0.1312	2.6600	0.0673	2.6602	1.4169	-0.1539	2	6	Edwards 1996
18	Arachnida	0.0300	2.9990	0.2210	0.1190	0.0300	2.9990	0.0300	2.9990	0.0294	2.9936	0.2531	0.6381	2	6	Edwards & Gabriel 1998
19	Arachnida	0.0175	3.1980	0.2210	0.1190	0.0175	3.1980	0.0175	3.1980	0.0166	3.1694	-0.2053	1.0516	2	6	Edwards & Gabriel 1998
20	Arachnida	0.0490	2.6690	0.2080	1.3670	0.0490	2.6690	0.0490	2.6690	0.0418	2.6691	0.6344	-0.1434	2	4	Díaz & Díaz 1990
21	Arachnida	0.0416	2.7710	0.2780	0.1750	0.0416	2.7710	0.0416	2.7710	0.0376	2.7710	0.5534	0.1100	2	6	Edwards & Gabriel 1998
22	Arachnida	0.0396	2.8290	0.2780	0.1750	0.0396	2.8290	0.0396	2.8290	0.0364	2.8289	0.5077	0.2481	2	6	Edwards & Gabriel 1998
23	Arachnida	0.1227	2.8450	0.2370	0.1260	0.1227	2.8450	0.1227	2.8450	0.0655	2.8448	1.3456	0.2502	2	6	Edwards 1996
24	Arachnida	0.0403	2.4680	0.1080	0.0760	0.0403	2.4680	0.0403	2.4680	0.0368	2.4756	0.5244	-0.5844	2	7	Ganihar 1997
25	Arachnida	0.0365	2.9110	0.1120	0.0560	0.0365	2.9110	0.0365	2.9110	0.0343	2.9096	0.3159	0.4383	2	8	Gowing & Recher 1984

26	Arachnida	0.0433	2.5320	---	---	0.0433	2.5320	0.0433	2.5320	0.0386	2.5355	0.5882	-0.4456	2	9	Gruner 2003
27	Arachnida	0.0760	2.2450	0.0240	0.0710	0.0760	2.2450	0.0760	2.2450	0.0531	2.2844	1.0367	-1.0374	2	10	Henschel *et al.* 1996
28	Arachnida	0.1044	2.2960	0.3740	0.2020	0.1044	2.2960	0.1044	2.2960	0.0613	2.3255	1.4054	-0.9406	2	11	Hódar 1996
29	Arachnida	0.0067	3.4130	0.0050	0.2450	0.0067	3.4130	0.0067	3.4130	-0.0033	3.3337	-0.9379	1.3872	1	12	Höfer & Ott 2009
30	Arachnida	0.0198	3.1600	0.0250	0.1180	0.0198	3.1600	0.0198	3.1600	0.0194	3.1376	-0.1193	0.9066	1	12	Höfer & Ott 2009
31	Arachnida	0.0165	3.2420	0.0010	0.0140	0.0165	3.2420	0.0165	3.2420	0.0152	3.2053	-0.2361	1.1366	1	13	Höfer & Ott 2009
32	Arachnida	0.0280	3.1800	0.0030	0.0790	0.0280	3.1800	0.0280	3.1800	0.0277	3.1545	0.1910	1.0131	1	13	Höfer & Ott 2009
33	Arachnida	0.0165	3.2420	0.0010	0.0160	0.0165	3.2420	0.0165	3.2420	0.0152	3.2053	-0.2358	1.1365	1	13	Höfer & Ott 2009
34	Arachnida	0.0170	3.8810	0.0030	0.1230	0.0170	3.8810	0.0170	3.8810	0.0159	3.6099	-0.2408	1.9536	1	13	Höfer & Ott 2009
35	Arachnida	0.0507	2.8990	0.0090	0.0160	0.0507	2.8990	0.0507	2.8990	0.0426	2.8979	0.7358	0.4125	1	13	Höfer & Ott 2009
36	Arachnida	0.0255	3.2880	0.0100	0.0810	0.0255	3.2880	0.0255	3.2880	0.0255	3.2415	0.1077	1.2081	1	13	Höfer & Ott 2009
37	Arachnida	0.0507	2.8990	0.0100	0.0180	0.0507	2.8990	0.0507	2.8990	0.0426	2.8979	0.7359	0.4126	1	13	Höfer & Ott 2009
38	Arachnida	0.0216	3.7100	0.0110	0.1140	0.0216	3.7100	0.0216	3.7100	0.0215	3.5201	-0.0379	1.7638	1	13	Höfer & Ott 2009
39	Arachnida	0.1253	2.0390	0.3430	0.2350	0.1253	2.0390	0.1253	2.0390	0.0661	2.1342	1.3375	-1.3882	2	16	Johnson & Strong 2000
40	Arachnida	0.0409	2.2180	0.1650	0.1220	0.0409	2.2180	0.0409	2.2180	0.0372	2.2633	0.5352	-1.0863	2	16	Johnson & Strong 2000
41	Arachnida	0.0124	1.5200	---	---	0.0124	1.5200	0.0124	1.5200	0.0090	1.8496	-0.4384	-1.8678	2	23	McLaughlin *et al.* 2010
42	Arachnida	0.0448	2.9290	0.1890	0.2940	0.0448	2.9290	0.0448	2.9290	0.0395	2.9270	0.6023	0.4669	2	30	Rogers *et al.* 1977
43	Arachnida	0.0500	2.7400	0.0100	0.1100	0.0500	2.7400	0.0500	2.7400	0.0423	2.7400	0.4550	-0.1051	1	31	Sabo *et al.* 2002
44	Arachnida	0.1188	2.2300	0.1500	0.1100	0.1188	2.2300	0.1188	2.2300	0.0647	2.2726	1.2790	-1.0625	2	47	Wardhaugh 2013
45	Arachnida	0.0150	3.0400	---	---	0.0150	3.0400	0.0150	3.0400	0.0131	3.0316	-0.3447	0.6840	2	3	Clausen 1983
46	Arachnida	0.0280	2.7300	---	---	0.0280	2.7300	0.0280	2.7300	0.0277	2.7300	0.1869	0.0109	2	3	Clausen 1983
47	Arachnida	0.0190	2.9600	---	---	0.0190	2.9600	0.0190	2.9600	0.0185	2.9567	-0.1477	0.5106	2	3	Clausen 1983
48	Arachnida	0.0160	3.0000	---	---	0.0160	3.0000	0.0160	3.0000	0.0146	2.9945	-0.2917	0.6036	2	3	Clausen 1983
49	Arachnida	0.0096	3.2400	---	---	0.0096	3.2400	0.0096	3.2400	0.0036	3.2037	-0.6904	1.0510	2	3	Clausen 1983
50	Arachnida	0.0165	2.9600	---	---	0.0165	2.9600	0.0165	2.9600	0.0152	2.9567	-0.2663	0.5232	2	3	Clausen 1983
51	Arachnida	0.0105	3.1700	---	---	0.0105	3.1700	0.0105	3.1700	0.0055	3.1460	-0.6239	0.9372	2	3	Clausen 1983
52	Arachnida	0.0436	2.6360	0.2650	0.1390	0.0436	2.6360	0.0436	2.6360	0.0388	2.6365	0.5969	-0.2084	2	6	Edwards & Gabriel 1998
53	Arachnida	0.0242	2.9990	0.2650	0.1390	0.0242	2.9990	0.0242	2.9990	0.0242	2.9936	0.0644	0.6380	2	6	Edwards & Gabriel 1998

54	Arachnida	0.1158	2.6530	0.1880	0.1020	0.1158	2.6530	0.1158	2.6530	0.0640	2.6533	1.3719	-0.1656	2	6	Edwards 1996
55	Arachnida	0.0130	1.3300	---	---	0.0130	1.3300	0.0130	1.3300	0.0100	1.7700	-0.3989	-2.0313	2	23	McLaughlin *et al.* 2010
56	Arachnida	0.0405	2.5950	0.1650	0.1750	0.0405	2.5950	0.0405	2.5950	0.0369	2.5962	0.5281	-0.2971	2	6	Edwards & Gabriel 1998
57	Arachnida	0.0203	3.0540	0.1650	0.1750	0.0203	3.0540	0.0203	3.0540	0.0200	3.0443	-0.0821	0.7570	2	6	Edwards & Gabriel 1998
58	Arachnida	0.0170	3.2320	0.0020	0.0290	0.0170	3.2320	0.0170	3.2320	0.0159	3.1972	-0.2262	1.1161	1	13	Höfer & Ott 2009
59	Arachnida	0.0531	2.8860	0.0200	0.0340	0.0531	2.8860	0.0531	2.8860	0.0438	2.8852	0.7715	0.3821	1	13	Höfer & Ott 2009
60	Arachnida	0.0248	2.9300	0.3290	0.1980	0.0248	2.9300	0.0248	2.9300	0.0248	2.9280	0.0894	0.4797	2	6	Edwards & Gabriel 1998
61	Arachnida	0.0278	2.8450	0.3290	0.1980	0.0278	2.8450	0.0278	2.8450	0.0276	2.8448	0.1890	0.2822	2	6	Edwards & Gabriel 1998
62	Arachnida	0.0590	3.0550	0.2000	0.0980	0.0590	3.0550	0.0590	3.0550	0.0465	3.0453	0.8385	0.7281	2	6	Edwards 1996
63	Arachnida	0.0450	2.1300	---	---	0.0450	2.1300	0.0450	2.1300	0.0396	2.1975	0.6229	-1.2286	2	3	Clausen 1983
64	Arachnida	0.0189	2.6470	0.2600	0.2090	0.0189	2.6470	0.0189	2.6470	0.0184	2.6473	-0.0711	-0.1341	2	6	Edwards & Gabriel 1998
65	Arachnida	0.0632	2.5300	0.2600	0.2090	0.0632	2.5300	0.0632	2.5300	0.0483	2.5336	0.9433	-0.4476	2	6	Edwards & Gabriel 1998
66	Arachnida	0.1606	2.7540	0.3820	0.2160	0.1606	2.7540	0.1606	2.7540	0.0725	2.7540	1.5123	0.0511	2	6	Edwards 1996
67	Arachnida	0.0270	2.8800	0.0022	0.1034	0.0270	2.8800	0.0270	2.8800	0.0268	2.8793	0.1587	0.3612	1	19	Lang *et al.* 1997
68	Arachnida	0.0125	1.1600	---	---	0.0125	1.1600	0.0125	1.1600	0.0091	1.7068	-0.4038	-2.0611	2	23	McLaughlin *et al.* 2010
69	Arachnida	0.0940	2.3600	---	---	0.0940	2.3600	0.0940	2.3600	0.0586	2.3794	1.1585	-0.8109	2	2	Breymeyer 1967
70	Arachnida	0.2750	1.9800	---	---	0.2750	1.9800	0.2750	1.9800	0.0868	2.0956	1.7575	-1.4787	2	2	Breymeyer 1967
71	Arachnida	0.0522	2.6950	0.2710	0.0930	0.0522	2.6950	0.0522	2.6950	0.0434	2.6950	0.7634	-0.0700	2	6	Edwards & Gabriel 1998
72	Arachnida	0.0387	2.8040	0.2710	0.0930	0.0387	2.8040	0.0387	2.8040	0.0358	2.8040	0.4864	0.1877	2	6	Edwards & Gabriel 1998
73	Arachnida	0.1296	2.8420	0.2800	0.0830	0.1296	2.8420	0.1296	2.8420	0.0669	2.8418	1.3576	0.2441	2	6	Edwards 1996
74	Arachnida	0.0326	2.7390	0.0027	0.0542	0.0326	2.7390	0.0326	2.7390	0.0315	2.7390	0.3269	0.0377	1	19	Lang *et al.* 1997
75	Arachnida	0.0500	2.4590	0.0030	0.0940	0.0500	2.4590	0.0500	2.4590	0.0423	2.4673	0.7249	-0.5830	1	13	Höfer & Ott 2009
76	Arachnida	0.0393	2.6820	0.0070	0.0760	0.0393	2.6820	0.0393	2.6820	0.0362	2.6821	0.5002	-0.0997	1	13	Höfer & Ott 2009
77	Arachnida	0.0370	2.9300	---	---	0.0370	2.9300	0.0370	2.9300	0.0346	2.9280	0.3918	0.4050	2	3	Clausen 1983
78	Arachnida	0.0210	3.2800	---	---	0.0210	3.2800	0.0210	3.2800	0.0208	3.2353	-0.0729	1.0115	2	3	Clausen 1983
79	Arachnida	0.0544	2.7400	0.3880	0.1960	0.0544	2.7400	0.0544	2.7400	0.0445	2.7400	0.8023	0.0381	2	6	Edwards & Gabriel 1998
80	Arachnida	0.0711	2.6170	0.3880	0.1960	0.0711	2.6170	0.0711	2.6170	0.0514	2.6178	1.0451	-0.2518	2	6	Edwards & Gabriel 1998
81	Arachnida	0.1374	2.9400	0.1770	0.1140	0.1374	2.9400	0.1374	2.9400	0.0685	2.9376	1.3854	0.4179	2	6	Edwards 1996

82	Arachnida	0.0132	2.3600	---	---	0.0132	2.3600	0.0132	2.3600	0.0103	2.3794	-0.4452	-0.8140	2	23	McLaughlin *et al.* 2010
83	Arachnida	0.0155	3.2720	0.1780	0.1820	0.0155	3.2720	0.0155	3.2720	0.0138	3.2290	-0.2961	1.1861	2	6	Edwards & Gabriel 1998
84	Arachnida	0.0447	2.7430	0.1780	0.1820	0.0447	2.7430	0.0447	2.7430	0.0394	2.7430	0.6204	0.0446	2	6	Edwards & Gabriel 1998
85	Arachnida	0.1300	2.8470	0.1330	0.1410	0.1300	2.8470	0.1300	2.8470	0.0670	2.8467	1.3772	0.2416	2	6	Edwards 1996
86	Arachnida	0.0271	3.0270	0.2890	0.1200	0.0271	3.0270	0.0271	3.0270	0.0269	3.0196	0.1617	0.6926	2	6	Edwards & Gabriel 1998
87	Arachnida	0.0358	2.9040	0.2890	0.1200	0.0358	2.9040	0.0358	2.9040	0.0338	2.9027	0.4146	0.4224	2	6	Edwards & Gabriel 1998
88	Arachnida	0.1126	2.9010	0.2380	0.1500	0.1126	2.9010	0.1126	2.9010	0.0633	2.8998	1.2518	0.3188	2	6	Edwards 1996
89	Arachnida	0.0200	2.7500	---	---	0.0200	2.7500	0.0200	2.7500	0.0197	2.7500	-0.1040	0.0625	2	3	Clausen 1983
90	Arachnida	0.0450	2.9500	---	---	0.0450	2.9500	0.0450	2.9500	0.0396	2.9472	0.5650	0.4595	2	3	Clausen 1983
91	Arachnida	0.0700	2.8390	0.3170	0.1770	0.0700	2.8390	0.0700	2.8390	0.0510	2.8388	1.0301	0.2732	2	6	Edwards & Gabriel 1998
92	Arachnida	0.0322	3.2290	0.3170	0.1770	0.0322	3.2290	0.0322	3.2290	0.0312	3.1948	0.3173	1.1034	2	6	Edwards & Gabriel 1998
93	Arachnida	0.2066	2.9070	0.2680	0.1050	0.2066	2.9070	0.2066	2.9070	0.0791	2.9057	1.6652	0.3490	2	6	Edwards 1996
94	Arachnida	0.0706	2.9450	0.3290	0.1470	0.0706	2.9450	0.0706	2.9450	0.0512	2.9424	1.0222	0.5168	2	6	Edwards & Gabriel 1998
95	Arachnida	0.0467	2.7430	0.2030	0.1950	0.0467	2.7430	0.0467	2.7430	0.0405	2.7430	0.6609	0.0450	2	6	Edwards & Gabriel 1998
96	Arachnida	0.0895	2.7410	0.3290	0.1470	0.0895	2.7410	0.0895	2.7410	0.0573	2.7410	1.2358	0.0403	2	6	Edwards & Gabriel 1998
97	Arachnida	0.1932	2.9730	0.2940	0.1320	0.1932	2.9730	0.1932	2.9730	0.0774	2.9691	1.5915	0.4980	2	6	Edwards 1996
98	Arachnida	0.3539	1.5160	2.7440	1.5360	0.3539	1.5160	0.3539	1.5160	0.0939	1.8478	2.2865	-2.0621	5	7	Ganihar 1997
99	Arachnida	0.0580	2.5590	0.0120	0.1040	0.0580	2.5590	0.0580	2.5590	0.0461	2.5614	0.8124	-0.3856	2	10	Henschel *et al.* 1996
100	Arachnida	0.0405	2.9160	0.7570	0.5310	0.0405	2.9160	0.0405	2.9160	0.0369	2.9144	0.5281	0.4332	2	11	Hódar 1996
101	Arachnida	0.0420	3.8790	0.0090	0.1190	0.0420	3.8790	0.0420	3.8790	0.0378	3.6089	0.5269	1.6724	1	13	Höfer & Ott 2009
102	Arachnida	0.0441	3.6220	0.0280	0.1050	0.0441	3.6220	0.0441	3.6220	0.0391	3.4692	0.5830	1.4882	1	13	Höfer & Ott 2009
103	Arachnida	0.0193	1.7400	---	---	0.0193	1.7400	0.0193	1.7400	0.0188	1.9564	-0.1285	-1.7673	2	23	McLaughlin *et al.* 2010
104	Arachnida	0.0172	1.8300	---	---	0.0172	1.8300	0.0172	1.8300	0.0162	2.0055	-0.2220	-1.6767	2	23	McLaughlin *et al.* 2010
105	Arachnida	0.0166	2.0700	---	---	0.0166	2.0700	0.0166	2.0700	0.0154	2.1552	-0.2576	-1.3412	2	23	McLaughlin *et al.* 2010
106	Arachnida	0.0151	2.9500	---	---	0.0151	2.9500	0.0151	2.9500	0.0133	2.9472	-0.3444	0.3050	2	23	McLaughlin *et al.* 2010
107	Arachnida	0.0129	2.2600	---	---	0.0129	2.2600	0.0129	2.2600	0.0098	2.2963	-0.4548	-1.0056	2	23	McLaughlin *et al.* 2010
108	Arachnida	0.0570	2.5890	0.0030	0.1030	0.0570	2.5890	0.0570	2.5890	0.0457	2.5904	0.8494	-0.2756	1	13	Höfer & Ott 2009
109	Arachnida	0.0468	2.4530	0.0060	0.0710	0.0468	2.4530	0.0468	2.4530	0.0406	2.4619	0.6868	-0.4930	1	13	Höfer & Ott 2009

110	Arachnida	0.0237	2.1650	0.2290	0.2320	0.0237	2.1650	0.0237	2.1650	0.0237	2.2231	0.0847	-1.0809	2	16	Johnson & Strong 2000
111	Arachnida	0.0081	3.4400	0.1000	0.1700	0.0081	3.4400	0.0081	3.4400	0.0003	3.3525	-0.7753	1.4689	2	47	Wardhaugh 2013
112	Arachnida	0.0078	3.4240	1.1060	0.3790	0.0078	3.4240	0.0078	3.4240	-0.0005	3.3414	-0.5314	1.4102	2	11	Hódar 1996
113	Chilopoda	0.0174	2.1800	0.3290	0.1210	0.0174	2.1800	0.0174	2.1800	0.0165	2.2343	-0.3505	-1.0815	2	8	Gowing & Recher 1984
114	Chilopoda	0.0036	2.6260	0.9060	0.2710	0.0036	2.6260	0.0036	2.6260	-0.0139	2.6266	-1.2238	-0.1946	2	11	Hódar 1996
115	Chilopoda	0.0001	3.2260	---	---	0.0001	3.2260	0.0001	3.2260	-0.0394	3.1924	-1.9076	1.1039	1	17	Klarner *et al.* 2017
116	Chilopoda	0.0007	2.5260	---	---	0.0007	2.5260	0.0007	2.5260	-0.0320	2.5298	-1.5538	-0.1415	1	18	Klarner *et al.* 2017
117	Chilopoda	0.0026	2.3560	---	---	0.0078	2.0186	0.0026	2.3561	-0.0186	2.3760	-1.4870	-0.7905	9	26	Ruiz-Lupión, D (unpublished)
118	Chilopoda	0.0020	2.9280	0.0004	0.1015	0.0020	2.9280	0.0020	2.9280	-0.0220	2.9260	-1.6203	0.4789	1	19	Lang *et al.* 1997
119	Chilopoda	0.0271	2.5780	---	---	0.0058	2.7327	0.0005	3.6617	-0.0342	3.4926	-2.0755	1.6806	9	46	Voigtländer 2000
120	Chilopoda	0.1922	1.3060	---	---	0.0165	2.2074	0.0698	1.5355	0.0509	1.8565	0.5742	-2.0357	9	46	Voigtländer 2000
121	Chilopoda	0.0102	2.9650	---	---	0.0025	3.0883	0.0035	2.9580	-0.0143	2.9548	-1.3490	0.5426	9	46	Voigtländer 2007
122	Chilopoda	0.0133	2.8670	---	---	0.0084	2.6367	0.0045	2.8625	-0.0103	2.8621	-1.2033	0.3276	9	46	Voigtländer 2007
123	Chilopoda	0.0072	2.2080	---	---	0.0246	2.1599	0.0045	2.4713	-0.0103	2.4787	-1.2039	-0.5800	9	27	Ruiz-Lupión, D (unpublished)
124	Chilopoda	0.0012	2.8420	0.6290	0.1970	0.0012	2.8420	0.0012	2.8420	-0.0276	2.8418	-1.6552	0.2754	2	7	Ganihar 1997
125	Chilopoda	0.0020	2.6160	---	---	0.0020	2.6160	0.0020	2.6160	-0.0220	2.6168	-1.5905	-0.2549	3	29	Richardson *et al.* 2000
126	Chilopoda	0.0373	2.1010	0.2490	0.1060	0.0373	2.1010	0.0373	2.1010	0.0348	2.1768	0.3635	-1.2900	2	7	Ganihar 1997
127	Diplopoda	0.0101	2.5430	0.5170	0.1720	0.0101	2.5430	0.0101	2.5430	0.0047	2.5460	-0.6546	-0.4128	2	8	Gowing & Recher 1984
128	Diplopoda	0.0001	3.9090	1.4870	0.4700	0.0001	3.9090	0.0001	3.9090	-0.0394	3.6236	-1.7074	2.0559	2	11	Hódar 1996
129	Diplopoda	0.0083	2.6010	---	---	0.0083	2.6010	0.0083	2.6010	0.0007	2.6021	-0.7648	-0.2937	3	29	Richardson *et al.* 2000
130	Diplopoda	0.0090	2.5580	---	---	0.0300	2.5580	0.0300	2.5580	0.0294	2.5604	0.2535	-0.3876	9	22	Mazantseva 1975
131	Diplopoda	0.0117	2.4560	---	---	0.0375	2.4681	0.0389	2.4557	0.0359	2.4643	0.4898	-0.6139	9	22	Mazantseva 1975
132	Diplopoda	0.0023	2.9900	---	---	0.0023	2.9900	0.0023	2.9900	-0.0202	2.9852	-1.5455	0.5823	2	23	McLaughlin *et al.* 2010
133	Diplopoda	0.0041	2.7400	---	---	0.0041	2.7400	0.0041	2.7400	-0.0118	2.7400	-1.2533	-0.0197	2	23	McLaughlin *et al.* 2010
134	Diplopoda	0.0137	2.4860	---	---	0.0222	2.7041	0.0456	2.4864	0.0399	2.4926	0.5705	-0.6386	9	41	Shinohara *et al.* 2007
135	Entognatha	0.1534	2.3000	0.1870	0.3010	0.1534	2.3000	0.1534	2.3000	0.0713	2.3288	1.0308	-1.3909	2	7	Ganihar 1997
136	Entognatha	0.0056	2.8090	---	---	0.0056	2.8090	0.0056	2.8090	-0.0066	2.8090	-1.0663	0.1494	2	9	Gruner 2003

137	Entognatha	0.0024	3.6760	0.2230	0.2560	0.0024	3.6760	0.0024	3.6760	-0.0196	3.5008	-1.5112	1.3965	2	11	Hódar 1996
138	Entognatha	0.0073	1.7500	---	---	0.0073	1.7500	0.0073	1.7500	-0.0017	1.9616	-0.8889	-1.7959	2	23	McLaughlin *et al.* 2010
139	Entognatha	0.0065	1.9920	0.0951	0.3067	0.0065	1.9920	0.0065	1.9920	-0.0039	2.1033	-0.8035	-1.3313	3	24	Mercer *et al.* 2001
140	Entognatha	0.0008	2.5000	0.0440	0.3800	0.0008	2.5000	0.0008	2.5000	-0.0311	2.5053	-1.5909	-0.5160	3	43	Tanaka 1970
141	Entognatha	0.0108	2.9040	---	---	0.0108	2.9040	0.0108	2.9040	0.0060	2.9027	-0.6497	-0.0090	8	44	Van Straalen 1989
142	Entognatha	0.0262	2.0180	---	---	0.0003	3.5538	0.0262	2.0175	0.0261	2.1199	-0.0867	-1.4575	9	27	Ruiz-Lupión, D (unpublished)
143	Entognatha	0.0072	1.4200	---	---	0.0072	1.4200	0.0072	1.4200	-0.0020	1.8064	-0.8985	-2.1627	2	23	McLaughlin *et al.* 2010
144	Entognatha	0.0056	2.7990	0.0159	0.1357	0.0056	2.7990	0.0056	2.7990	-0.0066	2.7990	-1.0675	0.0241	3	28	Petersen 1975
145	Entognatha	0.0063	2.8810	0.0362	0.2034	0.0063	2.8810	0.0063	2.8810	-0.0045	2.8803	-0.9970	0.1235	3	28	Petersen 1975
146	Entognatha	0.0085	3.2230	0.0333	0.2584	0.0085	3.2230	0.0085	3.2230	0.0012	3.1899	-0.8774	0.4133	3	28	Petersen 1975
147	Entognatha	0.0046	2.4390	0.0602	0.1631	0.0046	2.4390	0.0046	2.4390	-0.0099	2.4491	-1.1882	-0.6466	3	28	Petersen 1975
148	Entognatha	0.0046	2.4390	0.0602	0.1631	0.0046	2.4390	0.0046	2.4390	-0.0099	2.4491	-1.1883	-0.6464	3	28	Petersen 1975
149	Entognatha	0.0047	2.1830	0.0745	0.2091	0.0047	2.1830	0.0047	2.1830	-0.0096	2.2366	-1.1654	-1.1494	3	28	Petersen 1975
150	Entognatha	0.0007	2.5600	0.0790	0.8300	0.0007	2.5600	0.0007	2.5600	-0.0320	2.5623	-1.6348	-0.3831	3	43	Tanaka 1970
151	Entognatha	0.0008	2.9900	0.0550	0.5000	0.0008	2.9900	0.0008	2.9900	-0.0311	2.9852	-1.7703	0.5837	3	43	Tanaka 1970
152	Entognatha	0.0008	3.2800	0.0970	1.0200	0.0008	3.2800	0.0008	3.2800	-0.0311	3.2353	-1.8438	1.0260	3	43	Tanaka 1970
153	Entognatha	0.0092	2.7440	0.0185	0.0482	0.0092	2.7440	0.0092	2.7440	0.0028	2.7440	-0.7436	-0.1749	3	28	Petersen 1975
154	Entognatha	0.0073	2.8820	---	---	0.0073	2.8820	0.0073	2.8820	-0.0017	2.8812	-0.8924	0.1368	8	44	Van Straalen 1989
155	Entognatha	0.0010	2.5500	0.0870	0.9300	0.0010	2.5500	0.0010	2.5500	-0.0292	2.5527	-1.5198	-0.4056	3	43	Tanaka 1970
156	Entognatha	0.0058	1.2700	---	---	0.0058	1.2700	0.0058	1.2700	-0.0060	1.7469	-1.0393	-2.2928	2	23	McLaughlin *et al.* 2010
157	Entognatha	0.0010	2.2400	0.0550	0.6700	0.0010	2.2400	0.0010	2.2400	-0.0292	2.2805	-1.3888	-1.0089	3	43	Tanaka 1970
158	Entognatha	0.0062	3.1260	0.0251	0.2129	0.0062	3.1260	0.0062	3.1260	-0.0048	3.1084	-1.0043	0.6447	3	28	Petersen 1975
159	Entognatha	0.0056	2.7690	0.0319	0.1961	0.0056	2.7690	0.0056	2.7690	-0.0066	2.7690	-1.0669	0.0772	3	28	Petersen 1975
160	Entognatha	0.0079	4.1490	0.0367	0.2663	0.0079	4.1490	0.0079	4.1490	-0.0002	3.7309	-0.9848	1.1914	3	28	Petersen 1975
161	Entognatha	0.0070	3.4680	0.0617	0.2454	0.0070	3.4680	0.0070	3.4680	-0.0025	3.3715	-0.9583	0.9213	3	28	Petersen 1975
162	Entognatha	0.0068	2.7250	0.0125	0.0688	0.0068	2.7250	0.0068	2.7250	-0.0031	2.7250	-0.9378	-0.0234	3	28	Petersen 1975
163	Entognatha	0.0056	2.5320	0.0291	0.1544	0.0056	2.5320	0.0056	2.5320	-0.0066	2.5355	-1.0637	-0.4410	3	28	Petersen 1975

164	Entognatha	0.0101	3.2080	0.0835	0.1604	0.0101	3.2080	0.0101	3.2080	0.0047	3.1777	-0.7190	0.6138	3	28	Petersen 1975
165	Entognatha	0.0070	2.8880	0.0500	0.2649	0.0070	2.8880	0.0070	2.8880	-0.0025	2.8871	-0.9188	0.2809	3	28	Petersen 1975
166	Entognatha	0.0006	2.7500	0.0370	0.3400	0.0006	2.7500	0.0006	2.7500	-0.0331	2.7500	-1.6120	0.0593	3	43	Tanaka 1970
167	Entognatha	0.0032	2.5040	0.0309	0.0877	0.0032	2.5040	0.0032	2.5040	-0.0156	2.5091	-1.3565	-0.5049	3	28	Petersen 1975
168	Entognatha	0.1199	3.6270	0.0561	0.1434	0.1199	3.6270	0.1199	3.6270	0.0649	3.4722	-0.0027	-0.3449	3	28	Petersen 1975
169	Entognatha	0.1199	3.6270	0.0561	0.1434	0.1199	3.6270	0.1199	3.6270	0.0649	3.4722	-0.0026	-0.3456	3	28	Petersen 1975
170	Entognatha	0.0084	2.3500	---	---	0.0084	2.3500	0.0084	2.3500	0.0010	2.3708	-0.7898	-0.8290	2	23	McLaughlin *et al.* 2010
171	Entognatha	0.0613	2.9250	---	---	0.0573	3.0020	0.0574	3.0011	0.0458	2.9956	0.4543	0.2401	9	45	Vannier 1973
172	Insecta	0.0079	3.1810	0.3250	0.1560	0.0079	3.1810	0.0079	3.1810	-0.0002	3.1553	-0.7555	1.0166	2	33	Sample *et al.* 1993
173	Insecta	0.0080	3.4630	---	---	0.0080	3.4630	0.0080	3.4630	0.0000	3.3682	-0.8131	1.5204	2	9	Gruner 2003
174	Insecta	0.0246	2.8240	0.3730	0.1910	0.0246	2.8240	0.0246	2.8240	0.0246	2.8239	0.0766	0.2331	2	11	Hódar 1996
175	Insecta	0.0105	3.1730	0.2110	0.0910	0.0105	3.1730	0.0105	3.1730	0.0055	3.1486	-0.5415	1.0030	2	11	Hódar 1996
176	Insecta	0.0168	2.7520	---	---	0.0168	2.7520	0.0168	2.7520	0.0157	2.7520	-0.2515	0.0637	2	9	Gruner 2003
177	Insecta	0.0080	3.2140	0.5000	0.2030	0.0080	3.2140	0.0080	3.2140	0.0000	3.1826	-0.7432	1.0829	2	11	Hódar 1996
178	Insecta	0.0307	2.6390	---	---	0.0307	2.6390	0.0307	2.6390	0.0300	2.6394	0.2718	-0.2011	1	15	Jarošik 1989
179	Insecta	0.0237	2.7050	0.0028	0.0522	0.0237	2.7050	0.0237	2.7050	0.0237	2.7050	0.0404	-0.0439	1	19	Lang *et al.* 1997
180	Insecta	0.0136	2.8390	---	---	0.0908	2.6178	0.0453	2.8388	0.0398	2.8386	0.5732	0.2699	9	21	Marcuzzi 1987
181	Insecta	0.0073	2.8200	---	---	0.0073	2.8200	0.0073	2.8200	-0.0017	2.8199	-0.8889	0.2248	2	23	McLaughlin *et al.* 2010
182	Insecta	0.0041	3.3600	---	---	0.0041	3.3600	0.0041	3.3600	-0.0118	3.2957	-1.2586	1.1842	2	23	McLaughlin *et al.* 2010
183	Insecta	0.0037	4.0600	---	---	0.0037	4.0600	0.0037	4.0600	-0.0134	3.6931	-1.3283	1.7030	2	23	McLaughlin *et al.* 2010
184	Insecta	0.0011	4.6400	---	---	0.0011	4.6400	0.0011	4.6400	-0.0284	3.9074	-1.8654	2.1282	2	23	McLaughlin *et al.* 2010
185	Insecta	0.0059	3.1900	---	---	0.0059	3.1900	0.0059	3.1900	-0.0057	3.1628	-1.0346	0.9217	2	23	McLaughlin *et al.* 2010
186	Insecta	0.0072	2.8700	---	---	0.0072	2.8700	0.0072	2.8700	-0.0020	2.8694	-0.8986	0.3347	2	23	McLaughlin *et al.* 2010
187	Insecta	0.0138	2.1300	---	---	0.0138	2.1300	0.0138	2.1300	0.0113	2.1975	-0.4118	-1.2198	2	23	McLaughlin *et al.* 2010
188	Insecta	0.0720	2.4010	0.0110	0.0510	0.0720	2.4010	0.0720	2.4010	0.0517	2.4151	0.5423	-0.7440	1	31	Sabo *et al.* 2002
189	Insecta	0.0241	2.7550	0.2840	0.1330	0.0241	2.7550	0.0241	2.7550	0.0241	2.7550	0.0580	0.0711	2	33	Sample *et al.* 1993
190	Insecta	0.0020	3.5950	---	---	0.0215	2.8024	0.0024	3.5619	-0.0196	3.4325	-1.1442	1.6675	9	34	Santos Gómez 2013
191	Insecta	0.0100	3.0530	---	---	0.0100	3.0530	0.0100	3.0530	0.0045	3.0434	-0.5332	0.7635	9	35	Santos Gómez 2013

192	Insecta	0.0110	3.0150	---	---	0.0110	3.0150	0.0110	3.0150	0.0064	3.0085	-0.5901	0.6729	9	36	Santos Gómez 2013
193	Insecta	0.0230	2.6890	---	---	0.0230	2.6890	0.0230	2.6890	0.0230	2.6890	0.0139	-0.0838	9	37	Santos Gómez 2013
194	Insecta	0.0197	2.8480	0.5330	0.1870	0.0197	2.8480	0.0197	2.8480	0.0193	2.8477	-0.1073	0.2916	2	11	Hódar 1996
195	Insecta	0.0427	2.3710	0.4850	0.2120	0.0427	2.3710	0.0427	2.3710	0.0383	2.3889	0.5760	-0.7917	2	33	Sample *et al.* 1993
196	Insecta	0.0258	3.0830	0.6740	0.3250	0.0258	3.0830	0.0258	3.0830	0.0257	3.0705	0.1180	0.8145	2	11	Hódar 1996
197	Insecta	0.2444	2.2570	---	---	1.1413	2.1484	0.8145	2.2574	0.1242	2.2943	2.0962	-1.1182	9	21	Marcuzzi 1987
198	Insecta	0.0883	2.1710	0.4640	0.2780	0.0883	2.1710	0.0883	2.1710	0.0570	2.2276	1.2050	-1.1378	2	33	Sample *et al.* 1993
199	Insecta	0.0247	3.1020	---	---	0.0247	3.1020	0.0247	3.1020	0.0247	3.0873	0.0528	0.8085	2	9	Gruner 2003
200	Insecta	0.0131	3.1480	0.1730	0.2760	0.0131	3.1480	0.0131	3.1480	0.0101	3.1273	-0.5061	0.7413	3	1	Beaver & Baldwin 1975
201	Insecta	0.0370	2.4920	0.0850	0.5230	0.0370	2.4920	0.0370	2.4920	0.0346	2.4979	0.3930	-0.5305	2	4	Díaz & Díaz 1990
202	Insecta	0.0380	2.4630	0.0660	0.0420	0.0380	2.4630	0.0380	2.4630	0.0353	2.4710	0.4696	-0.5949	2	7	Ganihar 1997
203	Insecta	0.0367	2.6890	0.2580	0.1480	0.0367	2.6890	0.0367	2.6890	0.0344	2.6890	0.2658	-0.0832	2	8	Gowing & Recher 1984
204	Insecta	0.0339	2.3840	---	---	0.0339	2.3840	0.0339	2.3840	0.0324	2.4002	0.3627	-0.7565	2	9	Gruner 2003
205	Insecta	0.0336	2.3470	---	---	0.0336	2.3470	0.0336	2.3470	0.0322	2.3682	0.3555	-0.8271	2	9	Gruner 2003
206	Insecta	0.0410	2.6400	0.1950	0.0800	0.0410	2.6400	0.0410	2.6400	0.0372	2.6404	0.5398	-0.1982	2	11	Hódar 1996
207	Insecta	0.0569	2.1660	0.2260	0.1580	0.0569	2.1660	0.0569	2.1660	0.0456	2.2239	0.7367	-1.1803	2	16	Johnson & Strong 2000
208	Insecta	0.0392	2.5130	0.1950	0.1280	0.0392	2.5130	0.0392	2.5130	0.0361	2.5175	0.4229	-0.4834	2	16	Johnson & Strong 2000
209	Insecta	0.0059	2.9100	---	---	0.0059	2.9100	0.0059	2.9100	-0.0057	2.9086	-1.0329	0.4145	2	23	McLaughlin *et al.* 2010
210	Insecta	0.0192	3.0160	0.0217	0.0298	0.0192	3.0160	0.0192	3.0160	0.0187	3.0094	-0.1380	0.6722	3	24	Mercer *et al.* 2001
211	Insecta	0.0245	2.8540	---	---	0.0245	2.8540	0.0245	2.8540	0.0245	2.8537	0.0528	0.2036	3	29	Richardson *et al.* 2000
212	Insecta	0.0314	2.7900	0.1050	0.0500	0.0314	2.7900	0.0314	2.7900	0.0305	2.7900	0.2869	0.1576	2	30	Rogers *et al.* 1977
213	Insecta	0.0400	2.6400	0.1400	0.0600	0.0400	2.6400	0.0400	2.6400	0.0366	2.6404	0.2315	-0.2589	1	31	Sabo *et al.* 2002
214	Insecta	0.0299	2.6690	---	---	0.0299	2.6690	0.0299	2.6690	0.0293	2.6691	0.2505	-0.1314	7	32	Sage 1982
215	Insecta	0.0574	2.5570	---	---	0.0574	2.5570	0.0574	2.5570	0.0458	2.5594	0.8108	-0.3880	7	32	Sage 1982
216	Insecta	0.0389	2.4920	0.1750	0.0810	0.0389	2.4920	0.0389	2.4920	0.0359	2.4979	0.4900	-0.5293	2	33	Sample *et al.* 1993
217	Insecta	0.0246	1.9900	0.1600	0.2700	0.0246	1.9900	0.0246	1.9900	0.0246	2.1020	0.1395	-1.1231	2	38	Schoener 1980
218	Insecta	0.0351	2.1100	0.1020	0.1700	0.0351	2.1100	0.0351	2.1100	0.0333	2.1832	0.4030	-1.1009	2	39	Schoener 1980
219	Insecta	0.0378	1.9100	0.0950	0.1900	0.0378	1.9100	0.0378	1.9100	0.0352	2.0522	0.4652	-1.5757	2	40	Schoener 1980

220	Insecta	0.0408	2.5600	0.1400	0.0800	0.0408	2.5600	0.0408	2.5600	0.0371	2.5623	0.4518	-0.3789	2	47	Wardhaugh 2013
221	Insecta	0.0607	2.3150	---	---	0.0607	2.3150	0.0607	2.3150	0.0473	2.3413	0.8227	-0.9038	2	9	Gruner 2003
222	Insecta	0.1281	2.2540	0.5170	0.2620	0.1281	2.2540	0.1281	2.2540	0.0666	2.2916	1.4639	-1.0197	2	11	Hódar 1996
223	Insecta	0.0029	3.7220	---	---	0.0087	3.7759	0.0095	3.7217	0.0034	3.5266	-0.7001	1.7048	9	21	Marcuzzi 1987
224	Insecta	0.0198	2.9980	0.0190	0.0258	0.0198	2.9980	0.0198	2.9980	0.0194	2.9927	-0.1126	0.6341	3	24	Mercer *et al.* 2001
225	Insecta	0.0216	2.9430	0.0375	0.0475	0.0216	2.9430	0.0216	2.9430	0.0215	2.9405	-0.0379	0.5097	3	24	Mercer *et al.* 2001
226	Insecta	0.0843	1.5550	0.1025	0.2222	0.0843	1.5550	0.0843	1.5550	0.0558	1.8654	1.2144	-1.7591	3	24	Mercer *et al.* 2001
227	Insecta	0.0342	2.6400	0.3265	0.5371	0.0342	2.6400	0.0342	2.6400	0.0327	2.6404	0.3727	-0.1951	3	24	Mercer *et al.* 2001
228	Insecta	0.0264	2.8640	0.1532	0.1785	0.0264	2.8640	0.0264	2.8640	0.0263	2.8635	0.1387	0.3276	3	24	Mercer *et al.* 2001
229	Insecta	0.0252	2.9670	0.1496	0.2278	0.0252	2.9670	0.0252	2.9670	0.0252	2.9634	0.0975	0.5662	3	24	Mercer *et al.* 2001
230	Insecta	0.0199	3.0500	0.2450	0.1640	0.0199	3.0500	0.0199	3.0500	0.0196	3.0407	-0.1087	0.7405	2	30	Rogers *et al.* 1977
231	Insecta	0.0101	2.9390	0.3630	0.1500	0.0101	2.9390	0.0101	2.9390	0.0047	2.9366	-0.6276	0.5011	2	33	Sample *et al.* 1993
232	Insecta	0.0568	2.7060	0.7040	0.3480	0.0568	2.7060	0.0568	2.7060	0.0456	2.7060	0.8103	-0.0741	2	11	Hódar 1996
233	Insecta	0.0309	2.4830	0.5260	0.1700	0.0309	2.4830	0.0309	2.4830	0.0301	2.4895	0.2836	-0.5352	2	11	Hódar 1996
234	Insecta	0.0679	1.3080	---	---	0.0679	1.3080	0.0679	1.3080	0.0502	1.7614	0.9893	-2.1777	2	9	Gruner 2003
235	Insecta	0.0750	2.5820	0.2730	0.1090	0.0750	2.5820	0.0750	2.5820	0.0527	2.5836	1.0573	-0.3306	2	11	Hódar 1996
236	Insecta	0.1826	2.3410	---	---	1.1434	2.1391	0.6085	2.3408	0.1112	2.3630	1.8785	-0.9566	9	21	Marcuzzi 1987
237	Insecta	0.0865	2.4940	0.2580	0.1000	0.0865	2.4940	0.0865	2.4940	0.0564	2.4997	1.0902	-0.5283	2	33	Sample *et al.* 1993
238	Insecta	0.0023	3.3320	0.9110	0.3530	0.0023	3.3320	0.0023	3.3320	-0.0202	3.2750	-1.2538	1.2832	2	11	Hódar 1996
239	Insecta	0.0134	2.2600	0.0024	0.0974	0.0134	2.2600	0.0134	2.2600	0.0106	2.2963	-0.4107	-1.0041	1	19	Lang *et al.* 1997
240	Insecta	0.0092	2.8260	---	---	0.0000	5.4295	0.0305	2.8262	0.0298	2.8261	0.2591	0.1818	9	21	Marcuzzi 1987
241	Insecta	0.0068	2.0900	---	---	0.0323	3.2082	0.0068	2.0900	-0.0031	2.1691	-0.9230	-1.3083	2	23	McLaughlin *et al.* 2010
242	Insecta	0.0010	4.0260	0.0001	0.2880	0.0051	2.8752	0.0010	4.0260	-0.0292	3.6780	-1.8949	1.5530	1	31	Sabo *et al.* 2002
243	Insecta	0.0513	2.6690	0.4070	0.1500	0.0513	2.6690	0.0513	2.6690	0.0429	2.6691	0.7400	-0.1274	2	11	Hódar 1996
244	Insecta	0.0051	3.4620	---	---	0.0323	3.2082	0.0170	3.4620	0.0159	3.3675	-0.2414	1.4329	9	21	Marcuzzi 1987
245	Insecta	0.0474	2.6810	0.2040	0.0800	0.0474	2.6810	0.0474	2.6810	0.0409	2.6811	0.6273	-0.1019	2	30	Rogers *et al.* 1977
246	Insecta	0.0012	2.9830	---	---	0.0051	2.8752	0.0041	2.9830	-0.0118	2.9786	-0.8969	0.6195	9	42	Sokoloff *et al.* 1999
247	Insecta	0.0313	2.3580	---	---	0.0313	2.3580	0.0313	2.3580	0.0305	2.3776	0.2916	-0.7967	2	9	Gruner 2003

248	Insecta	0.0494	2.3440	0.5340	0.2820	0.0494	2.3440	0.0494	2.3440	0.0420	2.3657	0.7135	-0.8277	2	11	Hódar 1996
249	Insecta	0.0187	2.7600	0.1700	0.0900	0.0187	2.7600	0.0187	2.7600	0.0181	2.7600	-0.1611	0.0857	2	47	Wardhaugh 2013
250	Insecta	0.0080	2.7980	0.0730	0.0260	0.0080	2.7980	0.0080	2.7980	0.0000	2.7980	-0.7929	0.1721	6	7	Ganihar 1997
251	Insecta	0.0015	3.4970	0.6590	0.2510	0.0015	3.4970	0.0015	3.4970	-0.0253	3.3908	-1.5300	1.5544	2	11	Hódar 1996
252	Insecta	0.0240	2.2080	0.0400	1.0360	0.0240	2.2080	0.0240	2.2080	0.0240	2.2556	0.0000	-1.1042	2	4	Díaz & Díaz 1990
253	Insecta	0.0432	2.3450	0.1800	0.0980	0.0432	2.3450	0.0432	2.3450	0.0386	2.3665	0.5130	-0.8471	2	7	Ganihar 1997
254	Insecta	0.0104	2.7630	0.5240	0.2940	0.0104	2.7630	0.0104	2.7630	0.0053	2.7630	-0.6225	0.0933	2	11	Hódar 1996
255	Insecta	0.0186	2.6950	---	---	0.0186	2.6950	0.0186	2.6950	0.0180	2.6950	-0.1699	-0.0652	7	32	Sage 1982
256	Insecta	0.0102	2.1900	0.3040	0.6700	0.0102	2.1900	0.0102	2.1900	0.0049	2.2419	-0.5805	-0.9637	2	38	Schoener 1980
257	Insecta	0.0036	2.7200	0.2230	0.5100	0.0036	2.7200	0.0036	2.7200	-0.0139	2.7200	-1.1678	0.0103	2	39	Schoener 1980
258	Insecta	0.0063	2.3100	0.2490	0.4400	0.0063	2.3100	0.0063	2.3100	-0.0045	2.3371	-0.8960	-0.9137	2	40	Schoener 1980
259	Insecta	0.0061	3.1000	0.2000	0.1300	0.0061	3.1000	0.0061	3.1000	-0.0051	3.0856	-1.0125	0.7919	2	47	Wardhaugh 2013
260	Insecta	0.0747	1.6730	1.0150	0.4500	0.0747	1.6730	0.0747	1.6730	0.0526	1.9219	1.0047	-1.8863	2	7	Ganihar 1997
261	Insecta	0.1284	1.6980	0.0560	0.0320	0.1284	1.6980	0.1284	1.6980	0.0667	1.9346	1.4653	-1.8605	4	7	Ganihar 1997
262	Insecta	0.0747	1.6010	0.2920	0.1460	0.0747	1.6010	0.0747	1.6010	0.0526	1.8869	1.0587	-1.9723	2	11	Hódar 1996
263	Insecta	0.0292	2.4620	0.2670	0.1000	0.0292	2.4620	0.0292	2.4620	0.0288	2.4701	0.2290	-0.6045	2	7	Ganihar 1997
264	Insecta	0.0180	2.7200	---	---	0.0180	2.7200	0.0180	2.7200	0.0172	2.7200	-0.1933	-0.0143	2	9	Gruner 2003
265	Insecta	0.0255	2.6370	0.5610	0.2000	0.0255	2.6370	0.0255	2.6370	0.0255	2.6374	0.1080	-0.2010	2	11	Hódar 1996
266	Insecta	0.0488	2.5150	0.2840	0.1050	0.0488	2.5150	0.0488	2.5150	0.0417	2.5194	0.6326	-0.4815	2	30	Rogers *et al.* 1977
267	Insecta	0.0300	2.5500	0.0200	0.1500	0.0300	2.5500	0.0300	2.5500	0.0294	2.5527	0.0441	-0.5384	1	31	Sabo *et al.* 2002
268	Insecta	0.0200	2.7840	---	---	0.0200	2.7840	0.0200	2.7840	0.0197	2.7840	-0.1041	0.1356	7	32	Sage 1982
269	Insecta	0.0720	1.6500	0.3940	0.4700	0.0720	1.6500	0.0720	1.6500	0.0517	1.9105	1.0632	-1.8563	2	39	Schoener 1980
270	Insecta	0.0252	1.9600	0.6170	0.9400	0.0252	1.9600	0.0252	1.9600	0.0252	2.0830	0.1061	-1.5106	2	40	Schoener 1980
271	Insecta	0.0420	2.6100	0.1900	0.0900	0.0420	2.6100	0.0420	2.6100	0.0378	2.6109	0.3941	-0.3179	2	47	Wardhaugh 2013
272	Insecta	0.0136	3.1150	---	---	0.0136	3.1150	0.0136	3.1150	0.0110	3.0988	-0.4416	0.7760	2	9	Gruner 2003
273	Insecta	0.0425	1.6370	0.2840	0.3410	0.0425	1.6370	0.0425	1.6370	0.0381	1.9042	0.5731	-1.8141	2	11	Hódar 1996
274	Malacostraca	0.0291	2.2350	0.2780	0.0500	0.0291	2.2350	0.0291	2.2350	0.0287	2.2765	0.2835	-1.0519	4	7	Ganihar 1997
275	Malacostraca	0.0102	3.1600	0.5850	0.3430	0.0102	3.1600	0.0102	3.1600	0.0049	3.1376	-0.6474	0.9760	2	8	Gowing & Recher 1984

276	Malacostraca	0.0152	2.7700	---	---	0.0152	2.7700	0.0152	2.7700	0.0134	2.7700	-0.3024	0.1083	2	9	Gruner 2003
277	Malacostraca	0.0101	2.8440	0.5120	0.2040	0.0101	2.8440	0.0101	2.8440	0.0047	2.8438	-0.3863	0.2800	2	11	Hódar 1996
278	Malacostraca	0.0063	2.9100	---	---	0.0063	2.9100	0.0063	2.9100	-0.0045	2.9086	-0.9813	0.3970	2	23	McLaughlin *et al.* 2010
279	Malacostraca	0.0617	1.8540	---	---	0.0617	1.8540	0.0617	1.8540	0.0477	2.0192	0.9189	-1.6624	3	29	Richardson *et al.* 2000
280	Malacostraca	0.0347	3.3800	0.3500	0.2100	0.0347	3.3800	0.0347	3.3800	0.0330	3.3102	0.2695	0.9894	2	47	Wardhaugh 2013
281	Malacostraca	0.0107	2.4400	---	---	0.0107	2.4400	0.0107	2.4400	0.0058	2.4500	-0.6032	-0.6456	2	23	McLaughlin *et al.* 2010
282	Malacostraca	0.0044	3.3000	---	---	0.0044	3.3000	0.0044	3.3000	-0.0107	3.2507	-1.2120	1.0071	2	23	McLaughlin *et al.* 2010
283	Malacostraca	0.0031	3.6200	---	---	0.0031	3.6200	0.0031	3.6200	-0.0161	3.4680	-1.4091	1.3531	2	23	McLaughlin *et al.* 2010

*Code: Identification number of the equation.
*Taxonomic classification for each specimen (Class).
*a: Value standardized of scaling factor.
*b: Value of allometric factor.
*SE a: Standard error of the scaling factor a.
*SE b: Standard error of the allometric factor b.
*NLS a: Value of scaling factor a from fitted M-L equations using Nonlinear Least-Squares analysis (nls).
*NLS b: Value of allometric factor b fitted M-L equations using Nonlinear Least-Squares analysis (nls).
*OLS a: Value of scaling factor a fitted M-L equations using Ordinary Least-Squares analysis.
*OLS b: Value of allometric factor b fitted M-L equations using Ordinary Least-Squares analysis.
*Normal a: Normalized value of scaling factor a using Maximum Likelihood Estimation For Lambert W x F Distributions.
*Normal b: Normalized value of allometric factor b using Maximum Likelihood Estimation For Lambert W x F Distributions.
*Normal a2: Normalized value of scaling factor a using Maximum Likelihood Estimation For Lambert W x F Distributions on the residuals fo the model.
*Normal b2: Normalized value of allometric factor b using Maximum Likelihood Estimation For Lambert W x F Distributions on the residuals fo the model.
*Original equation: Type of equation used in the original study (Table S4).
*Site: Code of the point where field sampling of the original study was carried out by the authors in the Reference (Fig. 2, Table S3).
*Reference: Bibliographic reference.

