UNIVERSIDAD DE GRANADA
DEPARTAMENTO DE BIOLOGÍA ANIMAL

ECOLOGÍA DE LOS MACROINVERTEBRADOS EDÁFICOS EN UN ECOSISTEMA ÁRIDO MEDITERRÁNEO

ECOLOGY OF SOIL MACROINVERTEBRATES IN A MEDITERRANEAN ARID ECOSYSTEM

TESIS DOCTORAL

Enrique Doblas Miranda
Granada 2007

Editor: Editorial de la Universidad de Granada
Autor: Enrique Doblas Miranda
D.L.: Gr. 1272 - 2007
ISBN: 978-84-338-4365-4

ECOLOGÍA DE LOS MACROINVERTEBRADOS EDÁFICOS EN UN ECOSISTEMA ÁRIDO MEDITERRÁNEO

ECOLOGY OF SOIL MACROINVERTEBRATES IN A MEDITERRANEAN ARID ECOSYSTEM

Memoria que el Licenciado Enrique Doblas Miranda presenta para aspirar al Grado de Doctor por la Universidad de Granada

Esta memoria ha sido realizada bajo la dirección de:
Dr. Francisco Sánchez Piñero

Ldo. Enrique Doblas Miranda

Aspirante al Grado de Doctor

Granada, de 2007

Dr. Francisco Sánchez Piñero, Profesor Titular de Zoología de la Universidad de Granada

CERTIFICA

Que los trabajos de investigación desarrollados en la Memoria de Tesis Doctoral: ″Ecología de los Macroinvertebrados Edáficos en un Ecosistema Árido Mediterráneo″**, son aptos para ser presentados por el Ldo. Enrique Doblas Miranda ante el Tribunal que en su día se designe, para aspirar al Grado de Doctor por la Universidad de Granada.**

Y para que así conste, en cumplimiento de las disposiciones vigentes, extiendo el presente certificado a de 2007

Dr. Francisco Sánchez Piñero

Durante el tiempo de realización de esta Tesis Doctoral he disfrutado de una Beca del Programa Nacional de Formación de Personal Investigador del Ministerio de Educación y Ciencia Ref. (FP-2001-0578).

Este trabajo estuvo financiado por el proyecto BOS2001-3806 del CICYT.

La investigación presentada en esta Tesis Doctoral se ha realizado en el Departamento de Biología Animal de la Universidad de Granada.

“Lo esencial es invisible para los ojos”

A. de Saint-Exupéry

A mamá y papá y el resto de la troupe familiar

Agradecimientos

Me quedo corto,

si pongo mil nombres,

si escribo los detalles de cada uno de los todos,

o si escribo oficios

tampoco,

ni gremios, ni títulos, ni jerarquías

¡Es imposible saber cuantos fueron!

(si hasta el que me dio una sonrisa en el día concreto casi me valió para escribir el cielo)

GRACIAS

Gracias a todos

Que cada uno se guarde en su camisa lo que le place

que yo guardo en mi centro una masa de hombros

de apoyo, de lloro y de risa

¿Por qué habría de valer más uno que otro?

No se cuando empezó, no se si ya ha acabado, ni las consecuencias del proceso

Cómo puedo decidir quién, cuándo y de qué manera

Cómo podría saber yo el peso

de todos los alientos, sudores y aciertos

Si somos una amalgama de influencias

y todo lo que creamos nunca es nuestro,

¿quién soy yo para saber como agradecerlo?

Es más,

si ya este libro es un resumen concentrado

de los cientos de esfuerzos

¿Cómo podría hacerle eso a la mejor parte?

No, me niego

No habrá incluidos ni descartes

No habrá elecciones de importantes

Y aún menos compromisos, o apegos

GRACIAS

Gracias a todos

Sin listas, ni barullos, ni deprisa, ni corriendo

Sin ti,

nunca hubiera hecho todo esto

Espero que valga tantísimo como tu ayuda, si lo estás leyendo

INDICE

RESUMEN

Dentro de cualquier hábitat, la división entre el medio epigeo e hipogeo ha estado clásicamente descompensada hacia el estudio del primero, siendo sin embargo el segundo fuente de reciclaje de sustancias y parte de los ciclos más importantes para la vida. Este desconocimiento es aún mayor en los sistemas áridos, pese a ocupar cerca de una tercera parte de las tierras emergidas y poseer una heterogeneidad espacial y temporal de grandes contrastes. En los ecosistemas desérticos, a los macroinvertebrados se les ha estudiado escasamente, sin embargo, constituyen un grupo importante de organismos del suelo, participando activamente en el funcionamiento del ecosistema y las uniones que se establecen entre procesos superficiales y subterráneos. Por tanto, para profundizar en el conocimiento de la ecología de la macrofauna del suelo desértico, el primer paso es conocer su estructura y conocer los factores que determinan su distribución y abundancia.

En la presente tesis doctoral se estudia la distribución y ecología de la comunidad de macrofauna edáfica de una zona árida mediterránea del sureste peninsular. En este estudio se analizan la composición, las variaciones temporales (estacionales y anuales) y la distribución horizontal (por microhábitats) y vertical de dicha macrofauna edáfica. Posteriormente se examinan los factores (abióticos y bióticos) que influyen en esa distribución y variación espacio-temporal, incluyendo las interacciones entre los principales grupos tróficos. Finalmente se investiga uno de los procesos ecológicos más importantes en el funcionamiento de los sistemas áridos, la influencia de los macrodetritívoros edáficos en la degradación del detritus superficial.

Durante dos años, los macroinvertebrados fueron muestreados mensualmente, en los principales microhábitats de la zona (la matriz de suelo desnudo, los arbustos más característicos y los cúmulos de detritus de ciertos hormigueros), tanto a nivel de hojarasca como en el medio subterráneo (hasta 50 cm. de profundidad), por medio de sacatestigos. La temperatura y la humedad se midieron en cada unidad de muestreo. Para obtener la producción de recursos (hojarasca y raíces) se llevaron a cabo medidas estacionales durante la etapa de muestreo, además de analizar parte de las muestras con el fin de estimar la calidad de dichos recursos. Por último, se realizó un experimento de un año de duración en el área de estudio con bolsas de hojarasca para conocer la tasa de consumo de detritus.

Los resultados muestran que la comunidad estaba dominada por artrópodos, especialmente Formicidae, Coleoptera (larvas subterráneas), Embioptera y Margarodidae. La comunidad de la hojarasca mostró diferencias frente a la subterránea. En la hojarasca, los detritívoros dominaron la composición trófica, mientras que en el medio hipogeo la fauna mostró una proporción similar de detritívoros y herbívoros y un menor porcentaje de depredadores.

Las comunidades edáficas mostraron variaciones estacionales en riqueza, abundancia, biomasa y composición, siendo estas variaciones más marcadas para los habitantes de la hojarasca. Los patrones de variación estacional también mostraron diferencias entre los dos años de estudio, tanto para los invertebrados de la hojarasca, como para los subterráneos.

Los arbustos que actúan como isla de recursos y los acúmulos de detritus de los hormigueros soportaron mayor riqueza, abundancia y biomasa de macroinvertebrados que la matriz de suelo circundante. Los diferentes microhábitats se diferenciaron en la composición taxonómica y trófica, abundancia y biomasa de macroinvertebrados edáficos, tanto a nivel de hojarasca como en el medio subterráneo. Además, la distribución de invertebrados entre microhabitats sufrió variaciones a lo largo de los periodos de muestreo.

Los macroinvertebrados mostraron que su riqueza, abundancia y biomasa disminuyen gradualmente con la profundidad. Aunque las comunidades de la hojarasca y del hábitat subterráneo mostraron algunas diferencias importantes, hubo taxones que mostraron una preferencia por la combinación de los medios epigeo e hipogeo. Entre ellos larvas de Tenebrionidae, detritívoros que pueden alimentarse en ambos niveles y manifestaron migraciones verticales con periodicidad estacional.

La variabilidad espacio-temporal de la comunidad podría tener importantes implicaciones en el sistema de estudio, ya que los cambios en la composición de especies y la estructura trófica de las comunidades de invertebrados edáficos deben afectar a las interacciones entre especies y a las dinámicas de redes tróficas en el espacio y en el tiempo. Los microhábitats isla en los ecosistemas áridos, donde la fauna del suelo se agrega, son potencialmente mantenidos por complejas uniones que implican a los propios macroinvertebrados edáficos que allí habitan. Además, para estos animales la hojarasca y el medio subterráneo no forman compartimientos separados, y existe una gradación y conectividad vertical. Por lo tanto, integrar la variabilidad temporal (tanto estacional como anual) y espacial (tanto horizontal como vertical) es crucial para entender las dinámicas de las comunidades y redes tróficas edáficas, especialmente en sistemas heterogéneos y variables como son los desiertos.

Aunque la temperatura y la humedad afectaron a la distribución espacio-temporal de la macrofauna edáfica, los principales factores fueron la disponibilidad y, especialmente, la calidad de los recursos. Además, los distintos grupos tróficos también mostraron interrelaciones, destacando las producidas entre detritívoros y depredadores, que sugieren importantes conexiones entre los medios epigeo e hipogeo.

Los macroinvertebrados edáficos de la Hoya de Baza se distribuyen de forma parcheada, concentrados en los microhábitats que les ofrecen condiciones ambientales más favorables que la matriz de suelo, al ser donde principalmente se concentran los recursos. Son las diferencias en producción y especialmente en la calidad de los recursos entre los distintos microhábitats las que provocan una gran heterogeneidad espacial, que a su vez se combina con la alta variabilidad temporal del sistema. Como resultado, la comunidad varía en el tiempo y en el espacio, con importantes consecuencias en los ciclos de materia y energía.

La degradación del detritus en la zona de estudio estuvo principalmente afectada por las diferencias de calidad en el recurso. Estas diferencias se manifestaron tanto a nivel superficial como subterráneo, aunque en el medio hipogeo la tasa de degradación fue mayor. La fauna del suelo participa activamente en la descomposición, siendo sus efectos más patentes en los recursos de mayor calidad. Los detritívoros hipogeos también de alimentan del detritus superficial, y su contribución a la degradación es aún mayor que la de los detritívoros superficiales.

Así, las larvas de Tenebriónido, que realizan migraciones verticales en busca del mejor alimento, contribuyen a la interacción entre la hojarasca superficial y el medio subterráneo participando en la degradación del detritus superficial, uno de los procesos ecológicos más importantes en los ecosistemas terrestres.

INTRODUCCIÓN GENERAL

Introducción

Los ecosistemas terrestres están compuestos por un medio epigeo y otro hipogeo, interrelacionados de tal manera que el uno no podría existir sin el otro (Scheu, 2001; Van der Putten et al., 2001; Bardgett y Wardle, 2003; Ehrenfeld et al., 2005). Sin embargo, el medio subterráneo ha sido largamente ignorado a la hora de estudiar el medio natural (Wardle 2002). Generalmente, las especies superficiales son más fáciles de detectar y manipular que las subterráneas, pero nuestro conocimiento de los organismos edáficos y de cómo interaccionan con aquellos que viven en el medio epigeo es crucial para entender el funcionamiento del ecosistema completo (Wall y Reichman, 2000; Wardle, 2002). La biota del suelo es muy rica y diversa (Giller, 1996), incluyendo bacterias, hongos, plantas y una extensa fauna que abarca de microbios a vertebrados, y dicha diversidad es potencialmente necesaria para mantener la estructura y funcionamiento del ecosistema (Wall y Moore, 1999). Entre estos organismos, los invertebrados edáficos influyen de manera fundamental en procesos esenciales para los hábitat en los que se desarrollan (Coleman y Hendrix, 2000). Pueden alterar la producción primaria, la estructura del suelo, los patrones de actividad microbiana, las dinámicas de la materia orgánica y el ciclo de nutrientes (Petersen y Luxton, 1982; Seastedt, 1984; Stanton, 1988; Verhoef y Brussaard, 1990; Beare et al., 1992; Heal et al., 1996; Bonkowski et al., 2000). Por todo ello, estudiar la composición, la distribución y las dinámicas de las comunidades subterráneas es uno de los principales retos en la ecología actual (Wardle y Giller, 1996; Wardle, 2002; Bengtsson y Berg, 2005). Sin embargo, a pesar del papel fundamental en el mantenimiento de los ciclos de materia y energía, las comunidades subterráneas siguen siendo pobremente conocidas (Hunter, 2001). Dentro de estás comunidades, los macroinvertebrados constituyen una de las menos estudiadas, pese al destacado papel que desempeñan en el suelo (Wolters y Ekschmitt, 1997). Si bien un considerable número de artículos muestran la estructura de las comunidades subterráneas de macroinvertebrados en hábitat templados y tropicales (e.g. Decäens et al., 1998, 1999; Feijoo et al., 1999; Frouz y Ali, 2004), pocos estudios se han llevado a cabo en ecosistemas áridos y mediterráneos (Ghabbour y Shakir, 1980; Legakis, 1994). Por tanto, si queremos comprender la ecología y las dinámicas de la comunidad de macroartrópodos en un ecosistema desértico, tan desconocidos actualmente, es imprescindible conocer la estructura de dicha comunidad y los factores que determinan su distribución y abundancia. De esta manera podremos abordar el estudio de cómo dicha comunidad afecta los procesos ecológicos más importantes dentro de su ecosistema.

Es imprescindible para estudiar la ecología, estructura y dinámica de una comunidad de fauna, conocer las especies que la componen y su distribución espacio-temporal (Hanski, 1996; Holt, 1996; Cardinale et al., 2000; Ettema y Wardle, 2002). Los organismos viven en un mosaico espacial de condiciones físicas con variaciones en la composición y abundancia de los recursos (Bell et al., 1991; Polis et al., 1996), y cómo esta heterogeneidad afecta a las comunidades y sus dinámicas se ha convertido en una necesidad dentro de la investigación en ecología (Downing, 1986; Levin, 1992; Dutilleul, 1993). La heterogeneidad espacio-temporal debe afectar los principales canales de energía y las relaciones tróficas de las comunidades del suelo (Bengtsson y Berg, 2005; McCann et al., 2005). En consecuencia, en el ecosistema edáfico, la variabilidad espacial no es sólo estructural, es además potencialmente funcional (Legendre, 1993). Esta funcionalidad deriva de la influencia de la distribución de la fauna edáfica y los factores que la determinan en los patrones espaciales y temporales de descomposición, de herbivoría de raíces y, en último término, en la distribución de las comunidades vegetales (Ettema y Wardle, 2002). Sin embargo, los datos sobre los patrones espaciales y temporales de la fauna y los recursos edáficos son normalmente escasos (Wam, 1993; Ettema et al., 1998; Bengtsson y Berg, 2005).

Los factores ambientales, la heterogeneidad de los recursos del suelo y los procesos poblacionales interactúan para formar los patrones espaciales complejos propios de las comunidades edáficas (Ettema y Wardle, 2002). Principalmente, la humedad y la materia orgánica disponible son considerados los factores más importantes a la hora de explicar las variaciones de densidad en la fauna del suelo (Di Castri y Di Castri 1981). En el medio natural, los organismos edáficos muestran distribuciones parcheadas, influenciados por los microhábitat generados por las plantas y por otros animales (Szlavecz, 1985; Sánchez-Piñero y Gómez, 1995; Blomqvist et al., 2000; Ettema y Wardle, 2002). Debemos considerar además la tridimensionalidad del medio subterráneo, ya que una gran proporción de la variabilidad en las comunidades edáficas puede ser atribuida a la heterogeneidad vertical (Begtsson y Berg, 2005). Además, los patrones espaciales de la biota del suelo son dinámicos en el tiempo y pueden mostrar aún mayores fluctuaciones que los patrones de los correspondientes factores que los generan (Görres et al., 1998; Stoyan et al., 2000; Ettema et al., 2000). Por ultimo, la distribución y las dinámicas de una comunidad serán mejor comprendidas si se tienen en cuenta, no sólo las influencias externas, sino también las interacciones entre la fauna (Fralish, 2002).

Los ecosistemas áridos están caracterizados por condiciones extremas y limitantes (alto estrés hídrico y grandes oscilaciones de temperatura) y una alta heterogeneidad espacial y temporal (Polis, 1991; Whitford, 2002). Los nutrientes del suelo se encuentran muy parcheados, concentrados alrededor de los arbustos, en cúmulos de detritus de los hormigueros y en el nivel más superficial del suelo (Schlesinger et al., 1990; Aguiar y Sala, 1999; Bochet et al., 1999; Sarah, 2002). La disponibilidad de recursos y sus interacciones favorecen que dichos microhábitats actúen como “islas de fertilidad” (Garner y Steinberg, 1989; Lavee et al., 1998; Krämer y Green, 2000) afectando a la diversidad de las comunidades edáficas (Stanton y Tepedino, 1977). Además, las marcadas variaciones estacionales e interanuales en los patrones de disponibilidad de agua y nutrientes afectan fuertemente la estructura y producción vegetales (Noy-Meir, 1979/80; Pavón y Briones, 2000). Por tanto, en zonas áridas y semiáridas (especialmente mediterráneas), la alta heterogeneidad espacio-temporal es un factor clave que determina la actividad y las dinámicas de población de los organismos desérticos (Polis, 1991, Legakis, 1994; Whitford, 2002). En general, la macrofauna edáfica es un grupo importante de organismos en los ecosistemas desérticos, donde las condiciones extremas fuerzan a muchos animales a usar el hábitat subterráneo (Crawford, 1981; Wallwork, 1982). Las hormigas y termitas se consideran como taxa fundamentales en el funcionamiento de los ecosistemas áridos (MacKay, 1991; Whitford, 2000), pero también los escarabajos detritívoros de la familia Tenebrionidae son de una gran importancia (Crawford, 1991; Sánchez-Piñero, 1994).

Los macroinvertebrados edáficos representan un componente abundante y diverso dentro de las comunidades animales que habitan en el suelo (Lavelle et al., 1997), incluyéndose dentro de los tres principales grupos animales que influyen en el funcionamiento del ecosistema (Brusaard, 1998): 1) En la biota de las raíces, que comprende la microflora y los radicívoros, forman parte de los segundos como insectos (tanto adultos como larvas) que afectan al crecimiento vegetal (Brown y Gange, 1990; Blowsey y Hunt-Joshi, 2003); 2) En los descomponedores, compuestos por la microbiota y los transformadores de la hojarasca, constituyen parte de los últimos como lombrices, cochinillas, larvas de insectos, etc. que actúan como reguladores de las poblaciones microbianas por medio del consumo y la disgregación de los detritus (Hanlon y Anderson, 1980; Mordkovich y Afanas'ev, 1980; Wolters, 2000); 3) Y finalmente, como los principales ingenieros del ecosistema: lombrices, hormigas, termitas y larvas de escarabajo capaces de crear el microhábitat para otros seres vivos por medio de su manejo del suelo (Jones et al., 1994; Lavelle et al., 1997; Coleman y Hendrix, 2000).

Los macroinvertebrados, por tanto, afectan a los procesos del suelo de manera directa (consumo y redistribución de recursos) e indirecta (disgregación de la hojarasca y actividad escavadora que potencian la actividad microbial), causando substanciales modificaciones en el medioambiente del suelo y modulando procesos clave, como la producción primaria y el ciclo de nutrientes (Lavelle, 1997; Brussaard, 1998; Lobry de Bruyn y Conacher, 1990; MacKay, 1991; Seastedt, 2000; Wolters, 2000). Por último, pero no menos importante, pueden jugar un papel central en la ecología del ecosistema como fauna de tránsito, uniendo el compartimiento epigeo con el hipogeo (Coleman, 1996). Por tanto, la forma principal en que la macrofauna detritívora actúa dentro del ecosistema, a través del consumo de detritus, puede verse afectada por estás dinámicas entre los medios superficial y subterráneo. Aunque hay evidencias del papel de los descomponedores en los procesos de descomposición epigeos e hipogeos en muchos sistemas (Santos et al., 1981; Whitford et al., 1982; Herlitzius, 1983; Maraun y Scheu, 1996; Ouédrago et al., 2003; Vivanco y Austin, 2006), no hay evidencia empírica del papel de los descomponedores subterráneos en los procesos de descomposición superficiales. Uno de los principales grupos dentro de estos detritívoros edáficos son las larvas de la familia Tenebrionidae, que se consideran capaces de realizar en desiertos las funciones que son dominio de anélidos y otros macroinvertebrados en ambientes más húmedos (Lavelle et al., 1997) y podrían influir en la degradación de los detritus superficiales como adultos epigeos y como larvas hipogeas, con consecuencias directas en las dinámicas espaciales y temporales de la materia y energía entre los medios epigeo e hipogeo.

Objetivos y desarrollo de los capítulos

Los objetivos generales de la presente investigación son:

- Describir la composición taxonómica y trófica de la comunidad de macroinvertebrados en una zona mediterránea árida del suroeste español, en términos de abundancia y biomasa. Se tendrán en consideración tanto las diferencias entre la hojarasca y medio subterráneo, como entre el estado adulto o larvario de los individuos.

- Estudiar la variabilidad temporal de la comunidad de macroinvertebrados por medio de los cambios interanuales y estacionales en: la composición taxonómica, la riqueza de especies, el número de individuos y la biomasa de los mismos.
- Determinar la distribución horizontal de la comunidad por medio del estudio comparativo de la composición taxonómica y trófica, abundancia y biomasa de los macroinvertebrados en los microhábitats más característicos de la zona de estudio: el suelo desnudo, más extenso, y los que hemos considerado “microhabitats isla” (*Retama*, *Salsola*, *Artemisia*, esparto y los cúmulos de detritus creados por la hormiga *Messor* spp.), por sus especiales características como fuentes de recursos y microclima más suave, así como analizar la variabilidad temporal de dicha distribución.
- Conocer la distribución vertical de la comunidad a través de la estructura trófica, composición, diversidad, abundancia y biomasa de los macroinvertebrados. Se considera la hojarasca como nivel más superficial, más cinco niveles de suelo de 10 cm. de profundidad cada uno, hasta los 50 cm. de profundidad total. También se analizarán las variaciones en el patrón de distribución vertical debidas a los distintos microhábitat y la estacionalidad del ecosistema.
- Por medio de datos obtenidos sobre la variación espacio-temporal de los factores abióticos (temperatura y humedad) y bióticos (disponibilidad y calidad de los recursos), se pretende averiguar la influencia de dichas variables en las pautas obtenidas en la distribución espacio-temporal de la comunidad de macroinvertebrados.
- Investigar el consumo de detritus en la zona de estudio tanto en la superficie como en el medio subterráneo. Se analizarán: las diferencias en entre macrofauna, mesofauna y microflora, diferencias en el consumo superficial entre organismos epigeos e hipogeos, la influencia de la degradación química y la importancia de la

calidad del substrato. El experimento se realizará por medio de bolsas de hojarasca de peso conocido. Las bolsas son encerradas en cajas que excluyen a meso- y macrofauna, sólo a la macrofauna, o de acceso total. La "hojarasca" está compuesta de cebada o esparto en el medio superficial y de zanahoria o raíz de esparto en el subterráneo. El trabajo de campo se complementa con análisis químicos de las muestras recogidas.

En base a los objetivos planteados, el desarrollo de los capítulos de la tesis se establece de la siguiente manera: En la primera parte, más descriptiva, se presenta a la comunidad de macroartrópodos edáficos y se analizan los factores que influyen en su distribución. En el Capítulo 1 se describe a la comunidad de macroartrópodos y se estudia la variación temporal en dicha comunidad. La distribución espacial de aborda en los Capítulos 2 y 3, que incluyen los principales aspectos de la distribución horizontal y vertical de la comunidad, respectivamente. Por último, en el Capítulo 4, se analizan los factores tanto abióticos como bióticos que afectan a la distribución de la fauna estudiada. La segunda parte, mucho más experimental, esta constituida por el Capítulo 5, y en ella se analiza el consumo de detritus en la zona de estudio.

Bibliografía

Aguiar, M. R. y O. E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology & Evolution 14: 273-277.

Bardgett, R. D. y D. A. Wardle. 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84: 2258-2268.

Beare, M. H., R. W. Parmelee, P. F. Hendrix, W. Cheng, D. C. Coleman y D. A. Crossley, Jr. 1992. Microbial and faunal interactions and effects on litter nitrogen and descomposition in agroecosystems. Ecological Monographs 62: 569-591.

Bell, S. S., E. D. McCoy y H. R. Mushinsky. 1991. Habitat Structure. The Physical Arrangement of Objects in Space. Chapman and Hall, London.

Bengtsson, J. y M. P. Berg. 2005. Variability in food web structure across time and space. En: de Ruiter, P.C., V. Wolters y J.C. Moore (Eds.), Dynamic Food Webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, Oxford, pp. 201-210.

Blomqvist, M. M., H. Olff, M. B. Blaauw, T. Bongers y W. H. Van der Putten. 2000. Interactions between above- and belowground biota: importance for small-scale vegetation mosaics in a grassland ecosystem. Oikos 90: 582-598.

Blossey, B. y T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. Annual Review of Entomology 48: 521-547.

Bochet, E., J. L. Rubio y J. Poesen. 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. Catena 38: 23-44.

Bonkowski, M., W. Cheng, B. S. Griffiths, J. Alphei y S. Scheu. 2000. Microbial-faunal interactions in the rhizosphere and effects on plant growth. European Journal of Soil Biology: 135-147.

Brown, V. K. y A.C. Gange. 1990. Insect herbivory below ground. Advances in Ecological Research 20: 1-58.

Brussaard, L. 1998. Soil fauna, guilds, functional groups and ecosystem processes. Applied Soil Ecology 9 (1-3): 123-135.

Cardinale, B. J., K. Nelson y M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of the environmental context. Oikos 91: 175-183

Coleman, D. C. 1996. Energetics of detritivory and microbivory in soil in theory and practice. En: Polis, G. A. y K.O. Winemiller (Eds.), Food Webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp. 39-50.

Coleman, D. C. y P. F. Hendrix. 2000. Invertebrates as Webmasters in Ecosystems. CABI Publishing (CAB International), Wallingford, 336 pp.

Crawford, C. S. 1981. Biology of Desert Invertebrates. Springer-Verlag, New York, 314 pp.

Crawford, C. S. 1991. The community ecology of macroarthropod detritivores. En: Polis, G.A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 89-112.

Decaëns, T., T. Dutoit, D. Alard y P. Lavelle. 1998. Factors influencing soil macrofaunal communities in post-pastoral successions of western France. Applied Soil Ecology 9: 361-367.

Decaëns, T., L. Mariani y P. Lavelle. 1999. Soil surface macrofaunal communities associated with earthworm casts in grasslands of the Eastern Plains of Colombia. Applied Soil Ecology 13: 87-100.

Di Castri, F. y V. V. Di Castri. 1981. Soil fauna of Mediterranean-climate regions. En: Di Castri, F., D. W. Goodall y R. L. Specht (Eds.), Ecosystems of the World. 11. Mediterranean type shrublands. Amsterdam, Elsevier, pp. 445-478.

Downing, J. A. 1986. Spatial heterogeneity, evolved behaviour or mathematical artefact? Nature 323: 255-257.

Dutilleul, P. 1993. Spatial heterogeneity and the design of ecological field experiments. Ecology 74: 1646-1658.

Ehrenfeld, J. G., B. Ravit y K. Elgersma. 2005. Feedback in the plant-soil system. Annual Review of Environmental Resources 30: 75-115.

Ettema, C. H. y D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology & Evolution 17: 177-183.

Ettema, C. H., D. C. Coleman, G. Vellidis, R. Lowrance y S. L. Rathbun. 1998. Spatiotemporal distributions of bacteriovorous nematodes and soil resources in a restored riparian wetland. Ecology 79: 2721-2732.

Ettema, C. H., S. L. Rathbun y D. C. Coleman. 2000. On spatiotemporal patchiness and the coexistence of five species of Chronogaster (Nematoda: Chronogasteridae) in a riparian wetland. Oecologia 125: 444-452.

Feijoo M., A., E. Bronson Knappz, P. Lavelle y A. G. Moreno. 1999. Quantifying soil macrofauna in a Colombian watershed. Pedobiologia 43: 513-517.

Fralish, J. S. 2002. Community-based ordination: the problem of data handling and interpretation. Bulletin of the Ecological Society of America 83: 77-81.

Frouz, J. y A. Ali. 2004. Soil macroinvertebrates along a successional gradient in Central Florida. Florida Entomologist 87(3): 386-390.

Garner, W. y Y. Steinberger. 1989. A proposed mechanism for the formation of fertile islands in the desert ecosystem. Journal of Arid Environment 16: 257-262.

Ghabbour, S. I. y S. H. Shakir. 1980. Ecology of soil fauna of Mediterranean desert ecosystem in Egypt. III. Analysis of Thymelaea mesofauna populations at the Mariut frontal plain. Revue D'écologie et de Biologie du Sol 17 (3): 327-352.

Giller, K. E. 1996. The diversity of soil communities, the “poor man’s tropical rainforest”. Biodiversity and Conservation 5: 135-168.

Görres, J. H., M. J. Dichiaro, J. B. Lyons y J. A. Amador. 1998. Spatial and temporal patterns of soil biological activity in a forest and an old field. Soil Biology and Biochemistry 30: 219-230.

Hanlon, R. D. G. y J. M. Anderson. 1980. Influence of macroarthropod feeding activities on microflora in decomposing oak leaves. Soil Biology and Biochemistry 12: 255-261.

Hanski, I. 1996. Metapopulation ecology. En: Rhodes, O. E., K. K. Chesser Jr. y M. H. Smith (Eds.), Population Dynamics in Ecological Space and Time. University of Chicago Press, Chicago, pp. 13-43.

Heal, O. W., S. Struwe y A. Kjoller. 1996. Diversity of soil biota and ecosystem function. En: Walker, B. y W. Steffen (Eds.), Global Change and Terrestrial Ecosystems. University Press, Cambridge, pp 385-402.

Herlitzius, H. 1983. Biological decomposition efficiency in different woodland soils. Oecologia 57: 78-97.

Holt, R. D. 1996. Temporal and spatial aspect of food web structure and dynamics. En: Polis, G.A. y K.O. Winemiller (Eds.), Food Webs: Integration of patterns and dynamics. Chapman and Hall, New York, pp. 255-257.

Hunter, M. D. 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. Agricultural and Forest Entomology 3: 3-9.

Jones, C. G., J. H. Lawton y M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69: 373-386.

Krämer, S. y D. M. Green. 2000. Acid and alkaline phosphatase dynamics and their relationship to soil microclimate in a semiarid woodland. Soil Biology and Biochemistry 32: 179-188.

Lavee, H., A. C. Imeson y P. Sarah. 1998. The impact of climate change on geomorphology and desertification along a Mediterranean-arid transect. Land Degradation & Development 9: 407-422.

Lavelle, P. 1997. Faunal activities and soil processes: Adaptative strategies that determine ecosystem function. Advances in Ecological Research 27: 93-132.

Lavelle, P., D. E. Bignell, M. Lepage, V. Wolters, P. Roger, P. Ineson, O.W. Heal y S. Dhillion. 1997. Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology 33: 159-193.

Legakis, A. 1994. Community structure and species richness in the Mediterranean-type soil fauna. En: Arianoursou, M. y R. H. Groves (Eds.), Plant-Animal Interactions in Mediterranean-Type Ecosystems. Kluwer Academic Publishers, Netherlands, pp. 37-45.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659-1673.

Levin, S. 1992. The problem of pattern and scale in ecology. The Robert H. McArthur Award Lecture. Ecology 73: 1943-1967.

Lobry de Bruyn, L. A. y A. J. Conacher. 1990. The role of termites and ants in soil modification: a review. Australian Journal of Soil Research 28: 55-93.

MacKay, W. P. 1991. The role of ants and termites in desert communities. En: Polis, G. A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 113-150.

Maraun, M. y S. Scheu. 1996. Changes in microbial biomass, respiration and nutrient status of beech (*Fagus selvatica*) leaf litter processes by millipedes (*Glomeris marginata*). Oecologia 107: 131-140.

McCann, K., J. Rasmussen, J. Umbanhowar y M. Humphries. 2005. The role of space, time and variability in food webs dynamics. En: de Ruiter, P. C., V. Wolters y J. C. Moore (Eds.), Dynamic Food Webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, Oxford, pp. 56-70.

Mordkovich, V. G. y N. A. Afanas'ev. 1980. Transformation of steppe litter by darkling beetles (Coleoptera, Tenebrionidae). Ékologiya 3: 56-62.

Noy-Meir, I. 1979/80. Structure and function of desert ecosystems. Israel Journal of Botany 28: 1-19.

Ouédrago, E., A. Mando y L. Brussaard. 2003 Soil macrofaunal-mediated organic resource disappearance in semi-arid West Africa. Applied Soil Ecology 27: 259-267.

Pavón, N. P. y O. Briones. 2000. Root distribution, standing crop biomass and belowground productivity in a semidesert in México. Plant Ecology 146: 131-136.

Petersen, H. y M. Luxton. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39: 288-388.

Polis, G.A. 1991. The Ecology of Desert Communities. University of Arizona Press, Tucson, 456 pp.

Polis, G. A., R. D. Holt, B. A. Menge y K. O. Winemiller. 1996. Time, space, and life history: influences on food webs. En: Polis, G. A. y K. O. Winemiller (Eds.), Food Webs: Integration of patterns and dynamics. Chapman and Hall, London, pp. 435-460.

Sánchez-Piñero, F. 1994. Ecología de las comunidades de coleópteros en zonas áridas de la depresión de Guadix-Baza (Sureste de la Península Ibérica). Universidad de Granada, Granada, 313 pp.

Sánchez-Piñero, F. y J. M. Gómez. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. Journal of Arid Enviroments 31: 91-104.

Santos, P. F., J. Philipps y W. G. Whitford. 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62: 664-669.

Sarah, P. 2002. Spatial patterns of soil moisture as affected by shrubs, in different climatic conditions. Environmental Monitoring and Assessment 73: 237-251.

Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. Basic and Applied Ecology 2: 3-13.

Schlesinger W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrel, R. A. Virginia y W. G. Whitford. 1990. Biological feedbacks in global desertification. Science 247: 1043-1048.

Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29: 25-46.

Seastedt, T.R. 2000. Soil fauna and controls of Carbon Dynamics: Comparisons of rangelands and forests across latitudinal gradients. En: Coleman, D. C. y P. F. Hendrix (Eds.), Invertebrates as Webmasters in Ecosystems. CABI Publishing (CAB International), Wallingford, pp. 293-312.

Stanton, N. L. 1988. The underground in grasslands. Annual Review of Ecology and Systematics 19: 573-589.

Stanton, N. L. y V. J. Tepedino. 1977. Island habitats in soil communities. En: Lohm, U. y T. Persson (Eds.), Soil Organisms as Components of Ecosystems. Swedish Natural Science Research Council, pp. 514-515.

Stoyan, H., H. De-Polli, S. Böhm, G. P. Robertson y E. A. Paul. 2000. Spatial heterogeneity of soil respiration and related properties at the plant scale. Plant and Soil 222: 203-214.

Szlavecz, K. 1985. The effect of microhabitats on the leaf litter decomposition and on the distribution of soil animals. Holartic Ecology 8: 33-38.

Van der Putten, W. H., L. E. M. Vet, J. A. Harvey y F. L. Wäckers. 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends in Ecology & Evolution 16: 547-554.

Verhoef, H. A. y L. Brussaard. 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11: 175-211.

Vivanco, L. y A. T. Austin. 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America. Oecologia 150: 97-107.

Wall Freckman, D. H. y J. C. Moore. 1999. Interactions underground. Soil biodiversity, mutualism, and ecosystem processes. BioScience 49: 109-117.

Wall Freckman, D. H. y O. J. Reichman. 2000. Biotic manipulation involving belowground animals. En: Sala, O. E., R. B. Jackson, H. A. Mooney y R. H. Howarth (Eds.), Methods in Ecosystem Science. Springer-Verlag, New York, pp. 318-329.

Wallwork, J. A. 1982. Desert soil fauna. Praeger Publishers, New York, 296 pp.

Wam, D. 1993. Ecology of terrestrial Enchytraeidae. Pedobiologia 37 (1): 2-29.

Wardle, D. A. 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton & Oxford, 392 pp.

Wardle, D. A. y K. E. Giller. 1996. The quest for a contemporary ecological dimension to soil biology. Soil Biology and Biochemistry 28: 1549–1554.

Whitford, W. G. 2000. Keystone arthropods as webmasters in desert ecosystems. En: D. C. Coleman y P. F. Hendrix (Eds.), Invertebrates as Webmasters in Ecosystems. CABI Publishing (CAB International), Wallingford, pp. 25-41.

Whitford, W. G. 2002. Ecology of Desert Systems. Academic Press, London, 343 pp.

Whitford W. G., Y. Steinberger y G. Ettershank. 1982. Contributions of Subterranean Termites to the "Economy" of Chihuahuan Desert Ecosystems. Oecologia 55: 298-302.

Wolters, V. 2000. Invertebrate control of soil organic matter stability. Biology and Fertility of Soils 31: 1-19.

Wolters, V. y K. Ekschmitt. 1997. Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. En: Benckiser, G. (Ed.), Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production. Marcel Dekker Inc., New York, pp 265-306.

PRIMERA PARTE:

DISTRIBUCIÓN ESPACIO-TEMPORAL DE LOS MACROINVERTEBRADOS EDÁFICOS Y FACTORES IMPLICADOS

Capitulo 1

Soil macroinvertebrate fauna of a Mediterranean arid system: composition and temporal changes in the assemblage

E. Doblas-Miranda, F. Sánchez-Piñero, A. González-Megías

Soil biology and Biochemistry (in press)

Resumen

La variabilidad temporal es un factor clave para entender la estructura de las comunidades subterráneas. Las variaciones estacionales y anuales son especialmente relevantes en los impredecibles ecosistemas desérticos, donde a los macroinvertebrados se les conoce pobremente, a pesar de que constituyen un grupo importante de organismos edáficos. En el presente estudio se analiza la composición y variaciones temporales (estacionales y anuales) de los macroinvertebrados edáficos en una zona árida del sur español. Durante dos años, los macroinvertebrados fueron muestreados, tanto a nivel de hojarasca como en el medio subterráneo, por medio de sacatestigos. Los resultados muestran que la comunidad estaba dominada por artrópodos, especialmente Formicidae y Coleoptera. La comunidad de la hojarasca mostró diferencias frente a la subterránea. En la hojarasca los detritivoros dominaron la composición trófica, mientras que en el medio subterráneo la fauna mostró una proporción similar de detritívoros y herbívoros y un menor porcentaje de predadores. Las comunidades de la hojarasca y el medio subterráneo mostraron variaciones estacionales en riqueza, abundancia, biomasa y composición, siendo estas variaciones más marcadas en la hojarasca. Los patrones de variación estacional también mostraron diferencias entre los dos años de estudio, tanto para los invertebrados de la hojarasca, como para los subterráneos. La variabilidad estacional y anual de la comunidad tiene importantes implicaciones potenciales para la dinámica de comunidad en el sistema de estudio, ya que los cambios en la composición de especies y la estructura trófica de las comunidades de invertebrados del suelo debe de afectar a las interacciones entre especies y las dinámicas de redes tróficas en el tiempo. Por lo tanto, integrar la variabilidad temporal es probablemente crucial para entender las dinámicas de las comunidades y redes trófical edáficas, especialmente en sistemas heterogéneos y variables como son los desiertos.

Abstract

Temporal variability is a key factor to undertand the structure of belowground commuties. Seasonal and annual variations are especially relevant in unpredictable desert ecosystems, where macroinvertebrates are poorly known, despite constituting an important group of soil organisms. In the present study, we analyse the composition and temporal (seasonal and annual) variations of soil macroinvertebrates in an arid area of Southern Spain. During two years, macroinvertebrates were sampled in litter and belowground levels by means of soil cores. Results show that the assemblage was dominated by arthropods, especially Formicidae and Coleoptera. The assemblage differed between litter and belowground levels. In litter, detritivores dominanted the community, while belowground fauna showed a similar proportion of detritivores and herbivores and a low percentage of predators. Litter and belowground assemblages showed seasonal variations in richness, abundance, biomass and composition, although variations were more marked in litter than belowground. Patterns of seasonal variation also differed between the two study years for both litter and belowground invertebrates. The seasonal and annual variability of the assemblage has potentially important implications for community dynamics in the study system, since the changes in species composition and trophic structure of soil invertebrate assemblages may affect species interactions and food web dynamics over time. Therefore, integrating temporal variability is likely to be crucial to understand soil community dynamics and food webs, especially in heterogeneous, variable systems as deserts.

Key words

Soil ecology; Macroinvertebrates; Litter and belowground assemblages; Mediterranean arid ecosystem; Temporal variability

Introduction

The soil biota is extremely rich and comprises a high proportion of the diversity in most ecosystems (Anderson, 1975). However, despite their crucial role in ecosystem functioning soil communities are still poorly known (Wall and Moore, 1999; Hunter, 2001). A key aspect to understand community structure and dynamics of ecological systems is temporal variability, which may affect the main energy channels and the trophic relations of soil communities (McCann et al., 2005). Soil communities show seasonal and annual variability in composition, the analysis of temporal variations remaining as a relevant question to understand soil community structure and dynamics, especially in highly variable systems (Bengtsson and Berg, 2005).

Deserts are characterized by high temporal variability (Polis, 1991; Whitford, 2002). Seasonal and annual variations strongly affect primary production and population dynamics of desert organisms (Whitford, 2002). However, only few papers have analyzed seasonal changes in the soil fauna of deserts (Ghabbour and Shakir, 1980; Pen-Mouratov et al., 2004).

The soil macrofauna is a relevant group of organisms in deserts, where high water stress and large temperature oscillations force many animals (especially immature stages) to use the subterranean habitat (Wallwork, 1982). Soil macroinvertebrates affect soil processes and cause important modifications in the soil environment (Lavelle, 1997; Wolters, 2000), with potentially high implications in nutrient limited desert soils (Whitford, 2000).

In this paper, we analyze the composition and temporal variability of the macroinvertebrate assemblage in an arid zone of SE Spain. Because few studies have analyzed the structure of belowground macroinvertebrate communities in arid ecosystems (Ghabbour and Shakir, 1980; Legakis, 1994), we first describe the taxonomic and trophic composition of the soil (considering both the litter and belowground levels) macroinvertebrate assemblage in terms of richness, abundance and biomass. Then, we analyse the seasonal and annual variations in the structure of the litter and belowground assemblages.

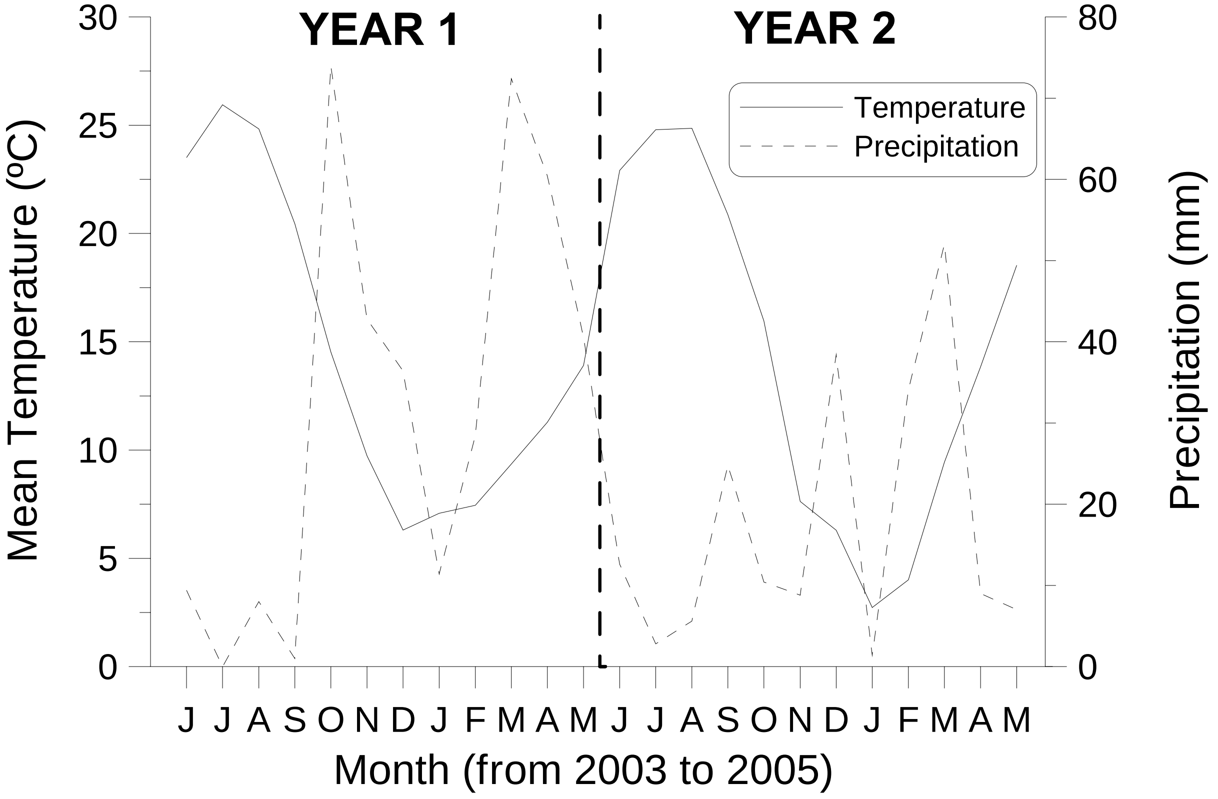
Materials and methods

Study site

The study was conducted at Barranco del Espartal, a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain), from June 2003 to May 2005. Potential evapo-transpiration exceeds three times the amount of annual rainfall (250-300 mm). Climate is Mediterranean continental, with strong temperature fluctuations (mean temperature 14.4 ºC, ranging from 40ºC to -14ºC), and highly seasonal. The sharp contrast between the hot, dry summer conditions and the cold, rainy winter conditions determine that autumn and winter do not appear as distinct seasons in the area (Castillo-Requena, 1989), only three seasons being actually recognizable: 1) a highly variable spring season, from March to May; 2) a summer season, with extreme heat and drought, from June to September; and 3) a cold and rainy winter season, from October to February. Temperature and precipitation records from a nearby meteorological station show that similar seasonal trends occurred during the two years of the study, both years differing principally in the amount of winter precipitation (Fig. 1).

The soil is a Gypsiric Regosol (WRBSR, FAO, 1998), characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (< 5% $CaCO_3$ content). Soil structure ranges from weak fine granular (in the upper centimetres of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually < 15-20 cm depth, being the first 1-2 cm where the organic matter concentrates, with values < 2% in all cases) and C (Sierra et al., 1990). As a general trait of desert soils, most ground surface is devoid of litter (58%), which only occurs under shrubs (usually forming a thin, distinct layer in the soil surface) and in ant-nest mounds.

Figure 1. Monthly mean temperature (ºC) and total amount of precipitation (mm) at the study area, during April 2003 to May 2005.



The vegetation is an arid open shrubsteppe dominated by *Artemisia herba-alba* Asso and *A. barrelieri* Bess and *Salsola oppositifolia* Desf. shrubs, tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.) and *Retama sphaerocarpa* L. brushes. In addition to plants, *Messor barbarus* L. and *M. bouvieri* Bondroit ant-nest mounds constitute important components of the study system, forming large detritus accumulations in which detritivorous arthropods aggregate (Sánchez-Piñero and Gómez, 1995).

Sampling design

To analyse the composition and distribution of the soil macroinvertebrates, we considered two levels in the soil: litter (which appears as a distinct layer of accumulated detritus on the soil surface) and belowground. To sample the litter level, we collected the litter (leaf litter under the shrubs or detritus accumulated around the ant-nest mouth) contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel. Belowground samples were collected in the same spot by using a 10 cm diameter auger. Soil cores were extracted up to 50 cm depth (maximum depth was selected based on preliminary data collected at the study site showing that all taxa and > 90% abundance occurred from 0-50 cm depth; Sánchez-Piñero et al., unpublished data). Both litter and core samples were collected in six different microhabitats: under the four dominant types of shrubs in the study site (*Artemisia*, *Salsola*, *Retama* and tussock grasses), in bare soil areas and in *Messor* ant-nests. We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the two years of study. To analyze seasonal variations, we distinguished six sampling periods comprising the three different seasons over the two years of study (thereafter, Summer-1, Winter-1, Spring-1, Summer-2, Winter-2 and Spring-2).