Table S1: Database used to evaluate scaling factor *a* and allometric factor *b* (cont'd).

Code	Class	n	min Length (mm)	max Length (mm)	Range length (mm)	Mean length (mm)	Reference mean length	Original equation	Site	Reference
1	Arachnida	7	0.400	3.900	3.500	2.150	Original	2	11	Hódar 1996
2	Arachnida	44	0.220	1.511	1.291	0.866	Original	9	20	LeBrun 1971
3	Arachnida	1759	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
4	Arachnida	281	0.582	0.730	0.148	0.485	Original	3	24	Mercer *et al.* 2001
5	Arachnida	25	0.110	1.020	0.910	0.319	Original	9	25	Newton & Proctor 2013
6	Arachnida	32	0.300	1.000	0.700	0.650	Original	2	30	Rogers *et al.* 1977
7	Arachnida	48	0.560	0.900	0.340	0.730	Original	3	24	Mercer *et al.* 2001
8	Arachnida	18	0.225	0.750	0.525	0.476	Original	9	25	Newton & Proctor 2013
9	Arachnida	1290	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
10	Arachnida	164	0.240	1.160	0.920	0.598	Original	3	24	Mercer *et al.* 2001
11	Arachnida	35	0.180	1.020	0.840	0.473	Original	9	25	Newton & Proctor 2013
12	Arachnida	21	0.400	1.000	0.600	0.700	Original	2	30	Rogers *et al.* 1977
13	Arachnida	43	0.140	1.643	1.503	0.582	Original	3	24	Mercer *et al.* 2001
14	Arachnida	21	0.110	0.640	0.530	0.281	Original	9	25	Newton & Proctor 2013
15	Arachnida	29	7.400	19.100	11.700	13.250	Original	2	6	Edwards & Gabriel 1998
16	Arachnida	29	7.400	19.100	11.700	13.250	Original	2	6	Edwards & Gabriel 1998
17	Arachnida	39	4.500	13.500	9.000	9.000	Original	2	6	Edwards 1996
18	Arachnida	26	4.000	14.100	10.100	9.050	Original	2	6	Edwards & Gabriel 1998
19	Arachnida	26	4.000	14.100	10.100	9.050	Original	2	6	Edwards & Gabriel 1998
20	Arachnida	12	3.000	17.000	14.000	10.000	Original	2	4	Díaz & Díaz 1990
21	Arachnida	1990	2.500	19.100	16.600	10.800	Original	2	6	Edwards & Gabriel 1998
22	Arachnida	500	2.500	19.100	16.600	10.800	Original	2	6	Edwards & Gabriel 1998
23	Arachnida	405	1.500	23.500	22.000	12.500	Original	2	6	Edwards 1996
24	Arachnida	114	1.000	12.700	11.700	6.850	Original	2	7	Ganihar 1997
25	Arachnida	100	2.000	20.000	18.000	11.000	Original	2	8	Gowing & Recher 1984

26	Arachnida	52	1.550	7.400	5.850	4.475	Original	2	9	Gruner 2003
27	Arachnida	138	1.100	10.000	8.900	5.550	Original	2	10	Henschel *et al.* 1996
28	Arachnida	18	1.300	27.100	25.800	14.200	Original	2	11	Hódar 1996
29	Arachnida	99	1.350	28.000	26.650	7.080	Original	1	12	Höfer & Ott 2009
30	Arachnida	99	1.350	28.000	26.650	7.080	Original	1	12	Höfer & Ott 2009
31	Arachnida	313	0.560	36.000	35.440	4.830	Original	1	13	Höfer & Ott 2009
32	Arachnida	225	---	---	---	1.250	Original	1	13	Höfer & Ott 2009
33	Arachnida	253	---	---	---	4.638	Original	1	13	Höfer & Ott 2009
34	Arachnida	60	---	---	---	1.474	Original	1	13	Höfer & Ott 2009
35	Arachnida	313	0.560	36.000	35.440	4.830	Original	1	13	Höfer & Ott 2009
36	Arachnida	225	---	---	---	1.250	Original	1	13	Höfer & Ott 2009
37	Arachnida	253	---	---	---	4.638	Original	1	13	Höfer & Ott 2009
38	Arachnida	60	---	---	---	1.474	Original	1	13	Höfer & Ott 2009
39	Arachnida	20	1.100	15.100	14.000	8.100	Original	2	16	Johnson & Strong 2000
40	Arachnida	51	0.800	9.900	9.100	5.350	Original	2	16	Johnson & Strong 2000
41	Arachnida	68	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
42	Arachnida	25	0.700	12.000	11.300	6.350	Original	2	30	Rogers *et al.* 1977
43	Arachnida	23	---	---	---	---	No Data	1	31	Sabo *et al.* 2002
44	Arachnida	99	1.500	9.600	8.100	5.550	Original	2	47	Wardhaugh 2013
45	Arachnida	92	4.000	7.000	3.000	5.500	Nentwig *et al*. 2019	2	3	Clausen 1983
46	Arachnida	63	6.000	13.000	7.000	8.750	Nentwig *et al*. 2019	2	3	Clausen 1983
47	Arachnida	38	7.000	11.000	4.000	8.750	Nentwig *et al*. 2019	2	3	Clausen 1983
48	Arachnida	193	5.500	8.750	3.250	7.667	Original	2	3	Clausen 1983
49	Arachnida	45	4.000	7.000	3.000	5.500	Nentwig *et al*. 2019	2	3	Clausen 1983
50	Arachnida	36	6.000	13.000	7.000	8.750	Nentwig *et al*. 2019	2	3	Clausen 1983
51	Arachnida	81	5.500	8.750	3.250	7.667	Original	2	3	Clausen 1983
52	Arachnida	26	2.500	11.100	8.600	6.800	Original	2	6	Edwards & Gabriel 1998
53	Arachnida	26	2.500	11.100	8.600	6.800	Original	2	6	Edwards & Gabriel 1998

54	Arachnida	27	2.200	8.500	6.300	5.500	Original	2	6	Edwards 1996
55	Arachnida	30	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
56	Arachnida	10	3.200	11.200	8.000	7.200	Original	2	6	Edwards & Gabriel 1998
57	Arachnida	10	3.200	11.200	8.000	7.200	Original	2	6	Edwards & Gabriel 1998
58	Arachnida	74	1.300	36.000	34.700	12.430	Original	1	13	Höfer & Ott 2009
59	Arachnida	74	1.300	36.000	34.700	12.430	Original	1	13	Höfer & Ott 2009
60	Arachnida	43	3.400	9.400	6.000	6.400	Original	2	6	Edwards & Gabriel 1998
61	Arachnida	43	3.400	9.400	6.000	6.400	Original	2	6	Edwards & Gabriel 1998
62	Arachnida	48	2.800	10.100	7.300	6.450	Original	2	6	Edwards 1996
63	Arachnida	15	1.500	1.700	0.200	1.600	Nentwig *et al.* 2019	2	3	Clausen 1983
64	Arachnida	43	2.500	5.400	2.900	3.950	Original	2	6	Edwards & Gabriel 1998
65	Arachnida	43	2.500	5.400	2.900	3.950	Original	2	6	Edwards & Gabriel 1998
66	Arachnida	23	1.500	5.500	4.000	3.500	Original	2	6	Edwards 1996
67	Arachnida	164	0.780	4.400	3.620	2.590	Original	1	19	Lang *et al.* 1997
68	Arachnida	29	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
69	Arachnida	68	3.000	12.000	9.000	7.500	Original	2	2	Breymeyer 1967
70	Arachnida	105	4.000	14.000	10.000	9.000	Original	2	2	Breymeyer 1967
71	Arachnida	83	4.000	16.800	12.800	10.400	Original	2	6	Edwards & Gabriel 1998
72	Arachnida	83	4.000	16.800	12.800	10.400	Original	2	6	Edwards & Gabriel 1998
73	Arachnida	19	2.000	23.500	21.500	12.750	Original	2	6	Edwards 1996
74	Arachnida	164	1.280	8.510	7.230	4.895	Original	1	19	Lang *et al.* 1997
75	Arachnida	68	0.670	4.300	3.630	1.460	Original	1	13	Höfer & Ott 2009
76	Arachnida	68	0.670	4.300	3.630	1.460	Original	1	13	Höfer & Ott 2009
77	Arachnida	79	---	---	---	---	No Data	2	3	Clausen 1983
78	Arachnida	79	---	---	---	---	No Data	2	3	Clausen 1983
79	Arachnida	31	2.900	12.500	9.600	7.700	Original	2	6	Edwards & Gabriel 1998
80	Arachnida	31	2.900	12.500	9.600	7.700	Original	2	6	Edwards & Gabriel 1998
81	Arachnida	26	2.000	7.000	5.000	4.500	Original	2	6	Edwards 1996

82	Arachnida	4	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
83	Arachnida	16	4.000	11.100	7.100	7.550	Original	2	6	Edwards & Gabriel 1998
84	Arachnida	16	4.000	11.100	7.100	7.550	Original	2	6	Edwards & Gabriel 1998
85	Arachnida	9	4.000	11.100	7.100	7.550	Original	2	6	Edwards 1996
86	Arachnida	86	3.400	10.800	7.400	7.100	Original	2	6	Edwards & Gabriel 1998
87	Arachnida	86	3.400	10.800	7.400	7.100	Original	2	6	Edwards & Gabriel 1998
88	Arachnida	24	4.000	10.100	6.100	7.050	Original	2	6	Edwards 1996
89	Arachnida	43	6.000	10.000	4.000	7.750	Nentwig *et al*. 2019	2	3	Clausen 1983
90	Arachnida	64	4.000	7.000	3.000	5.250	Nentwig *et al*. 2019	2	3	Clausen 1983
91	Arachnida	55	3.000	8.200	5.200	5.600	Original	2	6	Edwards & Gabriel 1998
92	Arachnida	55	3.000	8.200	5.200	5.600	Original	2	6	Edwards & Gabriel 1998
93	Arachnida	33	2.100	7.600	5.500	4.850	Original	2	6	Edwards 1996
94	Arachnida	52	2.600	8.200	5.600	5.400	Original	2	6	Edwards & Gabriel 1998
95	Arachnida	29	3.000	8.200	5.200	5.600	Original	2	6	Edwards & Gabriel 1998
96	Arachnida	52	2.600	8.200	5.600	5.400	Original	2	6	Edwards & Gabriel 1998
97	Arachnida	57	1.900	8.300	6.400	5.100	Original	2	6	Edwards 1996
98	Arachnida	10	4.900	8.600	3.700	6.750	Original	5	7	Ganihar 1997
99	Arachnida	53	2.000	7.000	5.000	3.500	Original	2	10	Henschel *et al.* 1996
100	Arachnida	10	2.600	6.400	3.800	4.500	Original	2	11	Hódar 1996
101	Arachnida	65	0.570	6.900	6.330	2.120	Original	1	13	Höfer & Ott 2009
102	Arachnida	65	0.570	6.900	6.330	2.120	Original	1	13	Höfer & Ott 2009
103	Arachnida	84	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
104	Arachnida	38	4.300	4.800	0.500	4.550	Van Duinen 2009-2018	2	23	McLaughlin *et al.* 2010
105	Arachnida	12	8.500	10.500	2.000	9.500	Van Duinen 2009-2018	2	23	McLaughlin *et al.* 2010
106	Arachnida	4	4.500	7.000	2.500	5.750	Van Duinen 2009-2018	2	23	McLaughlin *et al.* 2010
107	Arachnida	11	3.000	5.200	2.200	4.100	Van Duinen 2009-2018	2	23	McLaughlin *et al.* 2010
108	Arachnida	111	0.860	2.100	1.240	1.380	Original	1	13	Höfer & Ott 2009
109	Arachnida	111	0.860	2.100	1.240	1.380	Original	1	13	Höfer & Ott 2009

110	Arachnida	28	1.000	3.700	2.700	2.350	Original	2	16	Johnson & Strong 2000
111	Arachnida	22	1.500	2.100	0.600	1.800	Original	2	47	Wardhaugh 2013
112	Arachnida	7	10.200	26.750	16.550	18.475	Original	2	11	Hódar 1996
113	Chilopoda	38	4.000	47.000	43.000	25.500	Original	2	8	Gowing & Recher 1984
114	Chilopoda	10	10.000	81.000	71.000	45.500	Original	2	11	Hódar 1996
115	Chilopoda	49	3.900	28.000	24.100	15.950	Original	1	17	Klarner *et al.* 2017
116	Chilopoda	17	3.200	12.000	8.800	7.600	Original	1	18	Klarner *et al.* 2017
117	Chilopoda	60	5.412	31.600	26.188	19.861	Original	9	26	Ruiz-Lupión, D (unpublished)
118	Chilopoda	49	2.800	10.000	7.200	6.400	Original	1	19	Lang *et al.* 1997
119	Chilopoda	112	2.500	17.000	14.500	9.750	Original	9	46	Voigtländer 2000
120	Chilopoda	129	2.000	10.000	8.000	6.000	Original	9	46	Voigtländer 2000
121	Chilopoda	337	2.500	17.500	15.000	10.705	Original	9	46	Voigtländer 2007
122	Chilopoda	292	2.500	17.750	15.250	10.481	Original	9	46	Voigtländer 2007
123	Chilopoda	30	2.640	22.500	19.860	9.119	Original	9	27	Ruiz-Lupión, D (unpublished)
124	Chilopoda	10	13.000	48.000	35.000	30.500	Original	2	7	Ganihar 1997
125	Chilopoda	25	---	---	---	---	No Data	3	29	Richardson *et al.* 2000
126	Chilopoda	25	4.000	20.000	16.000	12.000	Original	2	7	Ganihar 1997
127	Diplopoda	10	11.000	47.000	36.000	29.000	Original	2	8	Gowing & Recher 1984
128	Diplopoda	10	11.000	39.000	28.000	25.000	Original	2	11	Hódar 1996
129	Diplopoda	62	---	---	---	---	No Data	3	29	Richardson *et al.* 2000
130	Diplopoda	500	12.000	80.000	68.000	46.000	Original	9	22	Mazantseva 1975
131	Diplopoda	300	18.000	44.000	26.000	31.000	Original	9	22	Mazantseva 1975
132	Diplopoda	25	---	---	---	20.000	VanDyk 2003-2019	2	23	McLaughlin *et al.* 2010
133	Diplopoda	91	14.000	25.000	11.000	19.500	Bon 2016	2	23	McLaughlin *et al.* 2010
134	Diplopoda	179	4.900	37.300	32.400	21.100	Original	9	41	Shinohara *et al.* 2007
135	Entognatha	10	1.160	2.480	1.320	1.820	Original	2	7	Ganihar 1997
136	Entognatha	33	1.700	3.850	2.150	2.775	Original	2	9	Gruner 2003
137	Entognatha	8	1.500	3.250	1.750	2.375	Original	2	11	Hódar 1996

138	Entognatha	4318	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
139	Entognatha	15	0.280	2.960	2.680	1.283	Original	3	24	Mercer *et al.* 2001
140	Entognatha	12	2.000	30.000	28.000	16.000	Original	3	43	Tanaka 1970
141	Entognatha	122	0.630	3.980	3.350	2.305	Original	8	44	Van Straalen 1989
142	Entognatha	58	0.684	5.409	4.725	2.238	Original	9	27	Ruiz-Lupión, D (unpublished)
143	Entognatha	1863	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
144	Entognatha	82	---	---	---	0.500	Original	3	28	Petersen 1975
145	Entognatha	57	---	---	---	0.480	Original	3	28	Petersen 1975
146	Entognatha	58	---	---	---	0.580	Original	3	28	Petersen 1975
147	Entognatha	34	---	---	---	0.630	Original	3	28	Petersen 1975
148	Entognatha	34	---	---	---	0.630	Original	3	28	Petersen 1975
149	Entognatha	27	---	---	---	0.630	Original	3	28	Petersen 1975
150	Entognatha	11	1.800	10.000	8.200	5.900	Original	3	43	Tanaka 1970
151	Entognatha	9	2.000	50.000	48.000	26.000	Original	3	43	Tanaka 1970
152	Entognatha	14	1.300	8.000	6.700	4.650	Original	3	43	Tanaka 1970
153	Entognatha	50	---	---	---	6.000	Hopkin 2019	3	28	Petersen 1975
154	Entognatha	92	0.830	3.800	2.970	2.315	Original	8	44	Van Straalen 1989
155	Entognatha	7	2.000	20.000	18.000	11.000	Original	3	43	Tanaka 1970
156	Entognatha	393	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
157	Entognatha	10	1.700	17.000	15.300	9.350	Original	3	43	Tanaka 1970
158	Entognatha	46	---	---	---	0.960	Original	3	28	Petersen 1975
159	Entognatha	26	---	---	---	1.000	Original	3	28	Petersen 1975
160	Entognatha	76	---	---	---	0.960	Original	3	28	Petersen 1975
161	Entognatha	41	---	---	---	1.000	Original	3	28	Petersen 1975
162	Entognatha	43	---	---	---	1.260	Original	3	28	Petersen 1975
163	Entognatha	26	---	---	---	1.260	Original	3	28	Petersen 1975
164	Entognatha	42	---	---	---	1.000	Original	3	28	Petersen 1975
165	Entognatha	23	---	---	---	1.260	Original	3	28	Petersen 1975

166	Entognatha	16	1.100	30.000	28.900	15.550	Original	3	43	Tanaka 1970
167	Entognatha	46	---	---	---	1.200	Palacios-Vargas & Salazar-Marínez 2014	3	28	Petersen 1975
168	Entognatha	23	---	---	---	1.000	Hopkin 2019 *T. elegans*	3	28	Petersen 1975
169	Entognatha	23	---	---	---	1.000	Hopkin 2019 *T. elegans*	3	28	Petersen 1975
170	Entognatha	2062	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
171	Entognatha	30	2.810	4.420	1.610	3.030	Original	9	45	Vannier 1973
172	Insecta	23	5.320	18.590	13.270	11.955	Original	2	33	Sample *et al.* 1993
173	Insecta	7	3.350	4.450	1.100	3.900	Original	2	9	Gruner 2003
174	Insecta	10	3.250	13.200	9.950	8.225	Original	2	11	Hódar 1996
175	Insecta	10	4.700	27.800	23.100	16.250	Original	2	11	Hódar 1996
176	Insecta	16	4.100	16.300	12.200	10.200	Original	2	9	Gruner 2003
177	Insecta	12	4.300	32.500	28.200	18.400	Original	2	11	Hódar 1996
178	Insecta	100	2.400	37.000	34.600	19.700	Original	1	15	Jarošik 1989
179	Insecta	167	2.880	24.000	21.120	13.440	Original	1	19	Lang *et al.* 1997
180	Insecta	76	4.167	32.260	28.093	18.214	Obtained from plots	9	21	Marcuzzi 1987
181	Insecta	524	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
182	Insecta	9	17.000	22.000	5.000	19.500	Roy & Comont 2019	2	23	McLaughlin *et al.* 2010
183	Insecta	10	3.000	4.000	1.000	3.500	Alford 2008	2	23	McLaughlin *et al.* 2010
184	Insecta	12	10.000	13.000	3.000	11.500	Alford 2008	2	23	McLaughlin *et al.* 2010
185	Insecta	6	---	---	---	12.000	VanDyk 2003-2019 *P. melanarius*	2	23	McLaughlin *et al.* 2010
186	Insecta	32	---	---	---	12.000	VanDyk 2003-2019 *P. melanarius*	2	23	McLaughlin *et al.* 2010
187	Insecta	16	---	---	---	12.000	VanDyk 2003-2019 *P. melanarius*	2	23	McLaughlin *et al.* 2010
188	Insecta	29	---	---	---	---	No Data	1	31	Sabo *et al.* 2002
189	Insecta	41	5.500	16.510	11.010	11.005	Original	2	33	Sample *et al.* 1993
190	Insecta	79	2.930	29.200	26.270	12.023	Original	9	34	Santos Gómez 2013
191	Insecta	272	2.930	20.890	17.960	10.805	Original	9	35	Santos Gómez 2013
192	Insecta	254	2.550	20.890	18.340	10.738	Original	9	36	Santos Gómez 2013
193	Insecta	178	2.930	18.470	15.540	10.783	Original	9	37	Santos Gómez 2013

194	Insecta	10	7.600	52.100	44.500	29.850	Original	2	11	Hódar 1996
195	Insecta	20	4.960	16.290	11.330	10.625	Original	2	33	Sample *et al.* 1993
196	Insecta	10	3.000	15.200	12.200	9.100	Original	2	11	Hódar 1996
197	Insecta	13	9.804	16.409	6.605	13.107	Obtained from plots	9	21	Marcuzzi 1987
198	Insecta	23	3.340	7.840	4.500	5.590	Original	2	33	Sample *et al.* 1993
199	Insecta	14	1.450	2.450	1.000	1.950	Original	2	9	Gruner 2003
200	Insecta	147	---	---	---	8.000	Original	3	1	Beaver & Baldwin 1975
201	Insecta	32	2.000	24.000	22.000	13.000	Original	2	4	Díaz & Díaz 1990
202	Insecta	175	1.200	22.000	20.800	11.600	Original	2	7	Ganihar 1997
203	Insecta	56	2.000	14.000	12.000	8.000	Original	2	8	Gowing & Recher 1984
204	Insecta	130	1.450	17.600	16.150	9.525	Original	2	9	Gruner 2003
205	Insecta	137	1.450	17.600	16.150	9.525	Original	2	9	Gruner 2003
206	Insecta	156	1.750	56.550	54.800	29.150	Original	2	11	Hódar 1996
207	Insecta	51	1.200	12.100	10.900	6.650	Original	2	16	Johnson & Strong 2000
208	Insecta	75	1.300	14.000	12.700	7.650	Original	2	16	Johnson & Strong 2000
209	Insecta	1083	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
210	Insecta	363	0.480	7.750	7.270	3.308	Original	3	24	Mercer *et al.* 2001
211	Insecta	575	---	---	---	---	No Data	3	29	Richardson *et al.* 2000
212	Insecta	151	0.900	34.000	33.100	17.450	Original	2	30	Rogers *et al.* 1977
213	Insecta	119	---	---	---	---	No Data	1	31	Sabo *et al.* 2002
214	Insecta	29	4.900	25.000	20.100	14.950	Original	7	32	Sage 1982
215	Insecta	29	4.900	25.000	20.100	14.950	Original	7	32	Sage 1982
216	Insecta	330	3.340	34.820	31.480	19.080	Original	2	33	Sample *et al.* 1993
217	Insecta	47	---	---	---	---	No Data	2	38	Schoener 1980
218	Insecta	150	---	---	---	---	No Data	2	39	Schoener 1980
219	Insecta	171	---	---	---	---	No Data	2	40	Schoener 1980
220	Insecta	132	1.400	25.000	23.600	13.200	Original	2	47	Wardhaugh 2013
221	Insecta	17	2.500	17.600	15.100	10.050	Original	2	9	Gruner 2003

222	Insecta	12	1.750	17.050	15.300	9.400	Original	2	11	Hódar 1996
223	Insecta	22	4.160	16.167	12.007	10.164	Obtained from plots	9	21	Marcuzzi 1987
224	Insecta	352	0.600	7.750	7.150	3.585	Original	3	24	Mercer *et al.* 2001
225	Insecta	235	3.060	8.360	5.300	6.180	Original	3	24	Mercer *et al.* 2001
226	Insecta	45	2.470	3.290	0.820	2.890	Original	3	24	Mercer *et al.* 2001
227	Insecta	21	3.530	4.590	1.060	4.050	Original	3	24	Mercer *et al.* 2001
228	Insecta	22	5.660	8.360	2.700	7.260	Original	3	24	Mercer *et al.* 2001
229	Insecta	29	3.930	5.570	1.640	4.540	Original	3	24	Mercer *et al.* 2001
230	Insecta	15	2.400	7.500	5.100	4.950	Original	2	30	Rogers *et al.* 1977
231	Insecta	33	5.640	16.940	11.300	11.290	Original	2	33	Sample *et al.* 1993
232	Insecta	10	4.200	13.600	9.400	8.900	Original	2	11	Hódar 1996
233	Insecta	10	8.100	56.550	48.450	32.325	Original	2	11	Hódar 1996
234	Insecta	22	3.000	4.500	1.500	3.750	Original	2	9	Gruner 2003
235	Insecta	10	4.150	32.500	28.350	18.325	Original	2	11	Hódar 1996
236	Insecta	7	17.083	27.083	10.000	22.083	Obtained from plots	9	21	Marcuzzi 1987
237	Insecta	27	2.240	24.790	22.550	14.515	Original	2	33	Sample *et al.* 1993
238	Insecta	10	2.000	28.000	26.000	15.000	Original	2	11	Hódar 1996
239	Insecta	133	2.200	3.600	1.400	7.900	Original	1	19	Lang *et al.* 1997
240	Insecta	11	5.947	8.563	2.616	7.255	Obtained from plots	9	21	Marcuzzi 1987
241	Insecta	328	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
242	Insecta	10	---	---	---	---	No Data	1	31	Sabo *et al.* 2002
243	Insecta	16	4.000	38.600	34.600	21.300	Original	2	11	Hódar 1996
244	Insecta	47	6.100	24.792	18.692	15.446	Obtained from plots	9	21	Marcuzzi 1987
245	Insecta	66	4.800	19.000	14.200	11.900	Original	2	30	Rogers *et al.* 1977
246	Insecta	159	3.069	7.653	4.584	5.361	Original	9	42	Sokoloff *et al.* 1999
247	Insecta	18	2.550	11.200	8.650	6.875	Original	2	9	Gruner 2003
248	Insecta	10	2.600	9.600	7.000	6.100	Original	2	11	Hódar 1996
249	Insecta	100	2.200	14.000	11.800	8.100	Original	2	47	Wardhaugh 2013

250	Insecta	8	7.000	22.000	15.000	14.500	Original	6	7	Ganihar 1997
251	Insecta	10	5.500	25.200	19.700	15.350	Original	2	11	Hódar 1996
252	Insecta	10	3.000	13.000	10.000	8.000	Original	2	4	Díaz & Díaz 1990
253	Insecta	25	2.370	13.500	11.130	7.935	Original	2	7	Ganihar 1997
254	Insecta	11	2.700	12.300	9.600	7.500	Original	2	11	Hódar 1996
255	Insecta	13	2.400	12.900	10.500	7.650	Original	7	32	Sage 1982
256	Insecta	13	---	---	---	---	No Data	2	38	Schoener 1980
257	Insecta	25	---	---	---	---	No Data	2	39	Schoener 1980
258	Insecta	20	---	---	---	---	No Data	2	40	Schoener 1980
259	Insecta	139	2.100	9.500	7.400	5.800	Original	2	47	Wardhaugh 2013
260	Insecta	10	6.000	13.000	7.000	9.500	Original	2	7	Ganihar 1997
261	Insecta	401	1.160	48.000	46.840	24.580	Original	4	7	Ganihar 1997
262	Insecta	10	3.000	10.000	7.000	6.500	Original	2	11	Hódar 1996
263	Insecta	10	5.000	34.000	29.000	19.500	Original	2	7	Ganihar 1997
264	Insecta	21	2.650	10.350	7.700	6.500	Original	2	9	Gruner 2003
265	Insecta	27	4.000	63.000	59.000	33.500	Original	2	11	Hódar 1996
266	Insecta	35	3.000	36.000	33.000	19.500	Original	2	30	Rogers *et al.* 1977
267	Insecta	42	---	---	---	---	No Data	1	31	Sabo *et al.* 2002
268	Insecta	36	4.600	60.000	55.400	32.300	Original	7	32	Sage 1982
269	Insecta	25	---	---	---	---	No Data	2	39	Schoener 1980
270	Insecta	10	---	---	---	---	No Data	2	40	Schoener 1980
271	Insecta	79	2.300	33.000	30.700	17.650	Original	2	47	Wardhaugh 2013
272	Insecta	40	1.500	3.150	1.650	2.325	Original	2	9	Gruner 2003
273	Insecta	6	1.200	3.000	1.800	2.100	Original	2	11	Hódar 1996
274	Malacostraca	10	2.440	9.000	6.560	5.720	Original	4	7	Ganihar 1997
275	Malacostraca	12	4.000	8.000	4.000	6.000	Original	2	8	Gowing & Recher 1984
276	Malacostraca	16	2.350	13.900	11.550	8.125	Original	2	9	Gruner 2003
277	Malacostraca	10	4.250	22.500	18.250	13.375	Original	2	11	Hódar 1996

278	Malacostraca	132	---	---	---	---	No Data	2	23	McLaughlin *et al.* 2010
279	Malacostraca	586	---	---	---	---	No Data	3	29	Richardson *et al.* 2000
280	Malacostraca	40	2.700	8.000	5.300	5.350	Original	2	47	Wardhaugh 2013
281	Malacostraca	82	---	---	---	13.000	VanDyk 2003-2019	2	23	McLaughlin *et al.* 2010
282	Malacostraca	22	---	---	---	17.000	VanDyk 2003-2019	2	23	McLaughlin *et al.* 2010
283	Malacostraca	12	---	---	---	8.000	VanDyk 2003-2019	2	23	McLaughlin *et al.* 2010

*Code: Identification number of the equation.
*Taxonomic classification for each specimen (Class).
*n: Sample size (number of individuals measured).
*min Length (mm): Length of the smallest individual.
*max Length (mm): Length of the largest individual.
*Range length (mm): max Length (mm) – min Length (mm).
*Mean length (mm): Average length of the individuals measured.
*Reference mean length: Origin of the measure of the Mean Length: 1) Original (from original bibliographic reference), 2) Obtained from plots of original bibliographic reference), 3) Other References (see below) and 4) No Data.
*Original equation: Type of equation used in the original study (Table S4).
*Site: Code of the point where field sampling of the original study was carried out by the authors in the Reference (Fig. 2, Table S3).
*Reference: Bibliographic reference.

Table S1: Database used to evaluate scaling factor *a* and allometric factor *b* (cont'd).

Code	Class	PCGM1	PCGM2	PCGM3	Feeding habits	Type of allometry	Latitude	Longitude	Altitude	MAT	MAP	NDVI	Original equation	Site	Reference
1	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	36.594	-2.448	925	14.3	474	0.252	2	11	Hódar 1996
2	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	51.409	5.588	95	9.8	814	0.595	9	20	LeBrun 1971
3	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	53.134	-8.261	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
4	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	-45.779	38.441	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
5	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	53.325	-113.314	613	3.0	452	0.412	9	25	Newton & Proctor 2013
6	Arachnida	-0.2750	0.0453	0.0083	Undefined	Evolutionary	38.463	-78.342	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
7	Arachnida	-0.3089	0.0389	-0.0143	Predator	Evolutionary	-48.003	39.641	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
8	Arachnida	-0.3089	0.0389	-0.0143	Predator	Evolutionary	52.172	-115.505	613	3.0	452	0.412	9	25	Newton & Proctor 2013
9	Arachnida	-0.1814	0.0825	0.0418	Decomposer	Evolutionary	52.505	-9.475	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
10	Arachnida	-0.1814	0.0825	0.0418	Decomposer	Evolutionary	-46.182	37.202	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
11	Arachnida	-0.1814	0.0825	0.0418	Decomposer	Evolutionary	52.230	-114.173	613	3.0	452	0.412	9	25	Newton & Proctor 2013
12	Arachnida	-0.1814	0.0825	0.0418	Decomposer	Evolutionary	38.898	-77.722	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
13	Arachnida	-0.2900	-0.0565	-0.0101	Predator	Evolutionary	-47.245	37.782	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
14	Arachnida	-0.2900	-0.0565	-0.0101	Predator	Evolutionary	53.611	-112.069	613	3.0	452	0.412	9	25	Newton & Proctor 2013
15	Arachnida	-0.0550	-0.0998	0.0291	Predator	Evolutionary	41.282	-71.233	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
16	Arachnida	-0.0550	-0.0998	0.0291	Predator	Evolutionary	40.409	-68.227	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
17	Arachnida	-0.0550	-0.0998	0.0291	Predator	Evolutionary	41.590	-71.088	23	9.8	1180	0.592	2	6	Edwards 1996
18	Arachnida	-0.0692	-0.0735	0.0600	Predator	Evolutionary	41.492	-72.298	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
19	Arachnida	-0.0692	-0.0735	0.0600	Predator	Evolutionary	41.837	-69.577	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
20	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	40.078	-2.239	1151	10.7	505	0.466	2	4	Díaz & Díaz 1990
21	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	40.202	-70.946	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
22	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	42.348	-68.480	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
23	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	41.825	-71.304	23	9.8	1180	0.592	2	6	Edwards 1996
24	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	14.753	73.764	75	27.2	2751	0.648	2	7	Ganihar 1997
25	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-36.080	149.108	760	11.1	737	0.673	2	8	Gowing & Recher 1984

26	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	19.244	-156.101	2577	9.6	871	0.381	2	9	Gruner 2003
27	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	50.502	9.731	289	9.0	646	0.571	2	10	Henschel *et al.* 1996
28	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	35.396	-3.934	925	14.3	474	0.252	2	11	Hódar 1996
29	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-24.007	-48.873	7	21.2	2108	0.808	1	12	Höfer & Ott 2009
30	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-26.355	-48.334	7	21.2	2108	0.808	1	12	Höfer & Ott 2009
31	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-1.513	-60.329	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
32	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-0.876	-58.118	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
33	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-2.371	-60.467	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
34	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	0.313	-60.636	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
35	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-1.574	-60.152	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
36	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-1.049	-61.558	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
37	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	0.382	-63.036	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
38	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-0.678	-59.126	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
39	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	18.260	-75.903	626	21.5	1869	0.756	2	16	Johnson & Strong 2000
40	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	18.887	-78.496	626	21.5	1869	0.756	2	16	Johnson & Strong 2000
41	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	51.625	-11.012	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
42	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	39.556	-77.765	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
43	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	39.132	-125.449	520	11.2	1568	0.812	1	31	Sabo *et al.* 2002
44	Arachnida	-0.0557	-0.0584	0.0458	Predator	Evolutionary	-16.062	145.217	27	25.5	2082	0.829	2	47	Wardhaugh 2013
45	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	55.954	10.519	72	7.9	620	0.588	2	3	Clausen 1983
46	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	57.389	11.373	72	7.9	620	0.588	2	3	Clausen 1983
47	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	55.554	12.243	72	7.9	620	0.588	2	3	Clausen 1983
48	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	56.044	11.934	72	7.9	620	0.588	2	3	Clausen 1983
49	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	55.550	10.482	72	7.9	620	0.588	2	3	Clausen 1983
50	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	54.102	12.362	72	7.9	620	0.588	2	3	Clausen 1983
51	Arachnida	-0.0251	-0.0840	0.0153	Predator	Ontogenetic	55.157	11.076	72	7.9	620	0.588	2	3	Clausen 1983
52	Arachnida	-0.0251	-0.0840	0.0153	Predator	Evolutionary	40.360	-71.689	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
53	Arachnida	-0.0251	-0.0840	0.0153	Predator	Evolutionary	39.892	-72.199	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998

54	Arachnida	-0.0251	-0.0840	0.0153	Predator	Evolutionary	40.513	-71.293	23	9.8	1180	0.592	2	6	Edwards 1996
55	Arachnida	-0.0251	-0.0840	0.0153	Predator	Evolutionary	51.279	-9.270	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
56	Arachnida	-0.0387	-0.1064	0.0453	Predator	Evolutionary	43.732	-69.935	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
57	Arachnida	-0.0387	-0.1064	0.0453	Predator	Evolutionary	43.850	-70.850	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
58	Arachnida	-0.0928	-0.0929	0.0493	Predator	Evolutionary	-0.770	-57.842	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
59	Arachnida	-0.0928	-0.0929	0.0493	Predator	Evolutionary	-2.742	-61.248	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
60	Arachnida	-0.0291	-0.0833	0.0455	Predator	Evolutionary	42.907	-71.158	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
61	Arachnida	-0.0291	-0.0833	0.0455	Predator	Evolutionary	41.245	-71.288	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
62	Arachnida	-0.0291	-0.0833	0.0455	Predator	Evolutionary	40.514	-70.303	23	9.8	1180	0.592	2	6	Edwards 1996
63	Arachnida	-0.0580	-0.0738	0.0644	Predator	Ontogenetic	55.413	10.941	72	7.9	620	0.588	2	3	Clausen 1983
64	Arachnida	-0.0580	-0.0738	0.0644	Predator	Evolutionary	42.289	-70.588	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
65	Arachnida	-0.0580	-0.0738	0.0644	Predator	Evolutionary	41.260	-71.018	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
66	Arachnida	-0.0580	-0.0738	0.0644	Predator	Evolutionary	41.519	-70.604	23	9.8	1180	0.592	2	6	Edwards 1996
67	Arachnida	-0.0580	-0.0738	0.0644	Predator	Evolutionary	48.312	10.790	519	8.0	932	0.525	1	19	Lang *et al.* 1997
68	Arachnida	-0.0580	-0.0738	0.0644	Predator	Evolutionary	50.908	-10.767	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
69	Arachnida	-0.0803	-0.0794	0.0694	Predator	Evolutionary	52.275	19.736	142	8.4	541	0.560	2	2	Breymeyer 1967
70	Arachnida	-0.0803	-0.0794	0.0694	Predator	Ontogenetic	52.612	18.291	142	8.4	541	0.560	2	2	Breymeyer 1967
71	Arachnida	-0.0803	-0.0794	0.0694	Predator	Evolutionary	42.704	-70.634	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
72	Arachnida	-0.0803	-0.0794	0.0694	Predator	Evolutionary	42.235	-70.843	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
73	Arachnida	-0.0803	-0.0794	0.0694	Predator	Evolutionary	42.939	-70.455	23	9.8	1180	0.592	2	6	Edwards 1996
74	Arachnida	-0.0803	-0.0794	0.0694	Predator	Evolutionary	48.767	10.217	519	8.0	932	0.525	1	19	Lang *et al.* 1997
75	Arachnida	-0.0959	-0.1036	0.0548	Predator	Evolutionary	-0.593	-58.821	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
76	Arachnida	-0.0959	-0.1036	0.0548	Predator	Evolutionary	-0.097	-59.568	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
77	Arachnida	-0.0670	-0.0061	0.0493	Predator	Ontogenetic	56.355	10.776	72	7.9	620	0.588	2	3	Clausen 1983
78	Arachnida	-0.0670	-0.0061	0.0493	Predator	Ontogenetic	54.226	11.366	72	7.9	620	0.588	2	3	Clausen 1983
79	Arachnida	-0.0670	-0.0061	0.0493	Predator	Evolutionary	40.651	-69.119	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
80	Arachnida	-0.0670	-0.0061	0.0493	Predator	Evolutionary	41.860	-70.452	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
81	Arachnida	-0.0670	-0.0061	0.0493	Predator	Evolutionary	41.662	-68.971	23	9.8	1180	0.592	2	6	Edwards 1996

82	Arachnida	-0.0670	-0.0061	0.0493	Predator	Evolutionary	52.590	-9.181	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
83	Arachnida	-0.0414	-0.0451	0.0238	Predator	Evolutionary	42.464	-71.327	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
84	Arachnida	-0.0414	-0.0451	0.0238	Predator	Evolutionary	42.145	-68.607	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
85	Arachnida	-0.0414	-0.0451	0.0238	Predator	Evolutionary	41.897	-70.289	23	9.8	1180	0.592	2	6	Edwards 1996
86	Arachnida	-0.0467	-0.0673	-0.0070	Predator	Evolutionary	39.589	-70.445	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
87	Arachnida	-0.0467	-0.0673	-0.0070	Predator	Evolutionary	41.848	-71.506	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
88	Arachnida	-0.0467	-0.0673	-0.0070	Predator	Evolutionary	42.889	-69.901	23	9.8	1180	0.592	2	6	Edwards 1996
89	Arachnida	-0.0259	-0.0865	0.0098	Predator	Ontogenetic	55.339	12.048	72	7.9	620	0.588	2	3	Clausen 1983
90	Arachnida	-0.0414	0.0813	0.0670	Predator	Ontogenetic	55.032	12.075	72	7.9	620	0.588	2	3	Clausen 1983
91	Arachnida	-0.0414	0.0813	0.0670	Predator	Evolutionary	42.958	-69.313	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
92	Arachnida	-0.0414	0.0813	0.0670	Predator	Evolutionary	42.921	-72.149	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
93	Arachnida	-0.0414	0.0813	0.0670	Predator	Evolutionary	41.806	-70.545	23	9.8	1180	0.592	2	6	Edwards 1996
94	Arachnida	-0.0688	0.0437	0.1115	Predator	Evolutionary	41.907	-70.081	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
95	Arachnida	-0.0688	0.0437	0.1115	Predator	Evolutionary	41.738	-70.564	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
96	Arachnida	-0.0688	0.0437	0.1115	Predator	Evolutionary	42.182	-70.572	23	9.8	1180	0.592	2	6	Edwards & Gabriel 1998
97	Arachnida	-0.0688	0.0437	0.1115	Predator	Evolutionary	41.430	-69.436	23	9.8	1180	0.592	2	6	Edwards 1996
98	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	15.507	73.847	75	27.2	2751	0.648	5	7	Ganihar 1997
99	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	49.425	9.766	289	9.0	646	0.571	2	10	Henschel *et al.* 1996
100	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	37.022	-4.022	925	14.3	474	0.252	2	11	Hódar 1996
101	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	-1.134	-60.140	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
102	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	-0.598	-61.475	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
103	Arachnida	-0.1565	0.1771	0.0323	Decomposer	Evolutionary	51.975	-10.318	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
104	Arachnida	-0.1424	0.2013	-0.0131	Decomposer	Ontogenetic	52.452	-8.034	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
105	Arachnida	-0.1424	0.2013	-0.0131	Decomposer	Ontogenetic	51.503	-8.728	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
106	Arachnida	-0.1424	0.2013	-0.0131	Decomposer	Ontogenetic	50.561	-9.556	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
107	Arachnida	-0.1706	0.1529	0.0777	Decomposer	Ontogenetic	51.653	-7.945	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
108	Arachnida	0.0221	0.0620	0.0705	Predator	Evolutionary	0.877	-60.330	198	26.5	2346	0.800	1	13	Höfer & Ott 2009
109	Arachnida	0.0221	0.0620	0.0705	Predator	Evolutionary	-2.132	-59.824	198	26.5	2346	0.800	1	13	Höfer & Ott 2009

110	Arachnida	0.0221	0.0620	0.0705	Predator	Evolutionary	17.428	-76.938	626	21.5	1869	0.756	2	16	Johnson & Strong 2000
111	Arachnida	0.0221	0.0620	0.0705	Predator	Evolutionary	-15.861	147.099	27	25.5	2082	0.829	2	47	Wardhaugh 2013
112	Arachnida	0.2687	0.0739	-0.2177	Predator	Evolutionary	38.682	-4.219	925	14.3	474	0.252	2	11	Hódar 1996
113	Chilopoda	0.3309	-0.0615	0.0367	Predator	Evolutionary	-34.463	149.190	760	11.1	737	0.673	2	8	Gowing & Recher 1984
114	Chilopoda	0.3309	-0.0615	0.0367	Predator	Evolutionary	37.554	-3.421	925	14.3	474	0.252	2	11	Hódar 1996
115	Chilopoda	0.3728	-0.0694	0.0162	Predator	Evolutionary	-0.518	103.728	67	26.7	2828	0.787	1	17	Klarner *et al.* 2017
116	Chilopoda	0.3309	-0.0615	0.0367	Predator	Evolutionary	-2.543	103.096	50	26.8	2522	0.805	1	18	Klarner *et al.* 2017
117	Chilopoda	0.3728	-0.0694	0.0162	Predator	Evolutionary	43.593	-3.052	761	10.7	859	0.572	9	26	Ruiz-Lupión, D (unpublished)
118	Chilopoda	0.3250	-0.0522	0.0156	Predator	Ontogenetic	48.754	10.289	519	8.0	932	0.525	1	19	Lang *et al.* 1997
119	Chilopoda	0.3179	-0.0492	0.0194	Predator	Ontogenetic	51.475	16.004	224	8.2	632	0.579	9	46	Voigtländer 2000
120	Chilopoda	0.3179	-0.0492	0.0194	Predator	Ontogenetic	52.490	15.404	224	8.2	632	0.579	9	46	Voigtländer 2000
121	Chilopoda	0.3179	-0.0492	0.0194	Predator	Ontogenetic	50.417	15.450	224	8.2	632	0.579	9	46	Voigtländer 2007
122	Chilopoda	0.3179	-0.0492	0.0194	Predator	Ontogenetic	52.168	13.726	224	8.2	632	0.579	9	46	Voigtländer 2007
123	Chilopoda	0.3214	-0.0507	0.0175	Predator	Evolutionary	44.056	-6.331	332	12.8	773	0.693	9	27	Ruiz-Lupión, D (unpublished)
124	Chilopoda	0.3330	-0.0815	0.0865	Predator	Evolutionary	14.812	74.379	75	27.2	2751	0.648	2	7	Ganihar 1997
125	Chilopoda	0.3330	-0.0815	0.0865	Predator	Evolutionary	17.157	-67.160	1143	18.2	2892	0.691	3	29	Richardson *et al.* 2000
126	Chilopoda	0.3056	-0.0552	0.0460	Predator	Evolutionary	14.643	73.693	75	27.2	2751	0.648	2	7	Ganihar 1997
127	Diplopoda	0.3464	-0.0352	0.0335	Decomposer	Evolutionary	-37.319	151.096	760	11.1	737	0.673	2	8	Gowing & Recher 1984
128	Diplopoda	0.3464	-0.0352	0.0335	Decomposer	Evolutionary	35.788	-5.184	925	14.3	474	0.252	2	11	Hódar 1996
129	Diplopoda	0.3464	-0.0352	0.0335	Decomposer	Evolutionary	17.811	-65.769	1143	18.2	2892	0.691	3	29	Richardson *et al.* 2000
130	Diplopoda	0.3318	-0.0795	0.1187	Decomposer	Ontogenetic	56.005	37.790	147	4.9	678	0.467	9	22	Mazantseva 1975
131	Diplopoda	0.3318	-0.0795	0.1187	Decomposer	Ontogenetic	53.053	36.432	147	4.9	678	0.467	9	22	Mazantseva 1975
132	Diplopoda	0.3318	-0.0795	0.1187	Decomposer	Ontogenetic	52.798	-9.155	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
133	Diplopoda	0.3496	0.0059	-0.0175	Decomposer	Ontogenetic	51.580	-7.704	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
134	Diplopoda	0.3578	-0.0320	-0.0007	Decomposer	Ontogenetic	27.726	128.608	69	22.1	2191	0.681	9	41	Shinohara *et al.* 2007
135	Entognatha	-0.1371	-0.1143	-0.0563	Decomposer	Evolutionary	14.136	74.312	75	27.2	2751	0.648	2	7	Ganihar 1997
136	Entognatha	-0.1371	-0.1143	-0.0563	Decomposer	Evolutionary	20.170	-155.533	2577	9.6	871	0.381	2	9	Gruner 2003
137	Entognatha	-0.1371	-0.1143	-0.0563	Decomposer	Evolutionary	38.019	-3.576	925	14.3	474	0.252	2	11	Hódar 1996

138	Entognatha	-0.1371	-0.1143	-0.0563	Decomposer	Evolutionary	52.617	-8.433	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
139	Entognatha	-0.1371	-0.1143	-0.0563	Decomposer	Evolutionary	-47.856	38.177	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
140	Entognatha	-0.1460	-0.1187	-0.1225	Decomposer	Evolutionary	33.369	131.761	78	16.1	1995	0.613	3	43	Tanaka 1970
141	Entognatha	-0.1460	-0.1187	-0.1225	Decomposer	Ontogenetic	52.265	4.095	-2	9.1	779	0.581	8	44	Van Straalen 1989
142	Entognatha	-0.1532	-0.1446	-0.0809	Decomposer	Evolutionary	43.110	-3.839	332	12.8	773	0.693	9	27	Ruiz-Lupión, D (unpublished)
143	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Evolutionary	52.061	-10.074	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
144	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	55.521	6.043	70	7.4	841	0.600	3	28	Petersen 1975
145	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	56.345	6.792	70	7.4	841	0.600	3	28	Petersen 1975
146	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	53.689	8.941	70	7.4	841	0.600	3	28	Petersen 1975
147	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	56.179	9.691	70	7.4	841	0.600	3	28	Petersen 1975
148	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	55.271	8.143	70	7.4	841	0.600	3	28	Petersen 1975
149	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Static	54.892	8.246	70	7.4	841	0.600	3	28	Petersen 1975
150	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Ontogenetic	32.522	133.371	78	16.1	1995	0.613	3	43	Tanaka 1970
151	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Ontogenetic	33.527	130.905	78	16.1	1995	0.613	3	43	Tanaka 1970
152	Entognatha	-0.1664	-0.1850	-0.0402	Decomposer	Ontogenetic	32.935	131.425	78	16.1	1995	0.613	3	43	Tanaka 1970
153	Entognatha	-0.1472	-0.1302	-0.0806	Decomposer	Ontogenetic	56.158	10.195	70	7.4	841	0.600	3	28	Petersen 1975
154	Entognatha	-0.1472	-0.1302	-0.0806	Decomposer	Ontogenetic	52.885	7.046	-2	9.1	779	0.581	8	44	Van Straalen 1989
155	Entognatha	-0.1418	-0.0726	-0.0787	Decomposer	Ontogenetic	30.478	131.498	78	16.1	1995	0.613	3	43	Tanaka 1970
156	Entognatha	-0.1960	-0.0016	-0.0553	Decomposer	Evolutionary	51.907	-9.368	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
157	Entognatha	-0.1960	-0.0016	-0.0553	Decomposer	Ontogenetic	31.479	131.071	78	16.1	1995	0.613	3	43	Tanaka 1970
158	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	56.348	8.385	70	7.4	841	0.600	3	28	Petersen 1975
159	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	55.784	11.739	70	7.4	841	0.600	3	28	Petersen 1975
160	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	54.932	8.203	70	7.4	841	0.600	3	28	Petersen 1975
161	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	56.048	9.645	70	7.4	841	0.600	3	28	Petersen 1975
162	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	54.860	9.785	70	7.4	841	0.600	3	28	Petersen 1975
163	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	54.709	8.199	70	7.4	841	0.600	3	28	Petersen 1975
164	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	55.832	9.681	70	7.4	841	0.600	3	28	Petersen 1975
165	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Static	56.325	10.136	70	7.4	841	0.600	3	28	Petersen 1975

166	Entognatha	-0.0908	-0.1501	0.0132	Decomposer	Ontogenetic	30.654	131.075	78	16.1	1995	0.613	3	43	Tanaka 1970
167	Entognatha	-0.0712	-0.1418	-0.0300	Decomposer	Ontogenetic	55.412	9.194	70	7.4	841	0.600	3	28	Petersen 1975
168	Entognatha	-0.2155	0.0995	-0.0108	Decomposer	Ontogenetic	55.301	10.590	70	7.4	841	0.600	3	28	Petersen 1975
169	Entognatha	-0.2155	0.0995	-0.0108	Decomposer	Ontogenetic	57.189	9.330	70	7.4	841	0.600	3	28	Petersen 1975
170	Entognatha	-0.1358	0.1080	0.0619	Decomposer	Evolutionary	50.163	-6.426	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
171	Entognatha	-0.1358	0.1080	0.0619	Decomposer	Ontogenetic	49.126	3.480	45	11.3	634	0.515	9	45	Vannier 1973
172	Insecta	0.0650	0.0132	0.1052	Decomposer	Evolutionary	34.946	-77.234	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
173	Insecta	0.0530	0.0365	0.1318	Herbivore	Evolutionary	19.223	-155.346	2577	9.6	871	0.381	2	9	Gruner 2003
174	Insecta	-0.0609	0.0555	0.0878	Decomposer	Evolutionary	37.425	-3.093	925	14.3	474	0.252	2	11	Hódar 1996
175	Insecta	0.1027	0.0954	-0.0288	Herbivore	Evolutionary	37.797	-1.473	925	14.3	474	0.252	2	11	Hódar 1996
176	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	20.529	-154.249	2577	9.6	871	0.381	2	9	Gruner 2003
177	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	39.110	-3.235	925	14.3	474	0.252	2	11	Hódar 1996
178	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	49.728	16.332	204	9.0	487	0.475	1	15	Jarošik 1989
179	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	49.287	12.203	519	8.0	932	0.525	1	19	Lang *et al.* 1997
180	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	44.410	15.206	0	16.2	558	0.454	9	21	Marcuzzi 1987
181	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	50.996	-9.233	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
182	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	51.573	-8.418	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
183	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	53.327	-8.395	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
184	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	52.265	-9.477	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
185	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	53.193	-8.900	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
186	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	52.291	-10.302	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
187	Insecta	-0.0114	0.0126	0.0453	Predator	Ontogenetic	52.376	-8.634	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
188	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	38.612	-122.609	520	11.2	1568	0.812	1	31	Sabo *et al.* 2002
189	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	36.515	-76.017	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
190	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	29.392	-16.146	665	16.2	510	0.334	9	34	Santos Gómez 2013
191	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	27.170	-18.664	781	15.6	525	0.334	9	35	Santos Gómez 2013
192	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	27.817	-16.289	1496	12.8	511	0.478	9	36	Santos Gómez 2013
193	Insecta	-0.0114	0.0126	0.0453	Predator	Evolutionary	27.218	-17.550	1753	11.9	507	0.426	9	37	Santos Gómez 2013