Litter and soil core samples were processed in the field using 1 mm mesh-size sieves. After sieving, the litter or soil held back in the sieve was placed in 20 x 15 cm white pans and macroinvertebrates were hand collected by carefully examining the litter or soil. Samples containing large numbers of macroinvertebrates were kept in plastic bags and examined in the laboratory. Immature stages were kept alive for laboratory rearing in order to identify the adult insects. Unknown or small (c.a., < 1 cm length) invertebrates were preserved in 70% ethanol for taxonomic identification and measurement (using a binocular scope equipped with a micrometer, 0.1 mm accuracy). Large specimens were measured in the field using a digital caliper. Body length was used to estimate macroinvertebrate biomass (dry weight) by means of allometric equations based on specimens from the study area (Hódar 1996). Macroinvertebrates were identified to the lowest taxonomic level possible.

Taxa were classified into five different trophic groups (Appendix I): Herbivores, detritivores, fungivores, predators and omnivores. All the above trophic groups consume exclusively or principally one type of food, except omnivores which diet includes always a proportion of plant material and animal prey. Because some taxa live in the soil but do not feed on soil resources or prey (e.g., pupae in the litter, ants or burrowing spiders at belowground level), an additional group, called as "non-*in situ*-consumers", was included in the analysis. Assignation of taxa to a trophic group was based on published information (e.g., Moore et al., 1988; Decaëns et al., 1998) and observations at the study site.

Statistical analysis

Beta diversity was calculated using two similarity indexes: the Sorensen index (qualitative, measuring whether assemblages differ in the species present) and the Morisita-Horn index (quantitative, which considers also the abundance of each species in the analysis; Magurran, 2004). Because of the high number of ants in some samples, Formicidae were excluded for the calculation of the Morisita-Horn index. To compare differences in richness (mean number of taxa per sample), abundance (mean number of individuals per sample) and biomass (mean dry weight per sample) among sampling periods or between years, non-parametric Kruskal-Wallis and Mann-Withney U tests were used because data were not normally distributed. To test whether the relative frequency of trophic groups differed among sampling periods, we used a Chi-square test. Sorensen and Morisita-Horn indexes were calculated using EstimateS 7.5.0 (Colwell, 2005), while the remaining statistical analyses were conducted using the Statistica software package (StatSoft Inc., Tulsa, USA).

Results

Taxonomic composition of the assemblage

A total of 19842 individuals belonging to 158 invertebrate taxa were collected (Appendix I). Density of macroinvertebrates was 101 individuals/m^2 (56 individuals/m^2

excluding ants) in litter and 1559 individuals/m^2 (217 individuals/m^2 excluding ants) belowground. Mean biomass was 0.50 g/m^2 in litter and 1.61 g/m^2 belowground.

The macroinvertebrate assemblage was amply dominated by arthropods, which comprised 99.9% of the total number of individuals and 94.7% of the total biomass. Litter and belowground levels differed in assemblage composition (Sorensen = 0.61; Morisita-Horn = 0.25; Appendix I). At the litter level, the most abundant arthropods were Hymenoptera (50.3%, mostly Formicidae), Embioptera (13.2%) and Aranei (12.7%). In terms of biomass, the composition of the litter assemblage was dominated by Coleoptera (55.5%, principally Tenebrionidae), Julida (18.4%) and spiders (7.9%).

Belowground, the composition of the assemblage was dominted by Hymenoptera (87.2%, mostly ants), Hemiptera (6.2%, mainly Margarodidae) and larval stages of Coleoptera (3.2%; principally Cebrionidae, Tenebrionidae and Curculionidae) in terms of abundance. In terms of biomass, the dominant taxa were Coleoptera (47.6%, mostly Tenebrionidae, Cebrionidae and Melolonthidae) and Hymenoptera (27.3%, mainly ants).

Trophic composition

Litter and belowground levels differed in the relative frequency of the abundances ($\chi^2 = 613.07$, $P < 0.0001$, d.f. = 5) and biomass ($\chi^2 = 92.08$, $P < 0.0001$, d.f. = 5; Table 1) of the different trophic groups. In the litter level, omnivores were the dominant group in terms of abundance, followed by detritivores and predators. In terms of biomass, however, detritivores largely dominated in this level (Table 1).

The belowground assemblage was amply dominated by non-*in situ*-consumers in terms of abundance, but detritivores, non-*in situ*-consumers and herbivores represented a similar proportion of biomass. Predators represented the lowest percentage of both abundance and biomass belowground (Table 1).

Table 1. Percentage of abundance and biomass of the different trophic groups in litter and belowground levels.

Trophic Group	Abundance		Biomass	
	Litter	Belowground	Litter	Belowground
Detritivores	25.87	3.35	72.85	32.31
Fungivores	0.08	0.01	0.04	0.78
Herbivores	4.05	8.22	8.05	27.11
Omnivores	49.70	0	3.59	0
Predators	18.14	0.80	13.19	10.01
Non-*in situ*-consumers	2.23	87.64	2.32	30.57

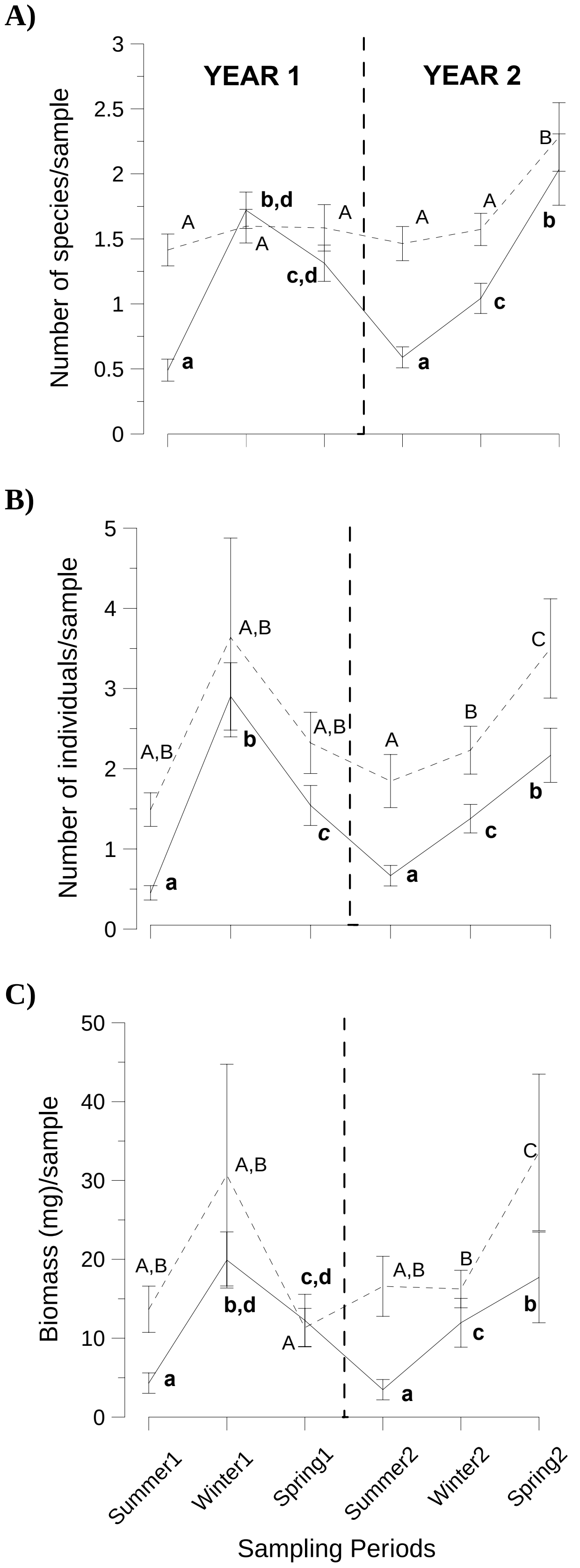
Annual variation

There were no differences in richness, abundance and biomass between the two years included in this study in both litter and belowground ($P \geq 0.18$ in all cases; Mann-Withney U test). Although the qualitative composition of the assemblages showed some differences between years (Sorensen index: Litter = 0.67; Belowground = 0.70), when the abundance of taxa was considered, a high similarity between the two years occurred in both litter (Morisita-Horn = 0.91) and belowground (Morisita-Horn = 0.95) assemblages.

Seasonal variations in assemblage composition

Richness ($H = 95.93$, $P < 0.0001$, d.f. = 5, 873), abundance ($H = 97.54$, $P < 0.0001$, d.f. = 5, 873) and biomass ($H = 90.75$, $P < 0.0001$, d.f. = 5, 873) varied significantly among sampling periods at the litter level (Fig. 2): For the three variables, the lowest values occurred in Summer-1, while Winter-1 and Spring-2 were the periods with the highest means. The pattern of seasonal variations differed between years in the three variables, reaching the highest values in winter during the first year, while the maximum values occurred in spring during the second year.

Figure 2. Species richness (mean number of species per sample; A), abundance (mean number of individuals per sample, excluding Formicidae; B), and biomass (mean mg of dry weight per sample; C) of soil macroinvertebrates per sampling period. Solid line: litter level; shaded line: belowground level.



At belowground level, only Spring-2 showed significantly higher values of richness (H = 11.68, $P < 0.05$, d.f. = 5, 873), abundance (H = 21.6, $P < 0.001$, d.f. = 5, 873) and biomass (H = 14.92, $P < 0.05$, d.f. = 5, 873; Fig. 2) than the rest of sampling periods.

Similarity in assemblage composition also varied between sampling periods (Table 2). At the litter level, the Sorensen index between sampling periods was about 50%, showing high differences between seasons. The Morisita-Horn index was higher than Sorensen index values in most cases, only Summer-1 showing a lower similarity than the other sampling periods, indicating that the abundance of dominant taxa remained similar between seasons. The Sorensen index between sampling periods was higher at belowground level than at the litter level, and the Morisita-Horn index showed higher variations belowground than at the litter level. Differences in similarity between seasons did not show a consistent pattern in both years, showing very different Morisita-Horn indexes between winter and summer at litter, and winter and spring belowground. Also, assemblage composition showed marked variations for the same season between the two years (Table 2).

Table 2. Similarity in species composition between sampling periods in A) litter and B) belowground levels. In each case, Sorensen index values are shown in lower diagonal and Morisita-Horn index values in upper diagonal. Bold numbers indicate similarities between consecutive seasons and between the same season in different years.

A) Litter

	Summer1	Winter1	Spring1	Summer2	Winter2	Spring2
Summer1	*	**0.35**	0.27	***0.49***	0.49	0.60
Winter1	**0.47**	*	**0.92**	0.87	***0.88***	0.79
Spring1	0.27	**0.52**	*	**0.77**	0.78	***0.71***
Summer2	***0.51***	0.56	**0.51**	*	**0.91**	0.84
Winter2	0.39	***0.57***	0.43	**0.55**	*	**0.85**
Spring2	0.44	0.58	***0.51***	0.52	**0.54**	*

B) Belowground

	Summer1	Winter1	Spring1	Summer2	Winter2	Spring2
Summer1	*	**0.75**	0.66	***0.82***	0.77	0.85
Winter1	**0.69**	*	**0.34**	0.99	***0.64***	0.96
Spring1	0.52	**0.57**	*	**0.40**	0.82	***0.43***
Summer2	***0.62***	0.65	**0.54**	*	**0.69**	0.98
Winter2	0.63	***0.70***	0.53	**0.66**	*	**0.73**
Spring2	0.52	0.59	***0.42***	0.54	**0.63**	*

Temporal variations in trophic structure

At the litter level, biomass of all trophic groups differed among seasons (H > 11.33, P < 0.05, d.f. = 5, 873 in all cases; Table 3), most trophic groups showing a common pattern of increase in Winter-1 and Spring-2 (except non-*in situ*-consumers, that only showed a small increase of biomass during the first spring). The relative frequency of trophic groups in the litter assemblage also varied among sampling periods ($\chi^2 > 10.18$, P < 0.05, d.f. = 4 in all cases).

At belowground level, the biomass of detritivores (H > 13.09, P < 0.05, d.f. = 5, 873) and predators (H = 18.05, P < 0.01, d.f. = 5, 873) differed significantly among seasons (Table 3), with higher biomass in Spring-2. There were also significant differences in the trophic structure among sampling periods belowground ($\chi^2 > 9.36$, P < 0.05, d.f. = 3 in all cases).

Discussion

Community composition

This study shows that macroinvertebrate assemblages of litter and belowground levels in the arid Baza Basin differed in taxonomic and trophic composition, abundance and biomass, as well as in the patterns of temporal variability.

Table 3. Mean biomass (± S.E.) of the different trophic groups in each sampling period in litter and belowground. Letters behind the numbers indicate statistically different means.

Trophic groups	**Sampling Periods**					
	Summer-1	**Winter-1**	**Spring-1**	**Summer-2**	**Winter-2**	**Spring-2**
Litter						
Detritivores	2.60 ± 1.14^{a}	13.43 ± 2.86^{b}	15.53 ± 6.00^{b,c}	2.91 ± 1.08^{d}	10.31 ± 2.98^{c}	12.56 ± 5.53^{b,c}
Fungivores	0	0	0.07 ± 0.07	0	0	0
Herbivores	0.82 ± 0.48^{a}	2.01 ± 0.71^{b}	1.01 ± 0.42^{b}	0.09 ± 0.04^{a}	0.57 ± 0.27^{a}	0.88 ± 0.61^{a,b}
Omnivores	0.22 ± 0.15^{a,d}	0.72 ± 0.23^{b}	0.27 ± 0.13^{a,b,c}	0.16 ± 0.03^{b,d}	0.15 ± 0.08^{a}	1.57 ± 0.56^{c}
Predators	0.60 ± 0.18^{a}	3.30 ± 1.20^{b,c}	1.35 ± 0.40^{a,b}	0.63 ± 0.15^{a}	0.89 ± 0.17^{b}	2.71 ± 1.49^{c}
Non-*in situ*-consumers	0.07 ± 0.07^{a}	0.48 ± 0.27^{a}	1.25 ± 0.63^{b}	0.19 ± 0.17^{a}	0.04 ± 0.03^{a}	0
Belowground						
Detritivores	3.53 ± 1.14^{a,b}	5.91 ± 1.56^{a,b}	2.32 ± 0.81^{a}	8.97 ± 3.53^{a}	5.17 ± 1.43^{b,c}	19.77 ± 6.74^{c}
Fungivores	0	0.70 ± 0.50	0	0	0	0
Herbivores	4.83 ± 1.23	6.09 ± 1.25	5.01 ± 1.33	4.59 ± 1.18	6.38 ± 1.55	4.05 ± 0.98
Predators	3.36 ± 2.38^{a}	2.71 ± 1.11^{a}	0.75 ± 0.35^{a}	0.62 ± 0.24^{a}	1.71 ± 0.87^{a}	3.00 ± 1.40^{b}
Non-*in situ*-consumers	1.96 ± 0.80	15.28 ± 13.89	3.26 ± 1.79	2.41 ± 0.76	2.99 ± 0.73	6.74 ± 4.58

The macrofaunal assemblage at the study site was dominated by arthropods both in terms of abundance and biomass. The assemblage differed to those reported in more humid temperate and tropical habitats, where Lumbricidae is generally the dominant group together with other taxa such as termites (in tropical regions), ants and beetles (e.g., Decaëns et al., 1998; Barros et al., 2002). The dominance of Formicidae and Coleoptera has been indicated as a general trait of ground dweeling assemblages in Mediterranean and desert systems (Ghabbour and Shakir, 1980; Legakis, 1994; Sánchez-Piñero, 1994, PhD Thesis).

The macroinvertebrate assemblages associated with litter and belowground levels showed marked differences in taxonomic and trophic composition. On the one hand, there was a relatively lower abundance of predators belowground than in litter, since most macroarthropod predators are only active at the soil surface (Wardle 1995). On the other hand, althouhg detritivores dominated at litter level, herbivores occurred in a relatively high proportion belowground. The dominance of detritivores in litter is explained by the availability of the food resources that they exploit, and it is in concordance with previous data from the study site (Sánchez-Piñero, 1994, PhD Thesis) as well as other studies in arid environments (Crawford, 1991; Legakis, 1994). In contrast, the high proportion of belowground herbivores suggest the relevance of belowground herbivory, usually a neglected question (e.g., Blossey and Hunt-Joshi, 2003) despite the fact that belowground primary productivity frequently exceeds aboveground production (e.g., Eissenstat and Yanai, 1997), especially in deserts (Pavón and Briones, 2000). Therefore, in our system belowground herbivory is potentially as important as detritivory or omnivory, generally considered as the main trophic pathways in arid ecosystems (Seely and Louw, 1980; Polis, 1991).

Temporal variability

Temporal variations at the study site were pronounced and showed significant differences between sampling periods. Differences in similarity between seasons showed that composition of the assemblage changed considerably both qualitatively and quantitatively for both litter and belowground assemblages. In addition to assemblage composition, other community descriptors (richness, abundance, biomass) also showed variations among sampling periods. Strong seasonality is a feature of most ecosystems (e.g., Wolda, 1988), particularly in Mediterranean habitats and deserts, where the seasonal fluctuations of temperature and rainfall create marked pulses of productivity and animal activity (Noy-Meir, 1979/80; Blondel and Aronson, 1999). Also, seasonal variations have been reported in soil meso- and macrofaunal assemblages of temperate (Berg et al., 1998), tropical (Rossi and Blanchart, 2005) and arid ecosystems (Ghabbour and Shakir, 1980; Pen-Mouratov et al., 2004).

The results highlight two interesting traits in the seasonal variations of the assemblage: the differences in seasonal variability between litter and belowground levels, and the differences in the seasonal pattern between years. First, the seasonal variations of the assemblage were more marked in litter than belowground. This result could be related to variations in abiotic conditions, fluctuations of temperature and moisture being less pronounced belowground than on the surface (Wallwork, 1982; Whitford, 2002).

Second, there were important differences between the two years considered in this study in the pattern of seasonal variations. These variations in the patterns between the two years are a common trait in unpredictable desert environments, where changes in temperature and precipitation usually have strong effects on resource availability and community composition and dynamics (Noy Meir, 1979/80; Seely and Louw, 1980; Mooney, 1981). Differential responses of specific taxa to changes in abiotic and biotic factors are responsible for strong annual differences in arid ecosystems (Thomas, 1979; Sánchez-Piñero and Avila, 2004).

The seasonal and annual variability of the assemblage has potentially important implications on community dynamics in the study system, since the changes in species composition and trophic structure of soil invertebrate assemblages may affect species interactions and food web dynamics over time. Therefore, integrating temporal variability is likely to be crucial to understand soil community dynamics and food webs, especially in heterogeneous, variable systems as deserts.

Acknowledgements

We thank all people who helped during the field work, especially José Manuel Herrera Vega, José Manuel Gómez Ros, Laura Pérez Zarcos, Elena Portellano and Niva. Voucher specimens were kindly identified by Manuel Baena (Hemiptera), Robert Bosman (Aranei), Imre Foldi (Margarodidade), Alberto Sendra (Diplura), Alberto Tinaut (Formicidae) and Dolores Trigo Haza (Lumbricidae). Francisco Martínez Peinado assisted us with the description of the soil. The owners of Barranco del Espartal, D. Julio and D. Fernando Gallardo, kindly allowed us to carry out the sampling, and Los Alamos provided logistic support. Comments by two anonimous referees improved the manuscript. This work was funded by CICYT. E.D.M. was supported by a F.P.I. grant from Ministerio de Ciencia y Tecnología.

Bibliography

Anderson, J.M., 1975. The enigma of soil animal species diversity. In: Vanek, J. (Ed.), Progress in Soil Zoology. Academia, Prague, pp. 51-58.

Barros, E., Pashanasi, B., Constantino, R., Lavelle, P., 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biology and Fertility of Soils 35, 338-347.

Bengtsson, J., Berg, M.P., 2005.Variability in food web structure across time and space. In: de Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, Oxford, pp. 201-210.

Berg, M.P., Kniese, J.P., Bedaux, J.J.M., Verhoef, H.A., 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. Biology and Fertility of Soils 26, 268-284.

Blondel, J., Aronson, J., 1999. Biology and wildlife of the Mediterranean Region. Oxford University Press, Oxford, 328 pp.

Blossey, B., Hunt-Joshi, T.R., 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. Annual Review of Entomology 48, 521-547.

Castillo Requena, J.M., 1989. El clima de Andalucía: clasificación y análisis regional de los tipos de tiempo. Instituto de Estudios Almerienses, Almería, 266 pp.

Colwell, R.K., 2005. EstimateS -statistical estimation of species richness and shared species from samples version 7.5. User's guide and application published at http://purl.oclc.org/estimates

Crawford, C.S., 1991. The community ecology of macroarthropod detritivores. In: Polis, G.A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 89-112.

Decaëns, T., Dutoit, T., Alard, D., Lavelle, P., 1998. Factors influencing soil macrofaunal communities in post-pastoral succesions of western France. Applied Soil Ecology 9, 361-367.

Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root life-span. Advances in Ecological Research 27, 1-60.

Ghabbour, S.I., Shakir, S.H., 1980. Ecology of soil fauna of Mediterranean desert ecosystem in Egypt. III. Analysis of Thymelaea mesofauna populations at the Mariut frontal plain. Revue D'écologie et de Biologie du Sol 17 (3), 327-352.

Hódar, J.A., 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17, 421-433.

Hunter, M.D., 2001. Out of sight, out of mind: the impacts of root-feeding insects in natural and managed systems. Agricultural and Forest Entomology 3, 3-9.

Lavelle, P., 1997. Faunal activities and soil processes: Adaptative strategies that determine ecosystem function. Advances in Ecological Research 27, 93-132.

Legakis, A., 1994. Community structure and species richness in the Mediterranean-type soil fauna. In: Arianoursou, M., Groves, R.H. (Eds.), Plant-Animal Interactions in Mediterranean-Type Ecosystems. Kluwer Academic Publishers, Netherlands, pp. 37-45.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, 256 pp.

McCann, K., Rasmussen, J., Umbanhowar, J., Humphries, M., 2005. The role of space, time and variability in food webs dynamics. In: de Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic Food Webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, Oxford, pp. 56-70.

Mooney, H.A., 1981. Primary production in Mediterranean-climate regions. In: di Castri, F., Goodall, D.W., Specht, R.L. (Eds.), Ecosystems of the world, Vol. 11: Mediterranean-type shrublands. Elsevier, Amsterdam, pp. 249-255.

Moore, J.C., Walter, D.E., Hunt, H.W., 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annual Review of Entomology 33, 419-439.

Noy-Meir, I., 1979/80. Structure and function of desert ecosystems. Israel Journal of Botany 28, 1-19.

Pavón, N.P., Briones, O., 2000. Root distribution, standing crop biomass and belowground productivity in a semidesert in México. Plant Ecology 146, 131-136.

Pen-Mouratov, S., Rakhimbaev, M., Barness, G., Steinberger, Y., 2004. Spatial and temporal dynamics of nematode populations under *Zygophyllum dumosum* in arid environments. European Journal of Soil Biology 40, 31-46.

Polis, G.A., 1991. The Ecology of Desert Communities. University of Arizona Press, Tucson, 456 pp.

Rossi J.P., Blanchart E., 2005. Seasonal and land-use induced variations of soil macrofauna composition in the Western Ghats, southern India. Soil Biology and Biochemistry 37, 1093-1104.

Sánchez-Piñero, F., Gómez, J.M., 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. Journal of Arid Enviroments 31, 91-104.

Sánchez-Piñero, F., Avila, J.M., 2004. Dung-insect community composition in arid zones of south-eastern Spain. Journal of Arid Enviroments 56, 303-327.

Seely, M.K., Louw, G.N., 1980. First approximation of the effect of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. Journal of Arid Environments 14, 131-143.

Sierra, C., Ortega, E., Quirantes, J., Lozano, J., Martínez, J., 1990. Proyecto LUCDEME. Mapa de suelos. Baza-994. M.A.P.A.-ICONA.

Thomas, D.B., 1979. Patterns in the abundance of some tenebrionid beetles in the Mojave Desert. Environmental Entomology 8, 568-574.

Wall, D.H., Moore, J.C., 1999. Interactions underground. Soil biodiversity, mutualism, and ecosystem processes. BioScience 49, 109-117.

Wallwork, J.A., 1982. Desert soil fauna. Praeger Publishers, New York, 296 pp.