194	Insecta	0.1239	0.0972	-0.1709	Herbivore	Evolutionary	35.654	-3.250	925	14.3	474	0.252	2	11	Hódar 1996
195	Insecta	0.1239	0.0972	-0.1709	Herbivore	Evolutionary	39.648	-78.198	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
196	Insecta	-0.0284	0.1725	0.0439	Herbivore	Evolutionary	38.188	-0.828	925	14.3	474	0.252	2	11	Hódar 1996
197	Insecta	-0.0284	0.1725	0.0439	Herbivore	Evolutionary	42.170	16.352	0	16.2	558	0.454	9	21	Marcuzzi 1987
198	Insecta	-0.0284	0.1725	0.0439	Herbivore	Evolutionary	38.336	-78.169	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
199	Insecta	-0.0247	0.1065	0.0139	Decomposer	Evolutionary	17.740	-153.845	2577	9.6	871	0.381	2	9	Gruner 2003
200	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	38.108	-107.368	3040	0.8	435	0.367	3	1	Beaver & Baldwin 1975
201	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	39.262	-1.520	1151	10.7	505	0.466	2	4	Díaz & Díaz 1990
202	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	15.466	73.787	75	27.2	2751	0.648	2	7	Ganihar 1997
203	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	-35.809	149.379	760	11.1	737	0.673	2	8	Gowing & Recher 1984
204	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	20.232	-155.782	2577	9.6	871	0.381	2	9	Gruner 2003
205	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	20.936	-156.615	2577	9.6	871	0.381	2	9	Gruner 2003
206	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	37.138	-3.369	925	14.3	474	0.252	2	11	Hódar 1996
207	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	18.006	-76.585	626	21.5	1869	0.756	2	16	Johnson & Strong 2000
208	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	19.543	-76.118	626	21.5	1869	0.756	2	16	Johnson & Strong 2000
209	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	51.809	-8.269	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
210	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	-46.370	37.396	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
211	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	17.124	-68.032	1143	18.2	2892	0.691	3	29	Richardson *et al.* 2000
212	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	36.893	-75.550	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
213	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	40.593	-124.877	520	11.2	1568	0.812	1	31	Sabo *et al.* 2002
214	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	28.914	-97.237	144	20.2	807	0.514	7	32	Sage 1982
215	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	29.836	-95.578	144	20.2	807	0.514	7	32	Sage 1982
216	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	37.651	-77.706	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
217	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	42.922	-71.285	11	9.4	1147	0.574	2	38	Schoener 1980
218	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	10.966	-85.816	87	26.7	1678	0.669	2	39	Schoener 1980
219	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	9.971	-83.826	274	25.0	4292	0.804	2	40	Schoener 1980
220	Insecta	0.0184	0.0828	-0.0117	Undefined	Evolutionary	-16.418	145.425	27	25.5	2082	0.829	2	47	Wardhaugh 2013
221	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	20.609	-156.276	2577	9.6	871	0.381	2	9	Gruner 2003

222	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	39.509	-3.589	925	14.3	474	0.252	2	11	Hódar 1996
223	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	43.185	15.248	0	16.2	558	0.454	9	21	Marcuzzi 1987
224	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	-44.391	35.616	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
225	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	-46.402	37.885	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
226	Insecta	0.0087	0.0782	-0.0252	Herbivore	Static	-48.429	38.295	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
227	Insecta	0.0087	0.0782	-0.0252	Herbivore	Static	-46.409	36.162	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
228	Insecta	0.0087	0.0782	-0.0252	Herbivore	Static	-45.395	40.355	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
229	Insecta	0.0087	0.0782	-0.0252	Herbivore	Static	-45.915	38.629	846	1.7	2644	0.475	3	24	Mercer *et al.* 2001
230	Insecta	0.0087	0.0782	-0.0252	Herbivore	Evolutionary	37.501	-78.366	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
231	Insecta	0.0536	0.0050	-0.0637	Herbivore	Evolutionary	37.414	-77.808	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
232	Insecta	-0.1197	0.2897	-0.0749	Predator	Evolutionary	36.770	-3.647	925	14.3	474	0.252	2	11	Hódar 1996
233	Insecta	0.0848	-0.0060	-0.0193	Predator	Evolutionary	38.616	-4.009	925	14.3	474	0.252	2	11	Hódar 1996
234	Insecta	-0.0797	0.1797	-0.0745	Decomposer	Evolutionary	20.866	-158.419	2577	9.6	871	0.381	2	9	Gruner 2003
235	Insecta	0.0355	0.0346	0.0240	Decomposer	Evolutionary	39.316	-3.755	925	14.3	474	0.252	2	11	Hódar 1996
236	Insecta	-0.0615	0.1452	0.0323	Decomposer	Evolutionary	41.460	17.162	0	16.2	558	0.454	9	21	Marcuzzi 1987
237	Insecta	-0.0615	0.1452	0.0323	Decomposer	Evolutionary	35.688	-78.589	19	14.2	1095	0.590	2	33	Sample *et al.* 1993
238	Insecta	0.1537	0.0095	-0.2147	Predator	Evolutionary	38.181	-4.853	925	14.3	474	0.252	2	11	Hódar 1996
239	Insecta	0.1537	0.0095	-0.2147	Predator	Evolutionary	47.833	11.459	519	8.0	932	0.525	1	19	Lang *et al.* 1997
240	Insecta	0.1537	0.0095	-0.2147	Predator	Evolutionary	41.290	14.691	0	16.2	558	0.454	9	21	Marcuzzi 1987
241	Insecta	0.1537	0.0095	-0.2147	Predator	Evolutionary	51.858	-8.605	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
242	Insecta	0.1537	0.0095	-0.2147	Predator	Evolutionary	38.726	-123.684	520	11.2	1568	0.812	1	31	Sabo *et al.* 2002
243	Insecta	-0.0615	0.1452	0.0323	Decomposer	Evolutionary	36.671	-2.324	925	14.3	474	0.252	2	11	Hódar 1996
244	Insecta	0.0355	0.0346	0.0240	Decomposer	Evolutionary	42.082	13.716	0	16.2	558	0.454	9	21	Marcuzzi 1987
245	Insecta	0.0355	0.0346	0.0240	Decomposer	Evolutionary	38.457	-76.913	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
246	Insecta	0.0355	0.0346	0.0240	Decomposer	Static	37.869	-119.137	1264	13.2	166	0.170	9	42	Sokoloff *et al.* 1999
247	Insecta	0.0963	0.1499	-0.0538	Decomposer	Evolutionary	20.625	-156.302	2577	9.6	871	0.381	2	9	Gruner 2003
248	Insecta	0.0963	0.1499	-0.0538	Decomposer	Evolutionary	36.405	-2.375	925	14.3	474	0.252	2	11	Hódar 1996
249	Insecta	0.0963	0.1499	-0.0538	Decomposer	Evolutionary	-17.314	145.341	27	25.5	2082	0.829	2	47	Wardhaugh 2013

250	Insecta	-0.0600	-0.1466	-0.0384	Predator	Evolutionary	15.654	74.271	75	27.2	2751	0.648	6	7	Ganihar 1997
251	Insecta	-0.0600	-0.1466	-0.0384	Predator	Evolutionary	36.291	-2.592	925	14.3	474	0.252	2	11	Hódar 1996
252	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	42.391	-3.095	1151	10.7	505	0.466	2	4	Díaz & Díaz 1990
253	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	15.280	70.333	75	27.2	2751	0.648	2	7	Ganihar 1997
254	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	36.466	-3.232	925	14.3	474	0.252	2	11	Hódar 1996
255	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	28.918	-98.541	144	20.2	807	0.514	7	32	Sage 1982
256	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	43.075	-69.676	11	9.4	1147	0.574	2	38	Schoener 1980
257	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	9.250	-83.507	87	26.7	1678	0.669	2	39	Schoener 1980
258	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	10.792	-84.040	274	25.0	4292	0.804	2	40	Schoener 1980
259	Insecta	-0.1401	-0.2325	-0.0070	Omnivore	Evolutionary	-15.858	146.948	27	25.5	2082	0.829	2	47	Wardhaugh 2013
260	Insecta	-0.0471	-0.1016	-0.1795	Decomposer	Evolutionary	15.122	74.713	75	27.2	2751	0.648	2	7	Ganihar 1997
261	Insecta	0.0452	0.0056	-0.0942	Undefined	Evolutionary	16.513	75.581	75	27.2	2751	0.648	4	7	Ganihar 1997
262	Insecta	-0.0471	-0.1016	-0.1795	Decomposer	Evolutionary	36.985	-3.726	925	14.3	474	0.252	2	11	Hódar 1996
263	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	15.348	72.699	75	27.2	2751	0.648	2	7	Ganihar 1997
264	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	20.018	-156.083	2577	9.6	871	0.381	2	9	Gruner 2003
265	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	40.264	-2.461	925	14.3	474	0.252	2	11	Hódar 1996
266	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	39.434	-76.434	63	13.0	1032	0.618	2	30	Rogers *et al.* 1977
267	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	40.957	-124.134	520	11.2	1568	0.812	1	31	Sabo *et al.* 2002
268	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	29.995	-100.079	144	20.2	807	0.514	7	32	Sage 1982
269	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	10.937	-87.171	87	26.7	1678	0.669	2	39	Schoener 1980
270	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	11.590	-83.650	274	25.0	4292	0.804	2	40	Schoener 1980
271	Insecta	0.0994	0.0135	-0.1905	Omnivore	Evolutionary	-15.621	146.501	27	25.5	2082	0.829	2	47	Wardhaugh 2013
272	Insecta	-0.1059	-0.1209	-0.0251	Decomposer	Evolutionary	18.267	-155.934	2577	9.6	871	0.381	2	9	Gruner 2003
273	Insecta	-0.1059	-0.1209	-0.0251	Decomposer	Evolutionary	39.001	-2.059	925	14.3	474	0.252	2	11	Hódar 1996
274	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	16.034	74.630	75	27.2	2751	0.648	4	7	Ganihar 1997
275	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	-37.616	150.493	760	11.1	737	0.673	2	8	Gowing & Recher 1984
276	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	18.636	-154.221	2577	9.6	871	0.381	2	9	Gruner 2003
277	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	38.483	-4.122	925	14.3	474	0.252	2	11	Hódar 1996

278	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	51.751	-10.195	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
279	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	17.322	-65.886	1143	18.2	2892	0.691	3	29	Richardson *et al.* 2000
280	Malacostraca	0.2189	0.1618	0.0514	Decomposer	Evolutionary	-14.497	146.331	27	25.5	2082	0.829	2	47	Wardhaugh 2013
281	Malacostraca	0.2076	0.1657	0.0652	Decomposer	Ontogenetic	51.273	-9.897	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
282	Malacostraca	0.2303	0.1579	0.0376	Decomposer	Ontogenetic	52.208	-9.276	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010
283	Malacostraca	0.2303	0.1579	0.0376	Decomposer	Ontogenetic	52.654	-7.940	71	10.1	1185	0.771	2	23	McLaughlin *et al.* 2010

*Code: Identification number of the equation.
*Taxonomic classification for each specimen (Class).
*PCGM1: It is the first shape principal component and it represents the slenderness with reduction of cephalic area (Fig. S2, Fig. S3, Fig. S4, Fig. S5, Fig. S6).
*PCGM2: It is the second shape principal componet and it represents the body thickness (Fig. S2, Fig. S3, Fig. S4, Fig. S5, Fig. S6).
*PCGM3: It is the third shape principal component and it represents the relative abdomen volume (Fig. S2, Fig. S3, Fig. S4, Fig. S5, Fig. S6).
*Feeding habits: Arthropods have been classified in 5 categories according to their feedin habits: 1) Decomposer, 2) Herbivores, 3) Omnivores, 4) Predators and 5) Undefined (Fig. S7).
*Type of allomety: Type of Mass-Length equation: 1) Static (intraspecific juvenile and intraspecific adult), 2) ontogenetic (intraspecific multi-instar) and 3) evolutionary (interspecific adult and interspecific multi-instar) (Fig. S8).
*Latitude: In sexagesimal degrees (e.g.: 52.135° in the Northern hemisphere or -52.135° in the Southern hemisphere).
*Longitude: In sexagesimal degrees (e.g.: 74.120° in the Eastern hemisphere or -74.120° in the Western Hemisphere).
*Altitude: In meters above sea level (m).
*MAT: Mean annual temperature in Celsius degrees (°C).
*MAP: Mean annual precipitation in milimeters (mm).
*NDVI: Normalized difference vegetation index varies between -1.0 and 1.0. Negative values correspond to wáter, negative values close to zero correspond to áreas of rock, sand or snow and positiva values represents vegetation.
*Original equation: Type of equation used in the original study (Table S4).
*Site: Code of the point where field sampling of the original study was carried out by the authors in the Reference (Fig. 2, Table S3).
*Reference: Bibliographic reference.

Table S1: Database used to evaluate scaling factor *a* and allometric factor *b* (cont'd).

Code	Group1	Group2	Group3	Class	Subclass	Infraclass	Superorder	Order	Suborder	Family	Genus	Species
1	Acari	Acari	Acari	Arachnida	Micrura	Acari	---	---	---	---	---	---
2	Acari	Acari	Acari	Arachnida	Micrura	Acari	---	---	---	---	---	---
3	Acari	Acari	Acari	Arachnida	Micrura	Acari	---	---			---	---
4	Acari	Acari	Acari	Arachnida	Micrura	Acari	---	---	---	---	---	---
5	Acari	Acari	Acari	Arachnida	Micrura	Acari	Acariformes	---	---	---	---	---
6	Acari	Acari	Acari	Arachnida	Micrura	Acari	---	---	---	---	---	---
7	Acari	Mesostigmata	Mesostigmata	Arachnida	Micrura	Acari	Parasitiformes	Mesostigmata	---	---	---	---
8	Acari	Mesostigmata	Mesostigmata	Arachnida	Micrura	Acari	Parasitiformes	Mesostigmata	---	---	---	---
9	Acari	Oribatida	Sarcoptiformes	Arachnida	Micrura	Acari	Acariformes	Sarcoptiformes	Oribatida	---	---	---
10	Acari	Oribatida	Sarcoptiformes	Arachnida	Micrura	Acari	Acariformes	Sarcoptiformes	Oribatida	---	---	---
11	Acari	Oribatida	Sarcoptiformes	Arachnida	Micrura	Acari	Acariformes	Sarcoptiformes	Oribatida	---	---	---
12	Acari	Oribatida	Sarcoptiformes	Arachnida	Micrura	Acari	Acariformes	Sarcoptiformes	Oribatida	---	---	---
13	Acari	Prostigmata	Trombidiformes	Arachnida	Micrura	Acari	Acariformes	Trombidiformes	Prostigmata	---	---	---
14	Acari	Prostigmata	Trombidiformes	Arachnida	Micrura	Acari	Acariformes	Trombidiformes	Prostigmata	---	---	---
15	Araneae	Araneae	Agelenidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Agelenidae	---	---
16	Araneae	Araneae	Agelenidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Agelenidae	---	---
17	Araneae	Araneae	Agelenidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Agelenidae	---	---
18	Araneae	Araneae	Amaurobiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Amaurobiidae	---	---
19	Araneae	Araneae	Amaurobiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Amaurobiidae	---	---
20	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
21	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
22	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
23	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
24	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
25	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---

26	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
27	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
28	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
29	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
30	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
31	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
32	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
33	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
34	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
35	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
36	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
37	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
38	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
39	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
40	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
41	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
42	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
43	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
44	Araneae	Araneae	Araneae	Arachnida	Micrura	Megoperculata	NA	Araneae	---	---	---	---
45	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona brevipes*
46	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona pallidula*
47	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona corticalis*
48	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona spp*
49	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona brevipes*
50	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona pallidula*
51	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	Clubiona	*Clubiona spp*
52	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	---	---
53	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	---	---

54	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	---	---
55	Araneae	Araneae	Clubionidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Clubionidae	---	---
56	Araneae	Araneae	Corinnidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Corinnidae	---	---
57	Araneae	Araneae	Corinnidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Corinnidae	---	---
58	Araneae	Araneae	Ctenidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Ctenidae	---	---
59	Araneae	Araneae	Ctenidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Ctenidae	---	---
60	Araneae	Araneae	Gnaphosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Gnaphosidae	---	---
61	Araneae	Araneae	Gnaphosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Gnaphosidae	---	---
62	Araneae	Araneae	Gnaphosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Gnaphosidae	---	---
63	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	Moebelia	*Moebelia penicillata*
64	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	---	---
65	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	---	---
66	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	---	---
67	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	---	---
68	Araneae	Araneae	Linyphiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Linyphiidae	---	---
69	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	---	---
70	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	Trochosa	*Trochosa ruricola*
71	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	---	---
72	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	---	---
73	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	---	---
74	Araneae	Araneae	Lycosidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Lycosidae	---	---
75	Araneae	Araneae	Oonopidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Oonopidae	---	---
76	Araneae	Araneae	Oonopidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Oonopidae	---	---
77	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	Philodromus	*Philodromus sp*
78	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	Philodromus	*Philodromus sp*
79	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	---	---
80	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	---	---
81	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	---	---

82	Araneae	Araneae	Philodromidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Philodromidae	---	---
83	Araneae	Araneae	Pisauridae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Pisauridae	---	---
84	Araneae	Araneae	Pisauridae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Pisauridae	---	---
85	Araneae	Araneae	Pisauridae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Pisauridae	---	---
86	Araneae	Araneae	Salticidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Salticidae	---	---
87	Araneae	Araneae	Salticidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Salticidae	---	---
88	Araneae	Araneae	Salticidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Salticidae	---	---
89	Araneae	Araneae	Segestriidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Segestriidae	Segestria	*Segestria senoculata*
90	Araneae	Araneae	Theridiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Theridiidae	Steatoda	*Steatoda bipunctata*
91	Araneae	Araneae	Theridiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Theridiidae	---	---
92	Araneae	Araneae	Theridiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Theridiidae	---	---
93	Araneae	Araneae	Theridiidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Theridiidae	---	---
94	Araneae	Araneae	Thomisidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Thomisidae	---	---
95	Araneae	Araneae	Thomisidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Thomisidae	Tmarus	---
96	Araneae	Araneae	Thomisidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Thomisidae	---	---
97	Araneae	Araneae	Thomisidae	Arachnida	Micrura	Megoperculata	NA	Araneae	Araneomorphae	Thomisidae	---	---
98	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
99	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
100	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
101	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
102	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
103	Opilionida	Opilionida	Opilionida	Arachnida	Dromopoda	NA	NA	Opilionida	---	---	---	---
104	Opilionida	Opilionida	Phalangiidae	Arachnida	Dromopoda	NA	NA	Opilionida	Palpatores	Phalangiidae	Lacinius	*Lacinius ephippiatus*
105	Opilionida	Opilionida	Phalangiidae	Arachnida	Dromopoda	NA	NA	Opilionida	Palpatores	Phalangiidae	Odiellus	*Odiellus spinosus*
106	Opilionida	Opilionida	Phalangiidae	Arachnida	Dromopoda	NA	NA	Opilionida	Palpatores	Phalangiidae	Rilaena	*Rilaena traingularis*
107	Opilionida	Opilionida	Sclerosomatidae	Arachnida	Dromopoda	NA	NA	Opilionida	Palpatores	Sclerosomatidae	Leiobunum	*Leiobunum blackwalli*
108	Pseudoscorpionida	Pseudoscorpionida	Pseudoscorpionida	Arachnida	Dromopoda	NA	NA	Pseudoscorpionida	---	---	---	---
109	Pseudoscorpionida	Pseudoscorpionida	Pseudoscorpionida	Arachnida	Dromopoda	NA	NA	Pseudoscorpionida	---	---	---	---

110	Pseudoscorpionida	Pseudoscorpionida	Pseudoscorpionida	Arachnida	Dromopoda	NA	NA	Pseudoscorpionida	---	---	---	---
111	Pseudoscorpionida	Pseudoscorpionia	Pseudoscorpionida	Arachnida	Dromopoda	NA	NA	Pseudoscorpionida	---	---	---	---
112	Scorpionida	Scorpionida	Scorpionida	Arachnida	Dromopoda	NA	NA	Scorpionida	---	---	---	---
113	Chilopoda	Chilopoda	Chilopoda	Chilopoda	---	---	---	---	---	---	---	---
114	Chilopoda	Chilopoda	Chilopoda	Chilopoda	---	---	---	---	---	---	---	---
115	Chilopoda	Chilopoda	Geophilomorpha	Chilopoda	Pleurostigmophora	NA	Epimorpha	Geophilomorpha	---	---	---	---
116	Chilopoda	Chilopoda	Geophilomorpha	Chilopoda	---	---	---	---	---	---	---	---
117	Chilopoda	Chilopoda	Geophilomorpha	Chilopoda	Pleurostigmophora	NA	Epimorpha	Geophilomorpha	---	---	---	---
118	Chilopoda	Chilopoda	Henicopidae	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	NA	Henicopidae	Lamyctes	*Lamyctes fulvicornis*
119	Chilopoda	Chilopoda	Lithobiidae	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	NA	Lithobiidae	Lithobius	*Lithobius erythrocephalus*
120	Chilopoda	Chilopoda	Lithobiidae	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	NA	Lithobiidae	Lithobius	*Lithobius microps*
121	Chilopoda	Chilopoda	Lithobiidae	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	NA	Lithobiidae	Lithobius	*Lithobius mutabilis*
122	Chilopoda	Chilopoda	Lithobiidae	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	NA	Lithobiidae	Lithobius	*Lithobius mutabilis*
123	Chilopoda	Chilopoda	Lithobiomorpha	Chilopoda	Pleurostigmophora	NA	NA	Lithobiomorpha	---	---	---	---
124	Chilopoda	Chilopoda	Scolopendromorpha	Chilopoda	Pleurostigmophora	NA	Epimorpha	Scolopendromorpha	---	---	---	---
125	Chilopoda	Chilopoda	Scolopendromorpha	Chilopoda	Pleurostigmophora	NA	Epimorpha	Scolopendromorpha	---	---	---	---
126	Chilopoda	Chilopoda	Scutigeromorpha	Chilopoda	Notostigmophora	NA	NA	Scutigeromorpha	---	---	---	---
127	Diplopoda	Diplopoda	Diplopoda	Diplopoda	---	---	---	---	---	---	---	---
128	Diplopoda	Diplopoda	Diplopoda	Diplopoda	---	---	---	---	---	---	---	---
129	Diplopoda	Diplopoda	Diplopoda	Diplopoda	---	---	---	---	---	---	---	---
130	Diplopoda	Diplopoda	Julidae	Diplopoda	Chilognatha	Helminthomorpha	Juliformia	Julida	NA	Julidae	Pachyiulus	*Pachyiulus flavipes*
131	Diplopoda	Diplopoda	Julidae	Diplopoda	Chilognatha	Helminthomorpha	Juliformia	Julida	NA	Julidae	Amblyiulus	*Amblyiulus continentalis*
132	Diplopoda	Diplopoda	Julidae	Diplopoda	Chilognatha	Helminthomorpha	Juliformia	Julida	NA	Julidae	Ophyiulus	*Ophyiulus pilosus*
133	Diplopoda	Diplopoda	Polydesmidae	Diplopoda	Chilognatha	Helminthomorpha	Merocheta	Polydesmida	NA	Polydesmidae	Polydesmus	*Polydesmus angustus*
134	Diplopoda	Diplopoda	Trigoniulidae	Diplopoda	Chilognatha	Helminthomorpha	Anocheta	Spirobolida	Trigoniulidea	Trigoniulidae	Trigoniulus	*Trigoniulus corallinus*
135	Collembola	Collembola	Collembola	Entognatha	Collembola	---	---	---	---	---	---	---
136	Collembola	Collembola	Collembola	Entognatha	Collembola	---	---	---	---	---	---	---
137	Collembola	Collembola	Collembola	Entognatha	Collembola	---	---	---	---	---	---	---

138	Collembola	Collembola	Collembola	Entognatha	Collembola	---	---	---	---	---	---	---
139	Collembola	Collembola	Collembola	Entognatha	Collembola	---	---	---	---	---	---	---
140	Collembola	Entomobryomorpha	Entomobryidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Entomobryidae	---	---
141	Collembola	Entomobryomorpha	Entomobryidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Entomobryidae	Orchesella	*Orchesella cincta*
142	Collembola	Entomobryomorpha	Entomobryomorpha	Entognatha	Collembola	NA	NA	Entomobryomorpha	---	---	---	---
143	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	---	---
144	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Folsomia	*Folsomia quadrioculata*
145	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Isotomiella	*Isotomiella minor*
146	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Isotoma	*Isotoma notabilis*
147	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Folsomia	*Folsomia quadrioculata*
148	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Isotomiella	*Isotomiella minor*
149	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Isotoma	*Isotoma notabilis*
150	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Folsomia	*Folsomia hasegawai*
151	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Folsomia	*Folsomia candida*
152	Collembola	Entomobryomorpha	Isotomidae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Isotomidae	Isotoma	*Isotoma trispinata*
153	Collembola	Entomobryomorpha	Tomoceridae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Tomoceridae	Tomocerus	*Tomocerus flavescens*
154	Collembola	Entomobryomorpha	Tomoceridae	Entognatha	Collembola	NA	NA	Entomobryomorpha	NA	Tomoceridae	Tomocerus	*Tomocerus minor*
155	Collembola	Poduromorpha	Hypogastruridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Hypogastruridae	Hypogastrura	*Hypogastrura cf manubrialis*
156	Collembola	Poduromorpha	Neanuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Neanuridae	---	---
157	Collembola	Poduromorpha	Neanuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Neanuridae	Neanura	*Neanura sp*
158	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus furcifer*
159	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus armatus*
160	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus furcifer*
161	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus armatus*
162	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus furcifer*
163	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus armatus*
164	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus furcifer*
165	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus armatus*

166	Collembola	Poduromorpha	Onychiuridae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Onychiuridae	Onychiurus	*Onychiurus spp*
167	Collembola	Poduromorpha	Tullbergiidae	Entognatha	Collembola	NA	NA	Poduromorpha	NA	Tullbergiidae	Tullbergia	*Tullbergia krausbaueri*
168	Collembola	Symphypleona	Katiannidae	Entognatha	Collembola	NA	NA	Symphypleona	NA	Katiannidae	Sminthurinus	*Sminthurinus aureus*
169	Collembola	Symphypleona	Katiannidae	Entognatha	Collembola	NA	NA	Symphypleona	NA	Katiannidae	Sminthurinus	*Sminthurinus flammeoulus*
170	Collembola	Symphypleona	Sminthuridae	Entognatha	Collembola	NA	NA	Symphypleona	NA	Sminthuridae	---	---
171	Collembola	Symphypleona	Sminthuridae	Entognatha	Collembola	NA	NA	Symphypleona	NA	Sminthuridae	Allacma	*Allacma fusca*
172	Coleoptera	Coleoptera	Alleculidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Alleculidae	---	---
173	Coleoptera	Coleoptera	Anobiidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Anobiidae	---	---
174	Coleoptera	Coleoptera	Aphodiidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Aphodiidae	---	---
175	Coleoptera	Coleoptera	Buprestidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Buprestidae	---	---
176	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
177	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
178	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
179	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
180	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
181	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
182	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Abax	*Abax parallelepipedus*
183	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Bembidion	*Bembidion lampros*
184	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Nebria	*Nebria brevicollis*
185	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Pterostichus	*Pterostichus crenatus*
186	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Pterostichus	*Pterostichus nigrita*
187	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	Pterostichus	*Pterostichus strenuus*
188	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
189	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
190	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
191	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
192	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---
193	Coleoptera	Coleoptera	Carabidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Adephaga	Carabidae	---	---

194	Coleoptera	Coleoptera	Cerambycidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Cerambycidae	---	---
195	Coleoptera	Coleoptera	Cerambycidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Cerambycidae	---	---
196	Coleoptera	Coleoptera	Chrysomelidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Chrysomelidae	---	---
197	Coleoptera	Coleoptera	Chrysomelidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Chrysomelidae	---	---
198	Coleoptera	Coleoptera	Chrysomelidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Chrysomelidae	---	---
199	Coleoptera	Coleoptera	Ciidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Ciidae	---	---
200	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
201	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
202	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
203	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
204	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
205	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
206	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
207	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
208	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
209	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
210	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
211	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
212	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
213	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
214	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
215	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
216	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
217	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
218	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
219	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
220	Coleoptera	Coleoptera	Coleoptera	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	---	---	---	---
221	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	---	---

222	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	---	---
223	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	---	---
224	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	---	---
225	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	Ectemnorhinus	---
226	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	Bothrometopus	*Bothrometopus elongatus*
227	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	Bothrometopus	*Bothrometopus parvulus*
228	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	Bothrometopus	*Bothrometopus randi*
229	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	Palirhoeus	*Palirhoeus eatoni*
230	Coleoptera	Coleoptera	Curculionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Curculionidae	---	---
231	Coleoptera	Coleoptera	Elateridae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Elateridae	---	---
232	Coleoptera	Coleoptera	Histeridae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Histeridae	---	---
233	Coleoptera	Coleoptera	Meloidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Meloidae	---	---
234	Coleoptera	Coleoptera	Nitidulidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Nitidulidae	---	---
235	Coleoptera	Coleoptera	Scarabaeidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Scarabaeidae	---	---
236	Coleoptera	Coleoptera	Scarabaeidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Scarabaeidae	---	---
237	Coleoptera	Coleoptera	Scarabaeidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Scarabaeidae	---	---
238	Coleoptera	Coleoptera	Staphylinidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Staphylinidae	---	---
239	Coleoptera	Coleoptera	Staphylinidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Staphylinidae	---	---
240	Coleoptera	Coleoptera	Staphylinidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Staphylinidae	---	---
241	Coleoptera	Coleoptera	Staphylinidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Staphylinidae	---	---
242	Coleoptera	Coleoptera	Staphylinidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Staphylinidae	---	---
243	Coleoptera	Coleoptera	Tenebrionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Tenebrionidae	---	---
244	Coleoptera	Coleoptera	Tenebrionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Tenebrionidae	---	---
245	Coleoptera	Coleoptera	Tenebrionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Tenebrionidae	---	---
246	Coleoptera	Coleoptera	Tenebrionidae	Insecta	Pterygota	Neoptera	Endopterygota	Coleoptera	Polyphaga	Tenebrionidae	Tribolium	*Tribolium brevicornis*
247	Insecta	Insecta	Blattodea	Insecta	Pterygota	Neoptera	Dictyoptera	Blattodea	---	---	---	---
248	Insecta	Insecta	Blattodea	Insecta	Pterygota	Neoptera	Dictyoptera	Blattodea	---	---	---	---
249	Insecta	Insecta	Blattodea	Insecta	Pterygota	Neoptera	Dictyoptera	Blattodea	---	---	---	---

250	Insecta	Insecta	Dermaptera	Insecta	Pterygota	Neoptera	Polyneoptera	Dermaptera	---	---	---	---
251	Insecta	Insecta	Dermaptera	Insecta	Pterygota	Neoptera	Polyneoptera	Dermaptera	---	---	---	---
252	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
253	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
254	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
255	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
256	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
257	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
258	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
259	Insecta	Insecta	Formicidae	Insecta	Pterygota	Neoptera	Endopterygota	Hymenoptera	Apocrita	Formicidae	---	---
260	Insecta	Insecta	Insecta	Insecta	Thysanura	---	---	---	---	---	---	---
261	Insecta	Insecta	Insecta	Insecta	Pterygota	Neoptera	Polyneoptera	---	---	---	---	---
262	Insecta	Insecta	Insecta	Insecta	Thysanura	---	---	---	---	---	---	---
263	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
264	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
265	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
266	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
267	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
268	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
269	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
270	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
271	Insecta	Insecta	Orthoptera	Insecta	Pterygota	Neoptera	Polyneoptera	Orthoptera	---	---	---	---
272	Insecta	Insecta	Psocoptera	Insecta	Pterygota	Neoptera	Paraneoptera	Psocoptera	---	---	---	---
273	Insecta	Insecta	Psocoptera	Insecta	Pterygota	Neoptera	Paraneoptera	Psocoptera	---	---	---	---
274	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
275	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
276	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
277	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---

278	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
279	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
280	Isopoda	Isopoda	Isopoda	Malacostraca	Eumalacostraca	NA	---	Isopoda	---	---	---	---
281	Isopoda	Isopoda	Oniscidae	Malacostraca	Eumalacostraca	NA	---	Isopoda	Oniscidea	Oniscidae	Oniscus	*Oniscus asellus*
282	Isopoda	Isopoda	Porcellionidae	Malacostraca	Eumalacostraca	NA	---	Isopoda	Oniscidea	Porcellionidae	Porcellio	*Porcellio scaber*
283	Isopoda	Isopoda	Porcellionidae	Malacostraca	Eumalacostraca	NA	---	Isopoda	Oniscidea	Porcellionidae	Porcellionides	*Porcellionides cingendus*

*Code: Identification number of the equation.
*Group 1: Classification level to acari, araneae, chilopoda, coleoptera, collembola, insecta, isopoda, opilionida, pseudoscorpionida and scorpionida.
*Group 2: Classification level to Group 1 plus mesostigmata, prostigmata, oribatida, entomobryomorpha, poduromorpha and symphypleona.
*Group 3: Classification to lowest available taxonomic level (from class to family)
*Taxonomic classification for each specimen (from class to species).

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Table S2. Number of mass-length equations ($M = aL^b$) detailed by taxonomic group. In bold, the principal groups and the total number of equations for that taxonomic category are in bold.

Taxonomic Group	Number of equations
Arachnida	**112**
Acari	8
Mesostigmata	1
Oribatida	4
Prostigmata	1
Araneae	83
Opilionida	10
Pseudoscorpion	4
Scorpion	1
Chilopoda	**14**
Diplopoda	**8**
Entognatha	**37**
Collembola	5
Entomobryomorpha	15
Poduromorpha	13
Symphypleona	4
Insecta	**102**
Endopterygota	
Coleoptera	75
Hymenoptera (ants)	8
Paraneoptera	
Psocoptera	2
Polyneoptera	1
Blattodea	3
Dermaptera	2
Orthoptera	9
Thysanura	2
Isopoda	**10**
Total	**283**

Table S3. Set of points around the world with the allometric equations used in this study. Each site was sampled by the authors in the reference, and we provide information about the code of the site, the number of equations by site, the reference, the location, the type of habitat and the biome according to the World Wildlife Fund (WWF).

Site	Reference	Number of equations	Location	Habitat	Biome
1	Beaver & Baldwin 1975	1	San Isabel National Forest, Wet Mountains, Colorado, EEUU	Temperate conifer forest	TCF
2	Breymeyer 1967	2	Poland	---	TMF
3	Clausen 1983	12	North Zealand, Denmark	Forest of linden trees (Tilia)	TMF
4	Díaz & Díaz 1990	3	Madrid and Segovia, Spain	Variety of habitats, from cereal crops to piornales	MEF
5	Edwards 1996, Edwards & Gabriel 1998	38	Frances Crane Management Area, Cape Cod, Massachusetts, EEUU	Temperate forest (Pine forest and scrub oaks)	TMF
6	Ganihar 1997	12	Bicholim taluk, Goa, India	Tropical forest	TSMF
7	Gowing & Recher 1984	5	Southern Tablelands of New South Wales, Australia	Eucalypt forest and woodland	TMF
8	Gruner 2003	13	Hawaiian Islands, EEUU	Subtropical islands	TCF
9	Henschel *et al*. 1996	2	Main River, Würzburg, Bavaria, Sounthern Germany	Riparian forest	TMF
10	Hódar 1996	26	Guadix-Baza Basin, Granada, Spain	Shrubsteppes, cereal crops, fallow lands and cleared oakwood	MEF
11	Höfer & Ott 2009	2	Reserva do Cachoeira, Antonina, Paraná, Brazil	Mata Atlântica	TSMF
12	Höfer & Ott 2009	16	Brazilian Agricultural Research Corporation, Brazil	Natural tropical forests and agroforestry (tree plantations)	TSMF
13	Jarošík 1989	1	Western and Central Bohemia, Czech Republic	Temperate forest	TMF
14	Johnson & Strong 2000	5	Jamaica Island	Temperate island	TSDF
15	Klarner *et al*. 2017	1	Bukit Duabelas National Park, Sumatra, Indonesia	Lowland Rainforest (jungle rubber, rubber and oil palm)	TSMF
16	Klarner *et al*. 2017	1	Harapan landscape, Sumatra, Indonesia	Lowland Rainforest (jungle rubber, rubber and oil palm)	TSMF
17	Lang *et al*. 1997	5	Agroecosystem research network, Munich, Germany	Arable land	TMF
18	LeBrun 1971	1	Commune Hamme-Mille, Val-Due, Moyenne, Belgium	Oak Forest, Poplar plantation and hayfield	TMF
19	Marcuzzi 1987	6	Gargano Promontory and Tremiti Islands, Foggia, Apulia, Italy	Mediterranean islands	MEF
20	Mazantseva 1975	2	Moscow, Russia	---	TMF
21	McLaughlin *et al*. 2010	30	River Lee, South-West Cork, Ireland	Deciduous alluvial forest	TMF
22	Mercer *et al*. 2001	12	Marion Island, Western Cape Province, South Africa	Sub-antartic island	TUN
23	Newton & Proctor 2013	4	Alberta, Canada	Mixed deciduous-coniferous forest, grassland and woodland	BOF

24	Ruiz-Lupión, D (unpublished)	1	Picos de Europa, Asturias, Spain	Beech Forest of *Fagus sylvatica*	TMF
25	Ruiz-Lupión, D (unpublished)	2	Asturias, Spain	Beech Forest of *Fagus sylvatica*	TMF
26	Petersen 1975	18	Juntland (Hestehave Wood at Kalo), Denmark	Beech Forest of *Fagus sylvatica*	TMF
27	Richardson *et al*. 2000	4	Luquillo Experimental Forest, Puerto Rico Island	Subtropical Forest of tabonuco, palm and colorado trees	TSMF
28	Rogers *et al*. 1977	7	Hanford Site, South-central Washington, EEUU	Arid lands	TMF
29	Sabo *et al*. 2002	5	Eel River, Mendocino County, California, EEUU	Mediterranean Forest of douglas fir and redwood trees	MEF
30	Sage 1982	4	Austin, Texas, EEUU	Natural habitats	TGS
31	Sample *et al*. 1993	7	Eastern West Virginia, EEUU	Forested area	TMF
32	Santos Gómez 2013	1	Basal stratum, Valley of Güimar, Tenerife, Canary Islands	Mediterranean mixed community of Cardón and Tabaibas	MEF
33	Santos Gómez 2013	1	Cloudy montane stratum, Valley of Güimar, Tenerife, Canary Islands	Laurisilva and Pine forest (*Pinus canariensis*)	MEF
34	Santos Gómez 2013	1	Summer-Xeric montane, Valley of Güimar, Tenerife, Canary Islands	Mixed community of Fabaceae and Lamiaceae	MEF
35	Santos Gómez 2013	1	Summit stratum, Valley of Güimar, Tenerife, Canary Islands	High mountain vegetation	MEF
36	Schoener 1980	2	Ipswich River Santuary, Massachusetts, EEUU	Temperate deciduous-conifer forest	TMF
37	Schoener 1980	3	Cañas, Guanacaste Province, Costa Rica	Tropical dry forest, including river-bottom forest	TSMF
38	Schoener 1980	3	Guapiles, Limon Province, Costa Rica	Tropical rainforest	TSMF
39	Shinohara *et al*. 2007	1	Okinawa Island, Okinawa Prefecture, Japan	Temperate island	TMF
40	Sokoloff *et al*. 1999	1	Bishop area, California, EEUU	---	MEF
41	Tanaka 1970	7	Mt. Sobo, central Kyushu, Japan	Temperate forests of *Tsuga sieboldii* or *Fagus crenata*	TMF
42	Van Straalen 1989	2	Roggebotzand, Netherlands	Pine stand (*Pinus nigra*) of the forest	TMF
43	Vannier 1973	1	Brunoy (Essone), Paris, France	Temperate zone (Park)	TMF
44	Voigtländer 2000, 2007	4	Neibetal, Görlitz, Germany	Deciduous forest (Laboratory rearing)	TMF
45	Wardhaugh 2013	7	James Cook University, Cape Tribulation, Queensland, Australia	Daintree Rainforest Observatory	TSGS

*TSMF (Tropical and Subtropical Moist Broadleaf Forest), TMF (Temperate Broadleaf and Mixed Forest), TCF (Temperate Conifer Forest), BOF (Boreal Forest or Taiga), TSGS (Tropical and Subtropical Grasslands, Savannas and Shrublands), TGS (Temperate Grasslands, Savannas and Shrublands), TUN (Tundra) and MEF (Mediterranean Forests, Woodlands and Scrub).

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Table S4. Set of original equations included in the database and the changes made to each type of equation. In Type I equations, the scaling and allometric factors were obtained directly from the publications without any further transformation. In Type II equations, the factors were obtained by calculating the anti-logarithms of the values provided in the publications. In Type III equations, we reconstructed the values by refitting the original equation and crossed the values with the original ones using an OLS model to calculate the fit (Fig. S1). In Type IV equations, because we had the original data, the values of the factors were obtained by fitting the equation directly.

Type	Original Equation		Number of Equation	Transformation	References
I	1	$M = aL^b$	31	No transformation was performed.	Hofer & Ott 2009; Jarošík 1989; Klarner *et al*. 2017; Lang *et al*. 1997; Sabo *et al*. 2002
II	2	$Ln\ M = Ln\ a + bLn\ L$	173	Linearization of the equation was reversed by removing the logarithms base e or base 10.	Breymeyer 1967; Clausen 1983; Díaz & Díaz 1990; Edwards 1996, Edwards & Gabriel 1998; Ganihar 1997; Gowing & Recher 1984; Gruner 2003; Henschel *et al*. 1996; Hódar 1996; Johnson & Strong 2000; McLaughlin *et al*. 2010; Rogers *et al*. 1976; Sample *et al*. 1993; Schoener 1980; Wardhaugh 2013
	3	$\log M = \log a + b\log L$	42		Beaver & Baldwin 1975; Mercer *et al*. 2001; Petersen 1975; Richardson *et al*. 2000; Tanaka 1970
III	4	$M = a + bL$	2	New data were generated from the original equation and the potential equation adjusted to the curve (Table S5).	Ganihar 1997
	5	$M = a + bLn\ L$	1		Ganihar 1997
	6	$M = ae^{bL}$	1		Ganihar 1997
	7	$Ln\ M = a + b_1L + b_2L^2$	4		Sage 1982
	8	$\log M = \log a_0 + a_1\log L + a_2\log^2 L$	2		Van Straalen 1989
IV	9	Original Dataset	27	In the original studies, the authors did not adjust an equation to the data or they adjusted a different type of equation. We adjusted the logarithmic equation (Type II on this table) to the original dataset.	Ruiz-Lupión, D (unpublished); de los Santos-Gómez 2013; LeBrun 1971; Marcuzzi 1987; Mazantseva 1975; Newton & Proctor 2013; Shinohara *et al*. 2007; Sokoloff *et al*. 1999; Vannier 1973 Voigtländer 2000, 2007

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Table S5. Fitting of the potential (allometric) equation to the original curve used by the authors (Fig. S1). And calculation of the coefficients of determination (R^2) and the error associated ($1-R^2$). Average error (± SD) calculated from the set of reconstructed equations was 1.51±1.74%.

Reference	Taxon	Original equation	R^2	$1 - R^2$
Ganihar 1997	Isopoda	$M = a + bL$	0.9366	0.0634
Ganihar 1997	Opilionida	$M = a + bLnL$	0.9869	0.0131
Ganihar 1997	Dictyoptera	$M = a + bL$	0.9861	0.0139
Ganihar 1997	Dermaptera	$M = ae^{bL}$	0.9771	0.0229
Sage 1982	Coleoptera	$LnM = a + b_1L + b_2L^2$	0.9966	0.0034
Sage 1982	Coleoptera	$LnM = a + b_1L + b_2L^2$	0.9962	0.0038
Sage 1982	Orthoptera	$LnM = a + b_1L + b_2L^2$	0.9863	0.0137
Sage 1982	Formicidae	$LnM = a + b_1L + b_2L^2$	0.9861	0.0139
Van Straalen 1989	Collembola	$logM = loga_0 + a_1\ logL + a_2log^2L$	0.9988	0.0012
Van Straalen 1989	Collembola	$logM = loga_0 + a_1\ logL + a_2log^2L$	0.9984	0.0016

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Table S6. Pearson correlation matrix of the variables included for analyses.

	PCGM1	PCGM2	PCGM3	Absolute latitude	Absolute longitude	Altitude	MAT	MAP	NDVI
PCGM1	1.00	0.16	-0.04	-0.14	0.06	0.11	0.16	0.02	0.01
PCGM2	0.16	1.00	0.03	-0.06	0.04	0.21	0.00	-0.03	-0.09
PCGM3	-0.04	0.03	1.00	0.03	-0.05	-0.11	-0.07	-0.04	0.14
Absolute latitude	-0.14	-0.06	0.03	1.00	-0.54	-0.23	-0.85	-0.59	-0.20
Absolute longitude	0.06	0.04	-0.05	-0.54	1.00	0.30	0.27	0.32	0.16
Altitude	0.11	0.21	-0.11	-0.23	0.30	1.00	-0.18	-0.16	-0.56
MAT	0.16	0.00	-0.07	-0.85	0.27	-0.18	1.00	0.53	0.35
MAP	0.02	-0.03	-0.04	-0.59	0.32	-0.16	0.53	1.00	0.54
NDVI	0.01	-0.09	0.14	-0.20	0.16	-0.56	0.35	0.54	1.00

Table S7. Summary of the results of the Base, Shape and Geographic LMs analyzing the scaling factor *a.*

Model	Variables included	Estimate	SE	F	d.f.	p (F)
Base model	(intercept)	0.4392	0.0582			
	b	-0.2570	0.0386	44.401	1, 273	***< 0.001***
	Class			49.076	5, 273	***< 0.001***
	NDVI	-0.2377	0.0462	26.512	1, 273	***< 0.001***
	lag1	0.3824	0.0525	53.056	1, 273	***< 0.001***
Shape model	(intercept)	0.6837	0.0780			
	b	-0.3396	0.0386	77.284	1, 270	***< 0.001***
	Class			50.793	5, 270	***< 0.001***
	PCGM1	0.4822	0.0754	40.909	1, 270	***< 0.001***
	PCGM2	0.0485	0.0439	1.221	1, 270	0.2703
	PCGM3	0.1793	0.0506	12.548	1, 270	***< 0.001***
	NDVI	-0.2241	0.0436	26.435	1, 270	***< 0.001***
	lag1	0.3593	0.0506	50.350	1, 270	***< 0.001***
Geographic model	(intercept)	0.6582	0.0753			
	b	-0.3680	0.0356	106.825	1, 267	***< 0.001***
	Class			33.589	5, 267	***< 0.001***
	PCGM1	0.3057	0.0743	16.920	1, 267	***< 0.001***
	PCGM2	0.1123	0.0408	7.556	1, 267	**0.0064**
	PCGM3	0.1074	0.0471	5.193	1, 267	*0.0235*
	Altitude	-0.2759	0.0551	25.079	1, 267	***< 0.001***
	Absolute latitude	-0.3997	0.0373	115.066	1, 267	***< 0.001***
	Longitude	0.0460	0.0436	1.117	1, 267	0.2915
	NDVI	-0.5568	0.0528	111.450	1, 267	***< 0.001***
	lag1	0.1051	0.0570	3.393	1, 267	0.0666

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

Table S8. Summary of the results of the Base, Shape and Geographic LMs analyzing the allometric factor *b.*

Model	Variables included	Estimate	SE	F	d.f.	p (F)
Base model	(intercept)	0.1746	0.1004			
	a	-0.3784	0.0869	18.943	1, 273	***< 0.001***
	Class			21.347	5, 273	***< 0.001***
	NDVI	-0.4183	0.0726	33.208	1, 273	***< 0.001***
	lag1	0.1324	0.0502	6.962	1, 273	**0.0088**
Shape model	(intercept)	0.5108	0.1234			
	a	-0.5466	0.0772	50.161	1, 270	***< 0.001***
	Class			37.410	5, 270	***< 0.001***
	PCGM1	0.7787	0.1096	50.496	1, 270	***< 0.001***
	PCGM2	-0.0708	0.0656	1.203	1, 270	0.2738
	PCGM3	0.4739	0.0712	44.296	1, 270	***< 0.001***
	NDVI	-0.3263	0.0640	26.037	1, 270	***< 0.001***
	lag1	0.0870	0.0481	3.269	1, 270	0.0717
Geographic model	(intercept)	0.5468	0.1211			
	a	-0.7246	0.0778	86.825	1, 267	***< 0.001***
	Class			23.127	5, 267	***< 0.001***
	PCGM1	0.5842	0.1101	27.852	1, 267	***< 0.001***
	PCGM2	0.0289	0.0626	0.213	1, 267	0.6452
	PCGM3	0.4065	0.0683	35.454	1, 267	***< 0.001***
	Altitude	-0.2794	0.0834	11.213	1, 267	***< 0.001***
	Absolute latitude	-0.3958	0.0601	43.369	1, 267	***< 0.001***
	Longitude	0.0855	0.0656	1.695	1, 267	0.1939
	NDVI	-0.6272	0.0817	58.883	1, 267	***< 0.001***
	lag1	0.0704	0.0494	2.032	1, 267	0.1552

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

Table S9. Summary of the results of the Full RLMs analyzing the scaling factor a and allometric factor b.

Factor	Variables included	Value	SE	F	d.f.	p (F)
	(intercept)	-0.0407	0.0284			
	b	-0.1147	0.0128	79.898	1, 267	***< 0.001***
	Class			14.197	5, 267	***< 0.001***
	PCGM1	0.0604	0.0265	5.1917	1, 267	*0.0235*
	PCGM2	0.0470	0.0145	10.591	1, 267	**0.0013**
	PCGM3	0.2750	0.0167	2.730	1, 267	*0.0100*
Scaling *a*	Altitude	-0.1550	0.0263	34.671	1, 267	***< 0.001***
	Absolute latitude	-0.2343	0.0510	21.070	1, 267	***< 0.001***
	Longitude	0.0022	0.0166	0.018	1, 267	0.8927
	MAT	-0.1105	0.0444	6.190	1, 267	*0.0135*
	MAP	-0.0047	0.0207	0.051	1, 267	0.8220
	NDVI	-0.1730	0.0196	77.937	1, 267	***< 0.001***
	(intercept)	-0.1115	0.0947			
	a	-0.5748	0.0726	62.705	1, 267	***< 0.001***
	Class			12.570	5, 265	***< 0.001***
	PCGM1	0.1811	0.0880	4.241	1, 267	*0.0404*
	PCGM2	-0.0024	0.0480	0.003	1, 267	0.9696
	PCGM3	0.2599	0.0542	23.043	1, 267	***< 0.001***
Allometric *b*	Altitude	-0.5782	-0.5782	47.579	1, 267	***< 0.001***
	Absolute latitude	-1.1679	-1.1679	54.849	1, 267	***< 0.001***
	Longitude	0.1871	0.1871	11.898	1, 267	***< 0.001***
	MAT	-0.9071	-0.9071	42.369	1, 267	***< 0.001***
	MAP	-0.2642	-0.2642	15.446	1, 267	***< 0.001***
	NDVI	-0.2133	-0.2133	9.848	1, 267	**0.0019**

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

Table S10. Summary of the results of the Full LMs analyzing the scaling factor *a* and allometric factor *b* for evolutionary allometries.

Factor	Variables included	Estimate	SE	F	d.f.	p (F)
	(intercept)	0.5007	0.0994	25.369	1, 199	***< 0.001***
	b	-0.4310	0.0508	72.061	1, 199	***< 0.001***
	Class			24.179	5, 199	***< 0.001***
	PCGM1	0.2819	0.0815	11.974	1, 199	***< 0.001***
	PCGM2	0.1022	0.0437	5.476	1, 199	*0.0203*
	PCGM3	0.1232	0.0596	4.267	1, 199	*0.0402*
Scaling *a*	Altitude	-0.5219	0.0975	28.649	1, 199	***< 0.001***
	Absolute latitude	-0.7309	0.1747	17.499	1, 199	***< 0.001***
	Longitude	0.0226	0.0552	0.167	1, 199	0.6830
	MAT	-0.4132	0.1648	6.285	1, 199	*0.0130*
	MAP	0.0852	0.0695	1.504	1, 199	0.2215
	NDVI	-0.6590	0.0704	87.629	1, 199	***< 0.001***
	(intercept)	-0.0432	0.1251	0.120	1, 199	0.7299
	a	-0.5932	0.0747	63.156	1, 199	***< 0.001***
	Class			20.187	5, 199	***< 0.001***
	PCGM1	0.2252	0.0998	5.091	1, 199	*0.0251*
	PCGM2	0.0728	0.0531	1.882	1, 199	0.1716
	PCGM3	0.3569	0.0690	26.780	1, 199	***< 0.001***
Allometric *b*	Altitude	-0.8594	0.1100	61.014	1, 199	***< 0.001***
	Absolute latitude	-1.7609	0.1834	92.228	1, 199	***< 0.001***
	Longitude	0.1900	0.0656	8.389	1, 199	**0.0042**
	MAT	-1.4848	0.1758	71.319	1, 199	***< 0.001***
	MAP	-0.2826	0.0821	11.837	1, 199	***< 0.001***
	NDVI	-0.2388	0.0958	6.211	1, 199	*0.0135*

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

Table S11. Summary of the results of the Shape LMs analyzing the scaling factor *a* and allometric factor *b* for ontogenetic allometries.