Wardle, D.A., 1995. Impacts of disturbance on detritus food-webs in agroecosystems of contrasting tillage and weed management practices. Advances in Ecological Research 26, 105-185.

Whitford, W.G., 2000. Keystone arthropods as webmasters in desert ecosystems. In: Coleman, D.C., Hendrix, P.F. (Eds.), Invertebrates as Webmasters in Ecosystems. CABI Publishing, Wallingford, pp. 25-41.

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, London, 343 pp.

Wolda, H., 1988. Insect seasonality: Why? Annual Review of Ecology and Systematics 19, 1-18.

Wolters, V., 2000. Invertebrate control of soil organic matter stability. Biology and Fertility of Soils 31, 1-19.

WRBSR, FAO, 1998. World Reference Base for Soil Resources. FAO-ISRIC-ISSS. Rome.

Appendix I. List of taxa, total number of individuals (No Indiv.) in litter and belowground, and trophic group of the macroarthropods collected at the study site during the two years of the study. In taxa with different trophic roles in litter and belowground, trophic group in each level (litter/belowground) is also indicated.

Class	**Order**	**Family**	**Genus/Species**	**No Indiv.**		**Trophic Group**
				Litter	**Belowg.**	
Oligochaeta	Opisthopora	Lumbricidae	*Allolobophora calliginosa*	0	10	Detritivore
Gastropoda	Stylommatophora	Helicidae	*Iberus gualtieranus*	1	0	Herbivore
Arachnida	Aranei	Anyphaenidae	*Anyphaena sp.*	1	0	Predator
		Ctenizidae	*Ummidia aedificatoria*	1	3	Predator/Non-*in situ*-consumer
		Cyrtaucheniidae	*Cyrtauchenius walckenaeri*	0	1	Non-*in situ*-consumer
		Dictynidae		2	0	Predator
		Eresidae	*Eresus cinnaberinus*	0	3	Non-*in situ*-consumer
		Filistatidae		1	0	Predator
		Gnaphosidae	*Berlandina spp.*	18	0	Predator
			Haplodrassus spp.	14	1	Predator/Non-*in situ*-consumer
			Micaria sp.	2	0	Predator
			Nomisia sp.	1	0	Predator
			Pterotricha sp.	7	0	Predator
			Zelotes sp.	11	0	Predator
			Unidentified Gnaphosidae	16	1	Predator/Non-*in situ*-consumer
		Lycosidae	*Hogna sp.*	0	1	Non-*in situ*-consumer
			Lycosa tarentula	10	0	Predator
			Pardosa sp.	3	0	Predator
		Miturgidae	*Cheiracanthium sp.*	2	0	Predator
		Nemesiidae	*Nemesia spp.*	8	18	Predator/Non-*in situ*-consumer
		Oonopidae	*Orchestina sp.*	1	0	Predator
		Oxyopidae	*Oxyopes spp.*	5	0	Predator
		Palpimanidae	*Palpimanus gibulus*	1	0	Predator
		Philodromidae	*Philodromus sp.*	1	0	Predator
		Salticidae		14	0	Predator
		Sicariidae	*Loxosceles rufescens*	0	1	Non-*in situ*-consumer
		Sparassidae	*Cebrennus ibericus*	2	0	Predator
		Theridiidae		1	0	Predator
		Thomisidae	*Misumenops sp.*	5	1	Predator/Non-*in situ*-consumer
			Ozyptila sp.	1	0	Predator
			Thomisus sp.	1	0	Predator
			Xysticus sp.	2	0	Predator
		Zodariidae	*Selamia reticulata*	12	2	Predator/Non-*in situ*-consumer
			Zodarion sp.	2	0	Predator
		Unidentified Juvenals		189	15	Predator/Non-*in situ*-consumer
	Laniatores	Gagrellidae	*Cosmobonus granaries*	1	0	Predator
	Solpugides	Daesiidae	*Gluvia dorsalis*	4	0	Predator
	Pseudoscorpiones			16	1	Predator
Malacostraca	Isopoda	Oniscidea	*Porcelio sp.*	26	9	Detritivore
Diplopoda	Penicillata			25	0	Detritivore
	Julida	Julidae	*Julus sp.*	48	13	Detritivore
Chilopoda	Lithobiomorpha			0	1	Predator
	Scolopendromorpha	Scolopendridae	*Scolopendra canidens*	3	5	Predator
		Cryptopidae	*Theatops erythrocephala*	0	1	Predator
	Geophilomorpha			10	45	Predator
Hexapoda	Diplura	Japygidae	*Monojapyx simplex*	7	6	Detritivore
			Protojapyx maior	0	2	Detritivore
	Microcoryphia			11	0	Detritivore
	Thysanura			26	20	Detritivore
	Blattodea	Blatellidae		6	0	Detritivore
	Dermaptera	Forficulidae	*Forficula*	0	1	Detritivore
	Embioptera	Oligotomidae	*Haploembia palaui*	349	325	Detritivore
	Psocoptera			13	0	Detritivore
	Thysanoptera			2	0	Herbivore
	Hemiptera	Margarodidae	*Dimargarodes mediterraneus*	5	1056	Herbivore
		Berytinidae	*Berytinus distinguendus*	3	0	Predator
		Reduviidae	*Rhinocoris erythropus*	4	0	Predator
		Pentatomidae	*Sciocoris sp.*	2	1	Herbivore
		Rhopalidae	*Agraphopus*	2	0	Herbivore
		Lygaeidae	*Plinthisus laevigatus*	1	2	Herbivore
			Plinthisus longicollis	2	0	Herbivore
			Engistus commendatorius	2	0	Herbivore
			Notochilus crassicornis	2	0	Herbivore
		Miridae	*Laurinia sp.*	4	0	Herbivore

			Halticus sp.	1	0	Herbivore
		Stenocephalidae	*Dicranocephalus*	1	0	Predator
		Aphidae		1	0	Herbivore
		Cercopidae	*Cercopis sp.*	1	1	Herbivore
		Cicadellidae		2	0	Herbivore
		Cicadidae		0	1	Herbivore
		Cydnidae		8	1	Herbivore
		Nabidae		1	0	Predator
		Unidentified Hemiptera		13	9	
	Neuroptera	Myrmeleontidae larva		1	0	Predator
	Coleoptera	Carabidae	*Harpalus tenebrosus*	1	0	Omnivore
			Cymindis lineola	1	0	Omnivore
			Ditomus capito	1	10	Herbivore/Non-*in situ*-consumer
			Demetrias atricapillus	1	0	Predator
			Carabus lusitanicus	1	0	Predator
			Microlestes spp.	44	5	Predator/Non-*in situ*-consumer
			Orthomus expansus	7	2	Predator/Non-*in situ*-consumer
			Singilis alternans	0	1	Non-*in situ*-consumer
			Synthomus fuscomaculatus	2	1	Predator/Non-*in situ*-consumer
			Unidentified larvae	23	10	Predator
		Staphylinidae	*Ocypus ophthalmicus*	1	0	Predator
			Unidentified adults	31	3	
		Histeridae	*Hister grandicollis*	1	0	Predator
		Thorictidae	*Thorictus sp.*	2	3	Detritivore/Non-*in situ*-consumer
		Melyridae	*Axynotarsus sp.*	1	0	Herbivore
			Unidentified species 1	0	1	Soil Dweller
			Unidentified larva 1	2	5	Detritivore
			Unidentified larva 2	0	1	Detritivore
			Unidentified larva 3	0	6	Detritivore
		Eucnemidae	Unidentified larvae	0	2	Detritivore
		Elateridae	*Cardiophorus sp.*	2	0	Herbivore
			Cardiophorus sp. larva	1	19	Herbivore
		Cebrionidae	*Cebrio granatensis* larvae	1	175	Herbivore
		Buprestidae	*Julodis onopordi*	0	1	Herbivore
			Julodis onopordi larvae	0	10	Herbivore
		Lathrydidae	Unidentified larvae	2	0	Fungivore
		Anobiidae		2	0	Detritivore
		Anthicidae		16	1	Detritivore
			Unidentified larva	1	0	Detritivore
		Meloidae	*Berberomeloe majalis* hypnotheca	0	1	Non-*in situ*-consumer
			Mylabrini hypnotheca	0	1	Non-*in situ*-consumer
		Melandrydae	Unidentified larvae	1	13	Detritivore
		Tenebrionidae	*Pimelia integra*	10	2	Detritivore
			Pimelia monticola	6	0	Detritivore
			Pimelia spp. larvae	7	19	Detritivore
			Morica hybrida	2	0	Detritivore
			Morica hybrida larvae	2	14	Detritivore
			Tentyria incerta	6	1	Detritivore
			Tentyria incerta larvae	10	6	Detritivore
			Scaurus spp. larvae	4	14	Detritivore
			Alphasida clementei	1	0	Detritivore
			Alphasida clementei larvae	0	17	Detritivore
			Heliotaurus ruficollis larvae	14	26	Detritivore
			Asida cincta	4	0	Detritivore
			Asida rectipennis	1	0	Detritivore
			Asida spp. larvae	1	11	Detritivore
			Phylan gibbulus	1	1	Detritivore
			Unidentified larvae	4	9	Detritivore
		Cetoniidae	Unidentified larva	0	1	Herbivore
		Dinastydae	Unidentified larva	0	1	Detritivore
		Geotrupidae	*Bolbelasmus bocchus*	0	2	Fungivore
		Aphodiidae	*Aphodius baeticus*	0	6	Detritivore
			Aphodius baeticus larvae	11	9	Detritivore
		Melolonthidae	*Elaphocera segurensis*	0	1	Herbivore
			Rhizotrogus toletanus	1	5	Herbivore/Non-*in situ*-consumer
			Rhizotrogus toletanus larvae	0	6	Herbivore
			Unidentified larvae	6	47	Herbivore
		Cerambicidae	*Iberodorcadion mucidum* larva	0	1	Herbivore
		Chrysomelidae	*Chryptocephalus sp.* larva	1	0	Herbivore
			Galeruca augusta	2	0	Herbivore
			Unidentified larvae	4	1	Herbivore
		Curculionidae	*Coniocleonus obliquus*	1	0	Herbivore
			Cycloderes submetallicus	0	1	Non-*in situ*-consumer

			Unidentified larvae	65	8	Herbivore
		Unidentified larvae		5	13	
	Diptera	Asilidae larvae		3	12	Predator
		Tipulidae larvae		4	2	Herbivore
		Unidentified Diptera		13	53	
	Lepidoptera	Noctuidae	*Agrotis spp.*	1	0	Herbivore
			Agrotis spp. larvae	5	1	Herbivore
		Geometridae larvae		1	0	Herbivore
		Pterophoridae pupae		13	48	Herbivore
		Pyralidae larvae		2	1	Herbivore
		Unidentified larvae		17	5	Herbivore
	Hymenoptera	Formicidae	*Crematogaster lestrigum*	123	24	Omnivore/Non-*in situ*-consumer
			Aphaenogaster sp.	1	1	Omnivore/Non-*in situ*-consumer
			Botryomirmex sp.	2	0	Omnivore
			Messor barbarus	286	1057	Omnivore/Non-*in situ*-consumer
			Messor bouvieri	58	493	Omnivore/Non-*in situ*-consumer
			Messor spp. pupae	0	14	Non-*in situ*-consumer
			Monomorium sp.	3	0	Omnivore
			Tapinoma nigerrimum	103	38	Omnivore/Non-*in situ*-consumer
			Diplorhoptrum sp.	28	1037	Omnivore/Non-*in situ*-consumer
			Pheidole palidula	40	158	Omnivore/Non-*in situ*-consumer
			Tetramorium semilaeve	92	10377	Omnivore/Non-*in situ*-consumer
			Plagiolepis pigmea	247	324	Omnivore/Non-*in situ*-consumer
			Plagiolepis schmitzi	136	475	Omnivore/Non-*in situ*-consumer
			Leptothorax specularis	95	319	Omnivore/Non-*in situ*-consumer
			Lasius niger	4	59	Omnivore/Non-*in situ*-consumer
			Camponotus sp.	4	0	Omnivore
			Oxyopomyrmex sp.	24	80	Omnivore/Non-*in situ*-consumer
			Unidentified Formicidae	64	128	Omnivore/Non-*in situ*-consumer
		Bethylidae		5	2	Predator
		Mutillidae		0	1	Predator
		Platygastridae		1	0	Predator
		Cynipidae		0	1	Non-*in situ*-consumer
		Chalcidoidea		1	0	Predator
		Sphecidae		0	1	Predator
		Unidentified pupae		2	6	Non-*in situ*-consumer

Capitulo 2

Patchiness in a desert landscape: implications of shrub islands and ant-nest mounds on soil macroinvertebrate distribution

E. Doblas-Miranda, F. Sánchez-Piñero, A. González-Megías

(Subbmited)

Resumen

La variabilidad, tanto espacial como temporal, es una de las claves fundamentales para entender la estructura de las poblaciones, las comunidades y los ecosistemas. La heterogeneidad espacial está causada en muchos casos por organismos que son capaces de modificar sus propios ambientes. Esto es especialmente relevante en sistemas áridos, donde organismos como arbustos y hormigas son capaces de crear parches de gran disponibilidad de nutrientes (islas de fertilidad) rodeados por una matriz de pocos nutrientes.

El principal objetivo de este estudio es analizar los efectos de determinadas especies de arbusto y los acúmulos de detritus de ciertos hormigueros en los patrones de distribución y en la estructura de las comunidades de los macroartrópodos edáficos, en una zona desértica del sureste español de marcada estacionalidad.

Los arbustos isla y los acúmulos de hormiguero mantuvieron mayor riqueza, abundancia y biomasa que la matriz de suelo circundante. Los diferentes microhábitat difirieron en la composición taxonómica y trófica, en la abundancia y en la biomasa de los macroinvertebrados edáficos, tanto a nivel de hojarasca como en el medio subterráneo. Además, la distribución por microhábitat de los invertebrados mostró variaciones a través de los periodos de muestreo. Así que la heterogeneidad espacio-temporal de la zona de estudio afectó a la distribución y dinámicas de la comunidad de macroinvertebrados.

Los microhabitat isla en los ecosistemas áridos, donde la fauna del suelo se agrega, son potencialmente mantenidos por uniones complejas en las que participan los macroinvertebrados edáficos.

Abstract

Spatial and temporal variability is one of the fundamental keys to understand the structure of populations, communities and ecosystems. Spatial heterogeneity is caused in many cases by organisms that are able to modify their environments. This is especially relevant in arid systems, where organisms such as shrubs and ants create patches of high nutrient availability (fertile islands) surrounded by a low nutrient matrix.

The principal aim of our study is to analyze the effects of different shrub species and ant-nest mounds on the spatial distribution patterns and structure of soil macroarthropod assemblages in a strongly seasonal desert location of SE Spain.

Shrub islands and ant-nest mounds maintained higher richness, abundance and biomass than the surrounding soil matrix. The different microhabitats differed in taxonomic and trophic composition, abundance and biomass of soil macroinvertebrates, at both litter and belowground levels. Also, invertebrate distribution among microhabitats showed variations throughout sampling periods. Thus the spatio-temporal heterogeneity of the study site affected the distribution and dynamics of the macroinvertebrate community.

Island microhabitats in arid ecosystems, where soil fauna aggregate, are potentially maintained by complex linkages involving soil macroinvertebrates.

Key words

Fertile islands; Litter and belowground assemblages; Mediterranean arid ecosystem; Microhabitat distribution; Soil ecology

Introduction

Spatial heterogeneity is a key factor to understand the structure and dynamics of populations, communities and ecosystems (Stewart, John & Hutchings 2000). This spatial heterogeneity is in many cases created and maintained by organisms that are able to profoundly modify their environments, exerting an important influence on community structure and ecosystem level processes via their effects on nutrient dynamics and the creation of microsites (Jones, Lawton & Shachak 1994).

Shrubs in arid ecosystems are able to modify their near environment creating high nutrient patches in a low-nutrient matrix (i.e., fertile islands), with important consequences on arid land dynamics (Charley & West 1975; Garner & Steinberg 1989; Schlesinger *et al.* 1996; Facelli & Brock 2000). Fertile islands appear through different mechanisms involving the effects of both the root system (through resource adquisition, nitrogen fixation, hydraulic lift, chemical interactions with the soil and by changing water retention) and the canopy (affecting light, moisture, temperature, the accumulation of litter and wind-blown material, and probably enhancing the collection of stemflow water; Whitford, Anderson & Rice 1997; Facelli & Brock 2000). Shrubs also offer perching or resting sites to animals, leading to accumulations of faeces or deposition of propagules (e.g., Dean, Milton & Jeltsch 1999) which in turn enhance the fertile island effect. Differences in structure and physiology among shrub species provoke differences in their effects as island microhabitats (Charley and West 1975, Schlesinger *et al.* 1996, Titus, Nowak & Smith 2002).

In addition to shrubs, animals can be important agents causing patchiness in soils of arid regions. Animal activity can affect soil properties creating patches of higher nutrient and water availability via burrowing and nest construction, increasing the amount of organic matter, nitrogen, phosphorus and the rates of mineralization compared with the surrounding soil over time (Wagner, Brown & Gordon 1997; Wagner & Jones 2006; Whitford 2002). Harvester ants, a dominant group in most arid and semi-arid systems (MacKay 1991), usually construct deep burrow systems and form large debris accumulation around their nests, affecting soil chemistry and water infiltration (Cammeraat *et al.* 2002; Wagner & Jones 2006). Accumulation of litter and nutrients in these patches usually supports different plant assemblages and favours the existence of higher abundance and diversity of microorganisms and invertebrates (Wagner *et al.* 1997; Boulton, Jaffee & Scow 2003; Sánchez-Piñero & Gómez 1995).

The distribution pattern of soil organisms considering the spatial heterogeneity created by different shrub species and animal created patches constitute an important question to understand the structure and dynamics of desert systems (Whitford 2002). Although a number of studies have analyzed fertile islands and their effects on different organisms (e.g., Pen-Mouratov *et al.* 2004; Boulton *et al.* 2003), few papers have studied the distribution patterns of soil macroinvertebrates in patchy, heterogeneous soils of arid and semi-arid regions (Peterson *et al.* 2001) despite the crucial role of soil macrofauna in soil processes (Lavelle 1997; Wolters 2000),

In this paper, we analyse the distribution patterns of soil macroarthropods in a strongly seasonal desert location of SE Spain and explore the effects of different shrubs and ant-nest mounds on the structure of the assemblage. Our goals are to describe the distribution of macroarthropods in a patchy desert environment in which shrubs and ant-nest mounds function as fertile islands. We hypothesise that: 1) shrubs and ant-nests harbour a higher richness, abundance and biomass of soil macroarthropods than the surrounding soil; 2) macroinvertebrate assemblages vary among different shrub species and ant-nests; 3) shrub species and ant-nest mounds affect the trophic structure of the assemblage; 4) the spatial mosaic is temporally dynamic in this extreme, strongly seasonal desert environment.

Methods

Study system

The study was conducted at Barranco del Espartal, a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain), from June 2003 to May 2005. Potential evapo-transpiration exceeds three times the amount of annual rainfall (250-300 mm). Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40ºC to -14ºC), and highly seasonal. The sharp contrast between the hot and dry summers and the cold and rainy winters determine that autumn do not appear as a distinct season in the area (Castillo-Requena 1989), only three seasons being actually recognizable: 1) spring, from March to May; 2) summer, from June to September; and 3) winter, from October to February.

The soil is a Gypsiric Regosol (WRBSR, FAO 1998) characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (< 5% $CaCO_3$ content). Soil structure ranges from weak fine granular (in the upper centimetres of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually 15-20 cm depth, being the first 1-2 cm where the organic matter concentrates, with values < 2% in all cases) and C (Sierra *et al.* 1990). As a general trait of desert soils, most ground surface is devoid of litter (58%), which only occurs under shrubs (usually forming a thin, distinct layer in the soil surface) and in ant-nest mounds.

The vegetation is an arid open shrubsteppe dominated by *Artemisia* (*A. herba-alba* Asso and *A. barrelieri* Bess) and *Salsola* (*S. oppositifolia* Desf.) shrubs, tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.) and *Retama* (*R. sphaerocarpa* L.) brushes. The dominant shrubs at the study site provoke a facilitation effect on annuals and these or similar species have been documented as creating fertile islands in different deserts (*Artemisia*: Charley & West 1975, Haase 2001; *Salsola*: Allen & Allen 1988, Cannon *et al.*

1995; *Retama*: Pugnaire, Haase & Puigdefábregas 1996, López-Pintor, Gómez-Sal & Rey-Benayas 2006; *Stipa*: Maestre *et al.* 2001, 2002). Also, mounds of *Messor* harvester ants constitute patches with increased amount of nutrients, affecting the distribution of different organisms in arid and semi-arid systems (Wagner & Jones 2006, Cammeraat *et al.* 2002, Boulton *et al.* 2003).

The soil macroinvertebrate assemblage at the study site is dominated by arthropods both in terms of abundance and biomass. The most important groups are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae and Cebrionidae), Hemiptera (Margarodidae) and Embioptera (Oligotomidae). Some taxa appear mainly associated to the litter (such as Araneae, Juliformia and Carabidae adults) or belowground (e.g. Cebrionidae and Melolonthidae larvae, Margarodidae), and few but important groups act as a connection between both levels (Embioptera, Tenebrionidae larvae and Geophilomorpha) (Doblas-Miranda, Sánchez-Piñero & González-Megías in press).

Sampling design

The study was conducted during two years, from June 2003 to May 2005. To analyse the distribution of the soil macroinvertebrates, we considered two levels in the soil: litter (which appears as a distinct layer of accumulated detritus on the soil surface) and belowground. To sample the litter level, we collected the litter (leaf litter under the shrubs or detritus accumulated around the ant-nest mouth) contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel. Belowground samples were collected in the same spot by using a 10 cm diameter auger. Soil cores were extracted up to 50 cm depth. To analyse the distribution patterns of macroinvertebrates, both litter and core samples were taken in six different microhabitats: 1) *Artemisia*, 2) *Salsola*, 3) *Retama* 4) tussock grasses, 5) ant nest mounds (thereafter ant nest), and in 6) the bare soil matrix (devoid of litter). We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the two years of study. In order to investigate seasonal variations, we have distinguished 6 sampling periods, which comprise the 3 different seasons over the two years of study.

Samples were processed in the field using fine-mesh sieves (1 mm mesh size). After sieving, the litter or soil held back in the sieve was placed in 20 x 15 cm white pans and invertebrates were hand collected by carefully examining the soil. Unknown or small (c.a., < 1 cm length) invertebrates were preserved in 70% ethanol for later identification and measurement (using a binocular scope equipped with a micrometer, 0.1 mm accuracy). Large specimens were measured in the field using a digital caliper. Lengths were used to estimate macroinvertebrate dry weight (biomass) by means of allometric equations based on specimens from the study site (Hódar 1996).

Taxa were classified into five different trophic groups (see Doblas-Miranda *et al.* in press): Herbivores, detritivores, fungivores, predators and omnivores. Because some taxa live in the soil but do not feed on soil resources or prey, an additional group, called as "non-*in situ*-consumers", was included in the analysis. Assignation of taxa to a trophic group was based on published information (e.g., Moore, Walter & Hunt 1988; Decaëns *et al.* 1998) and observations at the study site.

Statistical analysis

To determine whether the distribution of the macroinvertebrates was uniform, random or clumped, the index of dispersion (ID) was calculated. The ID tests the equality of the variance to mean in a Poisson series. When $n > 30$, a d statistic with a critical value = 1.96 identifies the type of distribution; if $d > 1.96$, a clumped distribution is indicated. When a clumped distribution occurred, the Green's index (GI) was used to determine the degree of aggregation in the samples. GI varies between 0, for random, and 1, for maximum clumping (Ludwig & Reynolds 1988).

Diversity of macrofauna was assessed by three measurements: 1) Observed richness (S_{obs}), the number of species obtained in the different microhabitats; 2) Michaelis Menten richness estimator (MM_{mean}), a species richness estimator computed for Mao Tau species accumulation curve; and 3) Hulbert's Probability of Interspecific Encounter (HP'), an index of evenness unbiased by sample size and easily interpreted as a probability. MM_{mean} richness estimator was generated using EstimateS v 7.5 (Colwell 2005). HP' was generated and statistically compared among microhabitats (accounting for differences in the number of individuals sampled by rarefaction) using EcoSim v5.53® (Gotelli & Entsminger 2005). Rarefaction uses iterative randomization (1000 iterations) to generate a 95% confidence interval of the studied indexes for a sample of a given number of individuals. Thus, according to EcoSim, a sample has the same proportional diversity of a second sample with an equal number of individuals if its diversity value falls inside the 95% confidence interval of the randomly generated diversity index for the second sample (see Gotelli & Entsminger 2005 for further details).