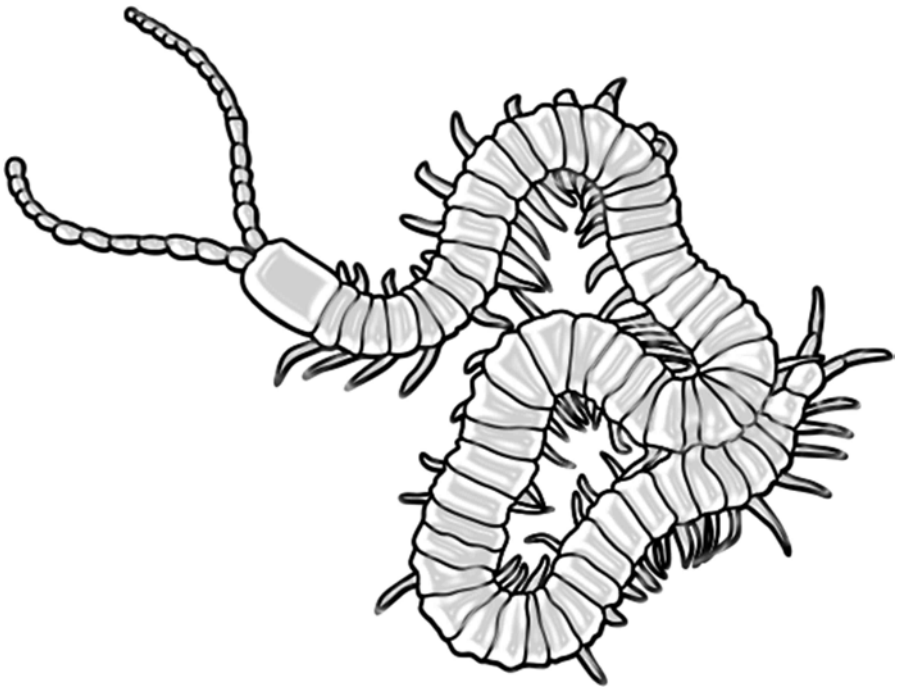
Factor	Variables included	Estimate	SE	F	d.f.	p (F)
Scaling *a*	(intercept)	0.7394	0.3159	5.479	1, 38	*0.0246*
	b	-0.7054	0.1007	49.094	1, 38	***< 0.001***
	Class			5.872	5, 38	***< 0.001***
	PCGM1	0.2213	0.7979	0.077	1, 38	0.7831
	PCGM2	0.4955	0.2120	5.462	1, 38	*0.0281*
	PCGM3	-0.1492	0.1645	0.822	1, 38	0.3703
	NDVI	-0.6053	0.1823	11.018	1, 38	**0.0019**
Allometric *b*	(intercept)	1.0382	0.3374	9.468	1, 38	**0.0039**
	a	-0.8716	0.1186	53.973	1, 38	***< 0.001***
	Class			3.151	5, 38	*0.0178*
	PCGM1	1.3108	0.8573	2.338	1, 38	0.1345
	PCGM2	0.4282	0.2322	3.401	1, 38	0.0730
	PCGM3	-0.1074	0.1792	0.359	1, 38	0.5526
	NDVI	-0.4790	0.2042	5.505	1, 38	*0.0243*

*p-values: ***Italic-bold < 0.001***, **bold 0.001 - 0.01**, *italic 0.01 - 0.05* and normal > 0.05.

Capítulo 3

New Litter Trap Devices Outperform Pitfall Traps for Studying Arthropod Activity

Dolores Ruiz-Lupión, Jordi Pascual, Nereida Melguizo-Ruiz, Oriol Verdeny-Vilalta & Jordi Moya-Laraño



New Litter Trap Devices Outperform Pitfall Traps for Studying Arthropod Activity

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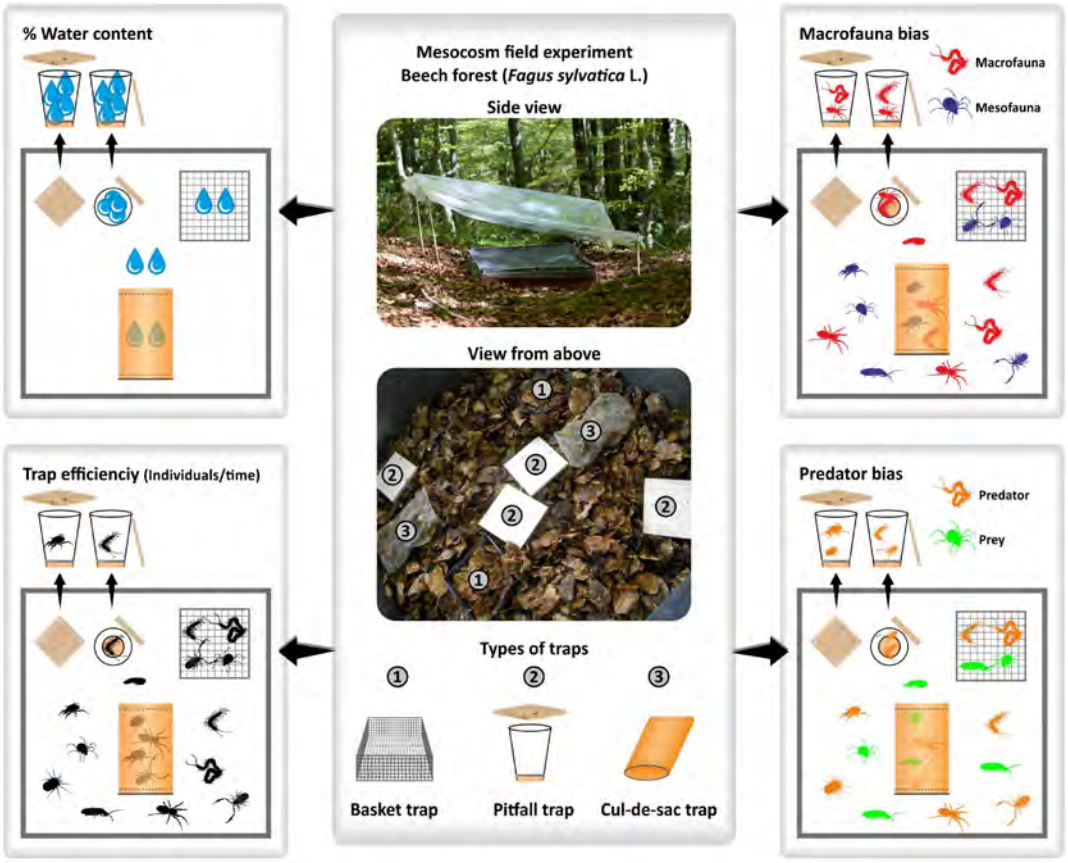
Abstract



Soil fauna play a key role in nutrient cycling and decomposition, and in recent years, researchers have become more and more interested in this compartment of terrestrial ecosystems. In addition, soil fauna can act as ecosystem engineers by creating, modifying, and maintaining the habitat for

other organisms. Ecologists usually utilize live catches in pitfalls traps as a standard method to study the activity of epigeic fauna in addition to relative abundance. Counts in pitfall traps can be used as estimates of relative activity to compare among experimental treatments. This requires taking independent estimates of abundance (e.g., by sifting soil litter, mark–recapture), which can then be used as covariates in linear models to compare the levels of fauna activity (trap catches) among treatments. However, many studies show that the use of pitfall traps is not the most adequate method to estimate soil fauna relative abundances, and these concerns may be extensible to estimating activity. Here, we present two new types of traps devised to study activity in litter fauna, and which we call "cul-de-sac" and "basket traps", respectively. We experimentally show that, at least for litter dwellers, these new traps are more appropriate to estimate fauna activity than pitfall traps because: (1) pitfall traps contain 3.5× more moisture than the surrounding environment, potentially attracting animals towards them when environmental conditions are relatively dry; (2) cul-de-sac and basket traps catch ca. 4× more of both meso- and macrofauna than pitfall traps, suggesting that pitfall traps are underestimating activity; and (3) pitfall traps show a bias towards collecting 1.5× higher amounts of predators, which suggests that predation rates are higher within pitfall traps. We end with a protocol and recommendations for how to use these new traps in ecological experiments and surveys aiming at estimating soil arthropod activity.

Keywords

Animal movement, dispersal, activity-density, abundance, activity, soil meso- and macrofauna, animal trapping.

1. Introduction

Soil fauna provide numerous and significant ecosystem functions and services in terrestrial ecosystems. First, they play a key role in nutrient cycling and storage, soil organic formation, and turnover via litter transformation; second, they create, modify, and maintain the soil habitat by acting as ecosystem engineers [1–3]; and third, given their recognized role as pest control agents [4,5] and their contribution to soil function, the sampling and analysis of soil fauna is essential in agroecosystem studies [6,7] and in food-web experimental ecology [8–10]. Moreover, there is an increasing interest in the study of the pedodiversity as a surrogate measure of above-ground biodiversity and as an indicator of below-ground biodiversity [11]. Indeed, through controlling above-ground processes, soil organisms can greatly contribute to the control and regulation of terrestrial ecosystems [12].

Thus, measuring the activity of soil fauna in field experiments becomes paramount. Pitfall trapping is the standard method for collecting ground-dwelling arthropods and soil fauna in studies of ecological and agricultural entomology [13]. The use of pitfall trap catches to obtain quantitative estimates of soil litter fauna relative abundances is a widespread technique [14]. However, the

relationship between actual abundances and pitfall trap catches has been shown to be either absent, weak, or highly variable among taxa, habitat, and time of the season [15]. Thus, it is not clear if the measure is activity, relative abundance, or a mixture of both. Indeed, pitfall trap catches in these types of studies are clearly biased towards surface-active arthropods, especially macrofauna (> 2 mm), such as Orthoptera, Diptera, and Coleoptera [15–17], and towards active hunting spiders and other epigeic predators [18–20].

The capture rate of arthropods in pitfall traps is proportional to their activity, and the number of individuals that each trap catches may or may not reflect their true abundance, and instead just their activity [21,22]. Thus, the rate of capture is proportional to the joint effects of abundance and activity [13,16,23,24], something that has very often been overlooked by ecologists for a long time [25]. Hence, pitfall trap catches could be better used to study the activity of soil fauna once controlling for actual absolute abundances [26], or when the aim of the study may be not affected by actual abundances and merely focuses on the study of differences in activity between the sexes after assuming a 1:1 sex ratio [27]. Nonetheless, activity estimates from pitfall trap catches can still be biased because of multiple factors such as the surrounding habitat structure [28] or the environmental conditions such as temperature and water availability. Additional factors could be the vertical distribution of the soil and leaf litter layers [20], as well as the attraction or repulsion of preservative fluids, detergents, or baits, the effects of which vary according to the taxon, sex, season, and environment [29–31]. Specifically, if a trap retains excessive amounts of water, it could act as an attractor for the fauna, especially during drought periods, therefore biasing the estimates of activity.

Here, we devised two novel trapping devices to assess the activity of soil litter fauna and compared their performance with standard pitfall traps in a field mesocosm experiment. The new traps were organza “cul-de-sac” traps and wireframe “basket” traps and were filled with leaf litter emptied of fauna and remained open, so that animals could freely enter and depart from the traps. Pitfall traps, on the other hand, were also filled with fauna-free leaf litter, but most animals could not escape from them. No preservatives, detergents, or baits were used so that fauna entered the traps according to their activity, without being attracted or repelled from them. Also, we established a watering treatment to minimize water gradients between the traps and the environment. We used the new trap devices described above to test if the activity of the entire community of soil litter mesofauna (0.2 - 2 mm) and macrofauna (> 2mm) in four beech forests (*Fagus sylvatica* L.) could be better estimated using these new trapping systems relative to using pitfall traps. To that end, we first simulated a drought, excluding rainfall by setting up plastic roofs covering each experimental mesocosm. Then, we placed the traps and started watering the plots and measuring animal activity. Litter samples served to estimate actual abundances, which were used as covariates in our linear models to study activity. We also measured the water content of each of the traps to test whether some of these devices retained excessive amounts of

water that could be used as attraction cues by the animals to set in, therefore biasing the estimates of activity.

2. Materials and Methods

2.1. Description of the Traps

All traps used in this mesocosm experiment (pitfall, cul-de-sac, and basket traps) were devised to capture live animals and therefore had no preservation fluids inside (Figure 1). Before setting the traps, we collected leaf litter from each site and extracted all the fauna (defaunation) by means of Berlese-Tullgren funnels (each equipped with an incandescent 55 W bulb) for 48 h, after which time the litter was completely dry and most (if not all) of the fauna were collected at the bottom of the funnel. This leaf litter was then used to fill the traps at the beginning of the experiment.

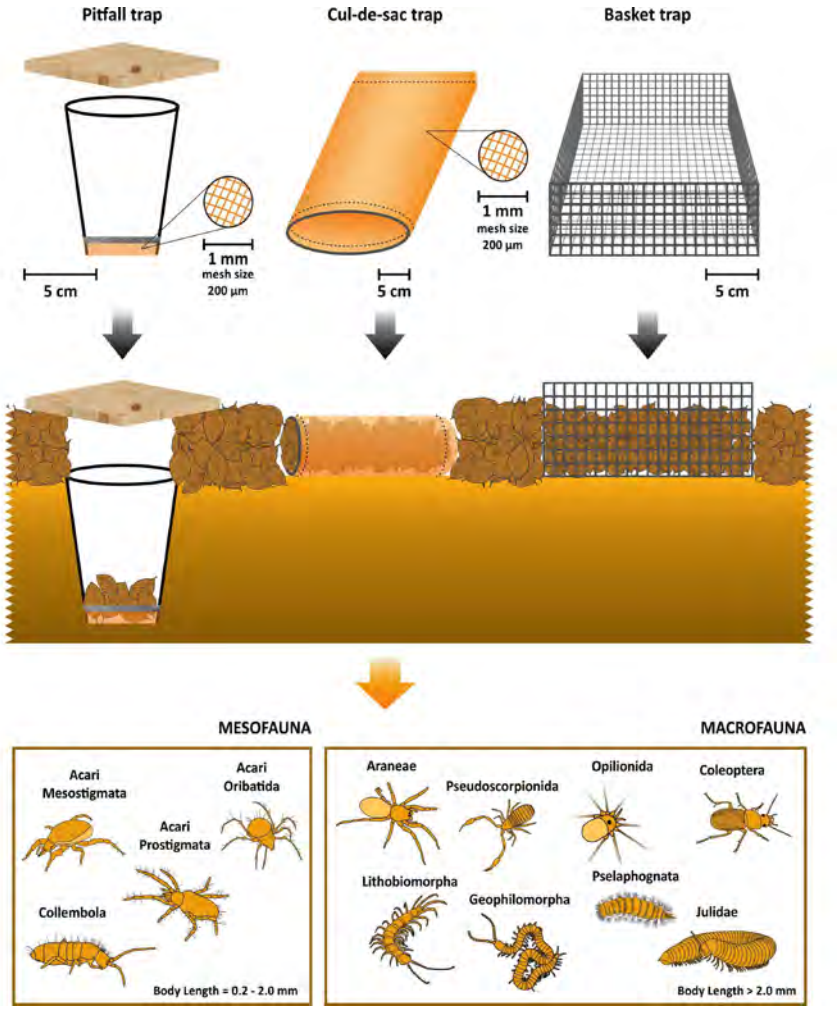


Figure 1. Trapping procedure of soil litter fauna. Black arrows represent how the traps were settled in the litter layer: pitfall traps were buried in the ground and their top lined at the bottom litter layer. Six leaves were included at the bottom of the trap and a wood lid was gently placed on top of the litter. Cul-de-sac and basket traps were embedded in the leaf litter layer. The orange arrow indicates the screening and classification of the fauna according to their size as meso- or macrofauna [1]. Mesofauna include mites (Acari) and springtails (Collembola), which have

body lengths between 0.2 and 2 mm (although some could be larger). Macrofauna include arthropods larger than 2 mm, such as arachnids in the Araenae and Pseudoscorpionida orders, Coleoptera, centipedes in the Lithobiomorpha and Geophilomorpha orders, and millipedes in the Julida and Pselaphognata orders.

2.1.1. Pitfall Traps

Pitfall traps (Figure 1) consisted of plastic cups, 8 cm Ø at the top, 5 cm Ø at the bottom, and 10 cm height, which were buried in the soil (lined on top with the bottom of the leaf litter level). A 10 × 10 × 1 cm^3 wood lid was gently placed on top, merely sitting on the litter. The lid was used to minimize incoming light in the trap because the aim of the study was to capture the active fauna within the leaf litter layer, which moves mostly in the dark. An open pitfall trap would have likely biased the results towards either nocturnal fauna or the small number of taxa that are active on top of the litter layer during daily hours (e.g., some species of carabid beetles, Jordi Moya-Laraño, personal observations). In order to prevent pitfall traps from flooding, the bottom of the cup was cut and a layer of nylon organza (mesh size ≈ 200 µm) attached to it by means of duct tape. This prevented most meso- and macrofauna from escaping through the bottom of the trap while allowing water to drain out. Moreover, in order to reduce as much as possible the occurrence of predation inside the trap (i.e., to minimize predation of small trapped animals by bigger trapped animals), as well as to have the same potential attractiveness as the other two trap types, we included some leaves inside. However, we only included a total of 6 leaves (dry mass mean: 2.67 ± 0.03 g) at the bottom of each pitfall trap, and to a maximum height of 3 cm, far enough from the trap opening as to prevent the largest animals from escaping by climbing out (Figure 1).

2.1.2. Cul-de-sac Traps

Cul-de-sac traps (Figure 1) were made up of 25 cm deep organza bags (mesh size ≈ 200 µm) with a 15 × 7 cm^2 ellipsoidal opening. At the opening end, the organza was sewed around with a 1 mm Ø wireframe which shaped the ellipsoidal opening and served to prevent the organza bag from folding on itself. These traps were filled with an average of 20.6 ± 0.1 g (mean ± SE) of defaunated dry beech leaf litter. To set up a trap, we carefully embedded it in the leaf litter layer after gently removing the litter corresponding to the volume of the trap and ensuring that the opening was in close contact with the surrounding litter (i.e., the cul-de-sac was placed horizontally in the litter), allowing a continuum (smooth transition) between the litter within the trap and the surrounding litter in the forest. The idea of this trap is that once moisture gradients have been removed (see below), any animal entering from the opening and remaining in the trap after that will reflect quasi-normal activity, with the exception that the probability of leaving the trap is not equal in all directions, as 3 of the 4 compass directions, as well as the top and the bottom, are closed. Thus, as pitfall traps, a cul-de-sac trap provides a picture of accumulated activity (Figure 1), but with the difference that fauna can potentially escape more easily from the latter and enter voluntarily rather than falling in.

2.1.3. Basket Traps

Basket traps (Figure 1) consisted of 20 × 20 × 7 cm^3 wireframe baskets (mesh size = 1 cm), open at the top and filled with 13.5 ± 0.1 g of dry and defaunated leaf litter up to a height of 3 cm. As with cul-de-sac traps, these traps were carefully embedded in the forest litter matrix after removing an equivalent volume of litter. These baskets, however, were in close contact with the surrounding litter through the 4 compass directions and also with the soil layer right below the basket (Figure 1). Therefore, all soil invertebrates could enter and leave the trap at all times with equal probabilities in all directions, hence truly reflecting normal activity (unlike cul-de-sac traps). Since these traps are open at all sides, they needed to be carefully approached for collection and rapidly placed in a bag or closed container to prevent animals from escaping down to the litter.

2.1.4. Comparison among Pitfall, Cul-de-sac, and Basket Traps

As stated above, pitfall and cul-de-sac traps serve to study cumulative activity, whereas basket traps serve to study instantaneous activity. In addition, in our design, the surface area for invertebrate catching differs among traps. Pitfall traps, with an 8 cm Ø circular opening at the top, each have a πr2 = 50.2 cm^2 catching surface or an interception perimeter of 25.1 cm. Cul-de-sacs, with r1 ≈ 7.5 cm and r2 ≈ 3.5 cm ellipsoidal opening, cover a catching area of πr1r2 ≈ 82.4 cm^2. Baskets, with a bottom area of 20 × 20 cm^2 as well as 4 side lateral contact surfaces of 20 × 3 cm^2, have a potential catching area of 640 cm^2 and is the only trap type that can collect animals coming from underground. Since pitfall traps and cul-de-sac traps work in a similar way by accumulating fauna, but the latter has a larger catching surface, we placed a pair of pitfall traps for each cul-de-sac trap to make both types more comparable to each other. To that end, the animals caught in two pitfall traps were added up for comparison with the other traps.

2.2. Experimental Design

2.2.1. Study Sites

The experiment was conducted in 4 beech forests (*Fagus sylvatica* L.) within the Cantabrian Mountains (Asturias, northwest of the Iberian Peninsula), which are separated by an average distance of 63.69 km (range 4.58 - 125.34 km). The sites were as follows: one forest site in the Integral Reserve of Muniellos (Cangas del Narcea) (43.0875° N, 6.6768° W), at 1075 m altitude; one forest site near the village of San Juan de Beleño (Ponga) (43.2038° N, 5.13908° W), at 961 m altitude, in the Ponga Natural Park; and another two forest sites in the Las Ubiñas–La Mesa Natural Park: one forest site near the village of Ricabo (Quirós) (43.0979° N, 5.9923° W), at 987 m, and the other forest site near to the village of Páramo (Teverga) (43.0895 N, 6.0447 W), at 1131 m of altitude.

2.2.2. General Description of the Experiment

We conducted a mesocosm experiment in the field from 24 May to 18 July 2013 in the four beech forests. For logistic reasons, the experiment was conducted in two temporal blocks: the first one included the sites of Muniellos and Páramo (24 May to 18 June) and the second the sites of Ricabo and Ponga (27 June to 18 July). The results presented here are part of an experiment in which we were interested in testing whether water availability drives activity among leaf-litter fauna. However, the present paper focuses on the performance comparison among trap types only, and the experimental results related to water availability will be published elsewhere. In each of the four forests, we established 2 pairs of 1 × 1 m^2 plots, with each plot next to each other within each pair (block). We dried the plots for a few days by excluding rainfall using a plastic roof, and we then established the traps and started to water each plot regularly to both induce animal activity and homogenize the moisture differences between the trap and the surrounding environment. Each plot was covered with a transparent 2 × 2 m^2 plastic sheet at an approximate height of 50 cm and with a slight incline to allow rainfall to run off from the roof (Figure 2a, b). Drying the plots prior to the mesocosm experiment was necessary to ensure that initial experimental conditions were of low water availability in all plots and sites and, most importantly, to homogenize as much as possible the moisture conditions between the traps (with dried litter from the lab) and the surrounding area (with normal amounts of rainfall if not covered). Differences in moisture could create gradients towards which animals could respond by migrating to wetter patches. Thus, this procedure allowed minimizing migration in or out of the traps and ensured that what the traps were measuring was true general activity effects in the litter. At the time that we established the rainfall covers, each 1 × 1 m^2 plot was fenced with a 40 cm height galvanized iron enclosure, buried 10 cm deep into the soil. Below the plastic roof, each fenced plot was covered with a 1.2 mm mesh fiberglass screen tightly attached to the enclosure walls (Figure 2c). This prevented emigrations from the plot during the drying period and immigrations during watering periods. Therefore, we could be sure that we were merely studying the activity of the fauna present in each 1 × 1 m^2 plot at the time of plot establishment and that our measures of activity were not biased by the attraction or repulsion of fauna due to the gradients induced by the experimental conditions.

2.2.3. Predrying Period

We induced a 15-day drought period for the present mesocosm experiment by placing the plastic roofs in the plot 15 days before the trapping began and before plot watering started. We believe that we had induced some water stress within the soil community, but not such a severe drought that could affect animal survival within the plot. We measured the excluded rainfall during the experiment by placing two pluviometers in each site and calculated average rainfall as (mean ± SE) 2.28 ± 0.19 L/m^2 day in the first temporal plot and only 0.08 ± 0.08 L/m^2 day in the second. According to the Digital Climatic Atlas of the Iberian Peninsula, rainfall in these four sites is (mean ± SE) 4.10 ± 2.12 L/m^2 day and 3.90 ± 3.00 L/m^2 day for the months of June and July, respectively [32], indicating that the year of the experiment was substantially drier than average.

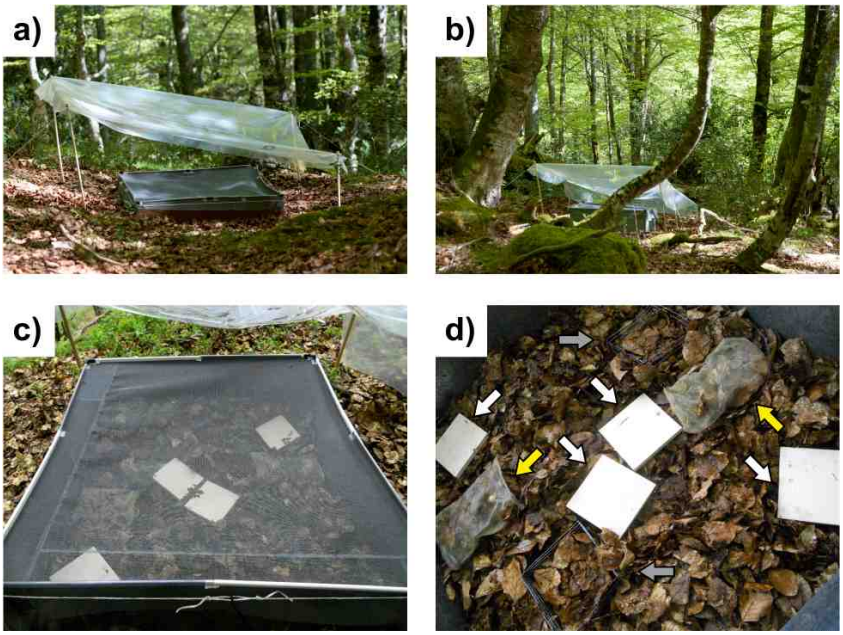


Figure 2. Pictures of the experimental design. (a) Lateral view of a 1 × 1 m^2 fenced plot, buried 10 cm deep into the soil and covered with a transparent 2 × 2 m^2 plastic cover at a height of 50 cm and with a slight incline to allow rainfall water runoff; (b) posterior view of a plot where the inclination of plastic cover is more evident; (c) dorsal view of a plot, below the plastic cover, to show how each enclosure was covered with a 1.2 mm mesh fiberglass screen tightly attached to the enclosure walls to prevent most soil litter fauna from coming in or leaving the plots; and (d) spatial arrangement of the traps within a plot: the white squares (white arrows) are the four wood lids of the pitfall traps, the yellowish bags (yellow arrows) are the two cul-de-sac traps, and the metallic squares (grey arrows) are the two basket traps. Photographs by Eva de Mas and Nereida Melguizo-Ruiz.

2.2.4. Trapping Establishment and Plot Watering

After the drying period, we set up 4 pitfalls, 2 cul-de-sacs, and 2 basket traps within each plot with the following arrangement: 1 pitfall trap in each of two opposite corners of the plot (following the diagonal), and being completely surrounded by litter (i.e., separated from the iron enclosure to avoid edge effects), and two in the middle. We then included 2 cul-de-sac and basket traps interdispersed among them and separated from each other, with the only constraint of not having the two traps of the same type on the same side of the plot (Figure 2d). We used a watering can with Font del Regàs-brand mineral water, pouring 12 L or 30 L total during the 11 days in which activity was measured, depending on whether the plot entered the low or the high water treatment, respectively. However, we stress that this factor was omitted in the present paper because it only aims at comparing trap performance. Differences in activity due to water availability, using only the appropriate type of traps, will be published elsewhere. These figures corresponded to 1.09 - 2.7 L/m^2 day, which falls within the normal regime of about 4 L/m2 day during the month of June in the area [32]. Water was supplied every other day in a total of 3 watering events, and the last watering took place three days before the last collection

(day 11). For watering, all the lids of the pitfall traps were removed and watering was accomplished by gently and homogeneously moving the water can around the plot.

2.3. Trap Collection and Counting of Fauna

Trap collection took place in two collecting rounds. The first round occurred four days after we first watered, for which we randomly collected 2 pitfall traps (one from the middle of the plot and the other from one of the corners), 1 cul-de-sac trap, and 1 basket trap. The remaining traps were collected at day 11 (second round), when all the plots were disassembled. All traps were collected carefully and quickly from the litter in order to prevent undesired migrations of fauna outside the traps (basket and cul-de-sac traps) or down into the litter (basket traps). Afterwards, each trap was immediately placed in a bag or closed plastic container. Upon arrival to the laboratory, the litter content of each trap was weighted to be later compared with the dry weight and obtain the water content (% of total mass) of each trap. Water content was assessed to test whether some of the traps could retain more water than others and therefore attract more animals, potentially biasing the estimates of activity. To extract all the fauna from the traps, we placed the content of each trap in a 40 × 80 × 15 cm^3 white tray, gently sorted through all the leaves, and collected, counted, and identified all the relatively large animals (> 0.5 mm). After this we placed the leaf litter in a Berlese–Tullgren funnel provided with a 55 W incandescent bulb, and we collected all of the animals within 48 h. The animals collected from the trays and those collected during the first two hours by the Berlese–Tullgren funnel were caught alive. The latter was accomplished by connecting the funnel extractor to a hermetic container which had a filter paper embedded with water at the bottom. These specimens were later used in an experiment to assess “who eats whom” in laboratory conditions (Jordi Moya-Laraño, unpublished results). After two hours, the Berlese-Tullgren funnels were connected to 100 mL vials containing 100% EtOH, which allowed preserving of the remaining animals. These were later counted and identified under the dissection microscope. Taxonomic identification was performed to different levels depending on the groups and always considering homogeneous criteria which took into account the common skills and knowledge of the researchers and field assistants. Because more than half of the animals had to be identified alive in situ, we could not reach a lower level of taxonomical detail. However, for the purpose of the present study, in which we simply distinguish between meso- and macrofauna, this level was sufficient. In mesofauna, we included mites and springtails. Mites were determined as Acari: Oribatida (decomposers) or Acari: Mesostigmata + Prostigmata (predators). Springtails were all included in the order Collembola. Macrofauna were all pooled in a single count per trap for statistical analysis and included spiders, pseudoscorpions, opilionids, centipedes, millipedes, and beetles (including larvae), and since not all observers were equally trained, a small proportion of animals (0.3%) could not be identified and were placed in the category “others”. The spiders were tabulated with the name Araneae. Centipedes were determined to order level (Lithobiomorpha or Geophilomorpha). Millipedes were identified at the family level as Julidae, Polydesmidae, or Polyxenidae. Adult beetles were divided between those easily identified at first sight (i.e., Carabidae, and Staphylinidae) and other groups of Coleoptera. Finally, after

all animals were removed from the traps and the leaf litter of each trap was put in a laboratory oven at 60 °C for 48 h, after which time we weighed it again to determine the dry weight, which was necessary to calculate the water content of the traps (see Table S1, Supplementary Material).

2.4. Assessment of Fauna Abundances Outside the Traps

One of the aims of ecological studies involving soil fauna is to distinguish animal activity from animal abundances [5,6,8,20,26]. One of the ways in which this can be done is by estimating animal abundances by an independent method of that used to study activity. Then, the differences between the "abundance" of animals in the activity trap and the abundance in the community is used as an accurate measure of animal activity. For instance, by including abundance as a covariate in the model when testing for activity. In leaf litter, this can be easily done by collecting litter to estimate abundances. To that end, before disassembling the plots and in order to have a good estimate of abundance of each animal group within each plot, we collected a total of 2 L of leaf litter per plot. The leaf litter was collected in 5 fractions of approximately equal volume: 4 fractions from close to each of the 4 corners and the other from the center of the plot. The procedures of sampling, counting, and identifying the animals from this litter were exactly the same as those for the traps, with a fraction of the animals also being extracted alive for inclusion in another study (see Table S1, Supplementary Material).

2.5. Assessment of Trap Bias

To assess whether all traps collected the same type of arthropod fauna, we built three bias indices: one for comparing the catches of macrofauna vs. mesofauna, another to compare the catches of predators vs. prey (fungivores and detritivores), and another to compare the catches of mites relative to that of springtails. The general formula of the index was:

$$\text{Bias Index} = \frac{\text{Activity 1 - Activity 2}}{\text{Activity 1 + Activity 2}}, \quad (1)$$

where 1 and 2 refers to each of the pairs of groups to be compared and activity is the number of individuals caught divided by the number of days elapsed since the trap was established (4 days for collecting in round 1 and 11 days for collecting in round 2). This index comparing the difference/sum ratio of two quantities has been shown to be statistically very robust and perform better than ratios or other similar indices [33]. We pooled all predators caught in a single trap, which included Acari: Mesostigamata, Acari: Prostigmata, spiders, pseudoscorpions, opilions, beetles, and centipedes; and all prey, which included Acari: Oribatida, Collembola, and millipedes. Similarly, all mite and springtail groups were pooled as single mite and springtail activity variables.

2.6. Statistical Analysis

All analyses were performed with either the function "lmer" for linear mixed models [34] or "glm" for generalized linear models (R 3.5.1 development core team 2018), testing for significant terms by means of Wald tests (lmer) or log-likelihood ratio tests (glm), respectively. Water content and animal numbers in each trap type (i.e., activity) were tested by means of linear mixed models and a Gaussian error. In all models, we first tested for the necessity to include plot or block (plot pair) effect as a random factor with a GLMM in which no fixed factors were included and only the random effect 'plot' was included, for which we used the function "ranova" in library "lmerTest" [35]. If the p-values of the random effect 'plot' and 'block' were > 0.25, we ran a GLM instead, leaving out these effects [36]. Otherwise, 'plot' and/or 'block' were included as random effects in a GLMM. We ran a separate model for the activity of mesofauna (mites and springtails) and another one for the activity of macrofauna (spiders, pseudoscorpions, opilionids, centipedes, millipedes, and beetles, including larvae). Both models included the log of ambient abundances of meso- or macrofauna, respectively, as covariates and trap type as a categorical fixed factor. The dependent variable (our measure of activity) was the number of individuals caught divided by the number of days elapsed since the trap was established (4 days for collecting in round 1 and 11 days for collecting in round 2). Since we found strong significant effects for the mesofauna, we then ran two separate models for each of the major mesofauna groups, (springtails and mites). To ensure normality of the residuals, animal counts were either log-transformed or transformed via a Box-Cox transformation using the library "MASS". Post-hoc tests among trap types were performed using the R library "multcomp".

3. Results

3.1. Water Content

Pitfall traps showed a strong bias towards high water content compared to cul-de-sac traps. Basket traps were assumed to have equivalent water content to the surrounding litter. In the final model, water content (% of total mass) was transformed via a Box-Cox transformation ($\lambda = 2.7$) to ensure normality of the residuals. 'Plot' and 'block' had no effect as random factors ($p = 0.567$ and $p = 1$, respectively) and they were therefore removed from the final GLM model. We found a significant effect of trap type ($\chi^2 = 364.620$, d.f. = 2, $p < 0.001$), and a post-hoc Tukey test showed that basket and cul-de-sac traps had the same water content (ca. 45%), while pitfall traps had around 30% more water than the other two (i.e., 75%) (pitfall vs. basket: $Z = 31.070$, $p < 0.001$; cul-de-sac vs. basket: $Z = -3.94$, $p = 0.443$ and cul-de-sac vs. pitfall: $Z = -35.010$, $p < 0.001$; Figure 3).

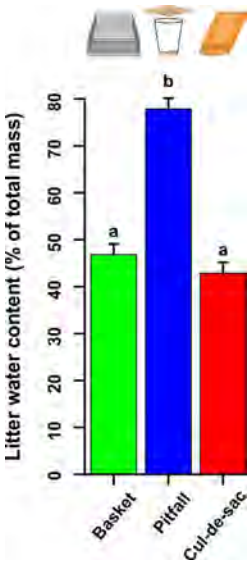


Figure 3. Litter water content (% of total mass) according to the type of trap. Green, blue, and red bars represent basket, pitfall, and cul-de-sac traps, respectively. Letters on top of bars denote statistical differences after a post-hoc Tukey test. Error bars represent standard errors of the mean.

3.2. Mesofauna Activity

The analysis of overall mesofauna activity showed that there were neither plot nor block effects ($p = 1$ and $p = 1$, respectively), and therefore a simple GLM was run for analysis. There were strong significant differences among trap types ($\chi^2 = 85.250$, d.f. = 2, $p < 0.001$). The abundance of mesofauna in the litter did not affect their activity ($\chi^2 = 0.002$, d.f. = 1, $p = 0.962$). Comparing trap efficiency among trap types, we found that pitfalls caught only 54% and 53% of the amount of fauna collected by basket and cul-de-sac traps, respectively (pitfall vs. basket: $Z = -1.220$, $p < 0.001$ and pitfall vs. cul-de-sac: $Z = 1.260$, $p < 0.001$; Figure 4a). Cul-de-sac and basket traps did not differ from each other in measuring mesofauna activity ($Z = 0.040$, $p = 0.965$). Next, we tested the performance of the traps by splitting the mesofauna into springtails (Collembola) and mites (Acari).

3.2.1. Collembola Activity

Analysis comparing the activity of springtails among trap types showed that there was a significant plot effect ($\chi^2 = 6.026$, d.f. = 1, $p = 0.014$) but no block effect ($\chi^2 = 0.950$, d.f. = 1, $p = 0.328$), and thus we removed the later from the final GLMM model. To ensure normality of the residuals, collembolan activity was transformed via a Box-Cox transformation ($\lambda = -0.4$). We found strong significant differences among trap types ($\chi^2 = 40.810$, d.f. = 2, $p < 0.001$). Importantly, the abundance of springtails in the litter did not significantly affect the amount of animals collected in the traps ($\chi^2 = 0.800$, d.f. = 1, $p = 0.796$). Comparing trap efficiency among each other with post-hoc Tukey tests, we found that pitfalls caught only 43% of the amount of collembolans collected by basket traps ($Z = -5.510$, $p < 0.001$; Figure 4b) and only 45% of the amount of collembolans collected by cul-de-sac traps ($Z = 5.21$, $p < 0.001$). We found no differences between cul-de-sac and basket traps ($Z = -0.300$, $p = 0.951$; Figure 4b).

3.2.2. Mite Activity

Analysis comparing the activity of mites among trap types showed that there were negligible plot (p = 1) and block effects (p = 1), and therefore a GLM without plot and block effects was run. There were strong significant differences among trap types (χ^2 = 99.410, d.f. = 2, p < 0.001). The abundance of mites in the litter did not significantly affect the amount of animals collected in the traps (χ^2 = 0.360, d.f. = 1, p = 0.548). Comparing trap efficiency among each other with a post-hoc Tukey test, we found that pitfalls caught only 33% and 32% of the amount of mites collected by basket and cul-de-sac traps, respectively (pitfall vs. basket: Z = −8.420, p < 0.001 and cul-de-sac vs. pitfall: Z = 8.830, p < 0.001; Figure 4c). Cul-de-sac and basket traps did not differ from each other in measuring mite activity (Z = 0.41, p = 0.912; Figure 4c).

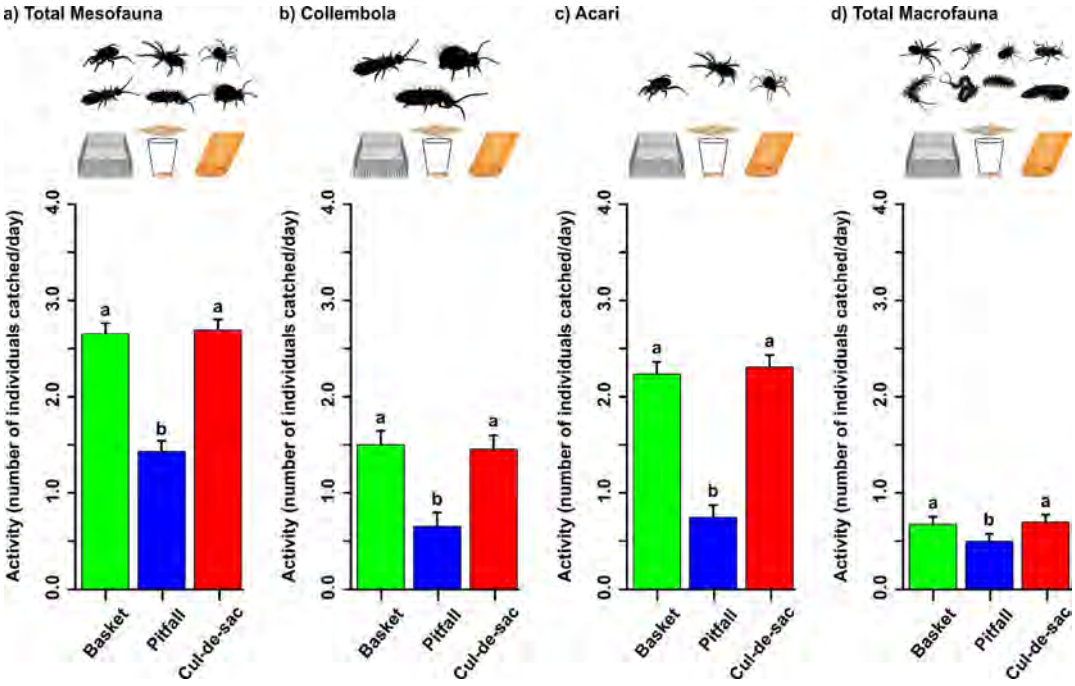


Figure 4. Activity of meso- and macrofauna (log-transform) according to the type of trap. (a) Total mesofauna; (b) Collembola; (c) Acari; and (d) total macrofauna. Green, blue, and red bars represent basket, pitfall, and cul-de-sac catches, respectively. Letters on top of bars denote statistical differences after a post-hoc Tukey test. Error bars represent standard errors of least-squares means (library "effects").

3.3. Macrofauna Activity

The analysis of macrofauna activity without fixed effects showed that there was a significant plot effect (p = 0.0014) but no block effect (p = 1), and therefore the final GLMM model included only 'plot' as a random factor. To ensure the normality of the residuals, activity was transformed via Box-Cox (λ = −0.9). We found significant differences among trap types (χ^2 = 8.900, d.f. = 2, p = 0.012). Importantly, the abundance of macrofauna in the litter did positively and significantly affect the amount of animals collected in the traps (estimate = 0.116, SE = 0.050, χ^2 = 5.390, d.f. = 1, p = 0.020). Comparing trap

efficiency among each other with a post-hoc Tukey test, we found that pitfalls caught only 73% of the amount of macrofauna collected by basket traps (Z = −2.490, p = 0.034; Figure 4d) and only 71% of the amount of macrofauna collected by cul-de-sac traps (Z = 2.670, p = 0.021). Cul-de-sac and basket traps did not differ from each other (Z = 0.180, p = 0.982; Figure 4d).

3.4. Trap Bias Index

The analysis of the trap bias index comparing macrofauna vs. mesofauna showed that there was a significant plot effect (p = 0.0479) but no block effect (p = 1), and therefore the final GLMM model included only 'plot' as a random factor. To ensure normality of the residuals, the bias index was transformed via Box-Cox (λ = −3.6, obtained after adding 2 to the bias index). We found significant differences among trap types (χ^2 = 12.640, d.f. = 2, p = 0.002). The bias index was 21% and 18% higher for pitfall traps compared to basket and cul-de-sac traps, respectively (pitfall vs. basket: Z = 3.320, p = 0.003 and cul-de-sac vs. pitfall: Z = −2.730, p = 0.017). The index did not differ between cul-de-sac and basket traps (Z = 0.580, p = 0.830; Figure 5a).

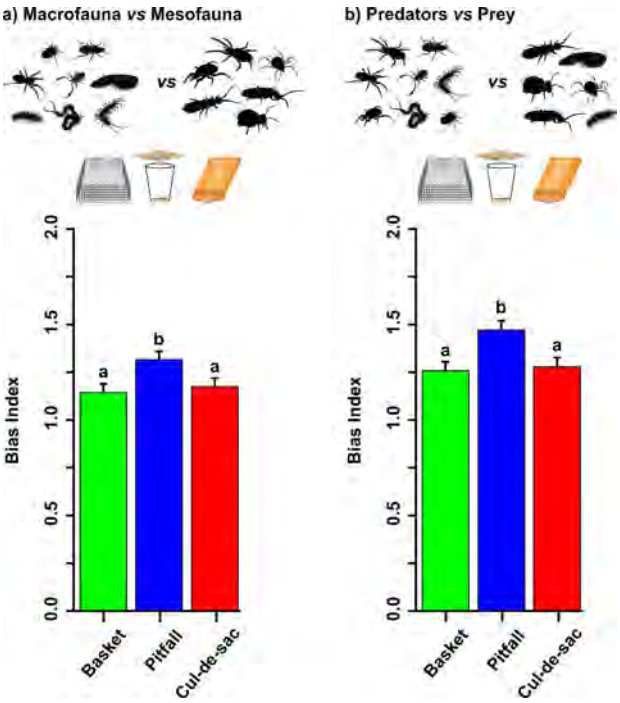


Figure 5. Trap bias. (a) Macrofauna vs. mesofauna and (b) predators vs. prey. Green, blue, and red bars represent basket, pitfall, and cul-de-sac catches, respectively. Letters on top of bars denote statistical differences after a post-hoc Tukey test. Error bars represent standard errors of least-squares means (library "effects"). Since the bias index reaches negative values, we enabled easier visualization and interpretation by adding a constant = 2 to the index.

The analysis of the trap bias index for predators compared to prey showed that there was a plot effect (p = 0.009) but that no block effect (p = 0.761), and thus we removed the latter from the GLMM.

To ensure normality of the residuals, the bias index was transformed via Box-Cox (λ = −1.4, obtained after adding 2 to the bias index). We found significant differences among trap types (χ^2 = 12.640, d.f. = 2, p = 0.002). The trap bias index for predators vs. prey was 29% and 28% higher for pitfall traps than for either basket or cul-de-sac traps (pitfall vs. basket: Z =−3.890, p <0.001 and cul-de-sac vs. pitfall: Z = −3.510, p = 0.001), indicating that pitfall traps tend to collect more predators (spiders, pseudoscorpions, larvae and adult beetles, and centipedes) than prey relative to the other traps. No differences were found between cul-de-sac and basket traps (Z = 0.390, p = 0.920) (Figure 5b). However, no bias was detected for the comparison of mites vs. collembolans (χ^2 = 0.800, d.f. = 2, p = 671).

4. Discussion

Pitfall traps were largely outperformed by cul-de-sac and basket traps in the study of both meso- and macrofauna activity. First, pitfall traps retained almost twice the amount of water that the other two trap types, potentially originating strong gradients which could encourage hygrophilous fauna to get into the traps. Second, despite this water bias in pitfall traps, cul-de-sac and basket traps collected around 3–5 times more animals per unit of time, both from mesofauna and macrofauna, than pitfall traps. As shown in Figure 5, pitfall traps biased their catches towards predators and towards macrofauna. Therefore, when the aim of the study is to disentangle activity from density in litter fauna, these two new trap types (cul-de-sac and basket traps) are to be preferred and should be used in all future studies involving hypotheses relating to animal activity; for instance, to test for the mobility dependence on climatic factors such as rainfall or temperature [37] or to study an increase or decrease in mobility induced by antipredatory behavior [38].

We do not disregard the idea that many predatory events took place within the traps and that this could explain why pitfall traps had such low efficiency compared to the other two, which had more litter and therefore could minimize predatory events much more efficiently. This, in addition, could explain why cul-de-sac traps did not accumulate more fauna than basket traps despite being open only on one end. However, if that were the case, we should have seen also a bias towards predators in cul-de-sac traps, which we did not. Thus, depending on whether one is interested in instantaneous vs. cumulative activity, basket or cul-de-sac traps, respectively, should be used. Additionally, since cul-de-sac traps have a single opening, they can be directional and collect animals coming from certain directions (e.g., in and out of shrubs).

We claim that these trap devices can be readily used in any system that has litter, not just in deciduous forests. For instance, these could be used in coniferous or evergreen forests, in tropical rainforests, and in fertility islands, in which litter accumulates underneath shrubs [39]. The size of the traps may need to be adjusted to the size of the shrub and the depth of the litter.

In order to use these new trap devices (cul-de-sac and basket traps) properly, we recommend following the protocol below:

(a) Collect litter from the habitat to be studied and carefully defaunate it in the laboratory. Using LED bulbs for longer periods (e.g., 7-14 days) instead of incandescent bulbs will minimize the death of animals in the litter, which could have some unwanted effects in terms of attracting scavengers and fungivores feeding on the fungi growing on the carcasses. In our case, we did check for large animals in the litter visually, and since the bias of a few inadvertently dead animals in the litter was the same for all trap types, we do not believe that it affected our results.

(b) Check the weather forecasts around the study area and get ready to set up the traps in the field right after the first sufficiently abundant rainfall event (e.g., of > 10 mm). Set the traps for the experiment before rainfall starts or before too much rain has fallen. This will ensure that the litter in the traps gets as wet as the litter in the habitat. Alternatively, set the trap when it has not been raining for a long time (i.e., when the litter in the field is as dry as the one that will be brought from the laboratory). However, in dry conditions, it is much less likely to be able to collect high amounts of fauna, and it may be necessary to wait until the next rainfall to collect the traps. If the intention is to include the traps in a mesocosm experiment, they must set in the inner parts of the plot and not at the edges. In our case, we set a pair of pitfall traps a few centimeters from the edge of the plot to minimize the bias due to catches from animals that were trying to leave the plot. A second pair of pitfall traps was set in the center of the plot to further dilute potential edge effects. Unfortunately, in our case, we pooled the data from edge and center traps without previously testing for edge effects. If traps of any type are to be included at the edges, it is important to test for differences between edge and inner traps before pooling the data.

(c) Check the traps 2-3 days after rainfall ceases (or a different number of days, which may depend on the particular system). Collect the traps and extract the fauna in the laboratory. Be aware that basket traps need to be collected fast and with care. Always try to prevent animals from escaping down into the litter or out from the sides. Place the trap in a bag or closed container as soon as it is removed from the field.

(d) The weather conditions on the day and timing of trap collection and differences among ecosystems can determine what one catches in the traps. Thus, for each ecosystem type, select a time of the day in which the edaphic fauna is active in the relevant the weather conditions. For instance, in the peak of summer in relatively dry ecosystems, most epigeic fauna are only active at night [40]. In addition, collect enough amounts of litter from the microhabitat's surrounding area (or inside the mesocosm) to estimate the abundances of all organisms under study.

(e) Run a GLMM or GLM to test for activity (animals caught by unit of time), and include the logarithm of the abundance or density of the group of interest as a covariate to control for animal availability in the litter to ensure that only activity is being tested for (not abundance). In our case, density was significant only in the case of macrofauna. If density is not significant, it means that activity is decoupled from the availability of individuals.

5. Conclusions

In conclusion, we believe that our new trap devices are a promising tool to help distinguishing abundance from activity in field experiments involving arthropod fauna that inhabit the leaf litter. We hope that future studies make use of these simple techniques to advance our knowledge on this important component of terrestrial ecosystems.

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Data accessibility statement

We confirm that the data supporting the results are archived in Ruiz-Lupión, Dolores; Pascual, Jordi; Melguizo-Ruiz, Nereida; Verdeny Vilalta, Oriol; Moya-Laraño, Jordi. 2019. "Activity-density of different traps of soil litter fauna [Dataset]" DIGITAL.CSIC https://digital.csic.es/handle/10261/174940.

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Table S1. Database of catches-abundance of different traps of soil litter fauna.

					Catches (individuals/trap)									
Site	**Trap Type**	**Plot**	**Block**	**% Water content**	**Acari Mesostigmata + Prostigmata**	**Acari Oribatida**	**Collembola**	**Araneae**	**Pseudoscorpionida**	**Opilionida**	**Carabidae**	**Staphylinidae**	**Other Coleoptera**	**Days of activation**
Muniellos	Basket	1	B1	53.41	9	51	25	0	1	0	0	0	0	4
Muniellos	Cul-de-sac	1	B1	36.61	7	65	41	0	0	1	0	0	0	4
Muniellos	Pitfall	1	B1	67.22	3	21	38	1	0	0	0	0	0	4
Muniellos	Basket	2	B1	49.54	16	91	128	0	0	1	0	0	1	4
Muniellos	Cul-de-sac	2	B1	42.88	5	135	102	0	0	1	0	0	0	4
Muniellos	Pitfall	2	B1	79.45	0	12	9	1	0	0	0	0	0	4
Muniellos	Basket	3	B2	38.16	2	23	16	1	0	1	0	0	0	4
Muniellos	Cul-de-sac	3	B2	27.56	5	76	5	0	2	0	0	0	0	4
Muniellos	Pitfall	3	B2	78.47	0	52	4	0	0	0	0	0	1	4
Muniellos	Basket	4	B2	55.35	3	68	18	1	0	0	0	0	0	4
Muniellos	Cul-de-sac	4	B2	42.29	4	75	32	0	2	0	0	0	0	4
Muniellos	Pitfall	4	B2	76.47	1	8	3	0	0	0	0	0	0	4
Muniellos	Basket	1	B1	16.25	0	60	9	1	1	0	0	0	0	11
Muniellos	Cul-de-sac	1	B1	25.92	9	84	13	0	0	0	0	0	0	11
Muniellos	Pitfall	1	B1	75.17	1	8	14	1	0	0	0	0	0	11
Muniellos	Basket	2	B1	57.41	19	171	86	0	1	0	0	0	0	11
Muniellos	Cul-de-sac	2	B1	44.10	8	246	48	2	0	0	0	0	0	11
Muniellos	Pitfall	2	B1	81.48	1	10	7	0	0	1	0	0	0	11
Muniellos	Basket	3	B2	16.93	1	18	1	0	0	0	0	0	0	11
Muniellos	Cul-de-sac	3	B2	19.37	5	55	8	2	0	0	0	0	0	11
Muniellos	Pitfall	3	B2	76.49	5	37	3	1	0	0	0	0	1	11
Muniellos	Basket	4	B2	41.01	15	74	10	0	0	0	0	0	0	11
Muniellos	Cul-de-sac	4	B2	47.50	4	93	33	0	0	0	0	0	0	11

Muniellos	Pitfall	4	B2	80.13	1	10	1	0	0	1	1	0	0	11
Páramo	Basket	1	B1	33.47	2	52	13	1	0	0	0	0	0	4
Páramo	Cul-de-sac	1	B1	31.64	5	105	25	3	2	0	1	0	0	4
Páramo	Pitfall	1	B1	78.04	3	12	3	1	0	1	0	0	1	4
Páramo	Basket	2	B1	52.95	0	28	38	1	0	0	0	0	0	4
Páramo	Cul-de-sac	2	B1	51.58	12	64	35	0	0	0	1	0	0	4
Páramo	Pitfall	2	B1	76.94	7	13	4	3	0	0	5	0	0	4
Páramo	Basket	3	B2	12.34	1	36	13	0	0	0	0	0	0	4
Páramo	Cul-de-sac	3	B2	27.29	3	69	2	0	0	2	0	0	0	4
Páramo	Pitfall	3	B2	78.50	0	6	3	0	0	3	7	1	0	4
Páramo	Basket	4	B2	54.82	5	80	11	1	1	0	0	0	0	4
Páramo	Cul-de-sac	4	B2	48.14	6	130	37	0	0	0	0	0	0	4
Páramo	Pitfall	4	B2	76.34	0	11	2	0	0	2	6	0	0	4
Páramo	Basket	1	B1	10.84	0	24	1	0	0	1	0	0	0	11
Páramo	Cul-de-sac	1	B1	58.34	0	35	0	0	0	1	0	0	0	11
Páramo	Pitfall	1	B1	81.95	2	22	2	0	0	0	3	1	0	11
Páramo	Basket	2	B1	28.36	7	111	11	0	0	0	0	0	0	11
Páramo	Cul-de-sac	2	B1	41.62	4	405	31	0	1	0	0	0	0	11
Páramo	Pitfall	2	B1	74.74	2	20	1	0	1	0	6	0	0	11
Páramo	Basket	3	B2	12.75	1	97	4	0	1	0	0	0	0	11
Páramo	Cul-de-sac	3	B2	13.84	1	119	8	0	2	2	0	0	1	11
Páramo	Pitfall	3	B2	78.03	4	36	6	0	0	3	31	1	0	11
Páramo	Basket	4	B2	52.68	12	101	26	0	0	1	0	0	0	11
Páramo	Cul-de-sac	4	B2	40.08	6	122	80	0	1	0	0	0	0	11
Páramo	Pitfall	4	B2	78.34	4	35	14	0	0	0	2	0	0	11
Ponga	Basket	1	B1	68.46	12	33	10	0	6	0	0	0	0	4
Ponga	Cul-de-sac	1	B1	45.23	6	20	13	0	0	1	0	7	0	4
Ponga	Pitfall	1	B1	81.95	1	0	2	1	0	1	0	0	0	4

Ponga	Basket	2	B1	69.74	11	82	21	0	6	0	0	3	0	4
Ponga	Cul-de-sac	2	B1	60.90	3	13	3	1	0	1	0	0	0	4
Ponga	Pitfall	2	B1	78.03	2	8	4	0	0	1	0	0	0	4
Ponga	Basket	3	B2	58.84	5	54	4	1	4	0	0	1	0	4
Ponga	Cul-de-sac	3	B2	52.46	6	19	1	0	3	2	0	0	0	4
Ponga	Pitfall	3	B2	79.10	0	6	5	0	0	0	0	0	0	4
Ponga	Basket	4	B2	67.71	3	44	13	1	4	2	0	1	0	4
Ponga	Cul-de-sac	4	B2	65.89	1	32	12	0	4	0	0	0	0	4
Ponga	Pitfall	4	B2	77.65	1	1	0	0	0	0	0	0	0	4
Ponga	Basket	1	B1	46.78	20	67	73	3	7	0	0	1	0	11
Ponga	Cul-de-sac	1	B1	41.37	7	54	13	1	6	0	0	0	0	11
Ponga	Pitfall	1	B1	81.70	0	20	13	0	0	0	0	0	0	11
Ponga	Basket	2	B1	65.35	25	93	122	2	3	0	0	0	0	11
Ponga	Cul-de-sac	2	B1	63.32	22	110	87	0	8	0	0	0	0	11
Ponga	Pitfall	2	B1	81.29	3	24	18	1	2	0	0	0	0	11
Ponga	Basket	3	B2	44.77	7	28	7	2	1	0	0	0	0	11
Ponga	Cul-de-sac	3	B2	35.56	13	35	9	0	2	1	0	1	1	11
Ponga	Pitfall	3	B2	75.20	2	13	2	0	0	0	1	1	0	11
Ponga	Basket	4	B2	65.67	20	95	106	0	2	0	0	4	0	11
Ponga	Cul-de-sac	4	B2	54.36	17	62	20	0	7	1	0	1	0	11
Ponga	Pitfall	4	B2	82.80	8	9	14	0	0	0	1	1	0	11
Ricabo	Basket	1	B1	51.52	3	27	10	0	1	1	0	0	1	4
Ricabo	Cul-de-sac	1	B1	44.22	10	36	30	1	0	0	0	0	0	4
Ricabo	Pitfall	1	B1	78.41	1	13	5	0	0	0	3	0	0	4
Ricabo	Basket	2	B1	61.91	16	39	59	0	0	1	0	0	0	4
Ricabo	Cul-de-sac	2	B1	53.96	10	19	25	0	1	1	1	0	0	4
Ricabo	Pitfall	2	B1	79.43	2	11	5	0	0	0	5	0	0	4
Ricabo	Basket	3	B2	59.06	13	20	20	0	1	4	0	0	0	4

Ricabo	Cul-de-sac	3	B2	40.96	6	11	9	0	0	1	0	0	0	4
Ricabo	Pitfall	3	B2	77.04	5	13	8	0	0	0	1	0	0	4
Ricabo	Basket	4	B2	67.24	13	17	25	0	0	0	0	0	0	4
Ricabo	Cul-de-sac	4	B2	56.98	8	11	16	0	0	0	0	0	0	4
Ricabo	Pitfall	4	B2	80.89	4	10	3	0	0	0	1	0	0	4
Ricabo	Basket	1	B1	24.28	6	43	18	0	4	0	0	0	0	11
Ricabo	Cul-de-sac	1	B1	30.08	10	30	6	0	7	0	0	0	0	11
Ricabo	Pitfall	1	B1	77.73	4	12	5	0	0	0	0	0	0	11
Ricabo	Basket	2	B1	63.13	38	67	57	0	1	0	0	0	0	11
Ricabo	Cul-de-sac	2	B1	45.17	54	113	158	0	1	0	0	0	0	11
Ricabo	Pitfall	2	B1	76.13	6	5	3	1	3	0	0	0	0	11
Ricabo	Basket	3	B2	44.13	52	56	42	0	1	0	0	0	0	11
Ricabo	Cul-de-sac	3	B2	34.26	12	38	37	1	2	1	0	0	0	11
Ricabo	Pitfall	3	B2	71.02	2	10	9	0	0	1	2	0	0	11
Ricabo	Basket	4	B2	53.18	15	96	31	1	0	0	0	1	0	11
Ricabo	Cul-de-sac	4	B2	48.55	26	40	64	0	1	0	0	0	0	11
Ricabo	Pitfall	4	B2	76.18	5	15	14	0	0	0	4	0	0	11

*Site: study sites (beech forests) where the experiment was conducted.
*Plot: in each forest site we established 2 pairs of 1x1m^2 contiguous plots.
*Block: each pair of contiguous plots.
*% Water content (mg): percentage of water in the litter.
*Catches: number of individuals caught by a given trap (individuals/trap).
*Days of activation: number of days since the trap was established until it was collected.

Table S1. Database of catches-abundance of different traps of soil litter fauna (cont'd).

					Catches (individuals/trap)								
Site	**Trap Type**	**Plot**	**Block**	**% Water content**	**Larvae Carabidae**	**Other Larvae**	**Diptera**	**Geophilomorpha**	**Lithobiomorpha**	**Julidae**	**Pselaphognata**	**Polydesmidae**	**Days of activation**
Muniellos	Basket	1	B1	53.41	0	0	0	0	0	0	1	0	4
Muniellos	Cul-de-sac	1	B1	36.61	0	0	0	0	0	0	0	0	4
Muniellos	Pitfall	1	B1	67.22	0	0	1	0	0	0	0	0	4
Muniellos	Basket	2	B1	49.54	0	1	1	0	0	0	0	1	4
Muniellos	Cul-de-sac	2	B1	42.88	0	0	0	0	1	0	0	0	4
Muniellos	Pitfall	2	B1	79.45	0	0	0	0	0	0	0	0	4
Muniellos	Basket	3	B2	38.16	0	0	0	0	0	0	0	0	4
Muniellos	Cul-de-sac	3	B2	27.56	0	1	1	0	0	0	0	0	4
Muniellos	Pitfall	3	B2	78.47	0	0	0	0	0	0	0	0	4
Muniellos	Basket	4	B2	55.35	0	0	1	0	0	0	0	0	4
Muniellos	Cul-de-sac	4	B2	42.29	0	0	1	0	0	0	0	0	4
Muniellos	Pitfall	4	B2	76.47	0	0	0	0	0	0	0	0	4
Muniellos	Basket	1	B1	16.25	0	0	0	0	0	0	1	0	11
Muniellos	Cul-de-sac	1	B1	25.92	0	0	1	0	2	0	0	0	11
Muniellos	Pitfall	1	B1	75.17	0	0	0	0	0	0	0	2	11
Muniellos	Basket	2	B1	57.41	0	0	1	0	0	0	0	0	11
Muniellos	Cul-de-sac	2	B1	44.10	0	0	0	0	4	0	1	0	11
Muniellos	Pitfall	2	B1	81.48	0	0	0	0	0	0	0	0	11
Muniellos	Basket	3	B2	16.93	0	1	0	0	0	0	0	0	11
Muniellos	Cul-de-sac	3	B2	19.37	0	0	0	0	1	0	2	0	11
Muniellos	Pitfall	3	B2	76.49	0	0	5	0	0	0	1	0	11
Muniellos	Basket	4	B2	41.01	0	0	0	0	0	0	0	0	11
Muniellos	Cul-de-sac	4	B2	47.50	0	0	0	0	0	0	0	0	11
Muniellos	Pitfall	4	B2	80.13	0	0	1	0	2	0	0	0	11

Páramo	Basket	1	B1	33.47	0	0	1	0	1	0	4	0	4
Páramo	Cul-de-sac	1	B1	31.64	0	0	1	0	1	0	7	0	4
Páramo	Pitfall	1	B1	78.04	0	0	0	1	0	0	0	0	4
Páramo	Basket	2	B1	52.95	0	1	2	0	0	0	1	0	4
Páramo	Cul-de-sac	2	B1	51.58	0	0	2	0	2	0	0	0	4
Páramo	Pitfall	2	B1	76.94	0	0	1	0	0	0	0	0	4
Páramo	Basket	3	B2	12.34	0	0	1	0	0	0	5	0	4
Páramo	Cul-de-sac	3	B2	27.29	0	1	0	0	1	0	8	0	4
Páramo	Pitfall	3	B2	78.50	0	0	0	0	0	0	0	0	4
Páramo	Basket	4	B2	54.82	0	0	1	0	1	0	1	0	4
Páramo	Cul-de-sac	4	B2	48.14	0	0	1	0	0	0	5	0	4
Páramo	Pitfall	4	B2	76.34	0	0	0	0	0	0	0	0	4
Páramo	Basket	1	B1	10.84	0	0	1	0	0	0	23	0	11
Páramo	Cul-de-sac	1	B1	58.34	0	0	0	0	0	0	42	0	11
Páramo	Pitfall	1	B1	81.95	0	0	1	0	0	0	0	0	11
Páramo	Basket	2	B1	28.36	0	0	1	0	0	0	5	0	11
Páramo	Cul-de-sac	2	B1	41.62	0	0	2	0	2	0	0	0	11
Páramo	Pitfall	2	B1	74.74	3	0	0	0	1	0	0	0	11
Páramo	Basket	3	B2	12.75	0	0	0	0	0	0	1	0	11
Páramo	Cul-de-sac	3	B2	13.84	0	0	0	0	0	0	18	0	11
Páramo	Pitfall	3	B2	78.03	0	0	0	0	2	0	0	0	11
Páramo	Basket	4	B2	52.68	0	1	4	0	2	0	11	0	11
Páramo	Cul-de-sac	4	B2	40.08	0	0	0	0	1	0	5	0	11
Páramo	Pitfall	4	B2	78.34	0	1	0	0	3	0	0	0	11
Ponga	Basket	1	B1	68.46	0	0	0	1	0	0	3	0	4
Ponga	Cul-de-sac	1	B1	45.23	0	0	1	0	0	0	0	0	4
Ponga	Pitfall	1	B1	81.95	0	0	2	0	0	0	0	0	4
Ponga	Basket	2	B1	69.74	0	0	0	0	0	0	0	0	4

Ponga	Cul-de-sac	2	B1	60.90	0	0	0	1	0	0	1	0	4
Ponga	Pitfall	2	B1	78.03	0	1	0	0	0	0	2	0	4
Ponga	Basket	3	B2	58.84	0	0	0	0	0	0	2	0	4
Ponga	Cul-de-sac	3	B2	52.46	0	0	0	0	1	0	4	0	4
Ponga	Pitfall	3	B2	79.10	0	0	0	0	0	0	0	0	4
Ponga	Basket	4	B2	67.71	0	0	0	0	0	0	0	0	4
Ponga	Cul-de-sac	4	B2	65.89	0	0	0	0	0	0	1	0	4
Ponga	Pitfall	4	B2	77.65	0	0	0	0	0	0	0	0	4
Ponga	Basket	1	B1	46.78	0	0	0	0	0	0	0	0	11
Ponga	Cul-de-sac	1	B1	41.37	0	0	0	0	0	0	2	0	11
Ponga	Pitfall	1	B1	81.70	0	0	0	0	0	0	0	0	11
Ponga	Basket	2	B1	65.35	0	1	1	0	0	0	0	0	11
Ponga	Cul-de-sac	2	B1	63.32	0	0	0	0	0	0	0	0	11
Ponga	Pitfall	2	B1	81.29	0	1	1	0	0	0	1	0	11
Ponga	Basket	3	B2	44.77	0	0	3	0	0	0	0	0	11
Ponga	Cul-de-sac	3	B2	35.56	0	0	0	0	0	0	3	0	11
Ponga	Pitfall	3	B2	75.20	0	0	0	0	0	0	0	0	11
Ponga	Basket	4	B2	65.67	0	1	0	0	0	0	0	0	11
Ponga	Cul-de-sac	4	B2	54.36	0	0	0	0	0	0	4	0	11
Ponga	Pitfall	4	B2	82.80	0	0	0	0	0	0	0	0	11
Ricabo	Basket	1	B1	51.52	0	1	0	0	0	0	0	0	4
Ricabo	Cul-de-sac	1	B1	44.22	0	0	0	1	0	0	1	0	4
Ricabo	Pitfall	1	B1	78.41	0	0	0	0	0	0	0	0	4
Ricabo	Basket	2	B1	61.91	0	0	0	1	1	0	0	0	4
Ricabo	Cul-de-sac	2	B1	53.96	0	0	0	0	0	0	0	0	4
Ricabo	Pitfall	2	B1	79.43	0	0	0	0	0	0	0	0	4
Ricabo	Basket	3	B2	59.06	0	3	0	0	1	0	0	0	4
Ricabo	Cul-de-sac	3	B2	40.96	0	0	0	0	0	0	0	0	4

Ricabo	Pitfall	3	B2	77.04	0	0	0	0	0	1	0	0	4
Ricabo	Basket	4	B2	67.24	0	0	0	0	2	0	0	0	4
Ricabo	Cul-de-sac	4	B2	56.98	0	0	0	0	0	0	0	0	4
Ricabo	Pitfall	4	B2	80.89	0	0	0	0	1	0	1	1	4
Ricabo	Basket	1	B1	24.28	0	0	0	0	0	0	1	0	11
Ricabo	Cul-de-sac	1	B1	30.08	0	0	0	0	0	0	2	0	11
Ricabo	Pitfall	1	B1	77.73	1	2	0	0	0	0	0	0	11
Ricabo	Basket	2	B1	63.13	0	1	0	0	0	0	0	0	11
Ricabo	Cul-de-sac	2	B1	45.17	0	0	0	0	1	0	2	0	11
Ricabo	Pitfall	2	B1	76.13	0	0	0	0	1	0	0	0	11
Ricabo	Basket	3	B2	44.13	0	0	0	1	1	0	1	0	11
Ricabo	Cul-de-sac	3	B2	34.26	0	0	1	1	1	0	2	0	11
Ricabo	Pitfall	3	B2	71.02	0	0	0	0	0	0	0	0	11
Ricabo	Basket	4	B2	53.18	0	0	0	0	1	0	0	0	11
Ricabo	Cul-de-sac	4	B2	48.55	0	0	1	0	1	0	2	0	11
Ricabo	Pitfall	4	B2	76.18	0	0	1	0	0	0	0	0	11

*Site: study sites (beech forests) where the experiment was conducted.
*Plot: in each forest site we established 2 pairs of 1x1m^2 contiguous plots.
*Block: each pair of contiguous plots.
*% Water content (mg): percentage of water in the litter.
*Catches: number of individuals caught by a given trap (individuals/trap).
*Days of activation: number of days since the trap was established until it was collected.

Table S1. Database of catches-abundance of different traps of soil litter fauna (cont'd).

					Abundance (individuals/2L leef litter)								
Site	**Trap Type**	**Plot**	**Block**	**% Water content**	**Acari Mesostigmata + Prostigmata**	**Acari Oribatida**	**Collembola**	**Araneae**	**Pseudoscorpionida**	**Opilionida**	**Carabidae**	**Staphylinidae**	**Other Coleoptera**
Muniellos	Basket	1	B1	53.41	106	212	146	2	1	2	0	0	1
Muniellos	Cul-de-sac	1	B1	36.61	106	212	146	2	1	2	0	0	1
Muniellos	Pitfall	1	B1	67.22	106	212	146	2	1	2	0	0	1
Muniellos	Basket	2	B1	49.54	51	86	73	0	1	0	0	1	2
Muniellos	Cul-de-sac	2	B1	42.88	51	86	73	0	1	0	0	1	2
Muniellos	Pitfall	2	B1	79.45	51	86	73	0	1	0	0	1	2
Muniellos	Basket	3	B2	38.16	56	139	39	17	5	0	0	0	0
Muniellos	Cul-de-sac	3	B2	27.56	56	139	39	17	5	0	0	0	0
Muniellos	Pitfall	3	B2	78.47	56	139	39	17	5	0	0	0	0
Muniellos	Basket	4	B2	55.35	59	369	71	14	12	0	0	0	3
Muniellos	Cul-de-sac	4	B2	42.29	59	369	71	14	12	0	0	0	3
Muniellos	Pitfall	4	B2	76.47	59	369	71	14	12	0	0	0	3
Muniellos	Basket	1	B1	16.25	106	212	146	2	1	2	0	0	1
Muniellos	Cul-de-sac	1	B1	25.92	106	212	146	2	1	2	0	0	1
Muniellos	Pitfall	1	B1	75.17	106	212	146	2	1	2	0	0	1
Muniellos	Basket	2	B1	57.41	51	86	73	0	1	0	0	1	2
Muniellos	Cul-de-sac	2	B1	44.10	51	86	73	0	1	0	0	1	2
Muniellos	Pitfall	2	B1	81.48	51	86	73	0	1	0	0	1	2
Muniellos	Basket	3	B2	16.93	56	139	39	17	5	0	0	0	0
Muniellos	Cul-de-sac	3	B2	19.37	56	139	39	17	5	0	0	0	0
Muniellos	Pitfall	3	B2	76.49	56	139	39	17	5	0	0	0	0
Muniellos	Basket	4	B2	41.01	59	369	71	14	12	0	0	0	3
Muniellos	Cul-de-sac	4	B2	47.50	59	369	71	14	12	0	0	0	3

Muniellos	Pitfall	4	B2	80.13	59	369	71	14	12	0	0	0	3
Páramo	Basket	1	B1	33.47	68	498	105	1	6	0	2	0	0
Páramo	Cul-de-sac	1	B1	31.64	68	498	105	1	6	0	2	0	0
Páramo	Pitfall	1	B1	78.04	68	498	105	1	6	0	2	0	0
Páramo	Basket	2	B1	52.95	105	257	204	0	1	0	1	0	0
Páramo	Cul-de-sac	2	B1	51.58	105	257	204	0	1	0	1	0	0
Páramo	Pitfall	2	B1	76.94	105	257	204	0	1	0	1	0	0
Páramo	Basket	3	B2	12.34	84	579	106	1	2	1	1	0	0
Páramo	Cul-de-sac	3	B2	27.29	84	579	106	1	2	1	1	0	0
Páramo	Pitfall	3	B2	78.50	84	579	106	1	2	1	1	0	0
Páramo	Basket	4	B2	54.82	57	580	147	10	3	0	0	1	0
Páramo	Cul-de-sac	4	B2	48.14	57	580	147	10	3	0	0	1	0
Páramo	Pitfall	4	B2	76.34	57	580	147	10	3	0	0	1	0
Páramo	Basket	1	B1	10.84	68	498	105	1	6	0	2	0	0
Páramo	Cul-de-sac	1	B1	58.34	68	498	105	1	6	0	2	0	0
Páramo	Pitfall	1	B1	81.95	68	498	105	1	6	0	2	0	0
Páramo	Basket	2	B1	28.36	57	580	147	10	3	0	0	1	0
Páramo	Cul-de-sac	2	B1	41.62	57	580	147	10	3	0	0	1	0
Páramo	Pitfall	2	B1	74.74	57	580	147	10	3	0	0	1	0
Páramo	Basket	3	B2	12.75	84	579	106	1	2	1	1	0	0
Páramo	Cul-de-sac	3	B2	13.84	84	579	106	1	2	1	1	0	0
Páramo	Pitfall	3	B2	78.03	84	579	106	1	2	1	1	0	0
Páramo	Basket	4	B2	52.68	105	257	204	0	1	0	1	0	0
Páramo	Cul-de-sac	4	B2	40.08	105	257	204	0	1	0	1	0	0
Páramo	Pitfall	4	B2	78.34	105	257	204	0	1	0	1	0	0
Ponga	Basket	1	B1	68.46	115	514	331	4	27	0	0	6	1
Ponga	Cul-de-sac	1	B1	45.23	115	514	331	4	27	0	0	6	1
Ponga	Pitfall	1	B1	81.95	115	514	331	4	27	0	0	6	1

Ponga	Basket	2	B1	69.74	44	206	63	5	18	0	0	2	0
Ponga	Cul-de-sac	2	B1	60.90	44	206	63	5	18	0	0	2	0
Ponga	Pitfall	2	B1	78.03	44	206	63	5	18	0	0	2	0
Ponga	Basket	3	B2	58.84	32	174	28	4	12	0	1	0	0
Ponga	Cul-de-sac	3	B2	52.46	32	174	28	4	12	0	1	0	0
Ponga	Pitfall	3	B2	79.10	32	174	28	4	12	0	1	0	0
Ponga	Basket	4	B2	67.71	24	63	89	3	9	0	0	1	2
Ponga	Cul-de-sac	4	B2	65.89	24	63	89	3	9	0	0	1	2
Ponga	Pitfall	4	B2	77.65	24	63	89	3	9	0	0	1	2
Ponga	Basket	1	B1	46.78	115	514	331	4	27	0	0	6	1
Ponga	Cul-de-sac	1	B1	41.37	115	514	331	4	27	0	0	6	1
Ponga	Pitfall	1	B1	81.70	115	514	331	4	27	0	0	6	1
Ponga	Basket	2	B1	65.35	44	206	63	5	18	0	0	2	0
Ponga	Cul-de-sac	2	B1	63.32	44	206	63	5	18	0	0	2	0
Ponga	Pitfall	2	B1	81.29	44	206	63	5	18	0	0	2	0
Ponga	Basket	3	B2	44.77	32	174	28	4	12	0	1	0	0
Ponga	Cul-de-sac	3	B2	35.56	32	174	28	4	12	0	1	0	0
Ponga	Pitfall	3	B2	75.20	32	174	28	4	12	0	1	0	0
Ponga	Basket	4	B2	65.67	24	63	89	3	9	0	0	1	2
Ponga	Cul-de-sac	4	B2	54.36	24	63	89	3	9	0	0	1	2
Ponga	Pitfall	4	B2	82.80	24	63	89	3	9	0	0	1	2
Ricabo	Basket	1	B1	51.52	42	255	77	0	6	0	0	0	0
Ricabo	Cul-de-sac	1	B1	44.22	42	255	77	0	6	0	0	0	0
Ricabo	Pitfall	1	B1	78.41	42	255	77	0	6	0	0	0	0
Ricabo	Basket	2	B1	61.91	36	260	59	0	3	0	0	0	0
Ricabo	Cul-de-sac	2	B1	53.96	36	260	59	0	3	0	0	0	0
Ricabo	Pitfall	2	B1	79.43	36	260	59	0	3	0	0	0	0
Ricabo	Basket	3	B2	59.06	75	176	196	1	6	0	0	0	1

Ricabo	Cul-de-sac	3	B2	40.96	75	176	196	1	6	0	0	0	1
Ricabo	Pitfall	3	B2	77.04	75	176	196	1	6	0	0	0	1
Ricabo	Basket	4	B2	67.24	65	102	34	0	5	0	0	0	0
Ricabo	Cul-de-sac	4	B2	56.98	65	102	34	0	5	0	0	0	0
Ricabo	Pitfall	4	B2	80.89	65	102	34	0	5	0	0	0	0
Ricabo	Basket	1	B1	24.28	42	255	77	0	6	0	0	0	0
Ricabo	Cul-de-sac	1	B1	30.08	42	255	77	0	6	0	0	0	0
Ricabo	Pitfall	1	B1	77.73	42	255	77	0	6	0	0	0	0
Ricabo	Basket	2	B1	63.13	65	102	34	0	5	0	0	0	0
Ricabo	Cul-de-sac	2	B1	45.17	65	102	34	0	5	0	0	0	0
Ricabo	Pitfall	2	B1	76.13	65	102	34	0	5	0	0	0	0
Ricabo	Basket	3	B2	44.13	75	176	196	1	6	0	0	0	1
Ricabo	Cul-de-sac	3	B2	34.26	75	176	196	1	6	0	0	0	1
Ricabo	Pitfall	3	B2	71.02	75	176	196	1	6	0	0	0	1
Ricabo	Basket	4	B2	53.18	36	260	59	0	3	0	0	0	0
Ricabo	Cul-de-sac	4	B2	48.55	36	260	59	0	3	0	0	0	0
Ricabo	Pitfall	4	B2	76.18	36	260	59	0	3	0	0	0	0

*Site: study sites (beech forests) where the experiment was conducted.
*Plot: in each forest site we established 2 pairs of 1x1m^2 contiguous plots.
*Block: each pair of contiguous plots.
*% Water content (mg): percentage of water in the litter.
*Abundance: estimate of abundance in 2L of leaf litter (individuals/2L leaf litter) collected at the plot level.

Table S1. Database of catches-abundance of different traps of soil litter fauna (cont'd).

					Abundance (individuals/2L leef litter)							
Site	**Trap Type**	**Plot**	**Block**	**% Water content**	**Larvae Carabidae**	**Other Larvae**	**Diptera**	**Geophilomorpha**	**Lithobiomorpha**	**Julidae**	**Pselaphognata**	**Polydesmidae**
Muniellos	Basket	1	B1	53.41	0	3	1	3	4	0	6	0
Muniellos	Cul-de-sac	1	B1	36.61	0	3	1	3	4	0	6	0
Muniellos	Pitfall	1	B1	67.22	0	3	1	3	4	0	6	0
Muniellos	Basket	2	B1	49.54	0	4	0	1	5	0	0	0
Muniellos	Cul-de-sac	2	B1	42.88	0	4	0	1	5	0	0	0
Muniellos	Pitfall	2	B1	79.45	0	4	0	1	5	0	0	0
Muniellos	Basket	3	B2	38.16	2	1	2	0	1	0	0	0
Muniellos	Cul-de-sac	3	B2	27.56	2	1	2	0	1	0	0	0
Muniellos	Pitfall	3	B2	78.47	2	1	2	0	1	0	0	0
Muniellos	Basket	4	B2	55.35	0	4	6	3	0	1	0	0
Muniellos	Cul-de-sac	4	B2	42.29	0	4	6	3	0	1	0	0
Muniellos	Pitfall	4	B2	76.47	0	4	6	3	0	1	0	0
Muniellos	Basket	1	B1	16.25	0	3	1	3	4	0	6	0
Muniellos	Cul-de-sac	1	B1	25.92	0	3	1	3	4	0	6	0
Muniellos	Pitfall	1	B1	75.17	0	3	1	3	4	0	6	0
Muniellos	Basket	2	B1	57.41	0	4	0	1	5	0	0	0
Muniellos	Cul-de-sac	2	B1	44.10	0	4	0	1	5	0	0	0
Muniellos	Pitfall	2	B1	81.48	0	4	0	1	5	0	0	0
Muniellos	Basket	3	B2	16.93	2	1	2	0	1	0	0	0
Muniellos	Cul-de-sac	3	B2	19.37	2	1	2	0	1	0	0	0
Muniellos	Pitfall	3	B2	76.49	2	1	2	0	1	0	0	0
Muniellos	Basket	4	B2	41.01	0	4	6	3	0	1	0	0
Muniellos	Cul-de-sac	4	B2	47.50	0	4	6	3	0	1	0	0
Muniellos	Pitfall	4	B2	80.13	0	4	6	3	0	1	0	0

Páramo	Basket	1	B1	33.47	1	5	1	3	4	0	86	0
Páramo	Cul-de-sac	1	B1	31.64	1	5	1	3	4	0	86	0
Páramo	Pitfall	1	B1	78.04	1	5	1	3	4	0	86	0
Páramo	Basket	2	B1	52.95	2	2	5	0	6	0	34	0
Páramo	Cul-de-sac	2	B1	51.58	2	2	5	0	6	0	34	0
Páramo	Pitfall	2	B1	76.94	2	2	5	0	6	0	34	0
Páramo	Basket	3	B2	12.34	3	0	0	0	0	0	48	0
Páramo	Cul-de-sac	3	B2	27.29	3	0	0	0	0	0	48	0
Páramo	Pitfall	3	B2	78.50	3	0	0	0	0	0	48	0
Páramo	Basket	4	B2	54.82	0	1	4	1	11	1	11	0
Páramo	Cul-de-sac	4	B2	48.14	0	1	4	1	11	1	11	0
Páramo	Pitfall	4	B2	76.34	0	1	4	1	11	1	11	0
Páramo	Basket	1	B1	10.84	1	5	1	3	4	0	86	0
Páramo	Cul-de-sac	1	B1	58.34	1	5	1	3	4	0	86	0
Páramo	Pitfall	1	B1	81.95	1	5	1	3	4	0	86	0
Páramo	Basket	2	B1	28.36	0	1	4	1	11	1	11	0
Páramo	Cul-de-sac	2	B1	41.62	0	1	4	1	11	1	11	0
Páramo	Pitfall	2	B1	74.74	0	1	4	1	11	1	11	0
Páramo	Basket	3	B2	12.75	3	0	0	0	0	0	48	0
Páramo	Cul-de-sac	3	B2	13.84	3	0	0	0	0	0	48	0
Páramo	Pitfall	3	B2	78.03	3	0	0	0	0	0	48	0
Páramo	Basket	4	B2	52.68	2	2	5	0	6	0	34	0
Páramo	Cul-de-sac	4	B2	40.08	2	2	5	0	6	0	34	0
Páramo	Pitfall	4	B2	78.34	2	2	5	0	6	0	34	0
Ponga	Basket	1	B1	68.46	2	1	4	0	3	0	24	0
Ponga	Cul-de-sac	1	B1	45.23	2	1	4	0	3	0	24	0
Ponga	Pitfall	1	B1	81.95	2	1	4	0	3	0	24	0
Ponga	Basket	2	B1	69.74	1	0	0	0	0	0	17	0

Ponga	Cul-de-sac	2	B1	60.90	1	0	0	0	0	0	17	0
Ponga	Pitfall	2	B1	78.03	1	0	0	0	0	0	17	0
Ponga	Basket	3	B2	58.84	3	4	0	0	1	0	13	0
Ponga	Cul-de-sac	3	B2	52.46	3	4	0	0	1	0	13	0
Ponga	Pitfall	3	B2	79.10	3	4	0	0	1	0	13	0
Ponga	Basket	4	B2	67.71	3	2	3	0	1	0	2	0
Ponga	Cul-de-sac	4	B2	65.89	3	2	3	0	1	0	2	0
Ponga	Pitfall	4	B2	77.65	3	2	3	0	1	0	2	0
Ponga	Basket	1	B1	46.78	2	1	4	0	3	0	24	0
Ponga	Cul-de-sac	1	B1	41.37	2	1	4	0	3	0	24	0
Ponga	Pitfall	1	B1	81.70	2	1	4	0	3	0	24	0
Ponga	Basket	2	B1	65.35	1	0	0	0	0	0	17	0
Ponga	Cul-de-sac	2	B1	63.32	1	0	0	0	0	0	17	0
Ponga	Pitfall	2	B1	81.29	1	0	0	0	0	0	17	0
Ponga	Basket	3	B2	44.77	3	4	0	0	1	0	13	0
Ponga	Cul-de-sac	3	B2	35.56	3	4	0	0	1	0	13	0
Ponga	Pitfall	3	B2	75.20	3	4	0	0	1	0	13	0
Ponga	Basket	4	B2	65.67	3	2	3	0	1	0	2	0
Ponga	Cul-de-sac	4	B2	54.36	3	2	3	0	1	0	2	0
Ponga	Pitfall	4	B2	82.80	3	2	3	0	1	0	2	0
Ricabo	Basket	1	B1	51.52	0	0	0	0	1	0	1	0
Ricabo	Cul-de-sac	1	B1	44.22	0	0	0	0	1	0	1	0
Ricabo	Pitfall	1	B1	78.41	0	0	0	0	1	0	1	0
Ricabo	Basket	2	B1	61.91	0	0	0	1	3	0	6	0
Ricabo	Cul-de-sac	2	B1	53.96	0	0	0	1	3	0	6	0
Ricabo	Pitfall	2	B1	79.43	0	0	0	1	3	0	6	0
Ricabo	Basket	3	B2	59.06	0	0	0	7	0	0	1	0
Ricabo	Cul-de-sac	3	B2	40.96	0	0	0	7	0	0	1	0

Ricabo	Pitfall	3	B2	77.04	0	0	0	7	0	0	1	0
Ricabo	Basket	4	B2	67.24	0	0	1	2	3	0	0	0
Ricabo	Cul-de-sac	4	B2	56.98	0	0	1	2	3	0	0	0
Ricabo	Pitfall	4	B2	80.89	0	0	1	2	3	0	0	0
Ricabo	Basket	1	B1	24.28	0	0	0	0	1	0	1	0
Ricabo	Cul-de-sac	1	B1	30.08	0	0	0	0	1	0	1	0
Ricabo	Pitfall	1	B1	77.73	0	0	0	0	1	0	1	0
Ricabo	Basket	2	B1	63.13	0	0	1	2	3	0	0	0
Ricabo	Cul-de-sac	2	B1	45.17	0	0	1	2	3	0	0	0
Ricabo	Pitfall	2	B1	76.13	0	0	1	2	3	0	0	0
Ricabo	Basket	3	B2	44.13	0	0	0	7	0	0	1	0
Ricabo	Cul-de-sac	3	B2	34.26	0	0	0	7	0	0	1	0
Ricabo	Pitfall	3	B2	71.02	0	0	0	7	0	0	1	0
Ricabo	Basket	4	B2	53.18	0	0	0	1	3	0	6	0
Ricabo	Cul-de-sac	4	B2	48.55	0	0	0	1	3	0	6	0
Ricabo	Pitfall	4	B2	76.18	0	0	0	1	3	0	6	0

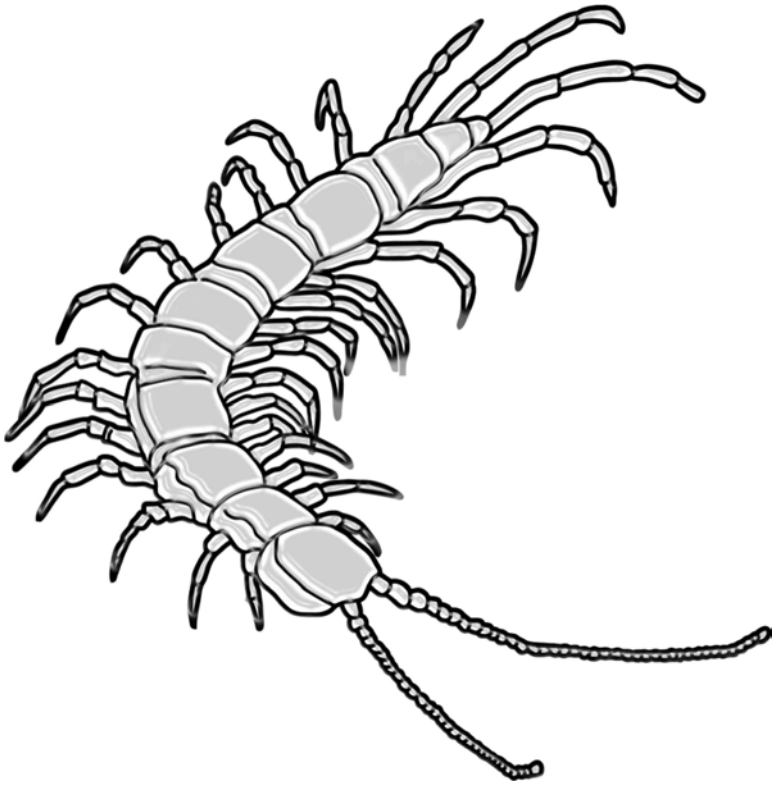
*Site: study sites (beech forests) where the experiment was conducted.
*Plot: in each forest site we established 2 pairs of 1x1m^2 contiguous plots.
*Block: each pair of contiguous plots.
*% Water content (mg): percentage of water in the litter.
*Abundance: estimate of abundance in 2L of leaf litter (individuals/2L leaf litter) collected at the plot level.

Capítulo 4

WEAVER 2.0:

Design and parameterization of multi-trophic meta-community experiments

Dolores Ruiz-Lupión, Gabriel Barrionuevo, Leocadio G. Casado, José María Gómez & Jordi Moya-Laraño



WEAVER 2.0: Design and parameterization of multi-trophic meta-community experiments.

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Manuscrito en preparación

Abstract

One of the principal challenges in ecology is understanding the long-term persistence and stability of complex food webs across space and time. To study this, we developed an extension of the multi-locus, multi-trait, multi-trophic ecoevolutionary and spatially explicit Individual Based Model WEAVER 1.0. With the new version, WEAVER 2.0, we want to simulate eco-evolutionary dynamics of multiple species embedded in complex food webs of beech litter-soil (*Fagus sylvatica* L.), with topologies obtained from the niche model, to study how food web persistence (a proxy of stability) is affected when: 1) the distance between islands rich in basal resources or moisture pockets is increased, and 2) one induces changes in the productivity of a central island while maintaining constant the global productivity of the simulated system. As part of this study we here present: 1) Some of the new features and functionalities of WEAVER 2.0, 2) the way to parameterize the simulations and to parameterize trophic networks, 3) how to obtain more realistic food webs using the niche model, and, 4) how to design scientifally sound experiments "in silico" in order to achieve our objetives and to test our hypotheses. We discuss how the design of experiments "in silico" is comparatively similar, and follows the same processes as the design of field or laboratory mesoscosm experiments.

Keywords

Individual Based Models, eco-evolutionary dinamics, design experiments "in silico", persistence, stability, niche model on food webs.

Introduction

Water is an essential resource in most terrestrial ecosystems, influencing the distribution and abundance of organisms at several spatial scales (Guernier *et al.* 2004; Blankinship *et al.* 2011; Chown & Nicolson 2004; Gear & Schmitz 2005; Melguizo-Ruiz *et al.* 2012; Hawkins *et al.* 2003). In many ecosystems water is even a limiting resource (McCluney & Sabo 2009; Noy-Meir 1974; Wolf & Walsberg 1996), shaping primary productivity and favouring higher rates of litter accumulation in soils (Loustau *et al.* 2001). Water has an important role not only in typical dry ecosystems (deserts and semiarid areas) but also in temperate deciduous forests where water is, in principle, not as limiting (e.g., European beech forests, *Fagus sylvatica* L.) (Verdeny-Vilalta & Moya-Laraño 2014). In these latter ecosystems there is an indirect water-mediated bottom-up effect of primary productivity on soil productivity (Capellesso *et al.* 2016), which would be expressed as higher fungal growth rates in the litter, a process that affects decomposition indirectly via its effects on the food web (Lensing & Wise 2006).

Water is often heterogeneously distributed at the micro-scale level (micro-topography) in beech forests (Herbst & Dikekkruger 2003; Jost *et al.* 2004; Melguizo-Ruiz *et al.* 2012; Schume *et al.* 2003). This is because after rainfall ceases the differential rate of soil desiccation produces the existence of dry patches intermingled with wet patches, which can be located underneath plants, in the base of rocks or under pits formed by fallen trees as well as at the bottom part of the slopes where water, leaf-litter and nutrients accumulate (Famiglietti *et al.* 1998; Melguizo-Ruiz *et al.* 2012). This spatial heterogeneity of moisture pockets may have important consequences for the dynamics, structure and persistence of food webs over time (Levins 1968; Levins 1969; Murdoch 1977; Holt & Lawton 1994; Briggs & Hoopes 2004; Lin *et al*. 2013; LeCraw *et al*. 2014). During the dry period, when the water pocket distribution is more heterogeneous, soil invertebrates are attracted to wet patches to avoid water loss (Verdeny-Vilalta 2013; Verdeny-Vilalta & Moya Laraño 2014). This results in higher densities of invertebrates in these moisture pockets relative to other parts of the forest (Melguizo-Ruiz *et al.* 2012; Verdeny-Vilalta 2013). However, if both preys and predators are attracted to the same humid areas, the preys will face a trade off between risk of desiccation and risk of predation. It is well known that larger arthropods can retain more water than small arthropods, either because of their lower surface/volume ratio or because their ability to store more water (Chown 1993; Renault & Coray 2004). Consequently, how litter organisms respond to moisture pockets could depend on their size, a feature that may have important consequences for the structure of food webs and the dynamics of the ecological systems. Fungivores and detritivores are attracted to patches with water and fungi, whereas predators are attracted indirectly toward these patches when searching for them (Verdeny-Vilalta *et al.*, unpublished data). In these patches predators also avoid desiccation at the same time that they are searching for preys. As a consequence, large predatory arthropods can contribute to the maintenance of leaf-litter community structure and they can couple energy

channels across space and contribute to global food wed stability (McCann *et al.* 2005; Rooney *et al.* 2006).

We can envision these systems of water pockets as multi-trophic meta-communities, i.e., communities linked by dispersal and trophic interactions (Haegeman & Loureau 2014; Holyoak *et al.* 2005; Melián *et al.* 2015; Pillai *et al.* 2011; Wilson 1992). In these meta-communities, species may form linear food chains or be otherwise embedded in complex food webs composed of a large number of species, different functional groups and genetically variable individuals (Bohan & Woodward 2013; Tamadoni-Nezhad *et al.* 2013; Winemiller & Polis 1996). The dynamics of these meta-communities is interesting, for example, as it has been demonstrated by simulations based on empirical data that the dispersal of individuals and the distance between resource-rich patches in heterogeneous landscapes are important drivers shaping local and regional richness (Melián *et al*. 2015). When distances among patches vary, species diversity tend to be highest at intermediate distances, due to the coupling of different search areas displayed by preys and predators. When the islands are adjacent to each other and the space is homogeneous, because the movement among islands is not constrained, the extinction of both preys and predators, and the collapse of the entire system, is very likely. Something similar happens when the islands are far apart, because the organisms cannot move among them, a feature resulting in low colonization rates, loss of genetic diversity, and high mortality and extinction rates from strong overgrazing and competition of preys that are not controlled from top predators (Moya-Laraño *et al.* 2014; Ruiz-Lupión *et al.*, unpublished data). Consequently, when habitat fragmentation occurs, either through human activity or naturally (e.g., form spatial heterogeneity of moisture pockets in leaf-litter of beech forests), the persistence of the food web at the landscape scale will depend on the size of patches, the distances between them and the dispersal distance of the species (Harrison & Taylor 1997; Stith *et al.* 1996). Under these circumstances, the existence of micro-ecological corridors, conceived as geographical spaces that connect fragments of natural habitats facilitating the dispersal of species and decreasing the degree of isolation of the patches (Bennett 1997, 1999), may be essential for the persistence of the food webs.

In this work, we use WEAVER 2.0, a Next Generation Individual-Based Model that describes autonomous individual organisms in complex food webs and simulates multi-trophic meta-community eco-evolutionary dynamics. This modelling platform considers a diversity of aspects that make simulations highly realist, such as inter- and intraspecific variability, local interactions, complete life cycles, individual behaviours responding to changing environments, trait-based approach and microevolution at fine spatial and temporal scale (Grimm *et al.* 2006; Grimm *et al.* 2017; Moya-Laraño et al 2014). The aims of this paper are: a) present an updated version of the modelling platform WEAVER 1.0 (WEAVER 2.0), which we have improved with several new functionalities, adding realism to the simulations, and b) how to design experiments "*in silico*" to

explore, at the micro-scale, the effects of 1) the distances among moisture pockets, and 2) the effects of the presence of a micro-ecological corridor that vary in productivity on the eco-evolutionary dynamics and persistence of a food web of beech leaf-litter (*Fagus sylvatica* L.), and the subsequent consequences for a key ecosystem process: litter decomposition.

New features and functionalities of WEAVER 2.0

WEAVER 2.0 is an Individual-Based Model computer program, implemented in C++, whose aim is the study of eco-evolutionary multi-trophic meta-community dynamics. This program is an extension of the WEAVER 1.0 platform (Moya-Laraño *et al*. 2014) which allowed the exploration of individual-based eco-evolutionary dynamics in multi-species food web across space but now substantially more realistic. This framework, links genes to ecosystems through space and provides information of ecological and evolutionary dynamics at the gene, individual, population and community levels and different spatial scales. We are going to describe the new features and functionalities implemented in WEAVER 2.0 model:

1. What is new in the implementation of time and space

For the current version WEAVER 2.0, time is going to be still considered to elapse in a daily basis. However, we are currently working and improving a new capability that corrects all events considering any time unit (from seconds to years) which we hope it can be ready soon for its use. Here, for the sake of generality we refer to each day as time step.

Relative to space, in WEAVER 1.0 space used cells as elementary units, and animals would move distances that were measured in numbers of cells. In WEAVER 2.0 space is now absolute and realistically measured in international units and in the present simulations the elementary cell unit has a volume of 10 x 10 x 10 mm^3. This realistic space setup allows ecosystem biomass and productivity to be incorporated in absolute terms and animals to move realistic distances in search for resources, similarly as they do in nature.

2. What is new in abiotic environmental conditions

To mimick rainfall events and micro-climate conditions, we can now include a Relative Humidity (RH) time series in each patch (moisture pocket or resource islands) where RH can change from day to day (step to step), mimicking seasonal trends in soil RH. In addition, each patch has its own "hygrostat", which similarly to a chemostat (renewal pulses of basal resources) in WEAVER 1.0, controls the strength and frequency of rainfall events which is mimicked through changes in RH in the soil and the rainfall decreases following a decay function until the next rainfall event. Similarly, to RH each patch has its own variable temperature, which is established by means of a time series (days or steps). By controlling the correlation among time series across patches one can control both the

micro- and mesoclimatic conditions of the simulation and even mimic the formation of soil pockets after a rainfall even.

3. What is new for the initialization of individuals

In WEAVER 1.0 model, to further include realism in the simulations, we initialized the density of each species and instar following mass-abundance allometric constraints (Reuman *et al*. 2009), using the equation $N = 74.8M^{-0.75}$ (Schneider *et al*. 2012), where N is the number of individuals and M is mass (mg). We assumed 69% of water body content, based on the mean value (68.8%) for all species of terrestrial arthropods study by Hadley 1994, to calculate the number of individuals of each instar and species. Note that this approach also assumes that water body content proportions do not change with body mass (e.g., perfect isometry) and thus that on average it does not affect Mass-Length allometric relationships. In the version WEAVER 2.0, we can choose type of initialization of density of individuals of each species and instar between the equation of Scheinder *et al*. (2012) or parameterizing the number of individuals for each species and instar based on real abundances measured in field experiments. For example, using the data obtained of abundance of beech soil and litter meso- and macrofauna in Ruiz-Lupión *et al*. (2019) (Chapter 3).

4. What is new in the food web features

Basal resources

Basal resources are the microbiota that grows in the litter, such as fungi and bacteria. In the present version WEAVER 2.0, however, since there are no bacterivores, we are not considering bacteria. Litter is considered here as a non-renewable resource which is consumed only by detritivores. In WEAVER 1.0, in each patch, the basal resource (fungi) grew according to a conventional logistic growth function, and its dynamics was updated following an update of the algorithm in Moya-Laraño *et al*. 2012. Since this equation was used to merely model the dynamics of a single cell, and not of the entire space in the simulation, and this equation generates chaotic dynamics beyond values near 2 for the intrinsic rate of increase *r*, we now merely model recursive exponential growth at the cell level. When fungi grow in excess of a certain limit value that we set for the cell, it expands to nearby cells as long as this value of carrying capacity has not been locally reached. Therefore, instead of a logistic growth curve we impose truncated exponential growth at the cell level.

As in other studies we define a total power for the system (Savage *et al*. 2004), here assumed to be the sum of the carrying capacities for all species of basal resources. In addition, in WEAVER 2.0 the growth of basal resources depends on RH in addition than on temperature (Figure 1). Moreover, we distinguish whether the simulation considers: a) non-competing species of fungi, within a cell growth occurs until the species carrying capacity is reached and therefore grows independently of what other species are doing; or b) competing species of fungi grow according to their own biomass and temperature-water dependent growth rate but share a common maximum cell carrying

capacity. Here, we consider the sum of the biomasses of all the fungus species and the biomass of each species grows as long as the sum of the total biomass considering all species does not exceed the cell carrying capacity. Note that this new functionality will also produce apparent competition (*sensu* Holt 1977) among fungus species, as differential predation upon one species will allow the non-preferred species to grow to fill the available fraction of the cell carrying capacity, producing a negative correlation between the abundances of both species.

When fungi grow in a patch beyond saturation, mycelia colonize neighboring patches, allowing the amount of extra-grown fungi to fill these patches up to the values of either the species-specific carrying capacity (non-competitive fungi) or the cell carrying capacity (competitive fungi) of the newly colonized patch. In addition, complete competitive exclusion among basal resources will never happen, because there is a threshold value of fungus biomass below which this fungus cannot be consumed by any the fungivorous species nor outcompeted by any of the other fungus species. This enables basal resources to recover within each of the cells, and entails a more realistic scenario, as not all parts of the basal resources are equally edible (e.g., old *vs* fresh mycelia).

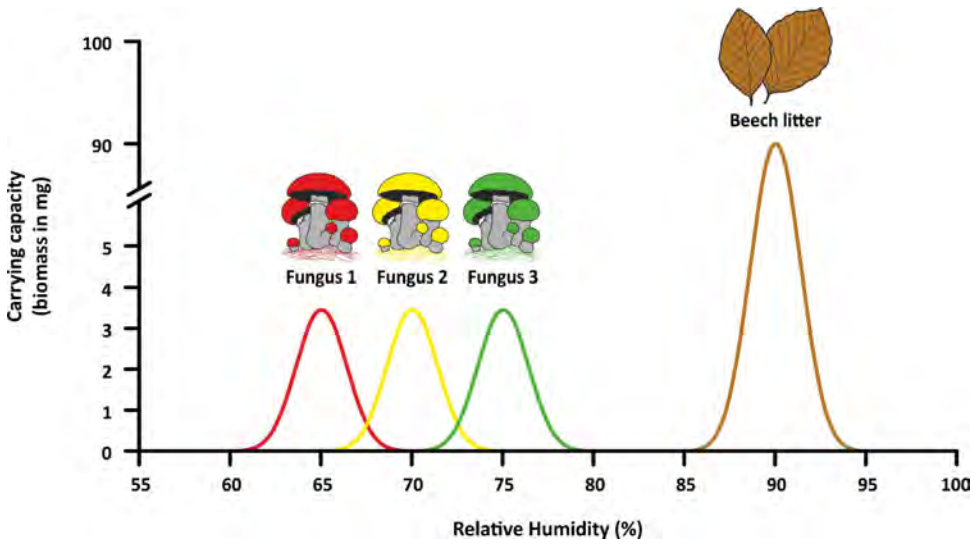

Figure 1. Relative humidity niche of the fungi and conditions for the non-renewable leaf-litter resource. The peaks of the parabolic curves correspond to the maximum carrying capacity values of each species. In our simulations for each cell the total carrying capacity are divided in 90% beech litter and 10% fungus species (i.e., 3.33% per fungus species).

Types of interaction between individuals

In WEAVER 1.0 the species are classified as predators than feed on fungivorous species, whether they are cannibals and/or intragremial predators in which case they would be trophic level omnivores (e.g., spiders and centipedes); and fungivorous species than only feed on fungi (basal resources) (e.g., Acari Oribatida and Collembola species). In WEAVER 2.0 we have implemented a

more inclusive type of omnivory, in the sense that a predator can now feed not only on other predators and on fungivores (preys), but also in fungi (basal resources). This conforms our food webs to niche model topologies, which was unfeasible with the assumption that no predator could feed on basal resources. Although the literature is not clear on this point, we have assumed that many species of Acari Mesostigamata and Prostigmata should be able to feed on these two types of resources. In the simulation, however, fungi are the least preferred and profitable food for predators.