To analyze similarity in assemblage composition, Beta diversity was calculated using two similarity indexes: the Sorensen index (qualitative, measuring whether assemblages differ in the species present) and the Morisita-Horn index (quantitative, which considers also the abundance of each species in the analysis; Magurran 2004). Because of the high number of ants in some samples, Formicidae were excluded to calculate the Morisita-Horn index. Beta diversity indexes were generated using EstimateS v 7.5 (Colwell 2005).

To compare differences in abundance (mean number of individuals per sample), biomass (mean dry weight per sample) or mean richness (mean number of species per sample) among microhabitats, Kruskal-Wallis and Mann-Whitney U tests were used. To analyze temporal differences in abundance, biomass and mean richness among microhabitats we carried out two different comparisons by means of Spearman rank correlation: 1) between adjacent seasons and 2) between the same season in different years. Non-parametric analyses were used because the data were not normally distributed. To test whether frequency distribution of trophic groups differed among microhabitats, we used a Chi-square test. To simplify the analysis, specific taxa were analyzed in terms of abundance and trophic groups in terms of biomass. Statistical analyses were conducted using Statistica software package (StatSoft Inc., Tulsa, USA).

Results

Aggregation

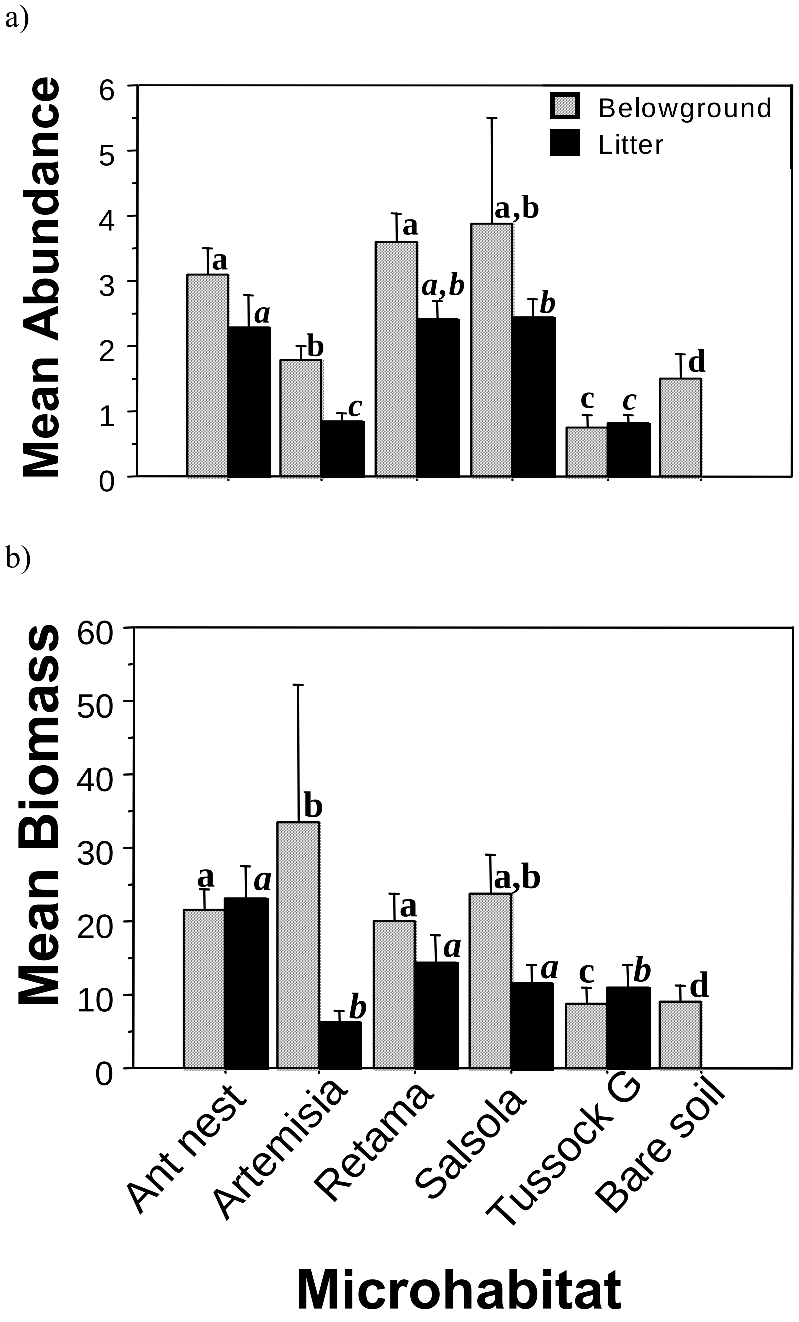
Considering the six microhabitats altogether, macroinvertebrates showed an aggregated distribution (d = 4359.3; GI = 0.27). Although macroinvertebrates aggregated at both litter and belowground ($d > 174.5$ in both cases), the two levels differed in aggregation, clumping being lower in litter (GI = 0.01) than belowground (GI = 0.36).

Within microhabitats, the distribution of macroinvertebrates was also clumped. Because of the low clumping in litter, only the distribution at belowground level was analysed for the different microhabitats. All the six microhabitats showed a clumped distribution of macroinvertebrates ($d \geq 78.42$ in all cases), although the degree of aggregation differed among microhabitats, being high in *Artemisia* (0.86) and bare soil (0.59), intermediate in *Salsola* (0.16) and tussock grasses (0.12), and low in *Retama* (0.08) and ant nest (0.07).

Microhabitat variability in abundance and biomass

At the litter level, the number of individuals (H = 57.44, $p < 0.0001$, d.f. = 4, 757) and biomass (H = 48.65, $p < 0.0001$, d.f. = 4, 757) of macroinvertebrates showed significant differences among microhabitats (Fig. 1). The highest abundance and biomass occurred in *Salsola*, *Retama* and ant nest, and the lowest in *Artemisia* and tussock grasses. At the belowground level, abundance (H = 121.32, p < 0.0001, d.f. = 5, 4542) and biomass (H = 122.38, p < 0.0001, d.f. = 5, 4542) also differed between microhabitats (Fig. 1). Ant nest, *Retama* and *Salsola* showed similar and high abundance of macroarthropods while tussock grasses showed the lowest abundance. For belowground biomass the pattern was similar, but in this case *Artemisia* showed the highest biomass.

Figure 1. Mean abundance (a, without Formicidae) and mean biomass (b) of soil macroinvertebrates per microhabitat.



Differences in microhabitat distribution was also observed in the dominant taxa ($H \geq 17.14$, $p < 0.01$, d.f. = 5, 5451 in all cases; Table 1). Although taxa showed different patterns in microhabitat distribution, in general most of them showed higher abundance in *Retama* and *Salsola*, while bare soil and tussock grasses were the microhabitats with the significantly lowest abundance in most taxa. In addition, some detritivore taxa (tenebrionid larvae, Embioptera, Oniscoidea, Thysanura) showed the highest abundances in ant-nest mounds.

Microhabitat variability in richness and diversity

Mean richness showed significant differences among microhabitats at both litter ($H = 48.65$, $p < 0.0001$, d.f. = 4, 757) and belowground levels ($H = 122.38$, $p < 0.0001$, d.f. = 5, 4542; Table 2). At the litter level, *Retama* and *Salsola* showed the highest values of mean richness, while the lowest richness corresponded to tussock grasses. At belowground level, the highest mean richness occurred in *Retama* and ant nest. Tussock grasses and bare soil were the microhabitats with the lowest richness (Table 2).

Observed richness followed a similar pattern than mean richness (Table 2). Michaelis Menten values also showed a similar pattern than richness, but at belowground level estimated richness was closer to the observed richness than at litter level (Table 2). Hulbert's PIE diversity was similarly high in *Retama*, *Salsola* and tussock grasses, while *Artemisia* showed low diversity values at both litter and belowground. Ant nest and bare soil showed also low diversity values at litter and belowground levels, respectively (Table 2).

Table 1. Mean abundance (± S.E.) of the main taxa in each microhabitat. Level column indicates the level where each group is predominant (L = Litter, B = Belowground, and L + B = both levels). Letters behind the numbers indicate statistically different means.

Taxa	**Level**	**Microhabitat**					
		Ant nest	**Retama**	**Salsola**	**Artemisia**	**Tussock G**	**Bare soil**
Araneae	L	0.048 ± 0.010 ^{a}	0.113 ± 0.018 ^{b}	0.147 ± 0.025 ^{b}	0.056 ± 0.011 ^{a}	0.059 ± 0.012 ^{a}	0 ^{c}
Oniscoidea	L	0.014 ± 0.007 ^{a,c}	0.005 ± 0.004 ^{b,c}	0.016 ± 0.006 ^{a}	0.001 ± 0.001 ^{b}	0.002 ± 0.002 ^{b}	0 ^{b}
Juliformia	L	0 ^{a}	0.029 ± 0.007 ^{b}	0.015 ± 0.004 ^{b}	0.002 ± 0.002 ^{a}	0.020 ± 0.005 ^{b}	0 ^{a}
Geophilomorpha	L + B	0.002 ± 0.002 ^{a}	0.026 ± 0.006 ^{b}	0.012 ± 0.004 ^{c}	0.010 ± 0.004 ^{a,c}	0.005 ± 0.002 ^{a,c}	0.004 ± 0.003 ^{a}
Thysanura	L	0.030 ± 0.012 ^{a}	0.010 ± 0.004 ^{a,b}	0.007 ± 0.003 ^{a,b}	0 ^{c}	0.004 ± 0.003 ^{b,c}	0 ^{c}
Embioptera	L + B	0.358 ± 0.088 ^{a}	0.180 ± 0.032 ^{a}	0.123 ± 0.017 ^{a}	0.051 ± 0.011 ^{b}	0.034 ± 0.008 ^{b}	0.002 ± 0.002 ^{c}
Margarodidae	B	0.111 ± 0.021 ^{a}	0.337 ± 0.051 ^{b}	0.427 ± 0.200 ^{b}	0.108 ± 0.024 ^{a,d}	0.045 ± 0.022 ^{c}	0.133 ± 0.044 ^{d}
Tenebrionidae (larvae)	L + B	0.087 ± 0.012 ^{a}	0.027 ± 0.006 ^{b}	0.022 ± 0.005 ^{b,c}	0.023 ± 0.005 ^{b}	0.011 ± 0.003 ^{c}	0.010 ± 0.003 ^{c}
Cebrionidae (larvae)	B	0.036 ± 0.007 ^{a}	0.034 ± 0.006 ^{a,b}	0.031 ± 0.006 ^{a}	0.052 ± 0.008 ^{b}	0.020 ± 0.005 ^{a}	0.022 ± 0.005 ^{a}
Carabidae (adults)	L	0.006 ± 0.003 ^{a}	0.038 ± 0.009 ^{b}	0.037 ± 0.010 ^{b}	0.003 ± 0.002 ^{a}	0.001 ± 0.001 ^{a}	0.001 ± 0.001 ^{a}
Formicidae	L + B	1.466 ± 0.387 ^{a}	1.213 ± 0.406 ^{a}	1.795 ± 0.483 ^{b}	12.23 ± 8.354 ^{b}	0.198 ± 0.092 ^{c}	1.134 ± 0.711 ^{c}

Table 2. Mean richness (± S.E.), Observed (S_{obs}) and expected (MMmean) richness, and Hulbert's probability of interspecific encounter diversity index (HP) for the different microhabitats in litter and aboveground. Letters behind the numbers indicate statistical differences.

Microhabitat	Mean Richness	S_{obs}	MMmean	HP
Litter				
Ant nest	1.230 ± 0.131^{a}	55	129.77	0.749^{a}
Retama	1.922 ± 0.168^{b}	74	92.42	0.906^{b}
Salsola	1.712 ± 0.135^{b}	83	121.65	0.931^{b}
Artemisia	$0.987 \pm 0.124^{a,c}$	58	104.75	0.892^{c}
Tussock grasses	0.697 ± 0.082^{c}	43	70.25	0.926^{b}
Belowground				
Ant nest	2.223 ± 0.177^{a}	49	57.02	0.574^{a}
Retama	2.195 ± 0.162^{a}	56	68.54	0.755^{b}
Salsola	$1.837 \pm 0.132^{a,b}$	50	60.39	0.781^{b}
Artemisia	1.560 ± 0.127^{b}	51	66.17	0.132^{c}
Tussock grasses	0.651 ± 0.074^{c}	32	47.36	0.788^{b}
Bare soil	1.007 ± 0.117^{d}	35	48.08	0.388^{d}

Species composition

As indicated by the Sorensen index, similarity between microhabitats was in general very low for both litter and belowground levels (Table 3). Morisita-Horn values were high for both levels (Table 3). At the litter level, the higher similarities were found between the shrubs, and the lower corresponded to ant nest compared with the rest. At the belowground level, Morisita-Horn values were in general higher than at litter level, and again ant nest showed the lower similarities with the other microhabitats.

Table 3. Species turnover between microhabitats. Sorensen index in lower diagonal and Morisita-Horn index in upper diagonal. Formicidae were not considered in the analysis.

a) Litter level.

	Artemisia	Ant nest	Retama	Salsola	Tussock G
Artemisia	*	0.58	0.86	0.79	0.83
Ant nest	0.59	*	0.76	0.45	0.50
Retama	0.58	0.57	*	0.74	0.78
Salsola	0.55	0.54	0.64	*	0.82
Tussock-Grasses	0.52	0.56	0.51	0.46	*

b) Belowground.

	Artemisia	Ant nest	Retama	Salsola	Bare Soil	Tussock G
Artemisia	*	0.72	0.89	0.83	0.90	0.97
Ant nest	0.67	*	0.69	0.60	0.55	0.73
Retama	0.61	0.67	*	0.98	0.96	0.89
Salsola	0.56	0.59	0.64	*	0.95	0.83
Bare Soil	0.57	0.60	0.53	0.53	*	0.89
Tussock-Grasses	0.51	0.57	0.53	0.55	0.53	*

Table 4. Mean biomass (± S.E.) of the different trophic groups in each microhabitat in litter and belowground. Letters behind the numbers indicate statistically different means.

Trophic groups	**Microhabitats**					
	Ant nest	**Retama**	**Salsola**	**Artemisia**	**Tussock G**	**Bare soil**
Litter						
Detritivores	19.85 ± 4.00 ^{a}	8.94 ± 2.75 ^{a}	6.32 ± 2.15 ^{a}	3.29 ± 1.48 ^{b}	9.91 ± 3.04 ^{b}	
Herbivores	1.35 ± 0.81 ^{a,c}	0.75 ± 0.28 ^{a,b}	1.58 ± 0.53 ^{b}	1.32 ± 0.58 ^{a,c}	0.29 ± 0.15 ^{c}	
Omnivores	0.64 ± 0.27 ^{a}	0.66 ± 0.23 ^{a}	0.55 ± 0.21 ^{a}	0.43 ± 0.15 ^{a}	0.09 ± 0.04 ^{b}	
Predators	1.24 ± 0.34 ^{a}	3.73 ± 1.63 ^{b}	2.06 ± 0.34 ^{b}	0.99 ± 0.30 ^{a}	0.63 ± 0.16 ^{a}	
Non-*in situ*-consumers	0	0.25 ± 0.25 ^{a}	1.14 ± 0.43 ^{b}	0.11 ± 0.09 ^{a}	0.01 ± 0.01 ^{a}	
Fungivores	0	0.026	0	0	0	
Belowground						
Detritivores	14.67 ± 2.22 ^{a}	7.31 ± 0.33 ^{b}	9.63 ± 2.42 ^{b}	4.71 ± 1.22 ^{c}	6.23 ± 1.70 ^{c}	0.39 ± 0.15 ^{d}
Herbivores	4.65 ± 0.99 ^{a}	3.09 ± 0.65 ^{a}	2.83 ± 0.57 ^{a}	2.79 ± 0.62 ^{a}	2.39 ± 0.78 ^{b}	2.71 ± 0.57 ^{b}
Predators	1.25 ± 0.40 ^{a}	4.83 ± 1.61 ^{b}	2.04 ± 0.45 ^{b}	1.24 ± 0.39 ^{a}	0.47 ± 0.11 ^{a}	0.29 ± 0.13 ^{c}
Non-*in situ*-consumers	1.39 ± 0.45 ^{a}	1.65 ± 0.47 ^{a}	2.97 ± 0.83 ^{a}	10.56 ± 9.45 ^{a}	0.40 ± 0.15 ^{b}	1.15 ± 0.88 ^{b}
Fungivores	0	0.013	0	0.206	0.267	0

Variations in trophic composition

The biomass of the different trophic groups showed significant variations among microhabitats at both litter ($H > 42.41$, $p < 0.0001$, d.f. = 5, 909 in all cases) and belowground levels ($H > 24.42$, $p < 0.001$, d.f. = 5, 4542 in all cases; Table 4). At litter most groups showed high biomass in *Salsola* and *Retama* while the lowest occurred in tussock grasses. Detritivores and omnivores showed also higher abundance in ant nest. At belowground most trophic groups showed also high biomass in *Retama* and *Salsola*, but *Artemisia* showed high quantities too. Detritivores and herbivores showed also high biomass in ant nest. The lowest biomass occurred in tussock grasses and bare soil for most trophic groups.

There were great fluctuations among the different microhabitats in the relative frequency of biomass of the different trophic groups, for both litter ($\chi^2 > 12.42$, $p < 0.05$, d.f. = 4 in all cases) and belowground levels ($\chi^2 > 13.54$, $p < 0.01$, d.f. = 3 in all cases). At litter level, the proportion of detritivores was much high in ant nest and tussock grasses, where we did not find non-*in situ*-consumers. Predators showed a high proportion in *Retama* and non-*in situ*-consumers in *Salsola*, while in *Artemisia* proportions were more even. Belowground assemblages were different of litter level: non-*in situ*-consumers dominated in *Artemisia*; both herbivores and detritivores shared the highest proportions in ant nest and tussock grasses. Also, detritivores were more representative in *Salsola* and herbivores in bare soil; in *Retama*, all groups shared approximately the same proportions, including predators.

Temporal variations in mean richness, abundance and biomass

The pattern of macroinvertebrate mean richness among microhabitats showed seasonal variations. At litter, all seasons showed a similar pattern (see Table 2a; $r_s \geq 0.9$, $p < 0.05$) except spring2 ($r_s \leq 0.2$, $p \geq 0.75$ compared with the rest) that showed high mean richness in *Artemisia* and tussock grasses. At belowground there were more seasonal variations, only both winters being correlated ($r_s = 0.83$, $p < 0.05$) and also the consecutives winter1 with spring1 ($r_s \geq 0.83$, $p < 0.05$) and spring1 with summer2 ($r_s \geq 0.94$, $p < 0.01$).

The pattern of macroinvertebrate abundance among microhabitats showed important variations among sampling periods in both litter and belowground levels. At litter, both summers showed the same pattern ($r_s = 1$, $p < 0.0001$) while the rest of the sampling periods were not correlated ($r_s \leq 0.67$, $p \geq 0.15$ in all cases). Interestingly, in spring2 macroinvertebrate abundance showed non-significant differences among microhabitats ($p = 0.33$). At belowground, summer1 was correlated with winter1 ($r_s > 0.89$, $p < 0.05$), but there were not more correlations ($r_s \leq 0.46$, $p \geq 0.35$ in all cases).

The pattern of macroinvertebrate biomass among microhabitats showed great seasonal variations in litter ($r_s \leq 0.70$, $p \geq 0.18$ in all cases). Moreover, in spring2 macroinvertebrate biomass did not show significant differences among microhabitats ($p = 0.29$). At belowground both summers were correlated ($r_s = 0.94$, $p < 0.01$), but there were not more correlations ($r_s \leq 0.77$, $p \geq 0.07$ in all cases).

From the most abundant taxa analyzed: Aranei, Juliformia, Embioptera, Margarodidae, Tenebrionidae, Carabidae and Formicidae showed also seasonal changes in the pattern of microhabitat distribution, the 4 remaining taxa showing non-significant differences among microhabitats for the distinct sampling periods. Formicidae was the only taxa that showed differences between all the sampling periods ($r_s \leq 0.66$, $p \geq 0.16$ in all cases), but for the rest there was not a common pattern of variation: all of these taxa showed differences both in consecutive seasons ($r_s \leq 0.77$, $p \geq 0.07$), and in the same season both years ($r_s \leq 0.74$, $p \geq 0.09$), but the sampling periods that showed correlations were different for the distinct taxa.

Discussion

Shrub islands and ant-nest mounds affected soil macroarthropods, which were more diverse and abundant in these microsites than in the surrounding bare soil. The different microhabitats in the study system showed differences in taxonomic and trophic composition, abundance and biomass of soil macroinvertebrates, at both litter and belowground levels. Also, invertebrate distribution among microhabitats showed variations among sampling periods, emphasizing the spatio-temporal heterogeneity of the system.

Distinct microenvironments created by shrubs are very important in arid and semi-arid systems, where extreme conditions can be tempered by these plants providing milder microclimate, higher resource availability and shelter (Schlesinger *et al.* 1996; Titus *et al.* 2002; Bochet, Rubio & Poesen, 1999). In the Baza Basin, macroinvertebrate distribution was affected by shrubs, richness, abundance and biomass being 2.3-3.6 fold higher in the shrub microhabitats than in the bare soil matrix. In addition to shrubs, ant nest mounds also supported 2.2-4.9 times higher richness, abundance and biomass of macroarthropods than bare soil areas. Debris accumulated in ant nests mounds have been reported to affect soil properties (Wagner & Jones 2006; Cammeraat *et al.* 2002) and the distribution of soil biota (Sánchez-Piñero & Gómez 1995, Wagner *et al.* 1997, Boulton *et al.* 2003).

The effect of plant species on the distribution of soil fauna may be important when individual plants are spaced at enough distance to have a dominating influence on resources (Wardle 2002), as in the study area, where bare soil represents ca. 60% of the soil surface. Therefore, soil macrofauna of the Baza Basin aggregated in island microhabitats and, in fact, soil fauna showed a clumped distribution, especially belowground. Clumped distribution is a feature of soil faunal communities (Ettema & Wardle 2002) related principally to the patchy distribution of biotic and abiotic factors (Stanton and Tepedino 1977; Ettema *et al.* 1998), like the island microhabitats in the study system. By enhancing the abundance of ground dwelling detritivores, shrubs and ant-nests may constitute a factor determining predator density and territory distribution (Hódar, Campos & Rosales 1996; Francisco Sánchez-Piñero, unpublished data), supporting the idea that ant-nests (as shrubs) may constitute hot-spots where interactions are more intense.

The different island microhabitats showed significant differences among them in macrofaunal diversity, abundance and biomass. Shrub species are known to differ in their contribution to fertile islands. Differences between plant species in enrichment ratios and in their effects on biota have been obtained in previous studies in desert (Charley & West 1975; Garner & Steinberger 1989; Schlesinger *et al.* 1996; Titus *et al.* 2002; but see Thompson *et al.* 2005 for a contrasting result) and temperate ecosystems (e.g., Innes, Hobbs & Bardgett 2004; Viketoft *et al.* 2005). Differential effects of shrub species on soil properties and biota can be due to differences in the nutrient concentration and mineralization of leaf litter (Charley and West 1975), shrub appearance (Whitford *et al.* 1997, Wezel, Rajot & Herbrit 2000), and to a complex combination of biotic and abiotic factors (Garner and Steinberger 1989). Differences in macroinvertebrate distribution among shrub species can be related to the different availability of both food resources (Wardle 2002) and shelter (Bochet *et al.* 1999, Sabo, Soykan & Keller 2005). Further, the clumped distribution of macroinvertebrates found within samples of the same shrub species suggests that differences in structure, location or productivity among individual plants are likely to increase patchiness in the system.