Selection of edible species

WEAVER 1.0 included a vector ("edibleSpecies") with the names of the species that predators could eat or of basal resources that fungivores could eat. As an example we show here two species [linkedSpeciesA.json and linkedSpeciesB.json]:

Predator: `linkedSpeciesA.json`

```
"edibleSpecies": ["speciesA","speciesB","speciesC","speciesD"],
```

Prey: `linkedSpeciesB.json`

```
"edibleSpecies": ["basalResourceA"],
```

Species A is a predator that can feed on members of its own species (cannibalism). Species B is a fungivore that can feed on a single species of fungus. In WEAVER 2.0, two different vectors have been implemented, one for the species of animals ("edibleAnimalSpecies") and another for the species of basal resources (fungi or beech litter) ("edibleFungusSpecies"). In the case that the species is omnivore, both vectors are filled; if it is a predator, only the vector of the animals is filled and if it is a prey, only the vector of the basal resources is filled. In addition, other four vectors have been implemented, two to indicate the preferences when feeding on animals and/or fungus species ("edibleAnimalPreferences" and "edibleFungusPreferences") and another two to modify, adding or subtracting (profitability) to the assimilation efficiency trait determining the profit that feeding on one or another species entails to the consumer ("edibleAnimalProfitability" animal "edibleFungusProfitability").

The sum of the preferences must be equal to or less than 0.99, and no species can have zero preference (they should be otherwise excluded from the edible vector) and in omnivorous species the preference for basal resources must be at least an order of magnitude lower than preferences for animal species. This forces omnivores to feed on fungi only when animal preys are not available. We show an example of parameterization for each type of species (predator, fungivorous prey and omnivore), as we can find it in the file of species parameters [linkedSpeciesA.json, linkedSpeciesB.json and linkedSpeciesC.json]:

Predator: `linkedSpeciesA.json`

```
“edibleAnimalSpecies”: [“speciesA”,“speciesB”,“speciesC”,“speciesD”],
“edibleAnimalPreferences”: [“0.50”,”0.17”,”0.17”,”0.17”],
“edibleAnimalProfitability”: [“0.2”,”0.1”,”0.1”,”0.1”],
“edibleFungusSpecies”: “”,
“edibleFungusPreferences”: “”,
“edibleFungusProfitability”:””,
```

Predator A is a highly cannibalistic species and takes more profit from feeding on conspecifics.

Fungivorous Prey: `linkedSpeciesB.json`

```
“edibleAnimalSpecies”: “”,
“edibleAnimalPreferences”: “”,
“edibleAnimalProfitability”: “”,
“edibleFungusSpecies”: [“basalResourceA”,“basalResourceB”,“basalResourceC”],
“edibleFungusPreferences”: [“0.33”,”0.33”,”0.33”],
“edibleFungusProfitability”: [“0.1”,”0.2”,”0.1”],
```

Mycophagous species B prefers equally all fungi. However, profitability is higher for basalResourceB.

Omnivorous species: `linkedSpeciesC.json`

```
“edibleAnimalSpecies”: [“speciesA”,“speciesB”,“speciesC”,“speciesD”],
“edibleAnimalPreferences”: [“0.22”,“0.30”,“0.22”,“0.22”],
“edibleAnimalProfitability”: [“0.1”,“0.2”,“0.1”,“0.1”],
“edibleFungusSpecies”: [“basalResourceA”,“basalResourceB”],
“edibleFungusPreferences”: [“0.025”,“0.025”],
“edibleFungusProfitability”: [“0.05”,“0.05”],
```

Omnivorous species C is cannibalistic, feeds on other prey and in addition can feed on fungi, even though these are less preferred and less profitable.

5. What is new in the searching and movement algorithm

In WEAVER 1.0, animals moved adaptively in 3D space. In addition, they remember the cells visited the same day and do not revisit then. Animals assess the 27 or 9 surrounding cells plus the cell where the animal is currently located in a given time in 3D or 2D simulations respectively. At each move, fungivores will move to cells with the lowest ratio between predation threat and fungus biomass; and predators behave in a similar way, they assess predator threat and prey availability (both fungivores and IGP-prey) and following the next mass ratio criterion for prey that would be fit as edible:

$$\log \frac{\text{mass Predator (mg)}}{\text{mass Prey (mg)}} \in [-1.21, 6.68] \qquad [1]$$

In addition, both prey and predators can jump at a distance which is established by drawing a random number from a uniform distribution ranging between 2 and its Search Area trait when food availability within the 27 neighboring cells (26 surrounding cells plus the cell where the animal is currently located) is zero (Moya-Laraño *et al*. 2014).

In WEAVER 2.0, the distances that the animals are allowed to travel per unit of time are still ruled by the trait "Search Area", but this time in mm not in cells, and the total distance travelled is corrected accordingly depending on whether space transitions are realized between adjacent or diagonal cells. Animals continue to move in 3D space and they remember the cells they visited not repeating the same cell during the same day. At each move, fungivore species will move to cells with fewer predators, greater fungus biomass and, if the species is social (i.e., Collembola species), with the highest number of conspecifics. This simulates that the animals can assess the consequences of Allee effect, that is, the population size is so small that the survival and/or reproductive rates decrease because individuals encounter each other to mate (Allee 1931). However, at very high densities, competition should be a problem and conspecifics should start avoiding each other. A series of coefficients tune the relative importance of food, predators or conspecifics in affecting the behavior of each individual. Predators behave in a similar way, they assess predator threat and prey availability (both fungivorous and IGP-prey species) as well as conspecifics. If it is also an omnivorous species, it asseses also the amount of fungus biomass. Now instead of a simple predator-prey size ratio to decide who eats whom, a realistic non-linear model based on the quasi-normal distribution of predator-prey ratios in terrestrial invertebrates (Brose *et al*. 2006) has been incorporated. This is now more realistic because large predators will refuse to feed on prey that are too small. In addition, instead of jumps when food is scarce, WEAVER 2.0 now includes the possibility of animals assessing cells farther away from neighboring cells at a touch distance. Remember that animals assess the 26 or 8 cells surrounding its cell in 3D or 2D simulations respectively. Now when food availability is zero they expand the search to 66 or 16 adjoining surrounding cells in 3D or 2D simulations respectively. If food availability is zero again, they expand the search in concentric circles until they reach their Search Area trait, the maximum distance that the animal can move per time step (Figure 2). Note that the animal assesses these cells at a distance, without moving to them until a prey is located. This is an especial type of algorithm that is triggered only when food nearby cannot be found.

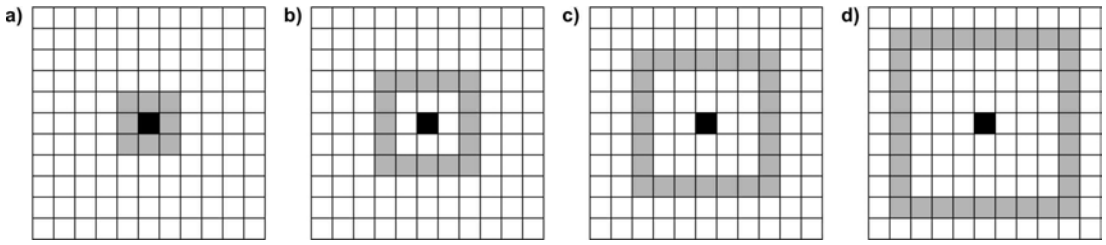

Figure 2. New algorithm for searching in WEAVER 2.0. World have 11 x 11 x 1 cells^3 dimensions, each cell measures 1000 mm^3 (10 x 10 x 10mm^3). In black, the cell where the animal is located and in gray, the cells asses in one step by one individual: a) circle of 8 surrounding cells to search, following the original algorithm but with the new searching criteria including the abundance of conspecifics, b) circle of 16 contiguous cells, c) circle of 24 contiguous cells and d) final circle of 32 cells (maximum Search Area of that particular individual).

6. What is new in the moulting algorithm

In WEAVER 1.0 the moulting algorithm depended on the shape of the animals, and thus the mass-length allometric relationship was taken into account to decide when the next instar should be achieved:

$$M = aL^b \quad [2]$$

where M is the body mass in mg, L is total body length without appendages in mm, a is a scaling factor an b is an allometric factor. This equation was used to transform the mass available for moulting into the length of the animal in order to allow for length growth to be governed by the trait fixed growth ratio. Since growth curves are not ruled by a single ratio parameter, as they usually have a sigmoid shape, we allowed animals to also plastically moult by including time as an alternative for moulting. A ratio between the time elapsed in the prior instar and the time elapsed in the present instar was included. The ratio between the time elapsed in the present time *vs* the time in past instars was established as a second rule of thumb to moult.

In the present version of WEAVER 2.0 we have included a more realistic growth curve based on real published growth curves at the species level. We included a real relationship between time (days) and length (mm) for each species of the simulation using our own database (see Table S1, Supplementary Material) and externally we adjust a von Bertalanffy growth curve (von Bertalanffy 1969), where each instar is considered a target length that the animal should follow to moult (Figure 3a, 3b):

$$L_t = L_\infty \left(1 - e^{-k\,(t - t_0)}\right) \quad [3]$$

where t is the age at time t, k is the growth coefficient, t_0 is a value that would estimate size when age is zero, L_∞ is an asymptotic size or maximum size. After feeding a non-linear regression we use the estimates of L_∞, k ant t_0 as parameters in the model. However, at any given body size, higher temperature leads to an exponentially greater metabolic rate (Gillooly *et al*. 2002). This effect (if uncompensated) would tend to decrease growth efficiency at higher temperatures. This general observation leads to the prediction that species from habitats with higher temperatures may exhibit a stronger effect of temperature on size. This is known as Temperature Size Rule (TSR) which denotes the plastic response of organismal body size to environmental temperature variation (Angilletta *et al*. 2003; Sears *et al*. 2004). Plastic organisms are capable of allowing their body size to change according to environmental temperature. For more realistic growth curves, individuals mature faster and they become adults at a larger size when temperature increases and at initialization we can implement in the parameterization the laboratory temperature (°C) at which the real growth curve was measured (Figure 3).

In the same way that in WEAVER 1.0, we used equation 2 to transform the mass available for moulting into the length of the animal, in WEAVER 2.0 we use our own database of mass-length allometric relationship (see Table S2, Supplementary Material) obtained from Table S1 Ruiz-Lupión *et al*. (Chapter 2). WEAVER 2.0 also includes the possibility for indeterminate growth; that is, individuals can continue to grow after sexual maturity and reproduction (e.g., as many Collembola species) (Figure 3a). In addition, includes holometabolism or complete metamorphosis, which is a form of insect development with four life stages: egg, larva, pupa, and imago or adult. Holometabolism is a synapomorphic trait of all insects in the superorder Endopterygota. Immature stages of holometabolous insects are very different from the mature stage. For this, now we can include in the parameterization two differents mass-length allometric relationship, one for larvae stage and another for the adult stage; and we can indicate the number of days that the individuals are in pupa stage during which they are not moving or feeding, nor do they suffer risk of predation.

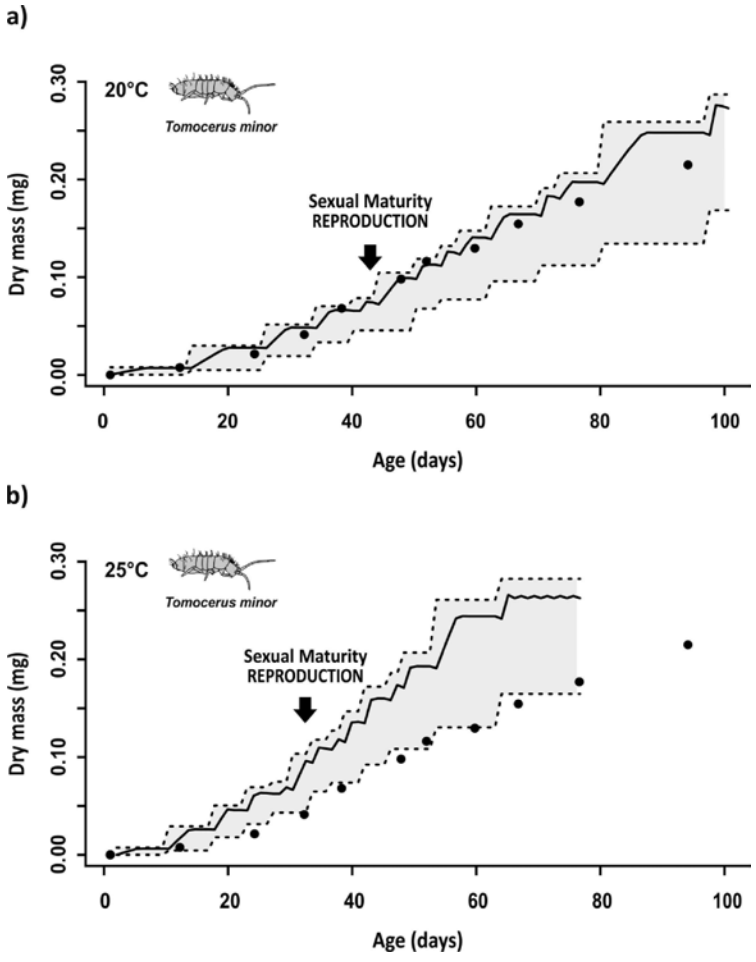

Figure 3. Real and simulated growth curves in dry mass (mg) of Collembola (*Tomocerus minor*) species implemented in WEAVER 2.0 model, with indeterminate growth. a) Growth curve at 20°C of temperature and b) growth curve at 25°C of temperature. Black points represent the real growth curve (Joosse & Veltkamp 1970) used to parameterize WEAVER 2.0; black lines represent the simulated growth curves and gray shadows

delimited by black dashed lines show the area or biological limits within which the animal can grow from plasticiy. The original temperature from laboratory is at 20°C.

7. What is new in the algorithm describing reproduction

Quantitative genetics with realistic recombination rates

The way genetics of the animal is considered has improved in the WEAVER 2.0. In addition to multidimensional quantitative genetics with Mendelian inheritance, we have modified the recombination and meiosis algorithms, including now the possibility for recombination and segregation. In the former version of this IBM framework, mini-AKIRA (Moya-Laraño *et al*. 2012), the genetic correlations were induced from pleiotropic effects by including all loci that affected the same traits in arrays which were called chromosomes. This was unrealistic because genetic correlations occur by both pleiotropic effects of quantitative genes and from linkage disequilibrium (Roff 1997), and we only considered the former. In linkage disequilibrium, loci that are close to each other in the chromosome tend to stay together for several generations (linkage), the number of which depends on their relative distance in the chromosome and on the recombination rate. We decided to improve our modelling of quantitative genetics by better mimicking true recombination. The formerly described loci vectors (Moya-Laraño *et al*. 2012), which are useful to induce the desired degrees of genetic correlations among traits, termed "correlosomes" in WEAVER 1.0 version (Moya-Laraño *et al*. 2014) and WEAVER 2.0 version.

Reproductive modes

As a novelty we have included separate sexes (males and females) although no sexual dimorphism has been implemented so far. Also, we consider three sexual modes: a) diploidy, in a diploid system both males and females contribute half of their genetic material to build a 2n zygote; b) haplodiploidy, in haplodiploids (i.e., mites) females that do not mate make gametes that produce haploid males which are the result of the female meiosis, and c) asexual reproduction, in asexual reproduction populations are only composed of females which produce other diploid (2n) females after meiosis (i.e., parthenogenesis), as it occurs in some species of springtails (Collembola).

Modularity of traits based on multidimensional quantitative genetics

In present version WEAVER 2.0, several changes have been made relative to the implementation of traits: a) Voracity, Speed and Search area traits are no longer the allometric factor "b" of the allometric equations (Trait = aM^b), but now they represent the scaling factor "a", b) the traits Q_{10} Voracity, Q_{10} Speed and Q_{10} Search Area have been replaced by the activation energy for Voracity, Speed and Search Area. In addition to the 13 traits present in WEAVER 1.0, WEAVER 2.0 includes 12 new traits scattered in 4 new 3-trait modules that we call "dummy" because they have the entire genetic machinery to work but these traits are not functional. Thus, if no further implementation is

added the genes associated to these traits behave neutrally and are thus subject to genetic drift. This alone is useful to document genetic drift during simulations However, the purpose of these genes is that an intermediate-level programmer in C++ can add new functional traits without having to deal with programming the entire genetic machinery. In this way, we have programmed the first dummy trait to become death by thermal shock. When temperature increase dramatically, individuals begin to synthesize Heat Shock Proteins (HSP) (Ritossa 1962), a family of proteins found in all living organisms, from bacteria to humans, that are produced in response to exposure to stressful conditions, such as extreme temperatures (Matz *et al*. 1995; Wu 1995) or UV light (Cao *et al*. 1999).

Everything else regarding genetics is very similar as in Moya-Laraño *et al*. (2012) and Moya-Laraño *et al*. (2014) (Chapter 1), and here we merely copy the text with the necessary details.

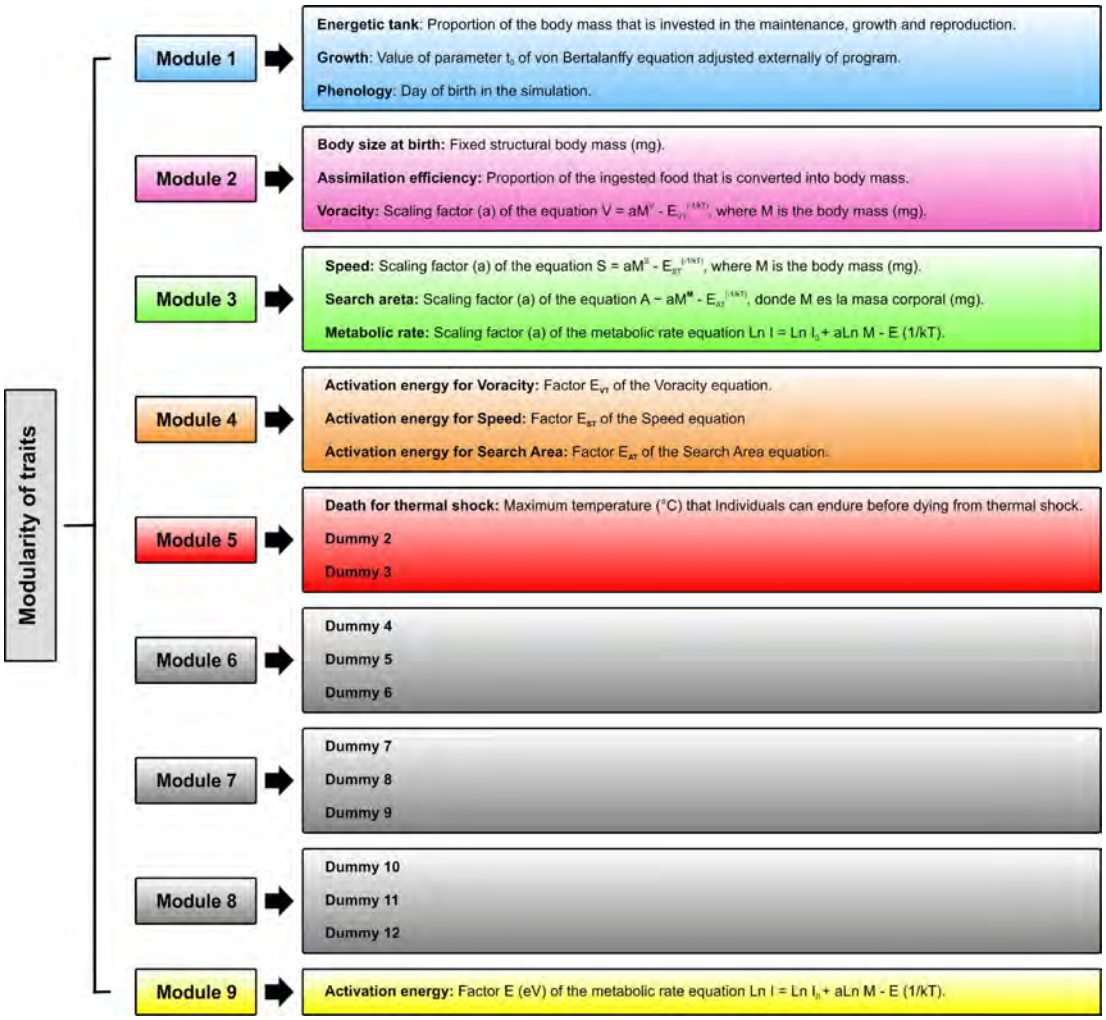

Figure 4. Modularity of traits based on multidimensional quantitative genetics. The traits are grouped into nine modules that are genetically independent of each other. Within each module the traits are correlated with each other, and the degree of correlation determines the degree of phenotypic integration.

Working flow of WEAVER 2.0

In summary, WEAVER 2.0 is more realistic than WEAVER 1.0 due to the implementation of novelties: it uses real space units (mm), temporal series of temperature and relative humidity, an initialization of individuals based on real data of abundance, syntopic basal resources with or without competition for space, new types of interactions between individuals and selection of edible species based on food preferences and assimilation efficiencies. Also the movement, moulting and reproduction algorithms have gained in realism. Figure 5 shows the working diagram of WEAVER 2.0.

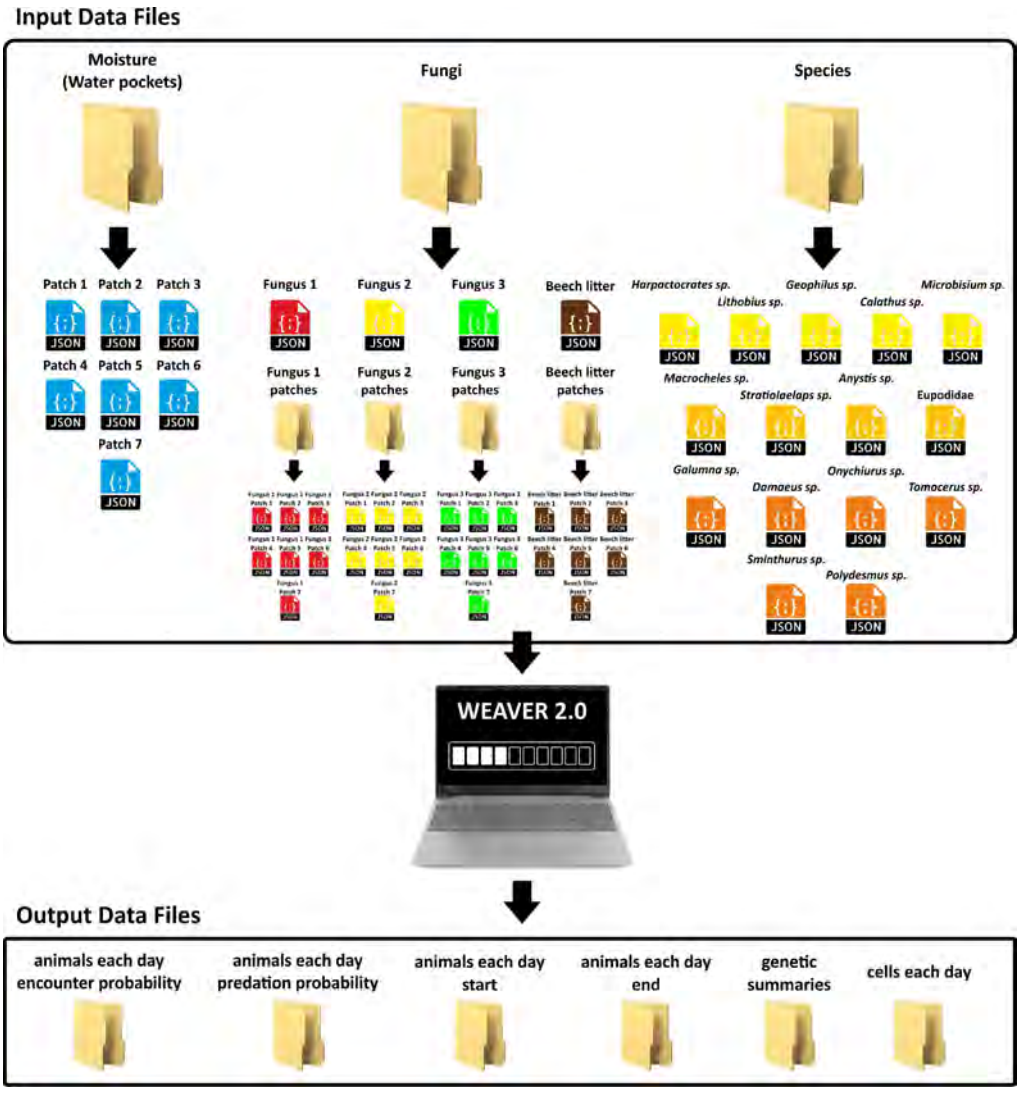

Figure 5. Working diagram of WEAVER 2.0. The moisture folder includes information about time series for temperature and relative humidity for each of the moisture spherical patches. The fungi folder includes all features for the fungi species and beech litter and how each of these basal resources is scattered around moisture patches. The species folder includes all features for each species (developmental and growth information, mass-length allometric relationship, traits based in quantitative genetics, feeding links, food preferences and profitabilities, etc). Finally, we get a diversity of outputs (number of encounters and predation events of each individual/day, amount of food consumed, traits values and genetics throughout the simulation, cells visited of each individual/day, time and energy spent in each step of the program, etc.).

Application to empirical data for simulated experimental design

Description of the food web, network analysis and niche model networks

We used the database of growth curves (see Table S1, Supplementary Material) for selecting the model species which are more similar to the real species or genera in the beech leaf-litter food web and then, we parameterized and implemented them for the current version WEAVER 2.0. Central to the functioning of this version continues to be mass-length allometric relationships (see above), for which we have performed a detailed bibliographical survey. We calculated the among species means of the "log(a)" and "b" for the mass-length relationships available (Chaper 2, Table S1, Table S2). The backtransformed means of scaling factors "log(a)" and the means of the allometric factors "b" are equal for juvenile and adults in species without holometabolisms and it is different for holometabolous species (see Table S3, Supplementary Material). And finally, for the implementation of the species in the food web we used real abundances of meso- and mesofauna of in beech-litter soil (Moya-Laraño & Melguizo-Ruiz, unpublished data).

With this dataset we built an initial leaf-litter food web of the beech forest composed of 19 species belonging to four trophic levels (Figure 6, 7a). The first trophic level is composed of 5 intraguild and cannibalistic predators: 4 large predators (a cursorial spider *Harpactocrates sp.,* 2 species of chilopoda, one Geophilomorpha *Geophilus sp.* and one Lithobiomorpha *Lithobius sp.,* and a carabid beetle *Calathus sp.*) with body length ranging between 10 and 40 mm as adults (Murakami 1958; Lewis 1961; Andersson 1990; Fisher & Vasconcellos-Neto 2005), and a 1 small predator (a Pseudoscorpion *Microbisium sp.*) of about 1.5 mm in body length as adult (Sakayori 1989). Predators account for 39% of the total biomass at the beginning of the simulation (Figure 6). The second trophic level included 4 omnivorous species that feed on other invertebrates as well as on fungi (2 Acari Mesostigmata *Macrocheles sp.* and *Stratiolaelaps sp.*, and 2 Acari Prostigmata *Anystis sp.* and Eupodidae). These species have a length ranging between 0.3 mm and 1.0 mm and represent 2% of the initial biomass (Sorensen *et al*. 1976; Cabrera *et al*. 2005; Abou-Awad *et al*. 2006; Mei-Fang *et al*. 2017; Balanzategui-Guijarro, unpublished data) (Figure 6). The third trophic level include 5 fungivorous species (2 Acari Oribatida *Galumna sp.* and *Damaeus sp.*, and 3 Collembola *Onychiurus sp.*, *Tomocerus sp.* and *Sminthurus sp.*) with length range of 0.3 - 4.0 mm, and accounting for 57% of the initial biomass (Maclagan 1932; Sengbusch & Sengbusch 1970; Joosse & Veltkamp 1970; Walsh & Bolger 1990, Balanzategui-Guijarro, unpublished data), and 1 large detritivorous species (a Diplopoda *Polydesmus sp.*) reaching 20 mm in body length but representing just 2% of the initial biomass (Snider 1981) (Figure 6). Finally, the fourth trophic level was composed of 4 basal resources with different Relative Humidity optimal for growth, 3 species of syntopic fungi (Fungus 1 RH Range = 60% - 70%; Fungus 2 RH Range = 65% - 75% and Fungus 3 RH Range = 70% - 80%) and beech leaf-litter (which is not renewable) (Figure 6).

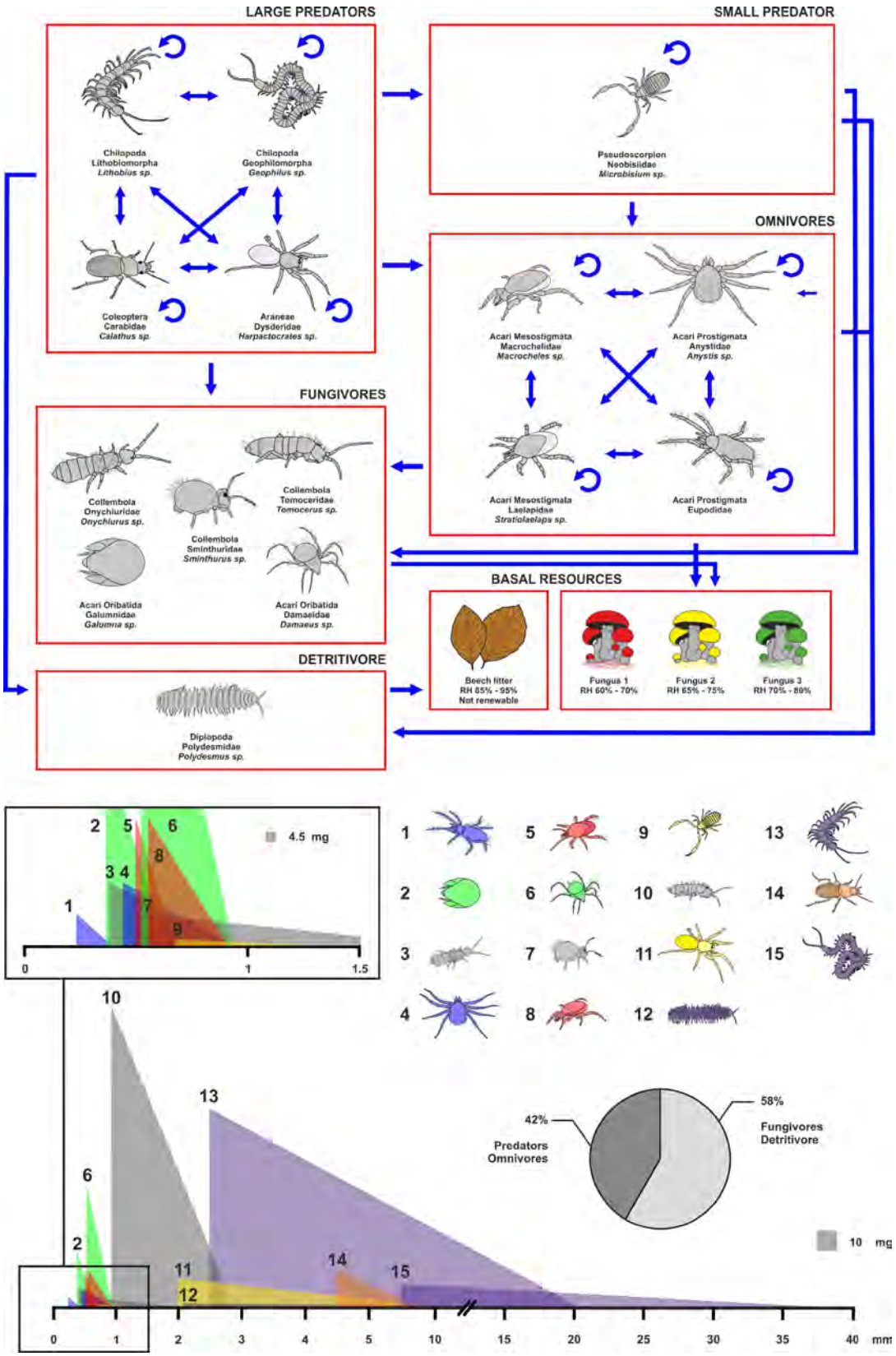

Figure 6. New food web of meso- and macrofauna of beech-litter soil. The blue arrows indicate who eats whom. Closed loops indicate that the species are cannibalistic. The shades of colors delimit the minimum and maximum body length (mm) from birth to adulthood of all species and they indicate the amount of biomass of each species and instar based on the number of individuals implemented in the simulations.

In the next step, we performed a network analysis to know the properties of the initial food web using Network3D program version 1.0.0.0. developed by ©Microsoft Corporation for Microsoft Research and PEaCE Lab. To that end, we loaded data from a predation matrix that describes our food web with all possible links constrained by food level as explained above (Figure 6, 7a, see Table S4, Supplementary Material). And finally, we obtained the 12 principal features of the initial food web: 1) Number of species, 2) links (L) per species (S), calculated as L/S, 3) connectance, calculated as L/S^2, 4) fraction of top species that have neither intra- nor interspecific predators, 5) fraction of intermediate species that have both predators and prey (in our study all predators and omnivores), 6) fraction of basal species (fungi and beech litter), 7) fraction of fungivorous and detritivorous species, 8) fraction of omnivorous species, 9) fraction of cannibalistic species, 10) standard deviation of generality; generality of a node is the number of species it consumes normalized by L/S, 11) standard deviation of vulnerability; vulnerability of a node is the number of species it is consumed by normalized L/S, and 12) standard deviation of connectivity; connectivity of a node is the number of species it is connected to as predator or prey normalized by 2L/S (Table 1) (Williams & Martinez, 2008).

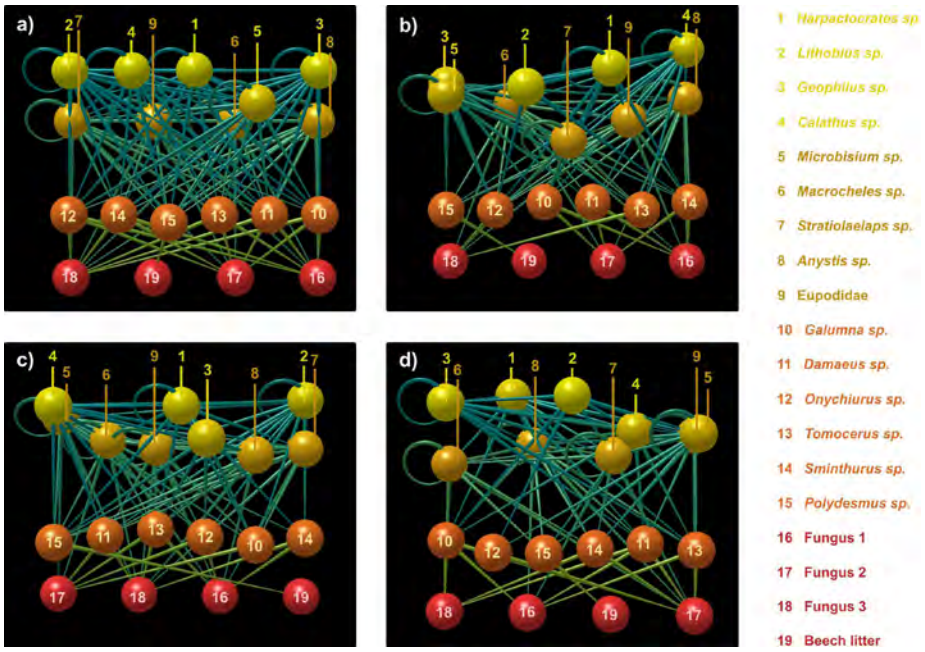

Figure 7. Beech forest (*Fagus sylvatica* L.) leaf-litter food webs implemented and simulated in the WEAVER 2.0 platform. a) Initial food web constrained by initial assumptions, b) niche model food web 1, c) niche model food web 2, and d) niche model food web 3. Yellow circles represent the fourth (top) trophic level (top predatory species), yellow mustard circles represent the third trophic level (omnivorous species), orange circles represent the second trophic level (fungivorous and detritivorous species) and red circles represents basal resources of the first trophic level (fungi and beech litter). Rings indicate cannibalistic species.

We use the topology of the initial food web and two empirical parameters, species number and a new value of connectance, to obtain a new food web matching the niche model. This was done by iteration of Network3D until a web with a given targeted connectance and which fitted to the niche model was obtained (Williams & Martinez, 2000). This procedure was run three times until three food webs were obtained, which were used as the replicates for simulation in WEAVER 2.0. These three food webs only differed in their topology (Figure 7b, 7c, 7d, see Table S5, Table S6, Table S7, Supplementary Material), with all other properties being identical (Table 1).

Table 1. Network analysis of initial and niche model food webs.

Property	Initial Food Web	Niche Model Food Webs
Number of species	19	19
Link per species	7.8	4.5 [4.3 – 4.7]
Connectance	0.40	0.25 [0.20 – 0.30]
Fraction Top species	0.00	0.10 [0.00 – 0.20]
Fraction Intermediate species	0.80	0.80 [0.60 – 0.90]
Fraction Basal species	0.20	0.20 [0.10 – 0.30]
Fraction Fungivorous and Detritivorous species	0.30	0.10 [0.00 – 0.20]
Fraction Omnivorous species	0.80	0.70 [0.60 – 0.80]
Fraction Cannibalistic species	0.50	0.30 [0.10 – 0.40]
Standard deviation of generality	0.80	0.90 [0.70 – 1.10]
Standard deviation of vulnerability	0.30	0.60 [0.30 – 0.80]
Standard deviation of connectivity	0.30	0.40 [0.30 – 0.50]

Design of Simulation Experiment 1

In experiment 1 we tested the effects of the distance among water pockets (resource islands) on the eco-evolutionary dynamics and persistence of the implemented food webs, as well as the subsequent consequences for a main ecosystem process: litter decomposition. To incorporate a spatial component, we simulated seven water pockets around a hexagon in which fungi were able to grow and beech litter was available for detritivorous species (Figure 8a). These islands were identical, had equal basal productivity (fungi and beech litter), shape (spheroids) and size (major axes = 100 mm, minor axis = 10mm, volume = 419 cm^3). The space surrounding water pockets was empty, without fungi or leaf-litter, and the individuals can only use it to move between resource islands. We minimized edge effects by controlling the distance between the outermost islands and the border of the microcosm by setting this distance to half the distance between islands for a given treatment. We established five distance treatments (adjacent, nearby, distant, very distant and remote islands) and included seven islands at 0, 10, 20, 30 and 40 cm distances between borders, or 10, 20, 30, 40 and 50 cm between centers respectively. The dimensions of the microcosms containing these islands were (width x length x depth): 30 x 28 x 1 cm^3, 60 x 54 x 1 cm^3, 90 x 82 x 1 cm^3, 120 x 108 x 1 cm^3 and

150 x 130 x 1 cm^3 respectively, and the distance to the edge of the microcosms were 0, 5, 10, 15 and 20 cm respectively (Figure 6a).

Note that in WEAVER 2.0 migration depends merely on an animal's mobility that in turn depends on several state variables (e.g., fungi or prey availability, predatory threat, social behaviour, internal stage and the trait searching area among others). We have not considered long distance dispersal (e.g., aerial dispersal in springtails and spiders). Finally, we evaluate the optimum distance at which greater species richness is maintained and the effect of the ecological corridor in food web persistence (Moya-Laraño, unpublished data, Ruiz-Lupión *et al*., unpublished data). To evaluate top-down effects of predators and their ability to couple the global dynamics, we estimated their dispersal distances in the simulations. We measured the average dispersal distances of each simulated species, from birth to first reproduction and obtained the "dispersal kernels" of each species using a normal distribution (Nathan *et al*. 2012), which are simply probability distributions that indicate the dispersal range of the individuals of each of these simulated species.

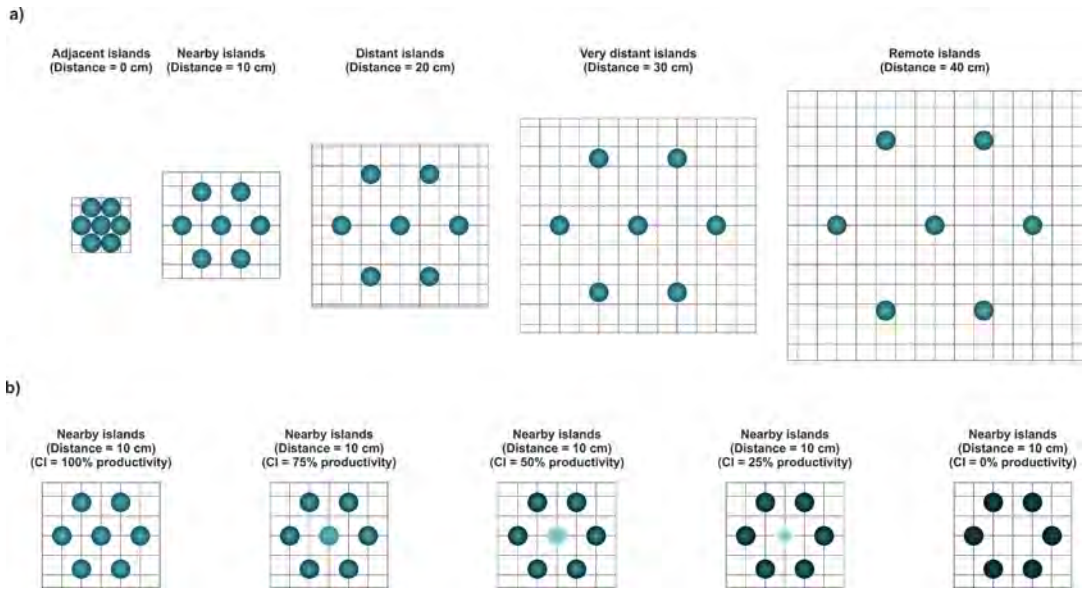

Figure 8. Spatial arrangement for experiments. a) Experiment 1: testing the effects of the distance among resource islands and b) experiment 2: testing the effect of variability in local productivity of a micro-ecological corridor at optimal distance among islands. Blue circles represent resource islands (water pockets in the beech forest floor in which fungi were able to grow and beech litter was available for detritivorous species at sufficiently high relative humidity for the animals to settle in). The clearer blue circles decrease (central island = CI) in productivity and the darker blue circles around the hexagon increase in productivity. The squares represent the size of the microcosm established for each simulation.

Design of Simulation Experiment 2

In experiment 2 we tested the effect of variability in local productivity of a micro-ecological corridor and the effect of spatial hetereogenety in the eco-evolutionary dynamics and persistence of the food webs obtained, and its consequences for litter decomposition. We used the island configuration of experiment 1 where the persistence of food webs was higher and the ecological dynamics were more persistent (optimal distance among islands) and we modified the productivity of the ecological corridor (central island hereafter) keeping the system productivity constant (Figure 8b). Therefore, as the productivity (fungi and beech litter) of the central island decrease, the productivity of the six outermost islands of the simulated hexagonal structure increase proportionally. We established five treatments based on a steady decrease in the productivity of the central island relative to the productivity of the peripheral islands. In decreasing order, very high productivity, high productivity, medium productivity, low productivity and zero productivity: 100%, 75%, 50%, 25% and 0%. The productivity of each peripheral micro-island increased proportionately in each treatment to keep the overall productivity of the system constant.

Simulations runs

To study the effect of the distance among islands, spatial hetereogenety and variability in local productivity of an ecological corridor in the eco-evolutionary dynamics and persistence of multi-trophic meta-community, we used a bifactorial design for the simulation experiments. In experiment 1, we will combine the three food webs and five distances among islands (Figure 9a). We will run 15 combinations of treatments that will be replicated 5 times, resulting in 75 simulations. Finally, we will calculate the dispersal kernels for each species at each distance, in total 19 species and 5 spatial arrangements, we will evaluate 95 dispersal kernels.

For experiment 2, we will combine the three food webs and the five treatments of productivity using the scenario were the distance among islands will be optimal in experiment 1. Again, we will run 15 combinations, although 3 of them will take the results of the ones already coming from the above optimal scenario of productivity and will be replicated 5 times, resulting in a total of 60 combinations (Figure 9b). All simulations will be run in 6 Ubuntu Virtual Machine clones (4 CPUs, 64 GB RAM and 100 GB hard disk running under Windows 10 as a guest operating system) which have been placed at our disposal by Supercomputing and Algorithms Group, Computer Department of the University of Almería.

Figure 9. Set of simulations to address questions 1 and 2: a) experiment 1, with a total of 75 combinations x 5 replicates, and b) experiment 2, with a total of 60 combinations x 5 replicates.

Conclusions

The implementation of simulation experimental designs or experiments "in silico" is very similar to how ecologists have traditionally used the scientific method in field and laboratory experiments. An experiment aims at predicting the outcome by introducing one or more independent variables, input or predictor variables. The change in one or more of these independent or input variables changes the result in one or more dependent variables, also referred to as output or response variables. Simulation models often have many input variables, and determining which ones have a significant impact on the response variables of interest can be a difficult task. Thus, in these types of simulation experiement we must choose the input variables carefully, minimizing as much as possible the uncertainty in their estimates, and ensuring that the documentation of the input method is sufficiently detailed. Note that, at the time in which this PhD Thesis was turned in WEAVER 2.0 is still at the debugging stage. Even though we are at the last steps of this time-demanding task, we could not be confident enough to run the simulations to be presented here. However, very soon we will be

able to use WEAVER 2.0 as a virtual laboratory and carry out the simulations described in this article and many other questions and hypotheses. Finally, we can conclude that within the context of Ecology, more and more IBMs are developing faster in order to perform "in silico" experiments that would be impossible to perform with traditional experimentation methods. WEAVER 2.0 is one of the most complete New Generation IBMs developed to date, and its potential will explode soon.

Acknowledgments

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Table S1. Database of arthropods growth curves. Dashed line (---) represents data not available.

Group	Species	Order or Family	Temperature from laboratory (°C)	Data available	Reference
Acari	*Euseius ho*	Mesostigmata	27.0	Stage-Age	Rêgo *et al*. 2012
Acari	*Stratiolaelaps scimitus*	Mesostigmata	21.0 – 23.0	Stage-Duration	Cabrera *et al*. 2005
Acari	*Acrogalumna longiplumus*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Belba kingi*	Oribatida	---	Stage-Duration	Hartenstein 1962
Acari	*Camisia spinifer*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Cepheus palmicinclum*	Oribatida	---	Stage-Duration	Michael 1888
Acari	*Ceratoppia bipilis*	Oribatida	---	Stage-Duration	Taberly 1957
Acari	*Ceratoppia bipilis*	Oribatida	17.0	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Ceratoppia bipilis*	Oribatida	20.0	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Ceratoppia quadridentata*	Oribatida	17.0	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Ceratoppia quadridentata*	Oribatida	20.0	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Ceratozetes gracilis*	Oribatida	---	Stage-Duration	Hartenstein 1962
Acari	*Ceratozetes jeweli*	Oribatida	---	Stage-Duration	Rockett & Woodring 1966
Acari	*Dameus boreus*	Oribatida	---	Stage-Duration	Sitnikova 1959
Acari	*Dameus clavipes*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Dameus onustus*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Eremobelba nervosa*	Oribatida	---	Stage-Duration	Hartenstein 1962
Acari	*Galumna confusa*	Oribatida	---	Stage-Duration	Woodring 1965
Acari	*Galumna elimatus*	Oribatida	---	Stage-Duration	Sengbusch 1954
Acari	*Galumna elimatus ilhacensis*	Oribatida	25.0	Stage-Age-Length	Sengbusch 1954
Acari	*Galumna longipluma*	Oribatida	---	Stage-Duration	Sengbusch 1954

(Continued)

Acari	*Galumna nervosus*	Oribatida	25.0	Stage-Age-Length	Sengbusch 1954
Acari	*Galumna nervosus*	Oribatida	20.0	Stage-Age-Length	Sengbusch 1954
Acari	*Galumna nervosus*	Oribatida	---	Stage-Duration	Sengbusch 1954
Acari	*Galumna nervosus*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Galumna parva*	Oribatida	---	Stage-Duration	Woodring 1965
Acari	*Hermannia scabra*	Oribatida	---	Stage-Duration	Jalil 1965
Acari	*Hypchthonius rufulus*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Minunthozetes semirufus*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Nanherinannia nana*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Nanhermannia* cf. *coronata*	Oribatida	20.0	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Nanhermannia* cf. *coronata*	Oribatida	22.5	Stage-Duration-Temperature	Ermilov & Lochynska 2008
Acari	*Nothrus silvestris*	Oribatida	---	Stage-Duration	Sengbusch 1958
Acari	*Oppia nitens*	Oribatida	---	Stage-Duration	Sengbusch & Sengbusch 1970
Acari	*Pergalumna nervous*	Oribatida	---	Stage-Duration	Rockett & Woodring 1966
Acari	*Platynothrus peltifer*	Oribatida	---	Stage-Duration	Hartenstein 1962
Acari	*Protoribates lophotrichus*	Oribatida	---	Stage-Duration	Hartenstein 1962
Acari	*Rostrozetes flavus*	Oribatida	---	Stage-Duration	Woodring 1965
Acari	*Scheloribates nudus*	Oribatida	---	Stage-Duration	Woodring 1965
Acari	*Scheloribates parabilis*	Oribatida	---	Stage-Duration	Woodring 1965
Acari	*Tectocepheus velatus*	Oribatida	---	Stage-Duration	Murphy&Jalil 1964
Acari	*Trypochthlonius tectorum*	Oribatida	---	Stage-Duration	Taberly 1953
Acari	*Tyrophagus curvipenis*	Oribatida	25.0	Stage-Duration-Length	Shi-Sen & Zhi-Qiang 2014
Acari	*Mononychellus tanajoa*	Prostigmata	27.0	Stage-Age	Rêgo *et al.* 2012
Acari	*Thermacarus nevadensis*	Prostigmata	---	Stage-Length	Mitchell 1961

(Continued)

Araneae	*Alpaida veniliae*	Araneidae	25.0	Stage-Duration	Benamú *et al*. 2011
Araneae	*Phoneutria boliviensis*	Ctenidae	25.0 – 27.0	Stage-Duration	Hazzi 2014
Araneae	*Atypena formosana*	Linyphiidae	25.0	Stage-Duration-Length	Sigsgaard *et al*. 2001
Araneae	*Meioneta mossica*	Linyphiidae	18.0 – 22.0	Stage-Age-Length	Schikora 2009
Araneae	*Aglaoctenus lagotis*	Lycosidae	26.7	Stage-Age	Moreira & Del-Claro 2011
Araneae	*Lycosa carbonelli*	Lycosidae	24.2	Stage-Duration	Francescoli & Costa 1991
Araneae	*Lycosa thorelli*	Lycosidae	24.2	Stage-Duration	Francescoli & Costa 1991
Araneae	*Pardosa astrigera*	Lycosidae	24.0	Stage-Duration-Weight	Xiao-qiong *et al*. 2011
Araneae	*Pardosa astrigera*	Lycosidae	24.0	Stage-Duration-Weight-Length	Ling *et al.* 2015
Araneae	*Pardosa lugubris*	Lycosidae	18.0	Stage-Age-Duration-Weight	Oelbermann & Scheu 2002
Araneae	*Aphirape n. sp.*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Cotinusa sp.*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Dendryphantes patagonicus*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Evophrys sutrix*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Lyssomanes pauper*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Phiale pantherina*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Phiale roburifoliata*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Sarinda marcosi*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Thiodina punctulata*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Tullgrenella serrana*	Salticidae	25.0 – 35.0	Stage-Duration	Galiano 1991
Araneae	*Loxosceles intermedia*	Sicariidae	21.4	Stage-Duration	Fisher & Vasconcellos-Neto 2005
Araneae	*Anelosimus* cf. *studiosus*	Theridiidae	24.0	Stage-Age	Viera *et al*. 2007
Araneae	*Enoplognatha ovata*	Theridiidae	23.0	Stage-Length	Seligy 1971
Araneae	*Enoplognatha ovata*	Theridiidae	23.0	Stage-Length	Seligy 1971

(Continued)

Araneae	*Enoplognatha ovata*	Theridiidae	23.0	Stage-Length	Seligy 1971
Araneae	*Latrodectus antheratus*	Theridiidae	20.0 – 23.0	Stage	González *et al.* 1998
Araneae	*Latrodectus corallinus*	Theridiidae	20.0 – 23.0	Stage	González *et al.* 1998
Araneae	*Latrodectus diaguita*	Theridiidae	20.0 – 23.0	Stage	González *et al.* 1998
Araneae	*Latrodectus mirabilis*	Theridiidae	20.0 – 23.0	Stage	González *et al.* 1998
Araneae	*Latrodectus variegatus*	Theridiidae	20.0 – 23.0	Stage-Duration	González *et al.* 1998
Araneae	*Steatoda retorta*	Theridiidae	23.0	Stage-Duration	González 1987
Araneae	*Tidarren sisyphoides*	Theridiidae	---	Stage-Duration	González 1982
Araneae	*Misumenops tricuspidatus*	Thomisidae	15.0	Stage-Duration-Temperature	Li 2002
Araneae	*Misumenops tricuspidatus*	Thomisidae	20.0	Stage-Duration-Temperature	Li 2002
Araneae	*Misumenops tricuspidatus*	Thomisidae	25.0	Stage-Duration-Temperature	Li 2002
Araneae	*Misumenops tricuspidatus*	Thomisidae	30.0	Stage-Duration-Temperature	Li 2002
Araneae	*Misumenops tricuspidatus*	Thomisidae	21.0	Stage-Duration-Temperature	Li 2002
Chilopoda	*Strigamia maritima*	Geophilomorpha	---	Stage-Age-Length	Lewis 1961
Chilopoda	*Bothropolys asperatus*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Bothropolys asperatus*	Lithobiomorpha	28.0 – 31.0	Stage-Length	Murakami 1958
Chilopoda	*Lamyctes fulvicornis*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lamyctes fulvicornis*	Lithobiomorpha	---	Stage-Length	Andersson 1984b
Chilopoda	*Lithobius calcaratus*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius calcaratus*	Lithobiomorpha	---	Stage-Length	Andersson 1982b
Chilopoda	*Lithobius crassipes*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius crassipes*	Lithobiomorpha	---	Stage-Length	Andersson 1981
Chilopoda	*Lithobius crassipes*	Lithobiomorpha	---	Stage-Length	Andersson 1981
Chilopoda	*Lithobius curtipes*	Lithobiomorpha	---	Stage-Age	Andersson 1990

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Chilopoda	*Lithobius curtipes*	Lithobiomorpha	---	Stage-Length	Andersson 1983
Chilopoda	*Lithobius curtipes*	Lithobiomorpha	---	Stage-Length	Andersson 1983
Chilopoda	*Lithobius erythrocephalus*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius erythrocephalus*	Lithobiomorpha	16.0	Stage-Length	Voigtländer 2000
Chilopoda	*Lithobius forficatus*	Lithobiomorpha	25.0	Stage-Age	Scheffel 1969
Chilopoda	*Lithobius forficatus*	Lithobiomorpha	18.0 – 22.0	Stage-Age	Joly 1966
Chilopoda	*Lithobius forficatus*	Lithobiomorpha	25.0	Stage-Length	Verhoeff 1902-25
Chilopoda	*Lithobius forficatus*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius forficatus*	Lithobiomorpha	---	Stage-Length	Andersson 1976
Chilopoda	*Lithobius melanops*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius melanops*	Lithobiomorpha	---	Stage-Length	Andersson 1980
Chilopoda	*Lithobius microps*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius microps*	Lithobiomorpha	---	Stage-Length	Andersson 1982a
Chilopoda	*Lithobius microps*	Lithobiomorpha	16.0	Stage-Length	Voigtländer 2000
Chilopoda	*Lithobius mutabilis*	Lithobiomorpha	16.0	Stage-Age-Length	Voigtländer 2007
Chilopoda	*Lithobius pachypedatus*	Lithobiomorpha	---	Stage-Length	Murakami 1960
Chilopoda	*Lithobius tenebrosus fennoscandius*	Lithobiomorpha	---	Stage-Age	Andersson 1990
Chilopoda	*Lithobius tenebrosus fennoscandius*	Lithobiomorpha	---	Stage-Length	Andersson 1984a
Chilopoda	*Lithobius variegatus*	Lithobiomorpha	---	Stage-Length	Lewis 2007
Chilopoda	*Lithobius variegatus*	Lithobiomorpha	---	Stage-Length	Lewis 2007
Chilopoda	*Lithobius variegatus*	Lithobiomorpha	---	Stage-Age	Roberts 1957
Coleoptera	*Abax ater*	Carabidae	---	Stage-Age-Length	Chaabane *et al*. 1997
Coleoptera	*Abax ater*	Carabidae	12.6	Stage-Age-Length	Chaabane *et al*. 1997
Coleoptera	*Amara aenea*	Carabidae	17.5	Stage	Saska & Honěk 2003

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Coleoptera	*Amara communis*	Carabidae	21.0	Stage-Duration	Hůrka & Jarošik 2001
Coleoptera	*Amara communis*	Carabidae	16.0	Stage-Duration-Temperature	Lopatina *et al*. 2011
Coleoptera	*Amara communis*	Carabidae	18.0	Stage-Duration-Temperature	Lopatina *et al*. 2011
Coleoptera	*Amara communis*	Carabidae	20.0	Stage-Duration-Temperature	Lopatina *et al*. 2011
Coleoptera	*Amara communis*	Carabidae	22.0	Stage-Duration-Temperature	Lopatina *et al*. 2011
Coleoptera	*Amara convexlor*	Carabidae	21.0	Stage-Duration	Hůrka & Jarošik 2001
Coleoptera	*Amara familiaris*	Carabidae	17.5	Stage	Saska & Honěk 2003
Coleoptera	*Amara fulvipes*	Carabidae	17.5	Stage	Saska & Honěk 2003
Coleoptera	*Amara littorea*	Carabidae	17.5	Stage	Saska & Honěk 2003
Coleoptera	*Amara makolskii*	Carabidae	21.0	Stage-Duration	Hůrka & Jarošik 2001
Coleoptera	*Amara ovata*	Carabidae	17.5	Stage	Saska & Honěk 2003
Coleoptera	*Amara pulpani*	Carabidae	21.0	Stage-Duration	Saska & Honěk 2003
Coleoptera	*Amara similata*	Carabidae	17.5	Stage	Saska & Honěk 2003
Coleoptera	*Parastethorus histrio*	Coccinellidae	23.0	Stage-Duration	Rioja *et al*. 2016
Coleoptera	*Creophilus maxillosus*	Staphylinidae	32.0	Stage-Duration-Temperature	Watson-Horzelski 2012
Coleoptera	*Creophilus maxillosus*	Staphylinidae	24.0	Stage-Duration-Temperature	Watson-Horzelski 2012
Coleoptera	*Creophilus maxillosus*	Staphylinidae	16.0	Stage-Duration-Temperature	Watson-Horzelski 2012
Coleoptera	*Drusilla canaliculata*	Staphylinidae	5.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Drusilla canaliculata*	Staphylinidae	10.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Drusilla canaliculata*	Staphylinidae	16.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Drusilla canaliculata*	Staphylinidae	23.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Drusilla canaliculata*	Staphylinidae	26.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Drusilla canaliculata*	Staphylinidae	28.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Geostiba circellaris*	Staphylinidae	5.0	Stage-Duration-Temperature	Schminke 1978

(Continued)

Coleoptera	*Geostiba circellaris*	Staphylinidae	10.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Geostiba circellaris*	Staphylinidae	16.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Oligota pygmaea*	Staphylinidae	23.0	Stage-Duration	Rioja *et al*. 2016
Coleoptera	*Oligota pygmaea*	Staphylinidae	25.0	Stage-Duration-Length	Perumalsamy *et al*. 2009
Coleoptera	*Zyras humeralis*	Staphylinidae	10.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Zyras humeralis*	Staphylinidae	16.0	Stage-Duration-Temperature	Schminke 1978
Coleoptera	*Tribolium confusum*	Tenebrionidae	---	Stage-Length	Metcalf & Flint 1939
Collembola	*Arrohopalites pygmaeus*	Entomobryidae	---	Stage-Age	Agrell 1948
Collembola	*Entomobrya nivalis*	Entomobryidae	20.0	Age-Length	Joosse & Veltkamp 1970
Collembola	*Entomobrya spp.*	Entomobryidae	---	Stage	South 1961
Collembola	*Lepidocyrtus cyaneus*	Entomobryidae	20.0	Age-Length	Joosse & Veltkamp 1970
Collembola	*Lobella maxillaris*	Entomobryidae	25.0	Stage-Age-Length	Choudhuri & Bhattacharyya 1978
Collembola	*Lobella sokamensis*	Entomobryidae	20.0	Age-Length	Youn - Joo *et al*. 2013
Collembola	*Orchesella cincta*	Entomobryidae	12.0	Stage-Age	Lindemann 1950
Collembola	*Orchesella cincta*	Entomobryidae	23.0	Stage-Age	Lindemann 1950
Collembola	*Orchesella cincta*	Entomobryidae	20.0	Age-Length	Ernsting & Isaaks 2002
Collembola	*Orchesella cincta*	Entomobryidae	20.0	Age-Length	Janssen & Joosse 1987
Collembola	*Orchesella cincta*	Entomobryidae	20.0	Age-Length	Joosse & Veltkamp 1970
Collembola	*Pseudosinella violenta*	Entomobryidae	---	Stage	Davis & Harris 1936
Collembola	*Tomocerus minor*	Entomobryidae	20.0	Age-Length	Joosse & Veltkamp 1970
Collembola	*Tomocerus minutus*	Entomobryidae	---	Stage	Uchida & Chiba 1958
Collembola	*Hypogastrura armata*	Hyogastruridae	24.0	Stage-Age	Britt 1951
Collembola	*Hypogastrura manubrialis*	Hyogastruridae	---	Stage-Age	Ripper 1930
Collembola	*Hypogastrura purpurescens*	Hyogastruridae	---	Stage-Age	Strebel 1932

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Collembola	*Hypogastrura sahbergi*	Hyogastruridae	---	Stage	Agrell 1948
Collembola	*Hypogastrura denticulata*	Hyogastruridae	8.0	Stage-Age	Hale 1965
Collembola	*Hypogastrura denticulata*	Hyogastruridae	15.0	Stage-Age	Hale 1965
Collembola	*Tullbergia krausbaueri*	Hypogastruridae	15.0	Stage-Age	Hale 1965
Collembola	*Folsomia 4-oculata*	Isotomidae	---	Stage	Agrell 1948
Collembola	*Folsomia candida*	Isotomidae	16.0	Age-Length	Mallard *et al.* 2015
Collembola	*Folsomia candida*	Isotomidae	12.0	Stage-Age-Length	Milne 1960
Collembola	*Folsomia candida*	Isotomidae	24.0	Stage-Age-Length	Milne 1960
Collembola	*Folsomia candida*	Isotomidae	8.0	Age-Length-Temperature	Johnson & Wellington 1980
Collembola	*Folsomia candida*	Isotomidae	16.0	Age-Length-Temperature	Johnson & Wellington 1980
Collembola	*Folsomia candida*	Isotomidae	24.0	Age-Length-Temperature	Johnson & Wellington 1980
Collembola	*Isotoma viridis*	Isotomidae	20.0	Age-Length	Joosse & Veltkamp 1970
Collembola	*Isotomurus palustris*	Isotomidae	---	Stage	James 1933
Collembola	*Neanura muscorum*	Neanuridae	15.0	Age-Length	Hoskins *et al.* 2015
Collembola	*Onychiurus furcifer*	Onychiuridae	15.0	Stage-Age	Hale 1965
Collembola	*Onychiurus furcifer*	Onychiuridae	15.0	Stage-Age	Hale 1965
Collembola	*Onychiurus furcifer*	Onychiuridae	15.0 – 25.0	Age-Length	Walsh & Bolger 1990
Collembola	*Onychiurus furcifer*	Onychiuridae	12.0	Stage-Age-Length	Milne 1960
Collembola	*Onychiurus latus*	Onychiuridae	15.0	Age-Length	Hale 1965
Collembola	*Onychiurus latus*	Onychiuridae	12.0	Stage-Age-Length	Milne 1960
Collembola	*Onychiurus procampatus*	Onychiuridae	15.0	Age-Length	Hale 1965
Collembola	*Onychiurus procampatus*	Onychiuridae	12.0	Stage-Age-Length	Milne 1960
Collembola	*Onychiurus tricampatus*	Onychiuridae	15.0	Age-Length	Hale 1965
Collembola	*Tullbergia krausbaueri*	Onychiuridae	12.0	Stage-Age-Length	Milne 1960

(Continued)

Collembola	*Sminthurides aquaticus*	Sminthuridae	---	Stage	Falkenhan 1932
Collembola	*Sminthurus viridis*	Sminthuridae	17.0	Stage-Age-Length	MacLagan 1932
Collembola	*Xenylla brevispina*	Sminthuridae	---	Age-Length	Itoh 1991
Collembola	*Xenylla grisea (Sminthurus viridis)*	Sminthuridae	8.0	Age-Length-Temperature	Johnson & Wellington 1980
Collembola	*Xenylla grisea (Sminthurus viridis)*	Sminthuridae	16.0	Age-Length-Temperature	Johnson & Wellington 1980
Collembola	*Xenylla grisea (Sminthurus viridis)*	Sminthuridae	24.0	Age-Length-Temperature	Johnson & Wellington 1980
Diplopoda	*Glomeris balcanica*	Glomeridae	---	Stage-Weight	Latrou & Stamou 1990
Diplopoda	*Glomeris balcanica*	Glomeridae	---	Stage-Length-Weight	Latrou & Stamou 1990
Diplopoda	*Brachydesmus polydesmoides calcivagus*	Julidae	---	Stage-Length	Kheirallah 1980
Diplopoda	*Cylindroiulus latestriatus*	Julidae	---	Stage-Length	Blower & Gabbut 1964
Diplopoda	*Cylindroiulus punctatus*	Julidae	---	Stage-Length	Blower & Gabbut 1964
Diplopoda	*Pachyiulus flavipes*	Julidae	---	Stage-Length-Weight	Dirsh 1937
Diplopoda	*Pachyiulus foetidissimus*	Julidae	---	Stage-Length-Weight	Striganova & Mazantseva 1979
Diplopoda	*Rossiulus kessleri*	Julidae	---	Stage-Length-Weight	Prishutova 2001
Diplopoda	*Tachypodoiulus niger*	Julidae	---	Stage-Length	Blower & Fairhurst 1968
Diplopoda	*Epibolus pulchripes*	Pachybolidae	18.0 – 20.0	Stage-Length	Dhaenes & VandenSpiegel 2006
Diplopoda	*Trigoniulus corallinus*	Pachybolidae	---	Stage-Length-Weight	Shinohara *et al.* 2007
Diplopoda	*Polydesmus inconstans*	Polydesmidae	10.0	Stage-Duration	Snider 1981
Diplopoda	*Polydesmus inconstans*	Polydesmidae	15.5	Stage-Duration	Snider 1981
Diplopoda	*Polydesmus inconstans*	Polydesmidae	21.0	Stage-Duration	Snider 1981
Diplopoda	*Polydesmus inconstans*	Polydesmidae	26.6	Stage-Duration	Snider 1981
Diplopoda	*Pseudopolydesmus pinetorum*	Polydesmidae	12.8 – 26.7	Stage-Length	Youngsteadt 2009
Oligochaeta	*Enchytraeus albidus*	Enchytraeidae	1.0 – 25.0	Stage-Duration-Length	Reynoldson 1942
Oligochaeta	*Enchytraeus crypticus*	Enchytraeidae	18.0	Age-Length	Bicho *et al.* 2015

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Oligochaeta	*Lumbricillus lineatus*	Enchytraeidae	1.0 – 25.0	Stage-Duration-Length	Reynoldson 1942
Opilionida	*Cynortoides cubanus*	Cosmetidae	---	Stage-Duration	Juberthie 1972
Opilionida	*Erginulus clavotibialis*	Cosmetidae	---	Stage-Duration	Goodnight & Goodnight 1976
Opilionida	*Vonones sayi*	Cosmetidae	---	Stage-Duration	Cokendolpher & Jones 1991
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Phareicarnaus calcariferus*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Santinezia serratotibialis*	Cranaidae	---	Stage-Length	Townsend Jr. *et al*. 2009
Opilionida	*Dicranolasma scabrum*	Dicranolasmatidae	---	Stage-Duration	Gruber 1996
Opilionida	*Discocyrtus pectinifemur*	Gonyleptidae	---	Stage-Duration	Matthiesen 1985
Opilionida	*Goniosoma speiaeum*	Gonyleptidae	---	Stage-Duration	Gnaspini 1995
Opilionida	*Goniosoma speiaeum*	Gonyleptidae	---	Stage-Age-Length	Gnaspini 1995
Opilionida	*Holoscotolemon queriihaci*	Gonyleptidae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Pachylus quinamavidensis*	Gonyleptidae	18.0	Stage-Age-Length	Muñoz-Cuevas 1971
Opilionida	*Pachylus quinamavidensis*	Gonyleptidae	---	Stage-Duration	Juberthie & Muñoz-Cuevas 1971
Opilionida	*Ischyropsalis luteipes*	Ischyropsalididae	---	Stage-Duration	Juberthie 1964, 1965

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Opilionida	*Ischyropsalis nodiferas*	Ischyropsalididae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Ischyropsalis pyrenaea*	Ischyropsalididae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Ischyropsalis strandi*	Ischyropsalididae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Ischyropsalis superba*	Ischyropsalididae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Nemastoma quadripuctatum*	Nemastomatidae	---	Stage-Duration	Immel 1954
Opilionida	*Paranemastoma sillii*	Nemastomatidae	---	Stage-Duration	Avram 1973
Opilionida	*Nipponopsalis abei*	Nipponopsalididae	---	Stage-Duration	Miyoshi 1942
Opilionida	*Lacinius ephippiatus*	Phalangiidae	---	Stage-Duration	Pfeifer 1956; Winkler 1957
Opilionida	*Lacinius horridus*	Phalangiidae	---	Stage-Duration	Pfeifer 1956; Parisot 1962
Opilionida	*Lophopilio palpinalis*	Phalangiidae	---	Stage-Duration	Pfeifer 1956
Opilionida	*Odiellus gallicus*	Phalangiidae	---	Stage-Duration	Juberthie 1957, 1960, 1964, 1965
Opilionida	*Oligolophus tridens*	Phalangiidae	---	Stage-Duration	Gueutal 1943; Pfeifer 1956
Opilionida	*Phalangium opilio*	Phalangiidae	---	Stage-Duration	Gueutal 1943; Todd 1949
Opilionida	*Platybunus bucephalus*	Phalangiidae	---	Stage-Duration	Immel 1955; Parisot 1962
Opilionida	*Platybunus triangularis*	Phalangiidae	---	Stage-Duration	Todd 1949; Pfeifer 1956
Opilionida	*Scotolemon doriae*	Phalangodidae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Scotolemon iespesi*	Phalangodidae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Scotolemon lucasi*	Phalangodidae	---	Stage-Duration	Juberthie 1964
Opilionida	*Homalenotus quadridentatus*	Sclerosomatidae	---	Stage-Duration	Juberthie 1957, 1964, 1965
Opilionida	*Cyphophthalmus duricorius*	Sironidae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Parasiro coiffaite*	Sironidae	---	Stage-Duration	Juberthie 1964, 1965
Opilionida	*Siro rubens*	Sironidae	---	Stage-Duration	Juberthie 1960, 1964, 1965
Opilionida	*Anelasmocephalus cambridgei*	Trogulidae	---	Stage-Duration	Pabst 1953
Opilionida	*Trogulus nepaeformis*	Trogulidae	---	Stage-Duration	Pabst 1953; Juberthie 1964

(Continued)

Trogulus tricarinatus	Trogulidae	---	Stage-Duration	Pabst 1953
Tyrannochthonius	Chthoniidae	---	Stage-Length	Sakayori 2002
Microbisium	Neobisiidae	---	Stage-Length	Sakayori 1989

*Data available can be:
Stage: number of instars of each species.
Age: age of Vn which each molt occurs.
Duration: time it takes a species between moult and moult.
Length: length (mm) after each moult.
Weight: weight (mg) after each moult.
Temperature: Laboratory temperature (°C) at which the growth curve was measured.

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Table S2. Values of scaling factor "a" and allometric factor "b" of mass-length relationship from a bibliographic database (Table S1 in Ruiz-Lupión *et al*. Chapter 2). From parameterization of each Model Species we used the backtransformation of the mean of the log of scaling factor "a" and the mean of allometric factor "b" among the equations available from close relatives and/or of very similar body shapes.

Feeding habits	Model Species	Taxonomic Level from equation	a	b	Reference
Large Predators	*Harpactocrates sp.*	Clubionidae	0.044	2.636	Edwards 1996
		Clubionidae	0.024	2.999	Edwards 1996
		Clubionidae	0.116	2.653	Edwards & Gabriel 1998
		Clubionidae	0.013	1.330	McLaughlin *et al.* 2010
		Clubiona brevipes	0.015	3.040	Clausen 1983
		Clubiona pallidula	0.028	2.730	Clausen 1983
		Clubiona corticalis	0.019	2.960	Clausen 1983
		Clubiona sp.	0.016	3.000	Clausen 1983
		Clubiona brevipes	0.010	3.240	Clausen 1983
		Clubiona pallidula	0.017	2.960	Clausen 1983
		Clubiona sp.	0.011	3.170	Clausen 1983
		Gnaphosidae	0.025	2.930	Edwards 1998
		Gnaphosidae	0.028	2.845	Edwards 1998
		Gnaphosidae	0.004	3.011	Edwards & Gabriel 1998
		Gnaphosidae	0.059	3.055	Edwards 1996
	Lithobius sp.	*Lithobius mutabilis*	0.010	2.965	Voigtländer 2007
		Lithobius mutabilis	0.013	2.867	Voigtländer 2007
		Lithobius erythrocephalus	0.027	2.578	Voigtländer 2000
		Lithobius micriops	0.192	1.306	Voigtländer 2000
	Geophilu sp.	Geophilomorpha	0.003	2.356	Klarner *et al.* 2017
		Geophilomorpha	$1 \cdot 10^{-4}$	3.226	Klarner *et al.* 2017
		Geophilomorpha	$1 \cdot 10^{-4}$	3.226	Ruiz-Lupión *et al.* (Chapter 2)
	Calathus sp. Larvae	Carabidae	0.034	2.162	Hódar 1996
	Calathus sp. Adult	Carabidae	0.017	2.752	Gruner 2003
		Carabidae	0.004	3.360	McLaughlin *et al.* 2010
		Carabidae	0.004	4.060	McLaughlin *et al.* 2010
		Carabidae	0.001	4.640	McLaughlin *et al.* 2010
		Carabidae	0.006	3.190	McLaughlin *et al.* 2010
		Carabidae	0.007	2.870	McLaughlin *et al.* 2010
		Carabidae	0.007	2.820	McLaughlin *et al.* 2010
		Carabidae	0.024	2.705	Lang *et al.* 1997
		Carabidae	0.008	3.214	Hódar 1996
		Carabidae	0.031	2.639	Jarošik 1989
		Carabidae	0.024	2.755	Sabo *et al.* 2002
		Carabidae	0.014	2.839	Marcuzzi 1987
		Carabidae	0.002	3.595	Santos Gómez 2013
		Carabidae	0.010	3.053	Santos Gómez 2013
		Carabidae	0.011	3.015	Santos Gómez 2013
		Carabidae	0.023	2.689	Santos Gómez 2013
Small Predator	*Microbisium sp.*	Pseudoscorpions	0.047	2.453	Höfer & Ott 2009
		Pseudoscorpions	0.024	2.165	Höfer & Ott 2009
		Pseudoscorpions	0.007	3.000	Johnson & Strong 2000
		Pseudoscorpions	0.008	3.440	Wardhaugh 2013

(Continued)

Omnivore Species	*Macrocheles sp.* *Stratiolaelaps sp.*	Acari	0.039	2.711	Hódar 1996
		Acari	0.053	2.494	LeBrun 1971
		Acari	0.040	2.761	McLaughlin *et al.* 2010
		Acari	0.005	3.000	Mercer *et al.* 2001
		Acari	0.142	3.093	Newton & Proctor 2013
		Acari	0.018	2.218	Rogers *et al.* 1977
		Mesostigmata	0.002	2.571	Mercer *et al.* 2001
		Mesostigmata	0.035	2.740	Newton and Proctor 2013
	Anystis sp. *Eupodidae*	Acari	0.039	2.711	Hódar 1996
		Acari	0.053	2.494	LeBrun 1971
		Acari	0.040	2.761	McLaughlin *et al.* 2010
		Acari	0.005	3.000	Mercer *et al.* 2001
		Acari	0.142	3.093	Newton & Proctor 2013
		Acari	0.018	2.218	Rogers *et al.* 1977
		Prostigmata	0.001	2.066	Mercer *et al.* 2001
		Prostigmata	0.010	1.909	Newton and Proctor 2013
Fungivore Species	*Galumna sp.* *Damaeus sp.*	Acari	0.039	2.711	Hódar 1996
		Acari	0.053	2.494	LeBrun 1971
		Acari	0.040	2.761	McLaughlin *et al.* 2010
		Acari	0.005	3.000	Mercer *et al.* 2001
		Acari	0.142	3.093	Newton & Proctor 2013
		Acari	0.018	2.218	Rogers *et al.* 1977
		Oribatida	0.003	2.519	McLaughlin *et al.* 2010
		Oribatida	0.052	2.790	Mercer *et al.* 2001
		Oribatida	0.003	3.000	Newton & Proctor 2013
		Oribatida	0.043	3.022	Rogers *et al.* 1977
	Onychiurus sp.	*Onychiurus furcifer*	0.007	2.725	Petersen 1975
		Onychiurus furcifer	0.006	3.126	Petersen 1975
		Onychiurus furcifer	0.010	3.208	Petersen 1975
		Onychiurus furcifer	0.008	4.149	Petersen 1975
	Tomocerus sp.	*Tomocerus flavescens*	0.009	2.744	Petersen 1975
		Tomocerus minor	0.007	2.882	Van Straalen 1989
	Sminthurus sp.	Sminthuridae	0.006	3.000	McLaughlin *et al.* 2010
		Allacma fusca	0.061	2.925	Vannier 1973
Detritivore Species	*Polydesmus sp.*	*Polydesmus angustus*	0.004	2.740	McLaughlin *et al.* 2010

References Table S2

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Table S3. Values of scaling factor "a" and allometric factor "b" of length-weight relationship for the simulated species (details of how these values were obtained in Table S2).

Feeding habit	Model Species	Juvenile		Adult	
		a	b	a	b
Large Predators	*Harpactocrates sp.*	0.0198	2.8136	0.0198	2.8136
	Lithobius sp.	0.0290	2.4287	0.0290	2.4287
	Geophilus sp.	0.0003	2.9360	0.0003	2.9360
	Calathus sp.	0.0338	2.1620	0.0086	3.1373
Small Predator	*Microbisium sp.*	0.0202	2.7294	0.0202	2.7294
Ominore species	*Macrocheles sp.*	0.0229	2.6775	0.0229	2.6775
	Stratiolaelaps sp.	0.0229	2.6775	0.0229	2.6775
	Anystis sp.	0.0195	2.5390	0.0195	2.5390
	Eupodidae	0.0195	2.5390	0.0195	2.5390
Fungivore species	*Galumna sp.*	0.0210	2.6468	0.0210	2.6468
	Damaeus sp.	0.0210	2.6468	0.0210	2.6468
	Onychiurus sp.	0.0076	3.3020	0.0076	3.3020
	Tomocerus sp.	0.0082	2.8130	0.0082	2.8130
	Sminthurus sp.	0.0141	2.7583	0.0141	2.7583
Detritivore species	*Polydesmus sp.*	0.0041	2.7400	0.0041	2.7400

* $M = aL^b$, where M is dry mass (mg), L is length (mm), a is the scaling factor and b is the allometric factor.

Table S4. Predation matrix of original food web.

PREDATOR	*Harpactocrates sp.*	*Lithobius sp.*	*Geophilus sp.*	*Amara sp.*	*Microbisium sp.*	*Macrocheles sp.*	*Stratiolaelaps sp.*	*Anystis sp.*	Eupodidae	*Galumna sp.*	*Damaeus sp.*	*Onychiurus sp.*	*Tomocerus sp.*	*Sminthurus sp.*	*Polydesmus sp.*	Fungus 1	Fungus 2	Fungus 3	Beech litter
Harpactocrates sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Lithobius sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Geophilus sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Amara sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Microbisium sp.	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
Macrocheles sp.	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Stratiolaelaps sp.	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Anystis sp.	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Eupodidae	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
Galumna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Damaeus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Onychiurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Tomocerus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Sminthurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Polydesmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREY

Table S5. Predation matrix of food web niche model 1.

PREDATOR	*Harpactocrates sp.*	*Lithobius sp.*	*Geophilus sp.*	*Amara sp.*	*Microbisium sp.*	*Macrocheles sp.*	*Stratiolaelaps sp.*	*Anystis sp.*	Eupodidae	*Galumna sp.*	*Damaeus sp.*	*Onychiurus sp.*	*Tomocerus sp.*	*Sminthurus sp.*	*Polydesmus sp.*	Fungus 1	Fungus 2	Fungus 3	Beech litter
Harpactocrates sp.	1	0	0	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0
Lithobius sp.	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
Geophilus sp.	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0
Amara sp.	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0
Microbisium sp.	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	0	0	0
Macrocheles sp.	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0
Stratiolaelaps sp.	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0
Anystis sp.	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0
Eupodidae	0	0	0	0	0	1	0	1	0	0	0	1	0	1	1	1	0	1	0
Galumna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Damaeus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Onychiurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tomocerus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sminthurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Polydesmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

PREY

Table S6. Predation matrix of food web niche model 2.

PREDATOR \ PREY	*Harpactocrates sp.*	*Lithobius sp.*	*Geophilus sp.*	*Amara sp.*	*Microbisium sp.*	*Macrocheles sp.*	*Stratiolaelaps sp.*	*Anystis sp.*	Eupodidae	*Galumna sp.*	*Damaeus sp.*	*Onychiurus sp.*	*Tomocerus sp.*	*Sminthurus sp.*	*Polydesmus sp.*	Fungus 1	Fungus 2	Fungus 3	Beech litter
Harpactocrates sp.	1	0	1	0	0	1	1	0	1	1	0	0	1	1	1	0	0	0	0
Lithobius sp.	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0
Geophilus sp.	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	0
Amara sp.	1	0	1	0	0	1	1	1	0	0	1	0	1	0	1	0	0	0	0
Microbisium sp.	0	0	0	0	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0
Macrocheles sp.	0	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	1	1	0
Stratiolaelaps sp.	0	0	0	0	0	1	0	1	0	1	1	1	0	0	1	1	0	1	0
Anystis sp.	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0
Eupodidae	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	0	1	0
Galumna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Damaeus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Onychiurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Tomocerus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Sminthurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Polydesmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S7. Predation matrix of food web niche model 3.

PREDATOR \ PREY	*Harpactocrates sp.*	*Lithobius sp.*	*Geophilus sp.*	*Amara sp.*	*Microbisium sp.*	*Macrocheles sp.*	*Stratiolaelaps sp.*	*Anystis sp.*	Eupodidae	*Galumna sp.*	*Damaeus sp.*	*Onychiurus sp.*	*Tomocerus sp.*	*Sminthurus sp.*	*Polydesmus sp.*	Fungus 1	Fungus 2	Fungus 3	Beech litter
Harpactocrates sp.	0	1	0	1	1	1	1	1	1	1	1	0	1	1	0	0	0	0	0
Lithobius sp.	0	1	0	1	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0
Geophilus sp.	0	1	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0
Amara sp.	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	0	0
Microbisium sp.	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0	0	0	0
Macrocheles sp.	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1	0	1	1	0
Stratiolaelaps sp.	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	1	1	0	0
Anystis sp.	0	0	0	0	0	1	1	1	0	1	1	0	1	1	1	1	1	0	0
Eupodidae	0	0	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0
Galumna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Damaeus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Onychiurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Tomocerus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Sminthurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Polydesmus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Fungus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fungus 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beech litter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Principales Resultados y Discusión General

En esta Tesis Doctoral hemos abordado distintos pasos del Ciclo de la Modelización. Partiendo de que este ciclo es un proceso iterativo y complejo, a modo de resumen y discusión integradora vamos a explicar cómo encaja cada capítulo de esta Tesis dentro de este proceso, así como los principales resultados procedentes de los diferentes estudios. La primera vuelta del Ciclo de la Modelización culminó con el desarrollo, implementación, análisis y comunicación del Modelo Basado en Individuos mini-AKIRA desarrollado en lenguaje R (R development Core Team 2012), descrito anteriormente en la Introducción General (Moya-Laraño *et al*. 2012). Tras este primer paso nos surgieron las siguientes preguntas: ¿cómo afecta la conectancia de una red trófica de la hojarasca de los hayedos (*Fagus sylvatica* L.), así como, el efecto de la variabilidad genética de los individuos y la estructuración espacial del hábitat en las dinámicas eco-evolutivas de dicha red trófica? La respuesta a estas preguntas exigía llevar a cabo una segunda vuelta del Ciclo de la Modelización en la que se desarrolló e implementó el Modelo Basado en Individuos de Nueva Generación WEAVER 1.0, que es una copia traducida del código fuente de mini-AKIRA en lenguaje R a lenguaje C++ al que se le incluyeron nuevas características y funcionalidades (Moya-Laraño *et al*. 2014), todo ello abordado en el **Capítulo 1**. Tras este paso, quisimos aportar más realismo y robustez a las simulaciones con una parametrización basada aún más en datos reales obtenidos de revisiones bibliográficas, así como de estudios de campo y laboratorio. De esta manera los resultados derivados de nuestras preguntas e hipótesis tendrían una mayor veracidad. Debido a esto fue necesario una tercera vuelta al Ciclo de Modelización que dio lugar a la comunicación de dos estudios paralelos como resultado de la mejora en la parametrización. El primer estudio está basado en un análisis comparativo de las alometrías longitud-peso ($M = aL^b$) en artrópodos del suelo a escala global descrito en el **Capítulo 2,** muy importante tanto en la versión WEAVER 1.0 como en las posteriores versiones pues la transformación entre longitud y masa se lleva a cabo a lo largo de muchos algoritmos del IBM durante la simulación. En el segundo estudio se realizó un experimento de mesocosmos de campo en hayedos (*Fagus sylvatica* L.) donde comparamos distintos tipos de trampas para el estudio de la actividad de meso- y macrofauna del suelo que detallamos en el **Capítulo 3**, con el cual pudimos determinar la metodología más adecuada para estudiar la actividad de los artrópodos de nuestro sistema de estudio. Con todos estos datos parametrizamos una nueva red trófica de la hojarasca de los hayedos basada únicamente en artrópodos y se mejoraron e implementaron nuevas funcionalidades a la versión WEAVER 1.0 descritas y comentadas en el **Capítulo 4**, creando así la versión WEAVER 2.0. Una característica primordial de esta nueva versión es que permite extrapolar WEAVER a nuevos sistemas ecológicos que están actualmente en proceso de parametrización e implementación.

1. Versión WEAVER 1.0 (Segunda vuelta del Ciclo de la Modelización)

WEAVER 1.0 se considera según los elementos y características descritas por Grimm & Berger 2016 un Modelo Basado en Individuos de Nueva Generación (Figura 1), a diferencia de mini-AKIRA que no es un Modelo de Nueva Generación. El hecho de pasar de trabajar con un código fuente desarrollado

en lenguaje R en un sistema operativo Windows 7 a trabajar con un código en lenguaje C++ en un sistema operativo Linux (concretamente utilizando el entorno de desarrollo Eclipse en Ubuntu 14.10) permitió que una simulación con los mismos parámetros de entrada y utilizando la misma máquina pasara de tardar 48 horas usando mini-AKIRA a 10 segundos utilizando WEAVER 1.0. Este gran paso fue decisivo no solo para incluir las nuevas funcionalidades descritas en el **Capítulo 1,** si no para hacer que las simulaciones fueran mucho más realistas. Así pudimos pasar de simular las dinámicas eco-evolutivas de una cadena trófica depredador-presa-hongo a poder simular dinámicas eco-evolutivas complejas de meta-comunidades multi-tróficas, con un gran número de individuos al inicio de la simulación, gracias también al acceso a la supercomputadora "Bullxual" de la Universidad de Almería formada por un clúster de 18 nodos y 8 GPUs (288 cores, 1152 GB de RAM y 2304 GB SSD). Por último, destacar que al igual que se llevó a cabo la descripción y publicación del modelo mini-AKIRA (Moya-Laraño *et al*. 2012) siguiendo los elementos descritos en el Protocolo ODD (Grimm *et al*. 2006) la descripción y publicación de la versión WEAVER 1.0 (Moya-Laraño *et al*. 2014, Capítulo 1), así como sus posteriores versiones también cumplen con dichos elementos (Ruiz-Lupión *et al.* en preparación).

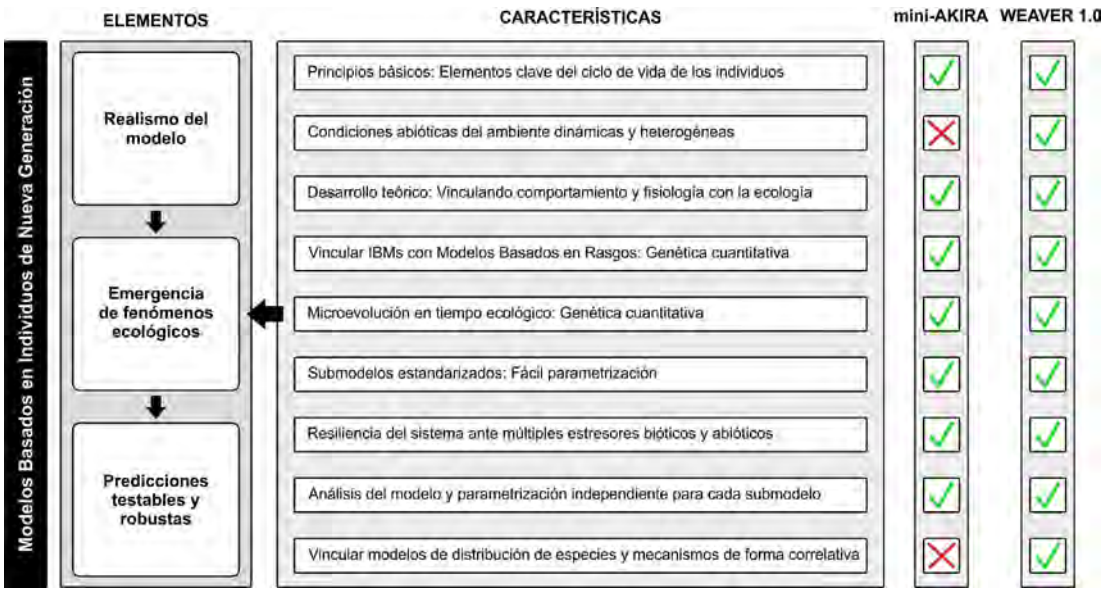

Figura 1. Elementos y características de los Modelos Basados en Individuos de Nueva Generación según Grimm & Berger 2016. Los ticks en verde reflejan los elementos que cumplen los modelos, las cruces rojas reflejan los que no cumplen.

1.1. Nuevas características y funcionalidades incluidas en el IBM de Nueva Generación WEAVER 1.0

A continuación, vamos a presentar un resumen comparativo de las principales características y funcionalidades modificadas y/o incluidas en la versión WEAVER 1.0 respecto a la versión mini-AKIRA (Tabla 1) descritas detalladamente en el **Capítulo 1**, como principal resultado de la segunda vuelta al Ciclo de la Modelización (Figura 2).

Tabla 1. Comparación entre los modelos mini-AKIRA y WEAVER 1.0. La línea discontinua (---) indica aquellas características o funcionalidades que no están incluidas en el modelo.

	Características y funcionalidades	mini-AKIRA	WEAVER 1.0
Tiempo y Espacio	**Lenguaje de programación**	R	C++
	Espacio	1D	3D
	Unidades espaciales	Celdas	Celdas
	Unidades tiempo de cada paso o "step"	Días	Días
	Tipo de modelo espacial	Semi-espacialmente expícito	Espacialmente explícito
Red trófica simulada	**Recursos basales**	Hongo	Hongo
	Tipo de crecimiento del hongo	Función logística	Función logística
	¿Dónde crece el hongo?	Todo el mundo	Bolsas de agua en el suelo
	Quimiostato	---	Pulsos biomasa hongo
	Inicialización de los recursos basales	99% capacidad carga celda	Parches esféricos
	Inicialización humedad del suelo	Todo el mundo	Parches esféricos
	Tipo de interacciones tróficas	Canibalismo Depredación intragremial Depredación active-hunting Depredación sit-and-wait --- --- Micofagia	Canibalismo Depredación intragremial Depredación active-hunting Depredación sit-and-wait Competencia depredadores Competencia presas Micofagia
	Nº total de depredadores	1	11
	Nº total de presas fungívoras	1	9
	Nº total de recursos basales	1	1
	Nº total de especies	3	21
	Inicialización de los individuos	Cada especie una abundancia Todos mismo instar	Relación alométrica masa-abundancia de Schneider *et al*. 2012.
	Inicialización posición de los individuos	Aleatoria	Aleatoria
Base genética cuantitativa multidimensional	**Número de rasgos incluidos**	13 rasgos	14 rasgos
	Modularidad de los rasgos	5 módulos	5 módulos
	Cromosomas	Vector 20 loci y 10 alelos	Correlosomas
	Correlación entre rasgos de cada módulo	Sí (parámetro $\rho \in [-1,1]$)	Sí (parámetro $\rho \in [-1,1]$)
	Variabilidad genética de cada rasgo	Sí (parámetro $\varphi \in [0,1]$)	Sí (parámetro $\varphi \in [0,1]$)
	Rangos y límites evolutivas por rasgo	Sí	Sí
	Rasgos dependientes de la temperatura	Sí	Sí
	Plasticidad fenotípica	Sí	Sí
	Efectos pleiotrópicos	Sí	Sí
	Tanque de agua	---	70% masa corporal Rasgo estático Sin base genética
Movimiento	**Movimiento Comportamiento adaptativo**	Recurso/Antidepredador	Recurso/Antidepredador
	Número de celdas evaluadas	3	27
	Salto si las celdas contiguas no hay recurso	Sí	Sí
	Probabilidad de encuentro y depredación	Sí	Sí

(Continuación)

Muda y Reproducción	**Evento de muda**	Energía para mudar	Energía para mudar
	Crecimiento	Ratio fijo tamaño ---	Ratio fijo tamaño Ratio tiempo
	Evento de reproducción	Energía para reproducirse	Energía para reproducirse
	Tipo de reproducción	Diploide	Diploide
	Búsqueda de pareja	---	Búsqueda de pareja

En este caso no se publicaron estudios paralelos como consecuencia del nuevo proceso de parametrización de la versión WEAVER 1.0 (Figura 2).

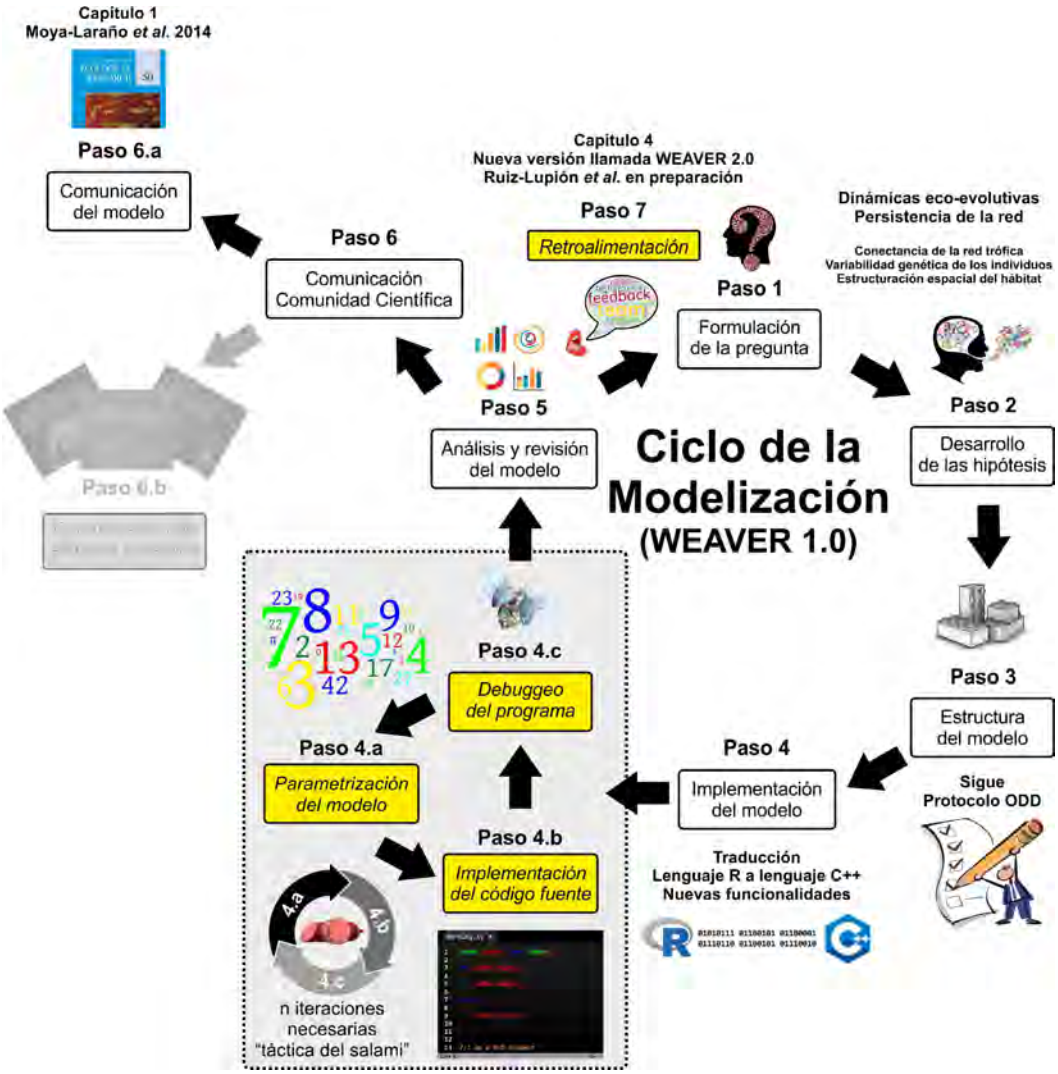

Figura 2. Pasos del Ciclo de la Modelización cumplidos por el IBM WEAVER 1.0. Los recuadros en blanco representan los 6 pasos originales descritos por Grimm & Railsback 2005 y los recuadros en amarillo son pasos intermedios considerados de gran importancia en el proceso de modelización. El recuadro en gris con borde negro discontinuo agrupa pasos intermedios interrelacionados. El paso en gris indica que no hubo publicaciones paralelas emergentes del proceso de parametrización.

1.2. Estudio de las dinámicas eco-evolutivas de la red trófica simulada

Gracias a todas estas nuevas características y funcionalidades incluidas en la versión WEAVER 1.0 pudimos estudiar el efecto de la conectancia, el grado de variabilidad genética de los individuos y el efecto de la distancia entre 4 islas equidistantes (o bolsas de agua en el suelo) ricas en recursos basales (hongo) sobre las dinámicas ecológicas, persistencia y estabilidad de la red trófica de la hojarasca de los hayedos compuesta por 11 depredadores intragremiales y caníbales, 9 presas fungívoras y 1 recurso basal (hongo) mediante simulaciones de 200 días "steps" (Capítulo 1), destacando lo siguiente:

1) Las dinámicas ecológicas de las redes tróficas con mayor conectancia (0.55 *vs* 0.30 y 0.10) muestran que el número de especies que sobreviven hasta el final de la simulación es mayor. No obstante, si observamos por separado depredadores y presas los patrones difieren. A mayor conectancia aumenta la tasa de extinción de las presas disminuyendo la proporción de estas especies respecto a la proporción de depredadores. De forma global vemos que redes altamente conectadas y con un cierto grado de omnivoría generalizado presentan una mayor estabilidad y persistencia en el tiempo (McCann & Hastings 1997; McCann 2000; Solé & Montoya 2001). Destacando que, además un alto grado de canibalismo y el comportamiento antidepredador, tanto de los depredadores como de las presas, contribuyen a que la red se estabilice (Rudolf 2007a, b), al igual que ocurre en los sistemas naturales (Woodward & Hildrew 2002).

2) En sistemas en los que la red trófica tiene una alta conectancia (0.55) y un alto grado de omnivoría, el aumento de la variabilidad genética de los 14 rasgos implementados en la versión WEAVER 1.0 promueve la persistencia y, así como, la estabilidad de dicha red en el tiempo. Como consecuencia de esta alta variabilidad genética se producen una gran diversidad de interacciones entre las especies embebidas en la red trófica, aumentando las fuerzas de interacción (Moya-Laraño 2011; Steiner & Masse 2013). Esto produce que aumente tanto la proporción de depredadores como de presas que sobreviven hasta el final de la simulación.

3) Para estudiar el efecto de la estructuración espacial del hábitat en las dinámicas de meta-comunidades se llevaron a cabo simulaciones con la red trófica altamente conectada (0.55) y con individuos con una alta variabilidad genética pues eran los dos escenarios que más favorecían la persistencia de la red trófica hasta el final de la simulación. Se encontró que cuando las islas ricas en recursos o bolsas de agua en el suelo se encuentran unas cerca de otras, creando un ambiente homogéneo, se produce un alto grado depredación sobre las presas haciendo que el sistema colapse rápidamente (McCann *et al*. 2005). En el caso contrario cuando las islas están muy alejadas (40 celdas), las especies más pequeñas que tienen un área de campeo menor a la distancia entre islas quedan aisladas siendo las especies de depredadores más grandes las únicas capaces de moverse entre islas. Sin embargo, los depredadores no consiguen llegar de una isla a otra con suficiente eficiencia para acoplar las cuatro islas, dejando de ejercer el efecto top-down sobre las presas y haciendo que estas colapsen por competencia (McCann *et al*. 2005; Rooney *et*

al. 2006, 2008). Este proceso de acoplamiento por control top-down sí se produce a distancias intermedias (10 celdas), y la estabilización del sistema por parte de los depredadores tiene más efecto debido a que por su amplia área de campeo llegan con suficiente frecuencia de una isla a otra para evitar la competencia del resto de especies de menor tamaño y la consecuente extinción en cadena y colapso del sistema. Como consecuencia los depredadores tienen que hacer un esfuerzo extra y moverse hacia distancias mayores para conseguir alimento.

Estos resultados se pudieron reproducir en simulaciones posteriores (Ruiz-Lupión, datos sin publicar), también utilizando la versión WEAVER 1.0 en el que usábamos la misma red trófica, con una conectancia de 0.55 y una alta variabilidad genética de los individuos. Sin embargo, en este caso utilizamos 7 islas ricas en recursos equidistantes en un hexágono para inducir que la isla central actuara como corredor ecológico. Pudimos comprobar que el aumento de la distancia entre islas produce una fuerte pérdida de riqueza de especies y número de alelos, con y sin isla central; que la distancia óptima donde había mayor riqueza de especies era a una distancia intermedia (10 celdas) y que evidentemente el corredor ecológico ejercía un fuerte efecto para el mantenimiento de la dinámica de la comunidad (Capítulo 1; Ruiz-Lupión *et al*., datos sin publicar). Para corroborar el efecto top-down de los depredadores y su capacidad para acoplar las dinámicas globales calculamos la distancia de dispersión media de cada especie simulada desde que nacen hasta que se reproducen por primera vez y obtuvimos los "dispersal kernels" de cada especie utilizando una distribución normal (Nathan *et al*. 2012), que son simplemente distribuciones de probabilidad que nos indican hasta donde pueden dispersarse los individuos de cada una de esas especies simuladas. Con este estudio calculamos la mayor distancia de dispersión de los depredadores grandes respecto a los depredadores pequeños y documentamos como el aumento de la distancia entre islas induce a que las especies hagan un mayor esfuerzo de dispersión aumentando la distancia media de dispersión (interacción masa del adulto*distancia entre islas, $p < 0.001$) (Ruiz-Lupión *et al*., datos sin publicar). Este último patrón emerge directamente del modelo pues, aunque la movilidad diaria sí es un parámetro en el modelo, ésta no explica toda la varianza de la distancia de dispersión, que viene además determinada por los parámetros ambientales (en este caso, la distancia entre islas). Estos resultados sugieren que la estructuración espacial de hábitat, así como el tamaño y la productividad de las islas, juegan un papel muy importante en el entendimiento de la persistencia y estabilidad de las dinámicas de las meta-comunidades multi-tróficas (Ruiz-Lupión, datos sin publicar).

Posteriormente, se seleccionó el escenario más estable en el que la red estaba altamente conectada (conectancia = 0.55), todos los individuos de las 20 especies simuladas tenían una alta variabilidad genética en sus 14 rasgos y la estructura espacial del hábitat estaba formada por 4 islas ricas en recursos dispuestas a 10 celdas de distancia entre ellas (Figura 1, Capítulo 1). Bajo este

escenario se estudiaron las dinámica eco-evolutivas multi-tróficas y espacio-temporales durante una simulación de 500 días, de la que podemos destacar los siguientes aspectos:

1) En una simulación a largo plazo de la red trófica más conectada de las 20 especies iniciales solamente 5 persisten hasta el final de la simulación, 2 grandes depredadores en especial uno muy abundante (un ciempiés del Orden Lithobiomorpha), 2 depredadores de pequeño tamaño (ácaros depredadores del Orden Prostigmata y Mesostigmata) y una especie de presa (un colémbolo del Suborden Symphypleona). La red trófica remanente de 5 especies es muy estable en el tiempo debido a las fuertes fuerzas de interacción, predominando el canibalismo y la depredación intragremial entre las poblaciones del depredador grande (ciempiés) y los depredadores pequeños (ácaros) que evitan la extinción de las poblaciones de colémbolos. En este caso el alto nivel de omnivoría (McCann 2000; McCann & Hastings 1997; Solé & Montoya 2001) y la fuerza de las interacciones podrían actuar estabilizando el sistema (Moya-Laraño 2011; Steiner & Masse 2013).

2) También hay que destacar que esta subred trófica de 5 especies presenta dinámicas espacio-temporales complejas como consecuencia de las diferencias de movilidad entre los grandes depredadores (ciempiés y opilión) respecto a los depredadores pequeños (ácaros) y la presa fungívora (colémbolo) que acoplan la dinámica espacial de la meta-comunidad (Abrams 2007; Amarasekare 2008; Koelle & Vandermeer 2005) e inducen patrones de extinción y persistencia a lo largo de toda la simulación (Figura 10, Capítulo 1).

3) Del estudio de las dinámicas evolutivas de la subred de 5 especies a lo largo de 500 días se desprende la idea de que la oscilación del valor de los rasgos (respuestas evolutivas) a lo largo de la simulación (Figura 12, Capítulo 1) se debe a que durante las dinámicas poblacionales los cambios en las presiones de selección provocan cambios en el número de individuos de cada especie que está embebida en la red trófica, así como en los patrones espaciales, dando lugar a las dinámicas emergentes y la relativa micro-evolución a corto plazo que surgió en este estudio. Debemos hacer hincapié en las dinámicas evolutivas de varios rasgos por su relevancia (Figura 12, Capítulo 1):

   Asignación de energía a la descendencia: En algunas especies aumenta la asignación de energía durante la reproducción por descendiente, lo que deberá afectar a la fecundidad (número de huevos), debido al compromiso entre el número de huevos y su tamaño (Fox & Czesak 2000).

   Crecimiento: La tasa de crecimiento tiende a aumentar en los depredadores, haciendo que se hagan más grandes, lo que les beneficia durante los encuentros depredador-presa y les permite tener una mayor inversión durante la reproducción. El colémbolo (presa), disminuye su tasa de crecimiento lo que puede indicar adaptación para evitar el riesgo de depredación en un ambiente cargado de depredadores.