Differences among microhabitats not only affected community descriptors as diversity, abundance, biomass, but also the taxonomic and trophic composition of the assemblage. The lowest similarities in assemblage composition corresponded to ant nest mounds, probably because of the distinct structure of this microhabitat (a detritus accumulation lacking a canopy and a rizhosphere). The rest of microhabitats, including bare soil, showed higher similarity in species composition, corroborating the idea that the roots extending outside the shrub canopy have also important effects (Li & Sarah 2003). However, these results should be taken with some caution, since the taxonomic resolution in some taxa known to show high host specificity, as Curculionidae (larvae could only be identified to family level), may result in lower similarity values among shrubs.

Our results also indicate that the spatial distribution of soil macroinvertebrates in the Baza Basin is dynamic in time, the distribution pattern of soil macroinvertebrates among microhabitats changing seasonaly. The temporal changes in the distribution pattern observed are probably related to seasonal variations in the macroinvertebrate fauna and to phenological differences among shrub species. Seasonality in the study site is strong and affects the structure of the macroinvertebrate assemblage (Doblas-Miranda *et al.*, in press). However, the temporal changes in distribution observed for specific taxa suggest that temporal variations of terrestrial invertebrates are also related with changes in the preferences for specific microhabitats, something reported in few studies (Sinclair, Lord & Thompson 2001). Thus, phenological differences among plant species may provoke changes in microhabitat selection among macroinvertebrates. Shrub species in the study site differ in their seasonal patterns of litter and root production and litter quality (Enrique Doblas-Miranda, unpublished data), factors related with the variations of abundance in the assemblage (E. D-M., F. S-P. & Adela González-Megías, unpublished data).

The spatio-temporal heterogeneity of the study site affected the distribution and dynamics of the macroinvertebrate community. Macrofauna was clumped in the distinct microhabitats, showing changes in their taxonomic and trophic composition. It has long been known that the soil faunal community has profound effects on plant growth, soil invertebrates being part of feedback loops linking C, N, microbial communities, and plants (Lavelle 1997; Wardle 1999; Ehrenfeld, Ravit & Elgersma 2005). Island microhabitats in arid ecosystems, where soil fauna aggregates, are thus potentially maintained by complex links that involve soil macroinvertebrates. Integrating macroinvertebrates in the study of the feedback interactions among soil organisms, soil processes and plants is likely to enhance our understanding of the formation and crucial role of fertile islands in desert ecosystems.

Bibliography

Allen, E.B., Allen, M.F., 1988. Facilitation of succession by the nonmycotrophyc colonizer Salsola kali (Chenopodiaceae) on a harsh site: effects of mycorrhizal fungi. American Journal of Botany 75, 257-266.

Bochet, E., Rubio, J.L., Poesen, J., 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. Catena 38, 23-44.

Boulton, A.M., Jaffee, B.A., Scow, K.M., 2003. Effects of a common harvester ant (Messor andrei) on richness and abundance of soil biota. Applied Soil Ecology 23, 257-265.

Cammeraat, L.H., Willott, S.J., Compton, S.G., Incoll, L.D., 2002. The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. Geoderma 105, 1-20.

Cannon, J.P, Allen, E.B., Allen, M.F., Dudley, L.M., Juniak, J.J., 1995. The effects of oxalates produced by Salsola tragus on the phosphorous nutrition of Stipa pulchra. Oecologia 102, 265-272.

Castillo-Requena, J.M., 1989. El clima de Andalucía: clasificación y análisis regional de los tipos de tiempo. Instituto de Estudios Almerienses, Almería, 266 pp.

Charley, J.L., West, N.E., 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. Journal of Ecology 63, 945-964.

Colwell, R.K., 2005. EstimateS -statistical estimation of species richness and shared species from samples version 7.5. User's guide and application published at http://purl.oclc.org/estimates

Dean, W.R.J., Milton, S.J., Jeltsch, F., 1999. Large trees, fertile islands, and birds in arid savanna. Journal of Arid Environments 41, 61-78.

Decaëns, T., Dutoit, T., Alard, D., Lavelle, P., 1998. Factors influencing soil macrofaunal communities in post-pastoral successions of western France. Applied Soil Ecology 9, 361-367.

Doblas-Miranda, E., Sánchez-Piñero, F., González-Megías, A., in press. Soil macroinvertebrate fauna of a Mediterranean arid system: composition and temporal changes in the assemblage. Soil Biology and Biochemistry.

Ehrenfeld, J.G., Ravit, B., Elgersma, K., 2005. Feedback in the plant-soil system. Annual Review of Environmental Resources 30, 75-115.

Ettema, C.H., Coleman, D.C., Vellidis, G., Lowrance, R., Rathbun, S.L., 1998. Spatiotemporal distributions of bacterivorous nematodes and soil resources in a restored riparian wetland. Ecology 79, 2721-2734.

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends in Ecology & Evolution 17, 177-183.

Facelli, J.M., Brock, D.J., 2000. Patch dynamics in arid lands: localized effects of Acacia papyrocarpa on soils and vegetation of open woodlands of south Australia. Ecography 23, 479-491.

Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of fertile islands in the desert ecosystem. Journal of Arid Environments 16, 257-262.

Gotelli, N.J., Entsminger, D.F., 2005. EcoSim: Null models software for ecology. Version 7.72. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm

Haase, P., 2001. Can isotropy vs. anisotropy in the spatial association of plant species reveal physical vs. biotic facilitation. Journal of Vegetation Science 12, 127-136.

Hódar, J.A., 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17, 421-433.

Hódar, J.A., Campos, F., Rosales, B.A., 1996. Trophic ecology of the Ocellated Lizard Lacerta lepida in an arid zone of southern Spain: relationships with availability and daily activity of prey. Journal of Arid Environments 33, 95-107.

Innes, L., Hobbs, P.J. & Bardgett, R.D., 2004. The impacts of individual plant species on rhizosphere microbial communities in soils of different fertility. Biology and Fertility of Soils 40, 7-13.

Jones, C.G., Lawton, J.H. & Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373-386.

Lavelle, P., 1997. Faunal activities and soil processes: Adaptative strategies that determine ecosystem function. Advances in Ecological Research 27, 93-132.

Li, X., Sarah, P., 2003. Arylsulfatase activity of soil microbial biomass along a Mediterranean-arid transect. Soil Biology and Biochemistry 35, 925-934.

López-Pintor, A., Gómez-Sal, A., Rey-Benayas, J.M., 2006. Shrubs as a source of spatial heterogeneity – the case of Retama sphaerocarpa in Mediterranean pastures of central Spain. Acta Oecologica 29, 247-255.

Ludwig, J.A., Reynolds, J.F., 1988. Statistical Ecology. Wiley Interscience, New York, 337 pp.

Maestre, F.T., Bautista, S., Cortina, J., Bellot, J., 2001. Potential of using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecological Applications 11, 1641-1655.

Maestre, F.T., Bautista, S., Cortina, J., Díaz, G., Honrubia, M., Vallejo, R., 2002. Microsite and mycorrhizal inoculum effects on the establishment of Quercus coccifera in a semi-arid degraded steppe. Ecological Engineering 19, 289-295.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Malden, 256 pp.

Moore, J.C., Walter, D.E., Hunt, H.W., 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annual Review of Entomology 33, 419-439.

Pen-Mouratov, S., Rakhimbaev, M., Barness, G., Steinberger, Y., 2004. Spatial and temporal dynamics of nematode populations under Zygophyllum dumosum in arid environments. European Journal of Soil Biology 40, 31-46.

Peterson, A.C., Hendrix, P.F., Haydu, C., Graham, R.C., Quideau, S.A., 2001. Single- shrub influence on earthworms and soil macroarthropods in the southern California chaparral. Pedobiologia 45, 509-522.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., 1996. Facilitation between higher plant species in a semiarid environment. Ecology 77, 1420-1426.

Sabo, J.L., Soykan, C.U., Keller, A., 2005. Functional roles of leaf litter detritus in terrestrial food webs. In: de Ruiter, P.C., Wolters, V., Moore, J.C. (Eds), Dynamic food webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, Oxford, pp. 211-222.

Sánchez-Piñero, F., Gómez, J.M., 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. Journal of Arid Enviroments 31, 91-104.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364-374.

Sierra, C., Ortega, E., Quirantes, J., Lozano, J., Martínez, J., 1990. Proyecto LUCDEME. Mapa de suelos. Baza-994. M.A.P.A.-ICONA.

Sinclair, B.J., Lord, J.M., Thompson, C.M., 2001. Microhabitat selection and seasonality of alpine invertebrates. Pedobiologia 45, 107-120.

Stanton, N.L., Tepedino, V.J., 1977. Island habitats in soil communities. In: Lohm, U., Persson, T. (Eds), Soil Organisms as Components of Ecosystems. Swedish Natural Science Research Council, Stockholm, pp. 514-515.

Stewart, A.J.A., John, E.A., Hutchings, M.J., 2000. The world is heterogeneous: ecological consequences of living in a patchy environment. In: Hutchings, M.J., John, E.A., Stewart

A.J.A. (eds), The ecological consequences of environmental heterogeneity. Blackwell Science, Oxford, pp. 1-8.

Thompson, D.B., Walker, L.R., Landau, F.H., Stark, L.R., 2005. The influence of elevation, shrubspecies, and biological soil crust on fertile islands in the Mojave Desert, USA. Journal of Arid Environments 61, 609-629.

Titus, J.H., Nowak, R.S., Smith, S.D., 2002. Soil resource heterogeneity in the Mojave Desert. Journal of Arid Environments 52, 269-292.

Viketoft, M., Sohlenius, B., Palmborg, C., Huss-Danell, K., Bengtsson, J., 2005. Plant species effects on soil nematode communities in experimental grasslands. Applied Soil Ecology 30, 90-103.

Wagner, D., Jones, J.B., 2006. The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biology and Biochemistry 38, 2593-2601.

Wagner, D., Brown, M.J.F., Gordon, D.M., 1997. Harvester ant nests, soil biota and soil chemistry. Oecologia 112, 232-236.

Wardle, D.A., 1999. How soil food webs make plants grow. TRENDS in Ecology & Evolution 14, 418-420.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton & Oxford, 392 pp.

Wezel, A., Rajot, J.L., Herbrig, C., 2000. Influence of shrubs on soil characteristics and their function in Sahelian agro-ecosystems in semi-arid Niger. Journal of Arid Environments 44, 383-398.

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, London, 343 pp.

Whitford, W.G., Anderson, J., Rice, P.M., 1997. Stemflow contribution to the ‘fertile island’ effect in creosotebush, Larrea tridentata. Journal of Arid Environments 35, 451-457.

Wolters, V., 2000. Invertebrate control of soil organic matter stability. Biology and Fertility of Soils 31, 1-19.

WRBSR, FAO, 1998. World Reference Base for Soil Resources. FAO-ISRIC-ISSS. Rome.

Capitulo 3

Vertical distribution of soil macrofauna in an arid ecosystem: are above- and belowground habitats compartmentalized?

E. Doblas-Miranda, F. Sánchez-Piñero, A. González-Megías

Resumen

Tradicionalmente, los medios epigeo e hipogeo han sido considerados compartimentos diferentes del ecosistema terrestre. Aunque recientemente se ha destacado la importancia de las conexiones que existen entre ambos compartimentos a través de interacciones indirectas mediante plantas y depredadores generalistas, menor atención ha recibido la conexión entre ambos sistemas debida a los movimientos de la fauna a través del ecotono entre la hojarasca y medio subterráneo. El flujo directo de organismos entre ambos medios podría aportar nuevas ideas sobre las interacciones que existen entre los medios epigeo e hipogeo. Con el propósito de analizar el grado de compartimentación de las comunidades de la hojarasca y el medio hipogeo, se estudió la distribución vertical de la comunidad de macroinvertebrados en un sistema árido del sureste de la Península Ibérica. Durante dos años, dichas comunidades fueron muestreadas en la capa de hojarasca y debajo del suelo mediante sacatestigos. Los resultados obtenidos muestran que la riqueza, abundancia y biomasa de los macroinvertebrados decrecen gradualmente con la profundidad del suelo. Aunque las asociaciones faunísticas de la hojarasca y el medio hipogeo muestran algunas diferencias importantes tanto en su composición taxonómica como trófica, hubo taxones presentes en ambos hábitats que actúan como elementos conectores entre ambos subsistemas. Además, las migraciones verticales de las larvas de tenebrionidos detritívoros indican que esta conexión varia en el tiempo, destacando la importancia de la variabilidad temporal en la conexión entre los medios epigeo e hipogeo. Es por ello que los resultados obtenidos demuestran que tanto la hojarasca como el hábitat hipogeo no se encuentran compartimentados, mostrando organismos que actúan como vínculos directos entre ambos subsistemas.

Abstract

Aboveground and belowground ecosystem levels have been classically considered different compartments of terrestrial ecosystems. Although connections between both compartment *via* indirect interactions through plants and generalist predators have been recently emphasized, less has been done on the direct connectivity between above- and belowground systems by the movement of animals through the litter-soil ecotone. The direct flux of organisms between both habitats could provide new insights on above-/belowground interactions. In order to analyze the degree of compartmentalization among litter and belowground communities, we studied the vertical distribution of macroinvertebrates in an arid area of Southeastern Spain. During two years, macroinvertebrates were sampled by means of soil cores in the litter layer and the soil beneath. Results showed that macroinvertebrate richness, abundance and biomass decreased gradually with soil depth. Although the faunal assemblages of the litter and belowground habitats showed some important differences in taxonomic and trophic composition, there were taxa inhabiting both habitats, acting as connectors between both subsystems. In addition, seasonal vertical migrations of detritivorous tenebrionid larvae indicate that this connection varies in time, emphasizing the importance of temporal variability in the conection between above- and belowground habitats. Therefore, our results show that litter and belowground habitats are not compartmentalized, some organisms acting as direct links connecting both subsystems.

Key words

Litter and belowground links; litter ecotone; Mediterranean arid ecosystem; vertical migration; soil ecology.

Introduction

Aboveground and belowground ecosystem levels have been classically considered different compartments of terrestrial ecosystems, the aboveground grazing food web viewed as being separate from the decomposer soil community (Pimm and Lawton 1980). However, producers and decomposers are implicitly dependent on each other, connecting both compartments (Wardle 1999; Van der Putten et al. 2001; Ehrenfeld et al. 2005), and the soil biota includes root herbivores, actively contributing to the feedbacks between above- and belowground habitats (Bardgett and Wardle 2003; Blossey and Hunt-Joshi 2003). Another link between both subsystems occur trough generalist aboveground predators that feed on adults emerging from subterranean larvae (Scheu 2001; Miyashita et al. 2003). However, connectivity between above- and belowground systems through the movement of animals at the litter ecotone have received little attention, despite the fact that the direct flux of organisms between both levels could provide new insights on above-/belowground interactions (Wardle 2002).

The litter level constitutes an ecological boundary between above- and belowground compartments, acting as an area of transition between contrasting elements that are functionally connected by fluxes of organisms, material and elements (sensu Cadenasso et al. 2003). However, few studies have considered the litter interface as an ecological boundary, probably because the position and characteristics of the litter interface have generated certain confusion. Thus, the litter level has been usually considered as belonging to the belowground compartment, especially in temperate forest ecosystems where the limit between litter and belowground is diffused due to a gradual change of properties (e.g. Setälä and Aarnio 2002; Bardgett 2005). As a consequence, most macroarthropods inhabiting the litter level, as carabids and spiders, have been considered as part of the belowground community (e.g. Ekschmitt et al. 1997), while most of these arthropods are also active at the ground surface where they are both predators and prey (Johnston 2000). In addition, detritivores have been commonly considered as belowground biota (e.g. Scheu 2001), but they also are one of the main components of the ground surface macroinvertebrate assemblages, especially in deserts (Crawford 1991, Sánchez-Piñero 1994) where they constitute an important component in the diet of aboveground predators, as lizards, rodents or birds (e.g. James 1991; Kronfeld-Schor and Dayan 1999; Hódar 2006). In the opposite, endogeous animals (as earthworms or termites) access ground surface resources (e.g. Cortez and Bouche 1998; Ouédraogo et al. 2004) with potentially important consequences on both above- and belowground systems. Therefore, whether aboveground (ground surface) animals penetrate belowground, and viceversa, through the permeable litter level is a crucial question to understand the conection between these adjacent habitats.

The vertical distribution of soil macrofauna provides an insight to analyze whether litter and belowground communities are compartmentalized or are connected by animals moving between the surface and deeper ground levels. Unfortunately, the vertical distribution of soil animals has been poorly studied (Schaefer and Schauermann 1990; Sadaka and Ponge 2003). Most of the studies on vertical distribution of soil fauna are focused on microarthropods (see review by André et al. 2002) and earthworms (e.g. Jiménez and Decaëns 2000; García and Fragoso 2002), but few studies have considered macroarthropod communities (Dowdy 1944; Frouz et al. 2004).

In arid and semiarid areas, the litter usually forms a thin, discrete layer that remains separated from the soil substrate (Whitford 1989, 2002), providing a simplified system to analyze the role of the litter level as an ecological boundary connecting above- and belowground systems. The principal aim of our study is to analyze the degree of compartmentalization among litter and belowground macroarthropod assemblages. Macroartrhopods are particularly relevant organisms connecting above- and belowground habitats (Coleman 1996, Wardle 2002), especially in arid ecosystems, where they constitute a dominant component (Crawford 1981; Sánchez-Piñero 1994). Extreme environmental conditions common to deserts usually provoke marked temporal variations in the community, a fact that may affect vertical distribution patterns and, consequently, the conection between the litter and soil systems. To answer the question of whether litter and belowground macroarthropod assemblages are compartmentalized, we analyzed: 1) the vertical distribution of macroinvertebrates in terms of diversity, abundance and biomass; 2) the vertical changes in taxonomic and trophic structure of the assemblage; 3) the temporal variations in the vertical distribution of macroinvertebrates.

Methods

Study System

The study was conducted at Barranco del Espartal, a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain), from June 2003 to May 2005. Potential evapo-transpiration exceeds three times the amount of annual rainfall (250-300 mm). Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40ºC to -14ºC), and highly seasonal. The sharp contrast between the hot, dry summer conditions and the cold, rainy winter conditions determine that autumn and winter do not appear as distinct seasons in the area (Castillo-Requena, 1989), only three seasons being actually recognizable: 1) spring, from March to May; 2) summer, from June to September; and 3) winter, from October to February.

The soil is a Gypsiric Regosol (WRBSR, FAO, 1998), characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (< 5% $CaCO_3$ content). Soil structure ranges from weak fine granular (in the upper centimetres of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually 15-20 cm depth, being the first 1-2 cm where the organic matter concentrates, with values < 2% in all cases) and C (Sierra et al., 1990). As a general trait of desert soils, the litter and the topsoil profile in the study area are poorly mixed, and most ground surface is devoid of litter (58%), which only occurs under shrubs (usually forming a thin, distinct layer in the soil surface) and in ant-nest mounds.

The vegetation is an arid open shrubsteppe dominated by Artemisia herba-alba Asso and A. barrelieri Bess and Salsola oppositifolia Desf. shrubs, tussock grasses (Stipa tenacissima Kunth and Ligeum spartum L.) and Retama sphaerocarpa L. brushes. In addition to plants, Messor barbarus L. and M. bouvieri Bondroit ant-nest mounds constitute important components of the study system, forming large detritus accumulations in which detritivorous arthropods aggregate (Sánchez-Piñero and Gómez, 1995).

The soil macroinvertebrate assemblage at the study site is dominated by arthropods both in terms of abundance (99%) and biomass (95%). The dominant groups are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae, Cebrionidae and Carabidae), Hemiptera (Dimargarodes mediterraneus Silvestri, 1908), Embioptera (Haploembia palaui Stefani, 1955), Araneae, Isopoda (Porcelio sp.), Julida (Julus sp.), Geophilomorpha, and Thysanura (Doblas-Miranda et al., in press), which constitute 92.2% of the total abundance and 76.1% of the total biomass of the assemblage (E. Doblas-Miranda, F. Sánchez-Piñero, A. González-Megías, unpublished data).

Sampling design

The study was conducted during two years, from June 2003 to May 2005. To analyse the vertical distribution of the soil macroinvertebrates, we first collected the litter (leaf litter under the shrubs or detritus accumulated around the ant-nest mouth) contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel (in the following considered as litter), and then we extracted soil cores of 10 cm diameter up to 50 cm depth, at 10 cm depth intervals: 0-10 cm depth (thereafter level 1); 10-20 cm (level 2); 20-30 cm (level 3); 30-40 cm (level 4); and 40-50 cm (level 5). Maximum depth was selected based on preliminary data collected at the study site showing that all taxa and > 90%

abundance occurred from 0-50 cm depth (Sánchez-Piñero et al., unpublished data). Samples were taken in six different microhabitats: under the four dominant shrubs in the study site (Artemisia, Salsola, Retama and tussock grasses), in bare soil areas and in ant-nests. We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the two years of study. In order to investigate seasonal variations we have distinguished 6 sampling periods, which comprise the 3 different seasons over the two years of study (Summer1, Winter1, Spring1, Summer2, Winter2 and Spring2).

Samples were processed in the field using fine-mesh sieves (1 mm mesh size), then the soil was placed in 20 x 15 cm white pans and invertebrates were hand collected by carefully examining the soil. Dissecting the soil horizons has been proved to be an efficient extraction method for macrofaunal groups (Ponge et al. 1997). Unknown or small (c.a., < 1 cm length) invertebrates were preserved in 70% ethanol for later identification and measurement (using a binocular scope equipped with a micrometer, 0.1 mm accuracy). Large specimens were measured in the field using a digital caliper. Body lengths were used to estimate macroinvertebrate dry weight (biomass) by means of allometric equations obtained from specimens from the study area (Hodar, 1996).

Taxa were classified into five different trophic groups (Doblas-Miranda et al., in press): Herbivores, detritivores, fungivores, predators and omnivores. Because some taxa live in the soil but do not feed on soil resources or prey, an additional group, called as “non-in situ-consumers”, was included in the analysis. Assignation of taxa to a trophic group was based on published information (e.g., Moore et al., 1988; Decaëns et al., 1994) and observations at the study site.

Statistical analysis

Richness and diversity of macrofauna was assessed by three measurements: 1) Observed richness (S_{obs}), the number of species obtained in the different depth levels; 2) Michaelis Menten (MM_{mean}), a species richness estimator computed for Mao Tau species accumulation curve; and 3) Hulbert's Probability of Interspecific Encounter (HP'), an index of evenness unbiased by sample size and easily interpreted as a probability. MM_{mean} was generated using EstimateS v 7.5 (Colwell, 2005). HP' was generated using EcoSim v5.53® (Gotelli and Entsminger, 2005) and it was statistically compared among depth levels accounting for differences in the number of individuals sampled by rarefaction. Rarefaction uses iterative randomization (1000 iterations) to generate a 95% confidence interval of the studied indexes for a sample of a given number of individuals. Thus, according to EcoSim, a sample has the same proportional diversity of a second sample with an equal number of individuals if its diversity value falls inside the 95% confidence interval of the randomly generated diversity index for the second sample (see Gotelli and Entsminger 2005 for further details).

To analyze similarity in assemblage composition between levels, beta diversity was calculated using two similarity indexes: the Sorensen index (qualitative, measuring whether assemblages differ in the species present) and the Morisita-Horn index (quantitative, which considers also the abundance of each species in the analysis; Magurran, 2004). Because of the high number of ants in some samples, Formicidae were excluded to calculate the Morisita-Horn index. Beta diversity indexes were generated using EstimateS v 7.5 (Colwell, 2005).

To compare differences in abundance (mean number of individuals per sample, excluding Formicidae), biomass (mean dry weight per sample) or mean richness (mean number of species per sample) among depth levels, Kruskal-Wallis and Mann-Whitney U tests were used because data were not normally distributed. To analyze temporal differences in abundance, biomass and mean richness among depth levels we carried out two different comparisons by means of Spearman rank correlation: 1) between adjacent seasons and 2) between the same season in different years. Spearman rank correlation was used also to analyze differences in the pattern of vertical distribution between microhabitats. To test whether frequency distribution of trophic groups differed between depth levels, we used a Chi-square test (Sokal and Rohlf 2003). To simplify the analysis, differences among taxa in vertical distribution were analyzed in terms of abundance and differences among trophic groups in terms of biomass. Statistical analyses were conducted using Statistica software package (StatSoft Inc., Tulsa, USA).

Results

1. Variations in abundance and biomass

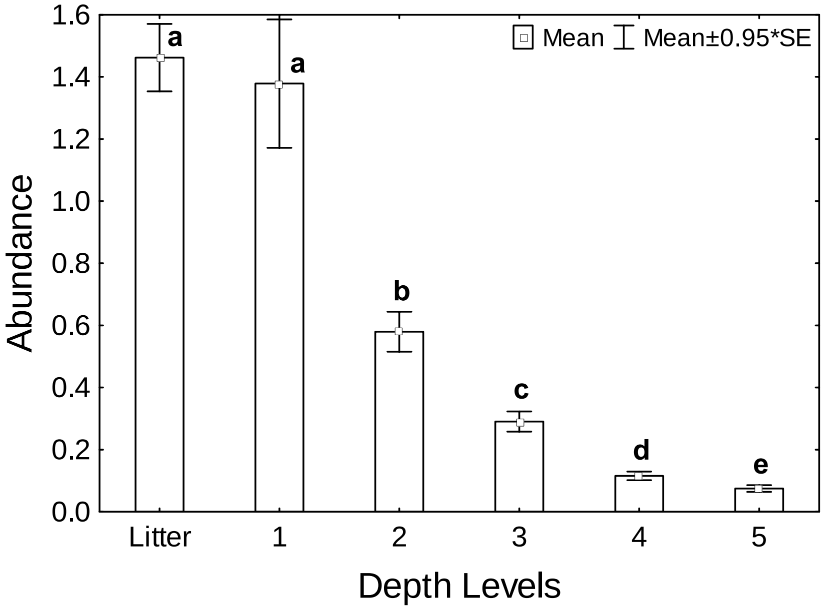
Abundance ($H = 679.5$, $p < 0.0001$, d.f. = 5, 5451) and biomass ($H = 663.2$, $p < 0.0001$, d.f. = 5, 5451) of macroinvertebrates showed significant differences among depth levels. The number of individuals and biomass decreased with soil depth, although in both cases no differences were found between litter and level 1 (Fig. 1a and 1b, respectively).

Differences in abundance among depth levels were also observed for the dominant taxonomic groups (Table 1). Some taxa were significantly more abundant at the litter level, like Aranei ($H = 684.57$, $p < 0.0001$, d.f. = 5, 5451), Isopoda ($H = 50.88$, $p < 0.0001$, d.f. = 5, 5451), Julida ($H = 137.03$, $p < 0.0001$, d.f. = 5, 5451), Thysanura ($H = 48.07$, $p < 0.0001$, d.f. = 5, 5451) and Carabidae ($H = 147.73$, $p < 0.0001$, d.f. = 5, 5451). Embioptera showed similar abundances in litter and level 1 ($H = 375.74$, $p < 0.0001$, d.f. = 5, 5451). Tenebrionidae ($H = 66.39$, $p < 0.0001$, d.f. = 5, 5451) and Geophilomorpha ($H = 14.58$, $p < 0.05$, d.f. = 5, 5451) showed small variations among litter and the more superficial levels. Ant abundance increased from litter to level 2 but decreased drastically from level 3 ($H = 265.9$, $p < 0.0001$, d.f. = 5, 5451). Finally, some taxa were found only at belowground levels: Margarodidae abundance decreased with depth ($H = 281.6$, $p < 0.0001$, d.f. = 5, 5451), while

Cebrionidae larvae showed similar abundances from level 1 to 3, decreasing at deeper levels (H = 98.55, p < 0.0001, d.f. = 5, 5451).

Figure 1. Mean total abundance (a) and biomass (b) of soil macroinvertebrates, per depth level. Letters indicate statistically different means.

a)



b)

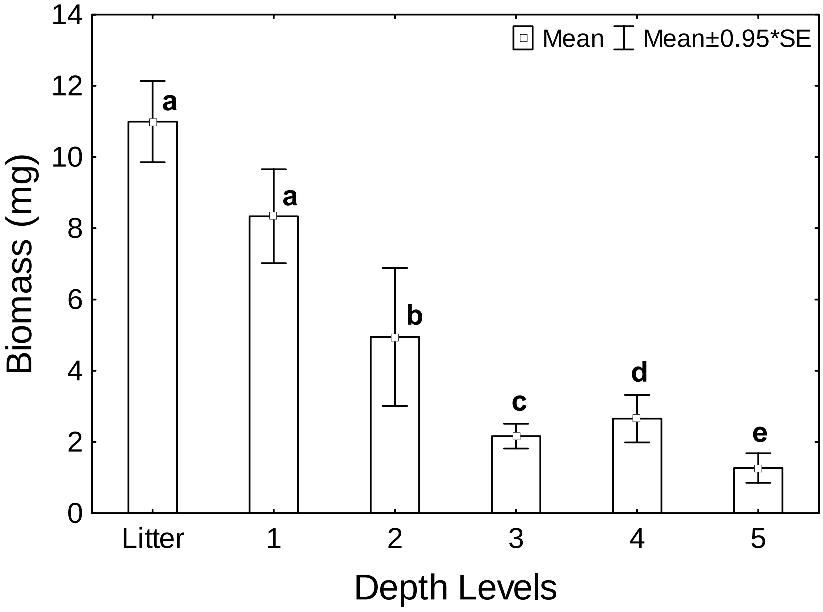


Table 1. Mean abundance (± S.E.) of the main taxa in each depth level. Letters behind the numbers indicate statistically different means.

Taxa	**Depth level**					
	Litter	**Level 1**	**Level 2**	**Level 3**	**Level 4**	**Level 5**
Aranei	0.371 ± 0.034 ^{a}	0.042 ± 0.007 ^{b}	0.011 ± 0.003 ^{c}	0.001 ± 0.001 ^{d}	0	0
Isopoda	0.029 ± 0.009 ^{a}	0.009 ± 0.004 ^{b}	0	0	0	0
Julida	0.053 ± 0.009 ^{a}	0.008 ± 0.003 ^{b}	0.004 ± 0.002 ^{b}	0	0	0
Geophilomorpha	0.012 ± 0.004 ^{a,b}	0.018 ± 0.005 ^{a}	0.014 ± 0.005 ^{a,b}	0.010 ± 0.003 ^{a,b}	0.003 ± 0.002 ^{b,c}	0.003 ± 0.002 ^{c}
Thysanura	0.030 ± 0.008 ^{a}	0.004 ± 0.002 ^{b}	0.003 ± 0.002 ^{b}	0.012 ± 0.010 ^{b}	0	0
Embioptera	0.384 ± 0.084 ^{a}	0.317 ± 0.043 ^{a}	0.039 ± 0.009 ^{b}	0	0	0
Margarodidae	0	0.666 ± 0.205 ^{a}	0.323 ± 0.062 ^{b}	0.129 ± 0.025 ^{c}	0.029 ± 0.010 ^{d}	0.015 ± 0.007 ^{d}
Tenebrionidae (larvae)	0.048 ± 0.009 ^{a,b}	0.066 ± 0.010 ^{a}	0.032 ± 0.006 ^{b}	0.011 ± 0.003 ^{c}	0.014 ± 0.004 ^{c}	0.007 ± 0.003 ^{c}
Cebrionidae (larvae)	0	0.058 ± 0.008 ^{a}	0.064 ± 0.009 ^{a}	0.046 ± 0.007 ^{a}	0.020 ± 0.005 ^{b}	0.004 ± 0.002 ^{c}
Carabidae (adults)	0.065 ± 0.012 ^{a}	0.018 ± 0.006 ^{b}	0.001 ± 0.001 ^{c}	0.003 ± 0.003 ^{c}	0	0
Formicidae	1.442 ± 0.256 ^{a}	6.180 ± 4.095 ^{b}	8.253 ± 7.235 ^{c}	1.206 ± 0.537 ^{c}	0.540 ± 0.194 ^{d}	0.302± 0.166 ^{e}

2. Richness and diversity

Mean richness showed significant differences among depth levels (H = 743.9, $p < 0.0001$, d.f. = 5, 5451), with a progressive decrease of the mean number of species from litter to the deepest level (Table 2). Observed richness also decreased from litter to level 5 (Table 2) and the values of Michaelis-Menten were relatively similar to observed richness except for the increase in level 4 (Table 2).

Table 2. Mean richness (± S.E.), Observed (S_{obs}) and expected (MMmean) richness, and Hulbert's probability of interspecific encounter diversity index (HP') for the different depth levels. Letters behind the numbers indicate statistically different means or indexes.

Microhabitat	**Mean Richness**	$\mathbf{S_{obs}}$	**MMmean**	**HP'**
Litter	1.097 ± 0.053 $^{\mathbf{a}}$	125	136	0.929 $^{\mathbf{a}}$
Level 1	0.735 ± 0.053 $^{\mathbf{b}}$	79	88.02	0.673 $^{\mathbf{b}}$
Level 2	0.394 ± 0.022 $^{\mathbf{c}}$	51	59.42	0.320 $^{\mathbf{c}}$
Level 3	0.243 ± 0.017 $^{\mathbf{d}}$	43	52.1	0.793 $^{\mathbf{d}}$
Level 4	0.125 ± 0.012 $^{\mathbf{e}}$	38	55.68	0.702 $^{\mathbf{b}}$
Level 5	0.080 ± 0.010 $^{\mathbf{f}}$	23	33.2	0.536 $^{\mathbf{e}}$

Hulbert's PIE diversity index was significantly higher in litter, but the differences belowground did not show a clear pattern: There were similar values for levels 1 and 4, the highest HP' corresponding to level 3 and the lowest to level 2 (Table 2). The lower diversity obtained in levels 1 and 2 was probably related with the dominance of ants in these levels.

3. Variations in species composition

There was a low similarity in species composition between depth levels (Table 3). Highest values of Sorensen index were produced between adjacent levels, lower values resulting as distance between levels increase. The Morisita-Horn index showed very low similarities between litter and the remaining depth levels, but there was not a general pattern among the depth levels underground (Table 3).

Table 3. Species turnover between depth levels. Sorensen index in inferior-left corner, and Morisita-Horn index in superior-right corner.

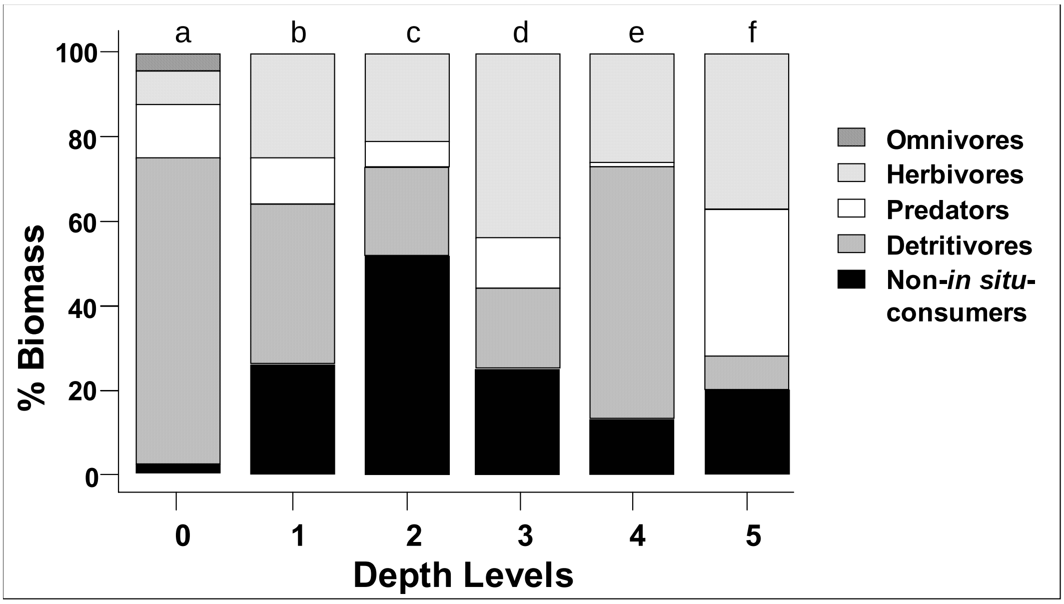
	Litter	**Level 1**	**Level 2**	**Level 3**	**Level 4**	**Level 5**
Litter	*	0.46	0.25	0.52	0.49	0.13
Level 1	0.63	*	0.87	0.42	0.59	0.45
Level 2	0.49	0.66	*	0.51	0.63	0.47
Level 3	0.39	0.57	0.68	*	0.69	0.28
Level 4	0.38	0.54	0.63	0.72	*	0.63
Level 5	0.28	0.39	0.55	0.59	0.61	*

4. Variations in trophic guilds

All trophic groups showed significant changes in biomass among depth levels ($H > 205.45$, $p < 0.0001$, d.f. = 5, 5451 in all cases; Table 4). Detritivores and predators showed the highest biomass in the litter level. Meanwhile, herbivores and non-in situ-consumers showed the highest biomass in levels 1 and 2.

In the other hand, all depth levels showed significant variations in the trophic composition of the assemblage ($\chi^2 > 25.16$, $p < 0.0001$, d.f. = 4 in all cases; Figure 2). Detritivores were the dominant trophic group at litter, showing a very high proportion compared with the other trophic groups. Herbivores showed a lower proportion at litter but then increased its relative abundance in deeper levels. Interestingly, predators maintained a similar proportion from litter to level 3.

Figure 2. Composition of the trophic assemblage, in % of total biomass, per depth level. Letters indicate statistically different compositions.



5. Variations in the vertical distribution among microhabitats

Bare soil was the only microhabitat that showed differences in the pattern of vertical distribution of richness and abundance ($r_s \leq 0.43$, $p \geq 0.39$). However, these differences were caused by the absence of litter in bare soil microhabitat, and when the litter level was not considered in the analysis, there were no differences among microhabitats in the pattern of vertical distribution of richness ($r_s \geq 0.9$, $p < 0.05$) and abundance ($r_s \geq 0.9$, $p < 0.05$).

There were differences in the vertical distribution of biomass among the different microhabitats: Artemisia and ant nest showed a similar pattern ($r_s = 0.9$, $p < 0.05$) of decreasing biomass with depth; Salsola and tussock grasses showed lower biomass in level 2 than in level 3 ($r_s = 0.9$, $p < 0.05$); Retama showed higher biomass in level 5 than levels 2, 3 and 4; and bare soil showed lower biomass in level 4 than in levels 3 and 5 ($r_s \leq 0.77$, $p > 0.07$).

Table 4. Mean biomass (± S.E.) of the different trophic groups in each depth level. Letters behind the numbers indicate statistically different means.

Trophic groups	**Depth level**					
	Litter	**Level 1**	**Level 2**	**Level 3**	**Level 4**	**Level 5**
Detritivores	8.01 ± 1.06 ^{a}	3.12 ± 0.56 ^{b}	1.03 ± 0.31 ^{c}	0.42 ± 0.19 ^{d}	1.60 ± 0.67 ^{d}	0.10 ± 0.04 ^{e}
Herbivores	0.89 ± 0.19 ^{a}	2.09 ± 0.37 ^{b}	1.06 ± 0.16 ^{c}	0.95 ± 0.23 ^{a}	0.69 ± 0.19 ^{d}	0.46 ± 0.14 ^{d}
Omnivores	0.39 ± 0.07	0	0	0	0	0
Predators	1.45 ± 0.29 ^{a}	0.95 ± 0.30 ^{b}	0.27 ± 0.12 ^{c}	0.25 ± 0.11 ^{c}	0.02 ± 0.01 ^{d}	0.45 ± 0.40 ^{d}
Non-*in situ*-consumers	0.25 ± 0.09 ^{a}	2.18 ± 1.14 ^{b}	2.59 ± 2.01 ^{c}	0.45 ± 0.17 ^{d}	0.28 ± 0.09 ^{a}	0.26 ± 0.10 ^{a}
Fungivores	0	0	0	0.089	0.068	0

6. Temporal changes

There were no differences in the pattern of vertical distribution of macrofauna among seasons considering mean richness ($r_s \geq 0.94$, $p < 0.01$) and abundance ($r_s \geq 0.83$, $p < 0.05$). However, vertical distribution of biomass showed temporal variations: In spring and winter biomass showed the general pattern (see Fig. 1b), but both summers were different between them ($r_s = 0.26$, $p = 0.62$) and with the adjacent seasons ($r_s \leq 0.77$, $p \geq 0.07$): in Summer1, level 5 showed higher biomass than levels 3 and 4, while in Summer2, level 4 showed higher biomass than the rest.

Tenebrionidae and Cebrionidae larvae were the only taxa out of the 11 dominant groups of the assemblage that showed temporal variations in their vertical distribution. Tenebrionid abundance distribution showed significant differences among adjacent seasons ($r_s \leq 0.70$, $p \geq 0.12$), but not between the same season in different years ($r_s \geq 0.94$, $p < 0.01$): in winter there was a gradual decrease in the number of individuals from litter to level 3 ($H = 36.55$, $p < 0.0001$, d.f. = 5, 2207) but in summer the abundance of larvae decreased at litter and increased in levels 1 and 2 ($H = 37.82$, $p < 0.0001$, d.f. = 5, 1960), while in spring there was not a clear pattern of vertical distribution ($H = 11.18$, $p = 0.048$, d.f. = 5, 1284). Cebrionidae showed a similar vertical distribution pattern in abundance between the same season in different years ($r_s \geq 0.98$, $p < 0.001$) and between spring and winter both years ($r_s \geq 0.86$, $p < 0.05$). There was a shift of maximum Cebrionidae abundance from level 1 in winter ($H = 59.49$, $p < 0.0001$, d.f. = 5, 2207) and spring ($H = 29.84$, $p < 0.0001$, d.f. = 5, 1284) to deeper levels (2 and 3) in summer ($H = 47.49$, $p < 0.0001$, d.f. = 5, 1960).

Discussion

The macroinvertebrates of the Baza Basin showed a vertical distribution pattern of gradual decrease in abundance, biomass and diversity, with important differences in taxonomic and trophic composition occurring among the different levels, especially between litter and belowground profiles. However, groups living in the litter-belowground interface and specific taxa that showed seasonal vertical migrations suggest the occurrence of direct connections between both habitats.

Richness, abundance and biomass decreased gradually with soil depth, in agreement with previous studies (Berg et al. 1998; Sadaka and Ponge 2003; Frouz et al. 2004). Interestingly, this vertical distribution pattern showed few variations among microhabitats except for biomass, a result probably related with differences in the presence or absence of specific taxa in each microhabitat (Tsukamoto and Sabang 2005). Nevertheless, there were great differences in diversity among levels, the litter layer maintaining a higher diversity than the underground profile, as previously indicated for Mediterranean ecosystems (Di Castri and Di Castri 1981). The distinction between both habitats was clearly shown by the species composition, and by the vertical distribution of the dominant taxa and trophic groups: predators were mainly litter dwellers, while soil herbivores occurred principally belowground, where they can find their resource, roots (Sadaka and Ponge 2003, Doblas-Miranda et al. in press).

However, despite the differences between litter and belowground communities, direct connection involving litter and belowground levels occurred in the study area. There were taxa like Tenebrionidae, Embioptera or Geophilomorpha (together constituting 27.3% of the species analized and as much as 52.4% and 23.1% of the total invertebrate biomass in litter and belowground, respectively; Doblas-Miranda et al. unpublished data), which inhabit both subsystems. Embioptera in Mediterranean ecosystems inhabit in silk galleries that ramify along the litter-soil interface (Ross 1966), showing that even in extreme environments, with no gradual transition between litter and soil, macrofauna is able to use the thin ecotone between the two subsystems. On the other hand, Geophilomorpha and Tenebrionidae were found along a wide range of depth levels. In fact, the first group has been recorded as predators usually found in both litter and deeper levels in the soil (Lewis 2003), while

Tenebrionidae larvae are detritivores that use resources in both habitats up to 80 cm depth (Sánchez-Piñero et al., unpublished data).

Interestingly, the vertical migrations of Tenebrionidae larvae (a dominant group in our system both in terms of abundance and biomass; Doblas-Miranda et al., in press) indicate that the conection between litter and belowground habitats varies in time. Thus, larvae used more frequently the surface litter during winter and spring, when detritus are more humid and edible (detritus edibility depends on moisture; Olear and Seastedt 1994), while in summer (when the litter is dry) larvae are mostly active deeper in the soil, where they feed on root detritus (Sánchez-Piñero et al., pers. obs.). These seasonal variations in the use of litter by Tenebrionidae larvae is likely to have a crucial impact on decomposition in the system since litter bag experiments in the study site show that belowground Tenebrionid larvae (representing 50% of the biomass of belowground detritivores; Doblas-Miranda et al. unpublished data) have significant effects in litter decomposition at the study site (González-Megías et al. unpublished manuscript). This pattern of temporal variability in the connections among different soil layers, principally related with seasonal environmental variations, may probably be a common feature in soil communities, as suggested by the occurrence of vertical migrations in diverse soil inhabiting taxa in different systems (Dowdy 1944, Briones et al 1998, Jiménez and Decaëns 2000, Frouz et al. 2004). Thus, temporal variability should be considered when analysing the relationships between aboveground and belowground communities and their consequences for ecosystem structure and function (see review by Bardgett et al. 2005, Begtsson and Berg 2005).

The study system showed a clear gradient in the vertical distribution of the macrofauna, with a few but relevant groups inhabiting in both litter and belowground levels and acting as connectors between both habitats. Detritivorous Tenebrionidae, feeding in both levels, showed seasonal vertical migrations with potential direct consequences in the dynamics of matter and energy between above- and belowground habitats, emphasizing the importance of considering temporal variability to understand the conection between these two subsystems, especially in highly seasonal and heterogeneous desert ecosystems (Doblas-Miranda et al., in press). Thus, litter and underground levels are not compartmentalized, and even in arid ecosystems the litter-soil interface is permeable to the fluxes of organisms.

Bibliography

André, H. M. et al.. 2002. Soil biodiversity: myth, reality or conning? - Oikos 96: 3-24.

Bardgett, R. D. 2005. The Biology Of Soil: A Community And Ecosystem Approach. - Oxford Univ. Press.

Bardgett, R. D. et al. 2005. A temporal approach to linking aboveground and belowground ecology. - Trends Ecol. Evol. 20: 634-641.

Bardgett, R. D. and Wardle, D. A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. - Ecology 84: 2258-2268.

Bengtsson, J. and Berg, M. P. 2005. Variability in food web structure across time and space. - In: de Ruiter P.C., Wolters V., Moore J.C. (eds), Dynamic Food Webs. Multispecies assemblages, ecosystem development and environmental change. Elsevier Academic Press, pp. 201-210.

Berg, M. P. et al. 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. - Biol. Fert. Soils 26: 268-284.

Blossey, B. and Hunt-Joshi, T. R. 2003. Belowground herbivory by insects: Influence on Plants and Aboveground Herbivores. - Annu. Rev. Entomol. 48: 521-547.

Briones, M. J. I. et al. 1998. Climate change and Cognettia sphagnetorum: effects on carbon dynamics in organic soils. - Funct. Ecol. 12: 528-535.

Cadenasso, M. L. et al. 2003. An interdisciplinary and synthetic approach to ecological boundaries. - Bioscience 53 (8): 717-722.

Castillo Requena, J. M. 1989. El clima de Andalucía: clasificación y análisis regional de los tipos de tiempo. - Instituto de Estudios Almerienses.

Coleman, D. C. 1996. Energetics of detritivory and microbivory in soil in theory and practice. - In: Polis, G. A. and Winemiller, K. O. (eds), Food Webs: Integration of patterns and dynamics. Chapman and Hall, pp. 39-50.

Colwell, R. K. 2005. EstimateS -statistical estimation of species richness and shared species from samples version 7.5. User's guide and application published at http://purl.oclc.org/estimates

Cortez, J. and Bouche, M. B. 1998. Field decomposition of leaf litters: earthworm-microorganism interactions--the ploughing-in effect. - Soil Biol. Biochem. 30: 795-804.

Crawford, C. S., 1991. The community ecology of macroarthropod detritivores. - In: Polis, G. A. (ed), The Ecology of Desert Communities. Univ. of Arizona Press, pp. 89-112.

Decaëns, T. et al. 1994. Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. - Eur. J. Soil Biol. 30: 157-168.

Di Castri, F. and Di Castri, V. V. 1981. Soil fauna of Mediterranean-climate regions. - In: Di Castri, F., Goodall, D. W. and Specht, R. L. (eds), Ecosystems of the World. 11. Mediterranean type shrublands. Elsevier, pp. 445-478.