Voracidad y área de campeo: Los rasgos denominados de personalidad animal (Carter *et al*. 2013; Wolf *et al*. 2007) como la voracidad y el área de campeo, son muy importantes en el balance entre la necesidad de encontrar alimento y el riesgo de depredación. Las presas evolucionan hacia un menor valor de estos rasgos, haciéndose más cautelosas debido a su pequeño tamaño y el riesgo de depredación. Por otra parte, los depredadores evolucionan hacia valores más altos, siendo más voraces y aumentando su área de campeo, esto es consistente con su bajo riesgo de depredación y con lo que ya hemos comentado anteriormente, cuando las islas ricas en recursos se encuentran muy alejadas los depredadores aumentan sus áreas de campeo y por ello sus tasas de dispersión mientras que las presas evolucionan hacia bajas tasas de dispersión agrupándose en las islas ricas en recursos (Pillai *et al*. 2012).

Velocidad de escapada: Los depredadores evolucionan teniendo mayores valores de velocidad de ataque y escapada, esto puede deberse al hecho del gran riesgo de depredación que sufren en las interacciones con otros depredadores, por canibalismo y depredación intragremial (Harvey & Pagel 1991), o a que así son más eficientes para cazar a sus presas.

Por último, cabe destacar que la red trófica está compuesta de tres especies de invertebrados no artrópodos (Familia Enchytraeidae), siendo una de esas tres especies la que persiste consistentemente hasta el día 200 de la simulación en el escenario más estable (alta conectancia, alta variabilidad genética y distancia intermedia entre islas). Por ello, estudiamos las dinámicas evolutivas en presencia y ausencia de depredadores de los 14 rasgos implementados en esta especie, para determinar cómo responden ante el cambio en las presiones de selección. Se vio que un ambiente en el que los depredadores estaban presentes la evolución de los rasgos fue más acusada y más oscilante, lo que puede ser debido a la gran complejidad y fluctuación de las presiones de selección como el número de especies de depredadores, o por co-evolución, debido a que la rápida evolución de los rasgos de los depredadores puede actuar como presiones de selección sobre los rasgos de las presas. Por el contrario, en un ambiente competitivo ausente de depredadores los enquitreidos evolucionan produciendo tamaños de puesta menores, lo que da lugar a adultos de menor tamaño y tiempos de desarrollo más cortos, pero con altos valores del tanque energético lo que supone una ventaja para prevenir la muerte por inanición. Justo lo contrario que ocurre en un ambiente con depredadores en el que los tamaños de puesta son mayores, dando lugar a adultos de mayor tamaño. Este aumento de tamaño puede considerarse una ventaja evolutiva frente a la depredación (Paine 1976; Wilson 1975).

1.3. Comparación con otros Modelos Basados en Individuos de Nueva Generación

Debido a todas las características y funcionalidades discutidas anteriormente y gracias a los estudios realizados, Grimm *et al*. 2017 consideraron a WEAVER 1.0 uno de los Modelos Basados en Individuos de Nueva Generación más completos en Ecología (Tabla 2).

Tabla 2. Características principales que definen el realismo estructural de una serie de Modelos Basados en Individuos dinámicos y espacialmente explícitos existentes que vinculan la estructura y función del ecosistema. La ticks en verde reflejan las características que incorporan los modelos, las cruces rojas reflejan las que no incorporan y las líneas discontinuas (---) representan características no documentadas. Modificado de la Tabla 1 de Grimm *et al.* 2017.

Elementos	Características	aDGM2	Madingley	OSMOSE	Giacomini	iLand	FORMIND	WIST	DOVE	WEAVER 1.0
	Aplicación de escala espacial	Global	Global	Regional	Regional	Paisaje	Estático	Local	Virtual	Micro-sitios
Escalas	Resolución espacial	X	X	X	---	√	√	√	---	√
	Resolución temporal	√	√	√	√	√	√	√	√	√
Estructura y función del ecosistema	Multi-trófico	X	√	√	√	X	X	√	√	√
	Multi-especies/Grupos funcionales	√	√	√	√	√	√	√	√	√
	Parametrización a nivel de especie	√	X	√	√	√	√	√	√	√
	Interacciones no-tróficas	√	X	X	X	√	√	√	X	√
	Flujos de masa y energía	X	√	√	√	X	X	√	√	√
	Biogeoquímica	√	X	√	X	√	√	√	X	X
Realismo estructural del modelo	Principios básicos	√	√	√	√	√	√	√	√	√
	Heterogeneidad espacio-temporal	√	√	√	√	√	√	X	X	√
	Aproximación basada en rasgos	√	√	X	√	X	√	√	√	√
	Microevolución	√	X	X	√	X	X	X	√	√
	Resiliencia	√	√	√	√	√	√	√	---	√
	Simulación de factores de estrés	√	---	√	---	√	√	---	---	√
	Vinculación especies con mecanismos	√	√	X	√	√	√	---	---	√
Estrategias de modelización	Desarrollo orientado a patrones	√	---	---	---	---	---	---	---	---
	Uso de submodelos estandarizados	√	√	√	√	√	√	√	√	√
	Uso de modelos de interacciones	√	√	√	√	√	√	√	√	√
	Pruebas de calibración	√	√	X	X	√	√	X	X	X
	Análisis de robustez	---	---	---	---	√	---	---	---	---
Dimensión humana	Incorporar acciones de manejo humanas	---	---	√	---	√	√	---	---	---

2. Versión WEAVER 2.0 (Tercera vuelta al Ciclo de la Modelización)

WEAVER 2.0, puesto que es una ampliación con nuevas funcionalidades de la versión WEAVER 1.0, cumple igualmente con los elementos y características descritas por Grimm & Berger 2016 para poder considerarse un Modelo Basado en Individuos de Nueva Generación (Figura 1). Se sigue trabajando con un código fuente en lenguaje C++ en un sistema operativo Linux (concretamente utilizando el entorno de desarrollo Eclipse en Ubuntu 14.10) o directamente a través software Linux que tiene instalado el sistema operativo Windows 10 PRO. Actualmente las simulaciones se realizan en una estación de trabajo llamada UTOPÍA con un procesador Intel(R) Xeon(R) CPU E5-2620 v4 (8 cores y 128 GB de RAM), aunque para simulaciones con muchos individuos seguimos teniendo acceso a la supercomputadora "Bullxual" de la Universidad de Almería formada por un clúster de 18 nodos y 8 GPUs (288 cores, 1152 GB de RAM y 2304 GB SSD). Por último, destacar que al igual que se llevó a cabo la descripción y publicación del modelo mini-AKIRA (Moya-Laraño *et al*. 2012) y WEAVER 1.0 (Moya-Laraño *et al*. 2014, Capítulo 1) siguiendo los elementos descritos en el Protocolo ODD (Grimm *et al*. 2006), para la descripción y publicación de las nuevas funcionalidades incluidas en la versión WEAVER 2.0 (Ruiz-Lupión *et al.* en preparación) se está siguiendo el mismo protocolo.

2.1. Nuevas características y funcionalidades incluidas en el IBM de Nueva Generación WEAVER 2.0

Las nuevas funcionalidades incluidas en la versión WEAVER 2.0 tienen como finalidad simular dinámicas eco-evolutivas en meta-comunidades multi-tróficas parametrizando nuevas y complejas redes tróficas de la hojarasca de los hayedos formadas únicamente por invertebrados artrópodos. No obstante, la parametrización de dichas redes implicó realizar una revision bibliográfica de la alometrías entre longitud y peso de los grupos de artrópodos de interés, lo que nos condujo a desarrollar un análisis comparativo a escala global de dichas alometrías descrito en el **Capítulo 2**. Nuestro objetivo era entender qué factores afectan a la variabilidad existente en los parámetros alométricos con el fin de que la parametrización fuera más robusta y realista. Entre ellos, destacamos el efecto en ambos parámetros de: 1) el bauplan morfológico que nos indica que los animales según su forma pueden tener una mayor capacidad de almacenar nutrientes y terminan almacenándolos, como por ejemplo los arácnidos con abdomen expandible donde almacenan grasas y otros nutrientes (Grassé 1949); 2) las variables geográficas, tanto la latitud como la altitud tiene un efecto sobre ambos factores indicándonos que los individuos que viven lejos del ecuador y a grandes altitudes se ven expuestos a un mayor número e intensidad de las interacciones, tendiendo en estas condiciones a favorecer un crecimiento rápido en longitud para un mayor almacenamiento de energía (Dobzhansky 1950; Pianka 1966; Moya-Laraño 2010; Laiolo & Obeso 2017; Roslin et al. 2017), además es muy importante la exposción crónica a condiciones de hipoxia a la que los individuos que viven a gran altitud están expuestos, los que les hace desarrollar un mayor sistema traqueal para compensar la falta de oxígeno (Dillon *et al*. 2005); 3) el importante efecto de la variables climáticas, un aumento de la temperatura genera un aumento de la tasa metabólica (Brown *et al*. 2004) y da lugar a tiempos de desarrollo más cortos haciendo que los adultos sean de

menor tamaño y por último, 4) destacar el efecto de la productividad primaria del ecosistema, parece indicar que los individuos que viven en ecosistemas con alta productividad se desarrollan más rápidamente sin acumular tanta masa por unidad de longitud, pues se encuentran en un ambiente muy rico en recursos. Además, se ha visto que este efecto es mayor en las especies de niveles tróficos altos respecto a las especies de los niveles tróficos basales. Por lo tanto, con este estudio demostramos la evidencia de que la energía es procesada por los individuos de manera diferente en las distintas partes del globo y en diferentes condiciones ambientales (Ehnes *et al*. 2014) y que es muy importante tener estos factores en cuenta a la hora de parametrizar las especies que queremos incluir en nuestra red trófica "in silico" dependiendo del ambiente que vamos a simular.

De igual forma nos pareció que la inicialización del número de individuos era más correcta si se basaba en datos reales de abundancia en la hojarasca y no en la relación alométrica masa-abundancia de Schneider *et al*. 2012. Además, el hecho de poder medir la actividad de los principales grupos de artrópodos correctamente en el campo sería un gran avance en la parametrización; esto dio lugar al estudio de mesocosmos de campo para comparar la idoneidad de las trampas de caída o "pitfalls" frente a dos nuevos tipos de trampas "basket" y "cul-de-sac" para medir la actividad de meso- y macrofauna de la hojarasca de los hayedos descrito en el **Capítulo 3**. De este estudio destacamos que las trampas de caída, el método más utilizado para este tipo de medidas, acumulaban el doble de agua en la hojarasca respecto a las otras dos trampas; recolectaban entre 3 y 5 veces menor cantidad de animales por unidad de tiempo, tanto mesofauna como macrofauna como consecuencia de los posibles eventos de depredación que ocurrían al permanecer los individuos vivos en las trampas y de ahí que este tipo de trampas tiendan a capturar mayor cantidad de macrofauna y depredadores. De manera que, desarrollamos de manera exitosa dos nuevos tipos de trampas fáciles de construir e instalar para el estudio de la actividad de la meso- y macrofauna del suelo, y extrapolables a cualquier otro tipo de ecosistema (ej.: bosques caducifolios, bosques de coníferas o de hoja perenne, bosques lluviosos tropicales o bosques mediterráneos).

Una vez hecho todo esto, utilizando el modelo de nicho (Williams & Martinez 2000), obtuvimos tres redes tróficas mediante el software Network3D program version 1.0.0.0. desarrollado por ©Microsoft Corporation para Microsoft Research y PEaCE Lab, en el que manteniendo constante el valor de la conectancia (0.25) y el mismo número de especies, se variaba la topología. Con estas nuevas redes parametrizadas diseñamos dos experimentos "in silico" para estudiar el efecto de la distancia entre 7 islas ricas en recursos (bolsas de agua en el suelo) equidistantes situadas en torno a un hexágono, y posteriormente evaluar el efecto que tiene modificar la productividad de los recursos basales (biomasa de hongos) en la isla central que actúa como micro-corredor ecológico, todo lo cual se encuentra descrito en el **Capítulo 4** junto a las principales características y funcionalidades modificadas y/o incluidas en la versión WEAVER 2.0 respecto a la versión WEAVER 1.0 (Tabla 3), resultado de la tercera vuelta al Ciclo de la Modelización (Figura 3).

Tabla 3. Comparación entre los modelos WEAVER 1.0 y WEAVER 2.0. La línea discontinua (---) indica aquellas características o funcionalidades que no están incluidas en el modelo.

	Características y funcionalidades	WEAVER 1.0	WEAVER 2.0
Tiempo y Espacio	**Lenguaje de programación**	C++	C++
	Espacio	3D	3D
	Unidades espaciales	Celdas	mm
	Unidades tiempo de cada paso o "step"	Días	Días
	Tipo de modelo espacial	Espacialmente explícito	Espacialmente explícito
Red trófica simulada	**Recursos basales**	Hongo ---	Hongo Hojarasca de haya
	Tipo de crecimiento del recurso basal	Función logística	Modelo recursivo exponencial
	Óptimos de crecimiento del recurso basal	No	Si
	¿El óptimo depende de humedad relativa?	No	Sí
	¿Dónde crece el recurso basal?	Bolsas de agua en el suelo	Bolsas de agua en el suelo
	Quimiostato/Higrostato	Pulsos biomasa hongo	Pulsos de agua
	Series temporales de temperatura	---	Sí
	Series temporales de humedad relativa	---	Sí
	Decaimiento de la humedad relativa	---	Sí
	Inicialización de los recursos basales	Parches esféricos	Parches esféricos
	Inicialización humedad del suelo	Parches esféricos	Parches esféricos
	Tipo de interacciones tróficas	Canibalismo Depredación intragremial Depredación active-hunting Depredación sit-and-wait Competencia depredadores Competencia presas --- Micofagia ---	Canibalismo Depredación intragremial Depredación active-hunting Depredación sit-and-wait Competencia depredadores Competencia presas Omnivoría trófica Micofagia Competencia hongos
	Nº total de recursos basales	1	Variable
	Preferencias de alimentación	No	Sí
	Diferentes eficiencias de asimilación	No	Sí
	Inicialización de los individuos	Relación alométrica masa-abundancia de Schneider *et al*. 2012.	Dependiente de abundancias reales
	Inicialización posición de los individuos	Aleatoria	Dependiente de la posición de sus recursos
Base genética cuantitativa multidimensional	**Número de rasgos incluidos**	14 rasgos	25 rasgos
	Modularidad de los rasgos	5 módulos	9 módulos
	Cromosomas	Genes ubicados en correlosomas	Ubicación aleatoria de genes en el cromosoma. Correlosomas sólo utilizado para inducir correlaciones genéticas
	Correlación entre rasgos por módulo	Sí (parámetro $\rho \in [-1,1]$)	Sí (parámetro $\rho \in [-1,1]$)

(Continuación)

Base genética cuantitativa multidimensional	**Variabilidad genética de cada rasgo**	Sí (parámetro $\varphi \in [0,1]$)	Sí (parámetro $\varphi \in [0,1]$)
	Rangos y límites evolutivas por rasgo	Sí	Sí
	Rasgos dependientes de la temperatura	Sí	Sí
	Plasticidad fenotípica	Sí	Sí
	Efectos pleiotrópicos	Sí	Sí
	Tanque de agua	70% masa corporal Rasgo estático Sin base genética	70% masa corporal Rasgo estático Sin base genética
	Proteínas de estrés por choque térmico	---	Sí
Movimiento	**Movimiento Comportamiento adaptativo**	Recurso/Antidepredador --- ---	Recurso/Antidepredador Repulsión o Atracción hacia conespecíficos
	Número de celdas evaluadas	27	Círculos concéntricos empezando por las 27 celdas contiguas hasta llegar al área de campeo
	Salto si las celdas contiguas no hay recurso	Aleatorio	A la celda más cercana con alimento.
	Probabilidad de encuentro y depredación	Ecuaciones dependientes de los rasgos	Ecuaciones dependientes de los rasgos
Muda y Reproducción	**Evento de muda**	Energía para mudar	Energía para mudar
	Crecimiento	Ratio fijo tamaño Ratio tiempo	Curva crecimiento von Bertalanffy Target curva de crecimiento Crecimiento indeterminado
	Holometabolismo	---	Sí Estado larvario Estado adulto Alometría $M = aL^b$ diferentes
	Diapausa	---	Sí
	Disminución tasa metabólica por inanición	---	Sí
	Evento de reproducción	Energía para reproducirse	Energía para reproducirse
	Tipo de reproducción	Diploide --- ---	Diploide Haplodiploide Asexual
	Sexos separados	No (hermafroditismo)	Sí
	Búsqueda de pareja	Sí	Sí

En este caso se completó el ciclo completamente y sí se desarrollaron estudios paralelos como consecuencia de la parametrización de la nueva red trófica de la hojarasca de los hayedos utilizada en la versión WEAVER 2.0 (Figura 3).

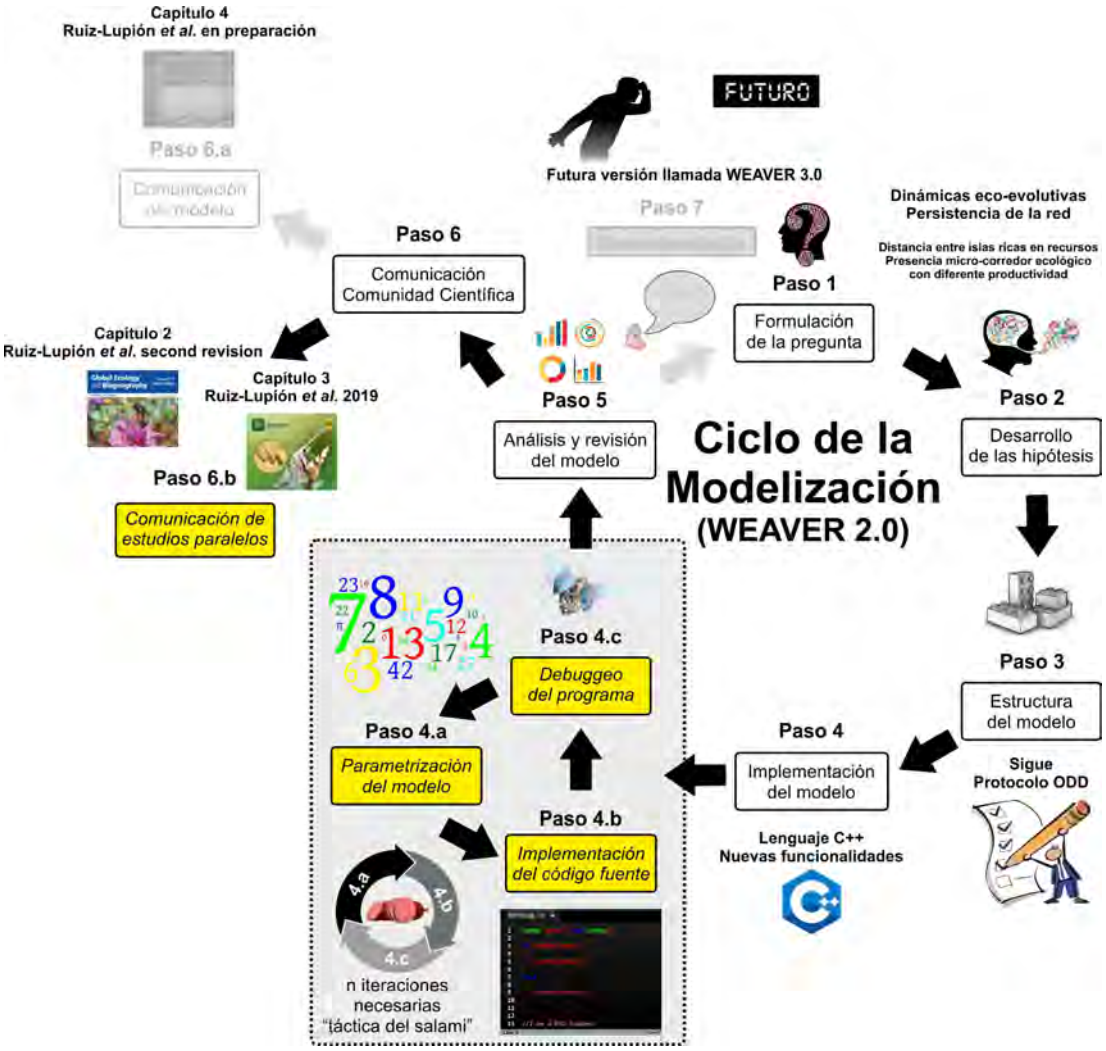

Figura 3. Pasos del Ciclo de la Modelización cumplidos por el IBM WEAVER 2.0. Los recuadros en blanco representan los 6 pasos originales descritos por Grimm & Railsback 2005 y los recuadros en amarillo son pasos intermedios considerados de gran importancia en el proceso de modelización. El recuadro en gris con borde negro discontinuo agrupa pasos intermedios interrelacionados.

3. Futura versión WEAVER 3.0 (Cuarta vuelta al Ciclo de la Modelización)

El Modelo Basado en Individuos de Nueva Generación WEAVER 2.0 puede considerarse en este momento un laboratorio virtual en el que testar hipótesis, teorías, comportamiento de los individuos o incluso testar modelos alternativos. Desde la creación del Modelo Basado en Individuos mini-AKIRA siempre se ha tenido en mente un Programa de Investigación Retroalimentada (PIR) en que máquina y datos reales de sistemas concretos trabajen de manera retroalimentada para resolver problemas comunes. Por ejemplo, hay estudios ya realizados en el Grupo de Investigación de Ecología Evolutiva y Funcional de la Estación Experimental de Zonas Áridas (EEZA-CSIC), de experimentos de mesocosmos de campo sobre la red trófica de la hojarasca de los hayedos en los que al eliminar los

depredadores más grandes se produce un gran impacto negativo en los niveles tróficos inferiores y en las tasas de descomposición, aunque no se produce una cascada trófica típica dado que todos los niveles tróficos se ven afectados negativamente, no sólo algunos de ellos (Melguizo-Ruiz *et al*. en revisión). Estos resultados inesperados podrían intentar replicarse utilizando la actual versión WEAVER 2.0 para poder reproducir las dinámicas intermedias que expliquen el patrón final inesperado de dicho experimento. Si además surgen patrones emergentes difíciles de detectar en campo, se podría diseñar otro experimento para estudiar esos nuevos patrones mediante este proceso PIR de Investigación Retroalimentada descrita detalladamente en la Introducción General.

Una funcionalidad ausente en WEAVER 2.0 es la biogeoquímica del sistema considerado. Esta característica arrastra un cuerpo teórico inmenso detrás y desde hace algunos años hemos realizado una revisión bibliográfica completa para determinar cuál es la mejor forma de incorporar la biogeoquímica en WEAVER, concretamente en la versión WEAVER 1.0. En aquél momento el modelo no estaba suficientemente desarrollado ni calibrado para implementar lo que se conoce como estequiometría ecológica, es decir, el estudio del equilibrio de múltiples sustancias químicas (nutrientes) en las interacciones y procesos ecológicos, como la depredación o la descomposición de la materia orgánica, o el estudio de sus desequilibrios. Los desequilibrios nutricionales en redes tróficas generan una demanda de algún tipo de nutriente en el consumidor que se encuentra en diferentes proporciones en las especies que componen su nicho nutricional (Sterner & Elser 2002). Evaluar cómo afecta la limitación de nutrientes y los desequilibrios nutricionales a la persistencia y estabilidad de las redes tróficas es una de las grandes preguntas que impulsan a que se produzca el cuarto Ciclo de la Modelización y llegar a desarrollar e implementar la versión 3.0.

Durante el desarrollo de todas las nuevas características y funcionalidades descritas en el **Capítulo 4**, y que han dado lugar a la presente versión WEAVER 2.0 estábamos, entre otras cosas preparando el modelo para implementar la estequiometría ecológica después de considerar tres grandes cuestiones nos llevaron a decidir cómo implementar la estequiometría ecológica en una versión futura de WEAVER 1.0 (Ruiz-Lupión, datos sin publicar):

1) ¿Qué implementar, la Teoría "Dynamic Energy Budget" o la Teoría Metabólica en Ecología?

Existe una gran controversia en la literatura sobre si es mejor implementar la Teoría "Dynamic Energy Budget" (Teoría DEB), que simplemente es un modelo diseñado para determinar cómo los animales adquieren energía y la asignan al mantenimiento, crecimiento y/o reproducción (Kooijman *et al*. 2004; Kooijman 2009; Sousa *et al*. 2008); o en caso contrario incluir el metabolismo en el Modelo Basado en Individuos mediante la Teoría Metabólica desarrollada por Brown *et al*. 2004. Ambas teorías son estáticas en el sentido de que ignoran por completo las dinámicas de los factores ambientales y también la ontogenia, no obstante, la Teoría Metabólica en Ecología (MTE) ya estaba implementa en la versión WEAVER 1.0 y se le había dado una dimensión dinámica mediante el uso

de rasgos como el Q_{10} en la velocidad de escapada, Q_{10} en el área de campeo, Q_{10} en la voracidad, así como la energía de activación de la tasa metabólica que inducían cambios por plasticidad en los rasgos con los cambios de temperatura mediante epistasis. Además, un factor a tener en cuenta es que los rasgos al igual que la tasa metabólica no sólo dependían de la temperatura si no que estaban escalados con la masa corporal de los individuos. En este punto parecía claro que la balanza se inclinaba a seguir con la MTE, aun así, hicimos una revisión de los diferentes modelos que se habían desarrollado incluyendo la Teoría DEB y que estudiaban las restricciones estequiométricas en el metabolismo y las interacciones entre organismos teniendo en cuenta la captación y uso de los nutrientes y sustratos, para un sistema depredador-presa muy básico (Kooijman *et al*. 2004), en el que solo tenían en cuenta un tanque energético, muy parecido el rasgo Tanque Energético que ya estaba implementado en WEAVER 1.0. Posteriormente, Sousa *et al*. 2008 realizaron una presentación y discusión de los patrones empíricos que caracterizan el metabolismo, formalizaron un modelo estándar que considera organismos isomorfos con una reserva y una estructura siguiendo la Teoría DEB y establecieron una relación entre la Teoría DEB y los parámetros entre diferentes especies. Incluso antes que eso, Kuijper *et al*. 2004 desarrolló un modelo teórico que incluía la Teoría DEB con dos tanques energéticos uno de proteínas y otro de hidratos de carbono, construyendo así un Modelo DEB nutricionalmente explícito. Más recientemente incluso se ha desarrollado un modelo teórico en el que se han estudiado los flujos de energía necesarios para cada uno de los estados diferentes a lo largo del ciclo de vida de un insecto holometábolo (Llandres *et al*. 2015) que podría implementarse en un IBM, pero sólo considera un tanque energético y no es nutricionalmente explícito. Después de esta revisión decidimos seguir desarrollando WEAVER de la versión 1.0 a la versión 2.0 sin incluir la Teoría DEB pues no había ningún modelo que incluyese todas las características que nuestro modelo necesitaba: 1) que fuera dinámico con las condiciones ambientales, 2) que tuviera en cuenta la ontogenia, y 3) que fuera nutricionalmente explícito. Además, poder desarrollar un modelo de ese calibre implicaría leer, entender y asimilar la Guía Básica de la Teoría Dynamic Energy Budget (DEB) (Kooijman *et al*. 2008), asistir al curso que se celebra cada dos años, el último fue en Noruega en el año 2017 (Kooijman *et al*. 2017) con el que aprendes a realizar ejercicios prácticos, lo que supone en total un mínimo de 2 años antes de aprender a manejar la teoría con soltura. Por último, y más importante, daría lugar a un Modelo Basado en Individuos extremadamente complejo con una sobre-parametrización difícil de calibrar y testar, seguramente innecesaria para los objetivos de WEAVER 2.0. Por lo tanto, lo mejor sería desarrollar a la carta un modelo nutricionalmente explícito que funcione eficientemente en WEAVER 3.0.

2) ¿Cómo desarrollamos un Modelo Basado en Individuos Nutricionalmente Explícito?

Una vez decidimos seguir adelante con la MTE y descartar la teoría DEB, era necesario incluir en el modelo no un tanque energético, si no diferentes tanques energéticos como proteínas, hidratos de carbono y fósforo (P) o tanques de carbono (C), nitrógeno (N) y fósforo (P) directamente. Para ello

nos centramos en el marco teórico basado en la Geometría de la Nutrición (Simpson & Raubenhaimer 2012), del que ya había sentado la bases Polis & Winemiller 1996 al definir los diagramas trofoquímicos. Este marco teórico se basa en que existe un espacio nutricional que puede estar construido por dos o más ejes (Figura 4a), en el que cada eje representa un componente del alimento (ej.: Proteínas *vs* Hidradtos de carbono). Cada alimento esta modelizado dentro del espacio nutricional por una cantidad o equilibrio de los nutrientes que contienen (ej.: el alimento "a" tiene 50% de proteínas y 50% de hidratos de carbono mientras que el alimento "b" tiene un 20% de proteínas y un 80% de hidratos de carbono) que se describen y representan como raíles nutricionales (Figura 4a). Cada especie (o individuo) que nosotros incluyamos en el modelo tendrá un óptimo nutricional que está representado en el espacio nutricional como un punto y que denominamos "intake target". Cada animal tiene un "intake target" que tiene que alcanzar siguiendo lo que se conoce como trayectorias nutricionales a lo largo del espacio nutricional (ej.: el animal tiene un "intake target" formado por un 35% de proteínas y un 65% de hidratos de carbono, así que debe alternar entre consumir uno u otro alimento a lo largo de su ontogenia para poder mudar) (Figura 4a). La capacidad de decisión de los individuos por un alimento rico en proteínas o rico en hidratos de carbono dependiendo de sus necesidades nutricionales ya está demostrada mediante experimentos con arañas, ortópteros, coleópteros e incluso mamíferos (Mayntz *et al*. 2005; Raubenheimer *et al*. 2007; Mayntz *et al*. 2009; Hawlena & Schmitz 2010). En base a esto cada vez que el individuo consiga llegar al "intake target" podrá pasar a la siguiente muda, de ahí que una de las nuevas funcionalidades de la versión WEAVER 2.0 sean curvas de crecimiento realistas basadas en "target" de longitud, dependientes de la cantidad de masa convertible a energía que adquieren con el alimento, y que tienen que alcanzar los individuos para poder mudar. Esta decisión la tomamos después de considerar otras formar de implementar la Geometría de la Nutrición en un IBM mediante la utilización de valores de vectores y ángulos entre la trayectoria nutricional y el "intake target", pero también nos parecía más complejo y computacionalmente más costoso (Lihoreau *et al*. 2015).

3) ¿Implementamos un espacio nutricional 2D o 3D?

Para poder decidir qué era más correcto estuvimos estudiando el "Molecular-kinetic Model" desarrollado por Dobberfuhl 1999 basado en el cálculo de la composición elemental del cuerpo y la tasa de crecimiento para una asignación dada de proteínas y ARN. Este modelo permitía conectar crecimiento y estequiometría ecológica mediada por la asignación de nutrientes. Este modelo se basa en la asunción de que el crecimiento está equilibrado, es decir, que la composición macromolecular y necesidades nutricionales no cambia a lo largo de la ontogenia. Este modelo además permite a partir del porcentaje de carbono, nitrógeno y fósforo determinar qué cantidad debe invertirse en proteínas, hidratos de carbono y ARN, es decir, fósforo para el crecimiento. Teniendo este modelo como referencia decidimos implementar un espacio tridimensional 3D de carbono (C), nitrógeno (N) y fósforo (P) sin necesidad de pasarlo a moléculas más complejas (Figura

4a). Esto implica que la versión WEAVER 3.0 debe incluir, además de un tanque energético como variable de estado, las variables de estado tanque de carbono, tanque de nitrógeno y tanque de fósforo, así como disgregar la eficiencia de asimilación en tres rasgos, pues no se asimilan de la misma manera los tres elementos. La obtención de los datos de C:N:P de cada especie se obtendrán de diversas bases de estequiometría ecológica (Fagan & Denno 2004; Fagan 2011) y además incluiremos variabilidad genética intraespecífica en la relación C:N:P (Figura 4b). Los tanques C:N:P tendrán una traducción directa en tanque energético al traducirse en biomasa total que ocuparán los tres elementos.

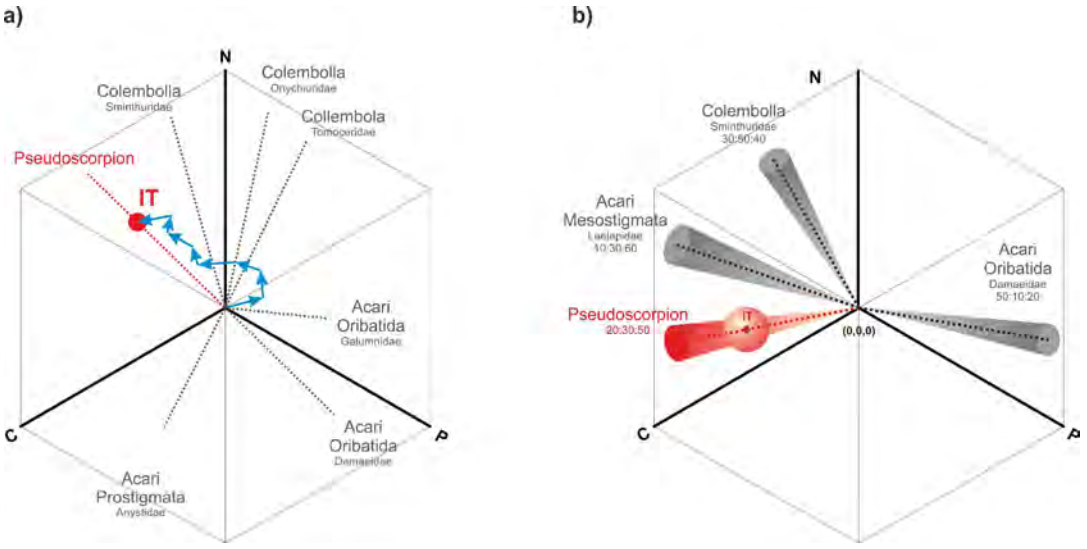

Figura 4. Marco teórico sobre geometría de la nutrición que se implementará en la futura versión WEAVER 3.0. a) Representa un espacio nutricional 3D y b) representa la variabilidad intraespecífica en el contenido C:N:P de los raíles nutricionales y del "intake target". Las líneas discontinuas representan los raíles nutricionales de especies hipotéticas pues no se basan en datos reales, las flechas azules representan la trayectoria nutricional y el punto rojo representa el "intake target" descrito para la especie representada. Los raíles en gris representan alimentos que aportarían un desequilibrio nutricional a la especie de estudio y el raíl en rojo representa el alimento totalmente equilibrado para dicha especie.

3.1. Otras consideraciones a tener en cuenta para la futura versión WEAVER 3.0

Para finalizar tenemos en mente una serie de consideraciones muy importantes que deben cumplir o implementarse como resultado de años de trabajo para poner a WEAVER al alcance de cualquier usuario:

1) Extrapolación a otros sistemas ecológicos

La creación de un Modelo Basado en Individuos de Nueva Generación tan complejo y con tantas funcionalidades no tiene ningún sentido si es sistema-dependiente. El objetivo inicial de la creación e

implementación de mini-AKIRA era estudiar las dinámicas eco-evolutivas en redes tróficas, concretamente en una red trófica de la hojarasca de los hayedos. Y tanto esta red trófica como el sistema de hayedos ha ido perfeccionándose a lo largo de las distintas versiones de WEAVER para hacer que las salidas del modelo sean cada vez más realistas. Pero no hay que olvidar que la utilidad primordial de WEAVER es poder implementar cualquier tipo de sistema ecológico, actualmente las versiones WEAVER 1.0 y WEAVER 2.0 ya se han utilizado en los siguientes estudios o se está en proceso de parametrización:

Estudio del efecto de la intensidad y frecuencia de las olas de calor sobre la capacidad de supervivencia de tres especies de una red trófica

Se implementó y parametrizo una red trófica en la versión WEAVER 2.0 formada por dos depredadores, una especie de araña cursorial o active-hunting (*Pardosa purbeckensis*) de la Familia Lycosidae, una araña sit-and-wait de la familia Linyphiidae y una especie de presa, en este caso un colémbolo (*Isotoma riparia*). Para esta red se capturaron individuos vivos en el campo en Schiermonnikoog (Holanda) y se mantuvieran en el laboratorio para obtener las curvas de crecimiento. Se corrieron simulaciones a 20°C, 25°C, 30°C, 40°C, 45°C, 50°C y 55°C para estudiar el efecto de la intensidad de las olas de calor y otro set de simulaciones con diferentes frecuencias de 4 olas de calor gracias a la implementación de las series temporales de temperatura en esta versión de WEAVER 2.0 (Franken *et al*. en preparación).

Ingeniería de redes tróficas para control biológico de plagas

Como futuras perspectivas del uso de mini-AKIRA se acuñó el término Ingeniería de Redes Tróficas (FWE) como una extensión del control biológico de plagas que integra la teoría general de las comunidades en ecología y la biología evolutiva en un agro-ecosistema, donde las comunidades son manejadas artificialmente. Cuando se aplique la FWE para el manejo de plagas, se necesitarán estrategias para diseñar un plan de alteración artificial de las interacciones con el potencial de influir la comunidad en general (Moya-Laraño *et al*. 2012, 2014, Capítulo 1). Actualmente se está parametrizando una red trófica para control biológico de plagas a la carta en un agro-ecosistema de cultivos de invernadero, incluyendo mosca blanca, y ácaros y heterópteros depredadores (Torres-Campos et al., en preparación).

Simulando redes tróficas de Dinosaurios (vuelta al pasado)

Últimamente, se están exportado las simulaciones a redes tróficas con dinosaurios. Para parametrizar los rasgos de los taxones de dinosaurios extintos, primero se están usando las curvas de crecimiento conocidas publicadas para algunas especies de dinosaurios (Erickson *et al*. 2007) y se acomodarán a los taxones presentes en el Maastrichtiano catalán. Por extraño que parezca hay casi más curvas de crecimiento de dinosaurios publicadas que de artrópodos del suelo, dado que gracias a la histología del hueso fósil se puede saber la edad de los dinosaurios cuando perecieron. Este

proyecto está aún en ciernes, parametrizando el primer dinosaurio, pero en WEAVER 2.0 ya se podrán simular ecosistemas que están siendo escalados 9 órdenes de magnitud respecto a los de los hayedos. Sin embargo, estas primeras simulaciones deberán necesariamente simular sólo los animales presa más grandes de las redes tróficas de los dinosaurios (vertebrados e insectos grandes), pero no las presas de éstos últimos. Para poder llevar a cabo la simulación de cientos de millones de individuos a todas las escalas, seguramente se tendrá que conseguir que WEAVER 3.0 pueda trabajar en diferentes capas de simulación, cada una a diferentes escalas, una para los individuos más grandes y otra para los más pequeños, de manera que las simulaciones se comuniquen.

2) Paralelización del código

La computación paralela o paralelización se caracteriza por que muchos cálculos o la ejecución de procesos se realizan simultáneamente en ordenadores o nodos diferentes que se comunican (Gottlieb & Almasi 1989). De esta manera si 1 ordenador tiene que realizar 3 cálculos tardará más que si 3 ordenadores que se comunican realizan cada uno 1 cálculo (Figura 5). Los algoritmos explícitamente paralelos, son más difíciles de escribir que los secuenciales, porque se introducen varias nuevas clases de posibles errores de software o "bugs". La comunicación y la sincronización entre las diferentes sub-tareas suelen ser algunos de los mayores obstáculos para obtener un buen rendimiento del programa paralelo (Hennessy 1999). La paralelización del código de la versión WEAVER 3.0 permitiría correr simulaciones en un super-ordenador con millones de individuos minimizando los problemas de memoria ni de tiempo.

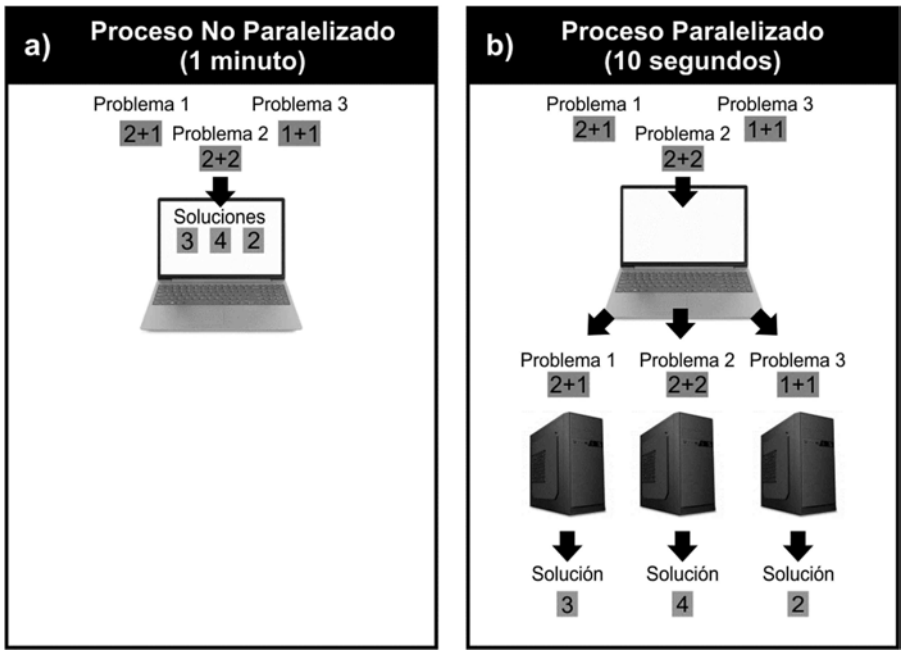

Figura 5. Características de un proceso paralelizado. a) Proceso no paralelizado: los 3 problemas son resueltos por un ordenador y b) proceso paralelizado: cada problema es enviado a un procesador independiente que lo resuelve y está sincronizado y comunicado con el portátil. Cada procesador resuelve 1 problema.

3) Aplicación de algoritmos de optimización

El volumen de información necesario y producido por WEAVER 2.0 como el tamaño de los históricos, sobre todo de los rasgos cuantitativos tienen un tamaño tan desmesurado que los métodos de optimización tradicionales, basados en algoritmos de búsqueda exhaustiva o en programación matemática (lineal, cuadrática, mixta, gradientes) son ineficientes y es preciso utilizar algoritmos más avanzados, tales como algoritmos genéticos. Estos algoritmos son un recurso común en ámbitos tan dispares como la Ingeniería, la Medicina, la Astrofísica, las Telecomunicaciones o la Economía. En general podemos definir los algoritmos genéticos o evolutivos como métodos robustos de optimización diseñados para resolver problemas complejos con elevado número de elementos, restricciones y variables y en los que, por lo general, coexisten una o varias soluciones óptimas que no pueden aproximarse utilizando los métodos tradicionales propios de la programación lineal (AndG 2012). Para la aplicación de este tipo de algoritmos contamos con la colaboración del Grupo de Supercomputación y Algoritmos de la Universidad de Almería (UAL), que cuentan con especialistas en este tipo de algoritmos y trabajan en colaboración con nosotros desde la primera versión de WEAVER 1.0.

4) Creación de una Interfaz gráfica

Ahora mismo la parametrización e implementación de los archivos de entrada de la versión WEAVER 2.0 se hace manualmente mediante documentos tipo [.json]. La gran cantidad de parámetros de entrada cuando se necesita simular redes tróficas complejas con una estructuración espacial también compleja hace que la entrada manual mediante editor de texto en sistema operativo Linux sea poco amigable para los que empiezan a trabajar con este modelo. La creación de una interfaz gráfica compuesta de ventanas, menúes, botones y otros elementos, a través de los cuáles se pueda interactuar con el programa fácilmente debe ser uno de los siguientes pasos a incorporar en la versión WEAVER 3.0. Casi todos los lenguajes de programación (C++, Phyton, etc) incluyen módulos específicos que provee las funciones necesarias para empezar a desarrollar una interfaz gráfica.

Aunque aún faltan algunas características muy importantes que implementar en la futura versión de WEAVER 3.0, el camino recorrido desde la publicación del IBM mini-AKIRA en el año 2012 aunque complejo ha dado lugar a uno de los Modelos Basados en Individuos de Nueva Generación más completos hasta la actualidad (Figura 6). Además de aportar grandes avances en el campo de la modelización también se ha convertido en un laboratorio virtual, donde muchos sistemas ecológicos diferentes puedes ser estudiados.

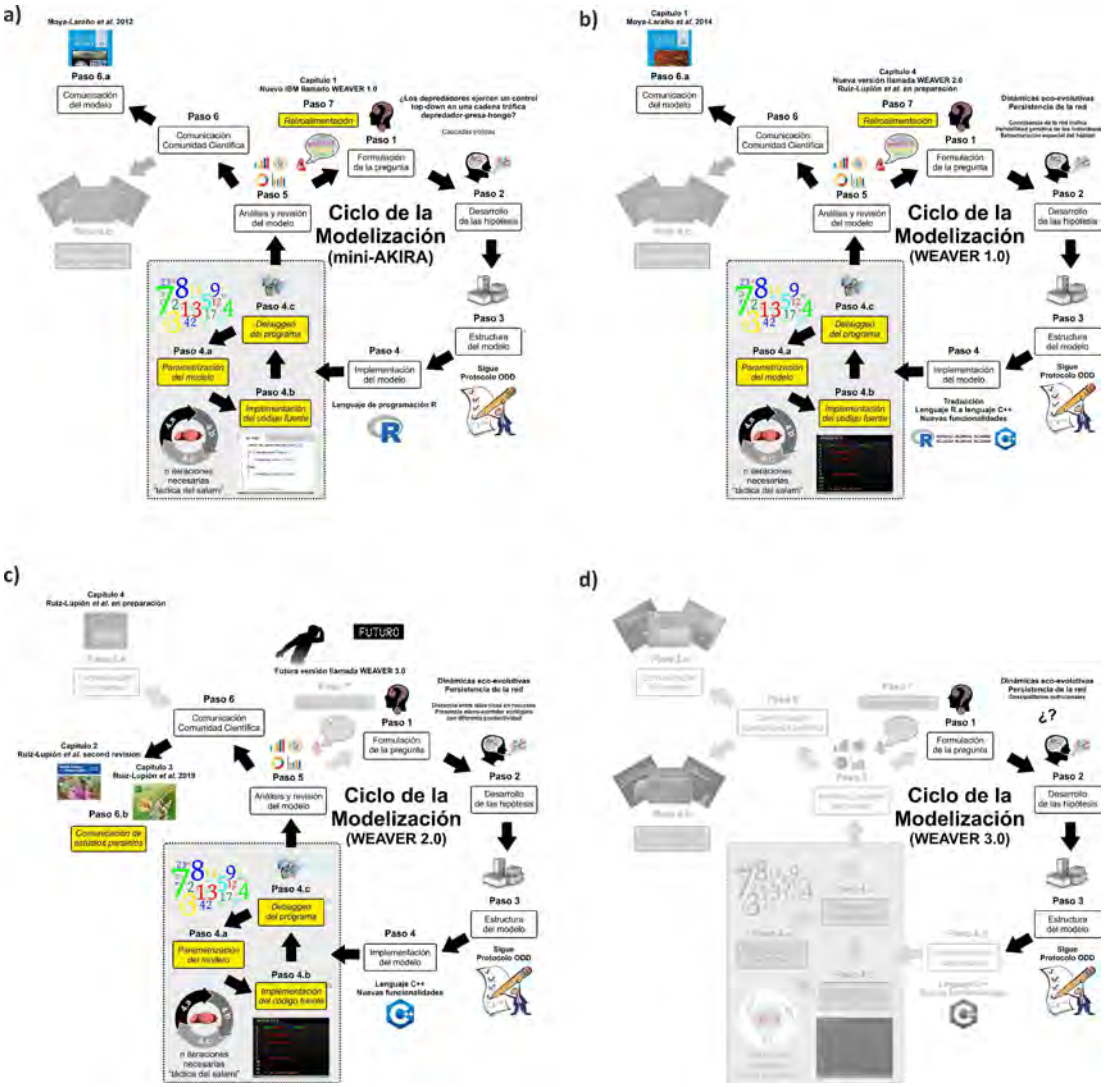

Figura 6. Historia desde el IBM mini-AKIRA hasta la futura versión WEAVER 3.0. a) Primera vuelta del Ciclo de la Modelización (mini-AKIRA), b) segunda vuelta del Ciclo de la Modelización (WEAVER 1.0), c) tercera vuelta del Ciclo de la Modelización (WEAVER 2.0) y d) pasos llevados a cabo hasta el momento de la cuarta vuelva del Ciclo de la Modelización (WEAVER 3.0). Los pasos en gris no se han cumplido durante el proceso del Ciclo de la Modelización.

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Conclusiones

1. La plataforma de simulación WEAVER 1.0 (extension de la plataforma mini-AKIRA), es un Modelo Basado en Individuos de Nueva Generación. Está considerado uno de los IBMs más completos en Ecología, ya que permite la exploración de dinámicas eco-evolutivas de meta-comunidades multi-tróficas a través del espacio y su utilización como laboratorio virtual para testar hipótesis "in silico" que son inabarcables con los métodos tradicionales de experimentación.

2. WEAVER 1.0 ha sido usado para explorar la dinámica ecológica de meta-comunidades multi-tróficas definidas por islas de recursos (bolsas de aguas) distribuidas en una matriz inhóspita y caracterizadas por una alta conectancia de la red, una gran variabilidad genética intraespecífica y una fuerte estructuración espacial del hábitat. La aplicación de WEAVER 1.0 sugiere que aquellas meta-comunidades donde las islas de recursos se encuentran a distancias intermedias (10 celdas) son más estables temporalmente, tanto en simulaciones a corto plazo (200 días) como a largo plazo (500 días). Varios factores contribuyen a esta persistencia: Por un lado, el alto grado de omnivoría, canibalismo, depredación intragremial y comportamiento antidepredador. Por otro, la gran diversidad de interacciones entre las especies de la red trófica, unido a un fuerte aumento de las fuerzas de las interacciones como consecuencia de una alta variabilidad genética. Y finalmente, una importante contribución del proceso de acoplamiento por control top-down que ejercen los depredadores a distancias intermedias.

3. Simulaciones a largo plazo (500 días) sugieren que una red persistente en el tiempo exhibe dinámicas espacio-temporales complejas como consecuencia de las diferencias de movilidad entre depredadores grandes y pequeños y entre éstos y las presas. A lo largo de la simulación hubo cambios concomitantes en las presiones selectivas y en el número de individuos de cada especie dando lugar a un proceso de evolución rápido en rasgos reproductivos, de crecimiento, voracidad, comportamiento de búsqueda y velocidad de escape o ataque.

4. Las tres especies de invertebrados no artrópodos (Familia Enchytraeidae) incluidas en nuestra red trófica persisten hasta el final de la simulación a corto plazo en el escenario más estable. En presencia de depredadores evolucionan hacia tamaños de puesta mayores, y por tanto adultos de mayor tamaño, lo que puede conllevar una ventaja evolutiva frente a la depredación. Sin embargo, en ambientes competitivos en ausencia de depredadores evolucionan hacia tamaños de puesta menores, dando lugar a adultos de menor tamaño y tiempos de desarrollo más cortos, pero con altos valores de energía disponible para el mantenimiento, crecimiento o reproducción, lo que supone una ventaja para prevenir la muerte por inanición.

5. Los parámetros alométricos "a" y "b" que relacionan longitud y masa de artrópodos del suelo se ven afectados por el bauplan morfológico de los grupos taxonómicos, la latitud, la altitud, la temperatura y la productividad primaria del ecosistema, lo que sugiere que la energía es

procesada por los individuos de manera diferente en las distintas partes del globo y en diferentes condiciones ambientales.

6. La metodología tradicional para medir abundancia y actividad de fauna del suelo mediante trampas de caída o "pitfalls" es ineficiente cuando se comparan con las nuevas trampas "basket" y "cul-de-sac", ya que acumulan el doble de agua en la hojarasca, recolectan entre 3 y 5 veces menor cantidad de animales por unidad de tiempo, y atrapan un mayor número de depredadores y macrofauna. Además, las nuevas trampas son fáciles de construir e instalar, y extrapolables a cualquier otro tipo de ecosistema con hojarasca.

7. El diseño y la parametrización de experimentos de simulación "in silico" sigue la misma metodología que el diseño experimental tradicional con un conjunto de variables de entrada que nos proporcionan una serie de variables respuesta. En Modelos Basados en Individuos la cantidad de variables de entrada es muy superior y por ello, se han de elegir cuidadosamente dichas variables para poder obtener resultados realistas, repetibles y, sobre todo, estadísticamente testables y robustos.

8. Las nuevas características y funcionalidades de WEAVER 2.0, tales como unidades de epacio reales, series temporales de temperatura y humedad relativa, una inicialización basada en abundancias reales, nuevos tipos de interacciones (omnivoría, sintopía y competencia entre hongos), diferencias en las preferencias y asimilación de los recursos, así como los nuevos algoritmos de movimiento, crecimiento (basado en curvas reales) y reproducción, permiten simular de forma más realista dinámicas eco-evolutivas en meta-comunidades multi-tróficas. Para ello se han parametrizado nuevas y complejas redes tróficas de la hojarasca de los hayedos.

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Te he dejado para el final, no por ello, eres menos importante, del Chumbo me llevo muchos amigos pero siempre será el sitio en el que te conocí. Este viaje ha sido difícil, muchos obstáculos para ti y para mi, espero seguir a tu lado muchos años, y no digo el resto de mi vida por que se que no crees en el romanticismo puro y duro, a pesar de que soy una chuche llena de azúcar, tú me elegiste y cada día te doy las gracias por que eres lo mejor que me ha pasado. Gracias por hacerme ver la vida siempre desde otro punto de vista, y sobre todo gracias por ser la trinchera de todas mis batallas.


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