Doblas-Miranda, E. et al. Soil macroinvertebrate fauna of a Mediterranean arid system: composition and temporal changes in the assemblage. - Soil Biol. Biochem., In press.

Dowdy, W. W. 1944. The influence of temperature on vertical migration of invertebrates inhabiting different soil types. - Ecology 25: 449-460.

Ekschmitt, K. et al. 1997. Spiders, carabids, and staphylinids: the ecological potential of predatory macroarthropods. - In: Benckiser, G. (ed), Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production. Marcel Dekker, pp. 307-362.

Ehrenfeld, J. G. et al. 2005. Feedback in the plant-soil system. - Annu. Rev. Env. Resour. 30: 75-115.

Frouz, J. et al. 2004. Horizontal and vertical distribution of soil macroarthropods along a spatio-temporal moisture gradient in subtropical Central Florida. - Environ. Entomol. 33: 1282-1295.

García, J. A., and Fragoso, C. 2002. Growth, reproduction and activity of earthworms in degraded and amended tropical open mined soils: laboratory assays. - Appl. Soil Ecol. 20: 43-56.

Gotelli, N. J. and Entsminger, D. F. 2005. EcoSim: Null models software for ecology. Version 7.72. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm

Hódar, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. - Acta Oecol. 17: 421-433.

Hódar, J. A. 2006. Diet composition and prey choice of the southern grey shrike Lanius meridionalis L. in South-eastern Spain: the importance of vertebrates in the diet. - Ardeola 53: 237-249.

James, C. D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (Ctenotus: Scincidae) in central Australia. - Oecologia 85: 553-561.

Jiménez Jaen, J. J., and Decaëns, T. 2000. Vertical distribution of earthworms in grassland soils of the Colombia Llanos. - Biol. Fert. Soils 32: 463-473.

Johnston, J.M. 2000. The contribution of microarthropods to aboveground food webs: a review ad model of belowground transfer in a coniferous forest. - Am. Midl. Nat. 143: 226-238.

Kronfeld-Schor, N and Dayan, T. 1999. The dietary basis for temporal partitioning: food habits of coexisting Acomys species. - Oecologia 121 (1): 123-128.

Lewis, J. G. E. 2003. Water relations, habitat and size in lithobiomorph and geophilomorph centipedes (Myriapoda; Chilopoda). - Bulletin of the British Myriapod and Isopod Group 19: 51-56.

Magurran, A. E. 2004. Measuring Biological Diversity. - Blackwell Publishing.

Miyashita, T. et al. 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. - Oikos 103: 31-36.

Moore, J. C. et al. 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. - Ann. Rev. .Entomol. 33: 419-439.

Olear, H. A. and Seastedt, T. R. 1994. Landscape patterns of litter decomposition in alpine tundra. - Oecologia 99 (1-2): 95-101.

Ouédraogo, E. et al. 2004. Soil macrofaunal-mediated organic resource disappearance in semi-arid West Africa. - Appl. Soil Ecol. 27: 259-267.

Petersen, H. and Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. - Oikos 39: 288-388.

Pimm, S. L. and Lawton, J. H. 1980. Are food webs divided into compartments? - J. Anim. Ecol. 49: 879-898.

Ponge, J. F. et al. 1997. Soil fauna and site assessment in beech stands of the Belgian Ardennes. - Can. J. Forest Res. 27: 2053-2064.

Ross, E. S. 1966. The Embioptera of Europe and the mediterranean region. - Bulletin of the British Museum (Natural History) Entomology 17: 275-326.

Rusek, J. et al. 1999. Improved method for comparing abundance data for soil zoological field studies. - Eur. J. Soil Biol. 35: 145-152.

Sadaka, N. and Ponge, J. F. 2003. Soil animal communities in holm oak forests: influence of horizon, altitude and year. - Eur. J. Soil Biol. 39: 197-207.

Sánchez-Piñero, F. 1994. Ecología de las comunidades de coleópteros en zonas áridas de la depresión de Guadix-Baza (Sureste de la Península Ibérica). - Univ. of Granada.

Sánchez-Piñero, F. and Gómez J. M. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. - J. Arid Environ. 31: 91-104.

Schaefer, M. and Schauermann, J. 1990. The soil fauna of beech forests: comparison between a mull and a moder soil. - Pedobiologia 34: 299–314.

Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. - Basic Appl. Ecol. 2: 3-13.

Schultz, G. B. and Crone, E. E. 2001. Edge-mediated dispersal behaviour in a prairie butterfly. - Ecology 82: 1879–1892.

Setälä, H. and Aarnio, T. 2002. Vertical stratification and trophic interactions among organisms of a soil decomposer food web - a field experiment using 15N as a tool. - Eur. J. Soil Biol. 38: 29-34.

Sierra, C. et al. 1990. Proyecto LUCDEME. Mapa de suelos. Baza-994. - M.A.P.A.-ICONA.

Sokal, R. R., Rohlf, F. J. 2003. Biometry: the principles and practice of statistics in biological research, third edn. - W. H. Freeman and company.

Tsukamoto, J. and Sabang, J. 2005. Soil macro-fauna in an Acacia mangium plantation in comparison to that in a primary mixed dipterocarp forest in the lowlands of Sarawak, Malaysia. - Pedobiologia 49: 69-80.

Van der Putten, W. H. et al. 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. - Trends Ecol. Evol. 16: 547-554.

Wardle, D. A. 1999. How soil food webs make plants grow. - Trends Ecol. Evol. 14: 418-420.

Wardle, D. A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton Univ. Press.

Whitford, W. G., 1989. Abiotic controls on the functional structure of soil food webs. Biol. Fert. Soils 8: 1-6.

Whitford, W. G., 2002. Ecology of Desert Systems. Academic Press.

WRBSR, FAO., 1998. World Reference Base for Soil Resources. FAO-ISRIC-ISSS.

Capitulo 4

Complexity in Mediterranean arid ecosystems: Abiotic and biotic factors controlling soil macroinvertebrates dynamic and distribution

Resumen

Describir los patrones de distribución y los mecanismos que explican estos patrones ha sido un objetivo en ecología desde hace mucho tiempo. Los factores ambientales, la heterogeneidad de los recursos y los procesos poblacionales interactúan juntos influyendo en la distribución de los organismos edáficos para determinar los complejos patrones espaciales observados en las comunidades del suelo. En los extremos ecosistemas áridos, el suelo bajo los arbustos muestra condiciones ambientales más suaves y una gran disponibilidad de recursos, así, estás plantas actúan como "islas de fertilidad", afectando en fuerte medida la distribución de las comunidades edáficas y favoreciendo las interacciones faunísticas. Nuestro objetivo es investigar los controles abióticos y de recurso sobre la distribución y dinámicas de la comunidad de macrofauna desértica en la Hoya de Baza. Durante dos años, los macroinvertebrados fueron muestreados por medio de sacatestigos y fueron registradas la temperatura y la humedad tanto en la hojarasca como bajo suelo, además fue medida la producción de hojarasca y raíces, así como las calidades de ambos recursos. Se realizó el análisis de los datos por medio de diferentes aproximaciones estadísticas. En contra de las ideas clásicas sobre los ecosistemas áridos, humedad y temperatura no fueron los únicos factores que afectaron a la fauna, y la producción de hojarasca y la calidad del recurso se revelaron como factores importantes en el control de la distribución de la macrofauna edáfica. Las interacciones entre los grupos tróficos fueron también un factor clave afectando las densidades de fauna y sugiriendo diferentes posibilidades de funcionamiento del ecosistema, con uniones entre los medios epigeo e hipogeo. Por lo tanto, los ecosistemas desérticos, y especialmente la fauna que allí habita, son complejos, ofreciendo la posibilidad de estudiar procesos ecológicos esenciales y mostrando ideas nuevas e importantes para futuras investigaciones.

Abstract

The description of species-distribution patterns and the mechanisms explaining these patterns have been an objective in ecology for a long time. Environmental controls, soil resource heterogeneity and population processes interact together influencing the distributions of soil organisms to determine the complex spatial patterns observed in soil communities. In the extreme arid and semi-arid ecosystems, the soil under the shrubs show milder climatic conditions and higher resource availability, this plants acting as "fertile islands", strongly affecting the distribution of soil communities and favouring faunal interactions. Our goal was to investigate abiotic and resource controls over desert soil macrofaunal community distribution and dynamics at the Baza Basin. During two years, macroinvertebrates were sampled by means of soil cores and temperature and moisture were registered both in litter and belowground levels, also litter and root productions as well as the quality of resource samples were measured. We perform the analysis using different statistical approximations. In contrast to classic ideas of arid ecosystems, moisture and temperature were not the only factors affecting fauna, and litter production and resource quality were revealed as important factors controlling soil macrofaunal distribution. Trophic groups interactions were also a key factor affecting the faunal densities and suggested different possibilities of ecosystem functioning, with above- belowground links. We thus conclude that desert ecosystems, and especially the soil macrofauna living there, are complex, offering the possibility of study essential ecological processes and showing new important ideas for future research.

Key words:

Faunal distribution; factors affecting distribution; resource quality; above- and belowground interactions; Structural Equation Models.

Introduction

The description of species-distribution patterns and the mechanisms explaining these patterns have been an objective in ecology for a long time (Begon et al. 1987, Ricklefs and Schluter 1993, Rosenzweig 1995, Gaston 2000, Whittaker et al. 2001). Organisms live in a spatial mosaic of physical traits with variations in the composition and abundance of resources affecting their distribution (Bell et al. 1991; Polis et al. 1996). In soil ecosystem, the effects of spatial variability in abiotic and resource factors are not only structural, but also functional (Legendre 1993), potentially influencing the spatial and temporal patterns of decomposition, root herbivory and ultimately, the distribution of animal and plant communities (Ettema and Wardle 2002).

Environmental controls, soil resource heterogeneity and population processes interact together influencing the distributions of soil organisms to determine the complex spatial patterns observed in soil communities (Ettema and Wardle 2002). Moreover, spatial patterns of abiotic factors, resources and soil biota are dynamic over time, showing great fluctuations (Görres et al. 1998; Stoyan et al. 2000; Ettema et al. 2000). The distribution of soil micro- and macrofauna is affected by environmental conditions (e.g. temperature, precipitation), resource abundance, elements distribution, soil structure and pH (Di Castri and Di Castri 1981, Ettema et al. 1998; Ponge 2000; Zimmer et al. 2000; Laiho et al. 2001; Verschoor et al. 2001; Maudsley et al. 2002; Hernández et al. 2003; Gongalsky et al. 2005). In addition, community distribution and dynamics may be better understood by taking into account not only the external influences, but also the faunal interactions (Fraslish 2002).

Faunal interactions are particularly relevant affecting the distribution of the more mobile soil macrofauna (Rossi et al. 1997; Margerie et al. 2001; Ettema and Wardle 2002). Soil macrofauna could constitute the principal approach to direct interactions among above- and belowground subsystems (Coleman 1996; Wardle 2002), and feedbacks among above- and belowground biota are major ecological drivers in terrestrial ecosystems (Wardle 2002).

Soil macroinvertebrates also affect soil processes and cause important modifications in the soil environment in all kinds of ecosystems (Lavelle 1997; Wolters 2000), but with potentially high implications in nutrient limited desert soils (Whitford 2000).

Soil macroarthropods constitute a relevant community of organisms in desert ecosystems (Wallwork 1982; Whitford 2000), where the characteristic high spatial and temporal heterogeneity determine the activity and the complex distribution of soil faunal communities (Polis 1991). In arid environments, soil food web dynamics have been considered principally affected by abiotic factors (Whitford 1989). In fact, deserts have been classically considered resource-pulse systems (Noy-Mair 1979/80), where the extreme abiotic conditions strongly affect plant production and consumers (Gutierrez and Whitford 1987; Wisdom 1991; Polis 1991). In the extreme arid and semi-arid ecosystems, the soil under the shrubs show milder climatic conditions and higher resource availability, this plants acting as "fertile islands" (Garner and Steinberg 1989; Schlesinger et al. 1996; Wagner and Jones 2006), and therefore, strongly affecting the distribution of soil communities and favouring faunal interactions (Stanton and Tepedino 1977; Wagner et al. 1997; Pen-Mouratov et al. 2004).

In the Baza Basin, the distribution of the macrofauna is strongly affected by these island microhabitats (Doblas-Miranda et al. *submitted*), but is crucial to known the factors that influence this patched distribution. Our goal was to investigate abiotic and resource controls over desert soil macrofaunal community distribution and dynamics at the Baza Basin, and to whether observed patterns are also affected by interactions among trophic groups, reflecting complex ecosystem processes. We perform the analysis using different statistical approximations.

Materials and methods

Study site

The study was conducted at Barranco del Espartal, a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain). Potential evapo-transpiration exceeds annual rainfall (250-300 mm) three times. Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40ºC to -14ºC), and highly seasonal. The sharp contrast between the hot, dry summer conditions and the cold, rainy winter conditions determine that autumn and winter do not appear as distinct seasons in the area (Castillo-Requena 1989), only three seasons being actually recognizable: 1) spring, from March to May; 2) summer, from June to September; and 3) winter, from October to February.

The soil is a Gypsiric Regosol (WRBSR, FAO 1998), characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (< 5% $CaCO_3$ content). Soil structure ranges from weak fine granular (in the upper centimetres of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually < 15-20 cm depth, being the first 1-2 cm where the organic matter concentrates, with values < 2% in all cases) and C (Sierra et al. 1990).

As a general trait of desert soils, most ground surface is devoid of litter (58%), which mainly occurs under shrubs (usually forming a thin, distinct layer in the soil surface). The vegetation is an arid open shrubsteppe dominated by *Artemisia herba-alba* Asso and *A. barrelieri* Bess and *Salsola oppositifolia* Desf. shrubs, tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.) and *Retama sphaerocarpa* L. brushes, which act as "islands of fertility" aggregating most soil macrofauna (Doblas-Miranda et al. *submitted*).

The soil macroinvertebrate assemblage at the study site is dominated by arthropods both in terms of abundance and biomass. The most important groups are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae and Cebrionidae), Hemiptera

(*Dimargarodes mediterraneus* Silvestri, 1908), Embioptera (*Haploembia palaui* Stefani, 1955), Araneae, Isopoda (*Porcelio sp.*), Julida (*Julus sp.*), Geophilomorpha, Thysanura and Carabidae beetles (Doblas-Miranda et al. *in press*), constituting 92.2% of the total abundance and 76.1% of the total biomass (unpublished data).

Sampling design

To study the effect of abiotic and biotic variables on macroinvertebrate distribution, we: 1) estimated macroinvertebrate abundance, 2) measured temperature and moisture and 3) measured productivity and quality of litter and roots. Samples were collected in five different microhabitats: under the four dominant types of shrubs in the study site, 1) *Artemisia*, 2) *Salsola*, 3) *Retama* and 4) tussock grasses, and in 5) bare soil areas. To analyze seasonal variations, we distinguished five sampling periods: Winter-1, Spring-1, Summer-1, Winter-2 and Spring-2, from October 2003 to May 2005.

To analyze the distribution of the soil macroinvertebrates, we considered two levels in the soil: litter and belowground. To sample the litter level, we collected the leaf litter under the shrubs contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel. Belowground samples were collected in the same spot by using a 10 cm diameter auger, up to 50 cm depth. We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the two years of study. Litter and soil core samples were processed in the field using 1 mm mesh-size sieves. After sieving, macroinvertebrates were hand collected by carefully examining the litter or soil.

Because of the large number of potential species interactions in the study site, it is methodologically better to focus on the interactions between selected functional groups of species (Rae et al. 2006). Macroinvertebrates were thus classified into five different trophic groups: detritivores, herbivores, predators, omnivores and fungivores, and an additional group, called as "non-*in situ*-consumers", which are taxa that live in the soil but do not feed on soil resources or prey (e.g., pupae at the litter level, burrowing spiders at belowground level). However, only detritivores, herbivores and predators were used in the analyses. Omnivorous Formicidae were not included in the analysis because they forage in wide areas and the affecting factors were measured only in the selected microhabitats; also, previous exploratory analyses including omnivores showed no significant interactions with influencing variables and other groups. Fungivores were too scarce to be included in the analyses. Finally, non-*in situ*-consumers are not affected by resource factors and, except for ants, were also scarce to carry out the analyses. Assignation of taxa to a trophic group was based on published information (e.g., Moore et al. 1988; Decaëns et al. 1998) and observations at the study site.

Temperature was measured in the litter and belowground, at 10 cm depth intervals, with a digital thermometer (precision ± 0.1 ºC). Moisture content in the samples of litter and soil was estimated using the gravimetric method. Also, precipitation records from a nearby meteorological station were used in most of the analyses in order to avoid gaps in the possible explanations related with one of the most important environmental factors in deserts (Noy-Mair 1979/80).

To estimate litter production, containers (18 x 18 x 12 cm) were placed under the four dominant shrubs in the study site (see above). In each microhabitat type, we placed 20 containers. Litter collected in the containers was sampled seasonally (see above). The litter was dried at 40ºC and weighted in the laboratory. Litter quality (C/N) was obtained from 12 individuals of each plant per season; Carbon and Nitrogen content were obtained by means of an Elemental Analysis Engine.

In order to study belowground primary production, we used the root in-growth technique (Flower-Ellis and Persson 1980; Cadwell and Virginia 1989): Soil cores were used to extract a soil volume of 10 cm diameter and 50 cm depth; this soil was sieved in the field using fine-mesh sieves (1 mm mesh size) to remove soil fauna and roots, and then was placed again in the hole. Marked cylinders of sifted soil were kept during a season for the in-growth of roots and then were extracted with soil cores of 8 cm diameter, up to 50 cm depth. Samples were taken under the five selected microhabitats (see above). We took 10 replicates per microhabitat each sampling period (see above). In-growth samples were processed in the laboratory, carefully sieving the soil (1 mm mesh size) and extracting fine roots, which were washed, dried at 40 ºC and weighted. Because there were not enough fine-root material per microhabitat to obtain the amounts of Carbon and Nitrogen seasonally by means of an Elemental Analysis Engine, root quality (C/N) was obtained from 5 different individuals of each species and categorized into 3 different values: low (tussock grasses C/N = 43.24 ± 2.2), medium (*Artemisia* C/N = 23.87 ± 0.1; bare soil C/N = 25.59 ± 2.5) and high (*Salsola* C/N = 16.95 ± 0.2; *Retama* C/N = 18.65 ± 1.1).

Statistical analysis

The data matrix was built with the mean data for each microhabitat at the five sampling periods ($n = 25$). The nine independent variables (precipitation, surface temperature, soil temperature, litter moisture, soil moisture, litter production, litter quality, root production and root quality) were logarithmically transformed, and densities of the six trophic groups (above- and belowground detritivores, herbivores and predators) were square root transformed prior to parametric analyses (Zar 1984). In order to test if the biotic and abiotic factors were correlated, Pearson product-moment correlations were calculated (Sokal and Rohlf 2003) using Statistica v7.1, Statsoft.

To evaluate the effect of the abiotic and resource variables on the distribution of the macroinvertebrate trophic groups, a canonical correspondence analysis was used (CCA; Ter Braak and Verdonschot 1995). We performed the CCA also to select the variables for the structural equation model. In the CCA, the principal axes are extracted in order to explain most of the total inertia (lack of independence between objects and variables), but also to maximize their correlation with additional variables (Quinn and Keough 2002). CCA was used to examine how the relative positions of the trophic groups were related to the values of the additional covariates (arrows) for each sampling unit (microhabitat x sampling period) in the obtained plot. Arrows may be extended in either direction to allow interpretation of the influence of the covariates on the trophic groups (Ter Braak 1986). The following environmental and resource variables were used like covariates: soil moisture, root production, surface temperature, litter quality and precipitation. CCA was performed using CANOCO for Windows 4.5 (Ter Braak and Smilauer 2002).

To analyze the influence of the different environmental and resource variables in the distribution of each trophic group of macroinvertebrates and also to select the variables for the structural equation model, we used General Linear Models (GLM; Christensen 1997) by Statistica v7.1, Statsoft. The abundances of aboveground trophic groups were regressed individually on the aboveground affecting variables: surface temperature, litter moisture and litter production and quality. The belowground groups were regressed on the belowground variables: soil temperature and moisture and root production and quality. Belowground detritivores were also regressed on litter production and quality because most belowground detritivores in the system are Embioptera, which live in the interface between litter and belowground, and active Tenebrionid larvae, which can perform vertical migrations in the soil and thus feed on both surface litter and subterranean resources (Doblas-Miranda et al. *submitted*).

We used Structural Equation Models (SEM; Proc SEPATH, Statistica v7.1, Statsoft) to analyse relationships among independent factors and density data, including the effect of the relationships among the trophic groups. SEM is a multivariate statistical methodology that includes factor and path analysis (Pugesek et al. 2003), providing a robust technique for studying interdependencies among a set of physical, chemical and biological variables, including if they are correlated (Arhonditsis et al. 2006). In contrast to multivariate regression or linear models, SEM allows us to explicitly test indirect effects that can be mediated by another intermediary variable (Arhonditsis et al. 2006). Correlated distributions of abundances can be interpreted as interactions among groups, but these may also be the result of correlated responses to environmental variation ("spurious correlations"; Wright 1921; Shipley 2000). If we differentiate among species interactions and spurious effects, we can then analyze the interactions within the context of variation that results from responses to abiotic or resource variables (Rae et al. 2006).

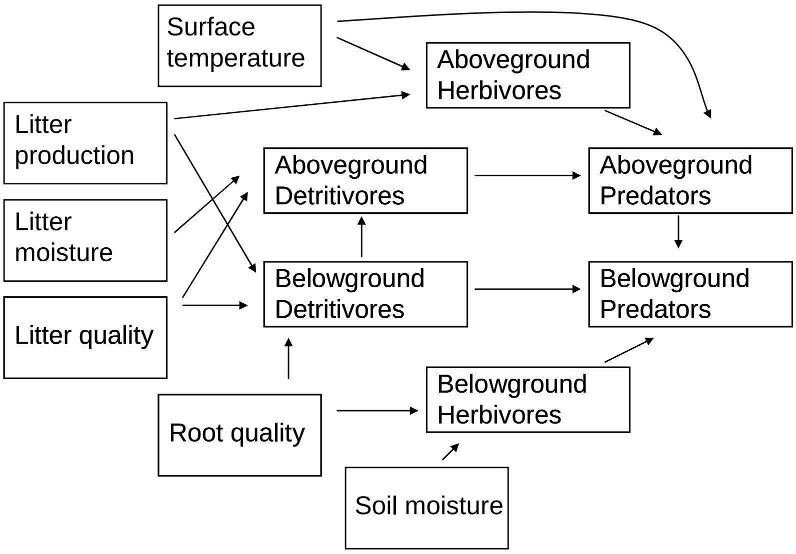
The first step in model selection lies in articulating a practical set of hypotheses (Johnson and Omland 2004). In this technique, preconceptualizations or existing knowledge is necessary to create the initial framework for the model development (Arhonditsis et al. 2006). Accordingly, previous analysis, observations, and our knowledge on life cycles, allowed us to built two *a priori* analytical basic models, which include all potential links between variables, based on two different possibilities about the system functioning: first, consumers affect the number of predators, and second, predators influence the abundance of consumers (Fig. 1). The exogenous, influencing variables on the models (surface temperature, litter and soil moisture, litter production and quality and root quality) were selected based on the previous analysis and the endogenous variables corresponded to the trophic groups, both hypotheses differing in the direction of the arrows that link primary consumers with predators (Fig. 1).

Resource variables were measured in order to study how the different plant species affect the distribution of the macrofauna, but we did not consider proposing top-down effects from primary consumers to producers (differences in quality and productivity among species were not large enough to assume that the variability was due to their interaction). We assumed in the two models that surface detritivores were affected by belowground detritivores (by subterranean migrating larvae; Doblas-Miranda et al. *submitted*) and subterranean predators by aboveground predators (myriapodes and carabid larvae from the surface; Doblas-Miranda et al., *submitted*), principally because previous exploratory analysis including the opposite direction in both pathways showed no significant results. Finally, we considered that above and belowground herbivores in the study had no possibility to affect one to each other; root feeders could affect the plants on which they feed, however, herbivores living in the soil surface do not represent the fauna associated to the shrub canopy, principally looking for shelter into the litter accumulations (Moore et al. 2004). Also, previous exploratory analysis including this pathway between root and litter herbivores showed no significant interactions.

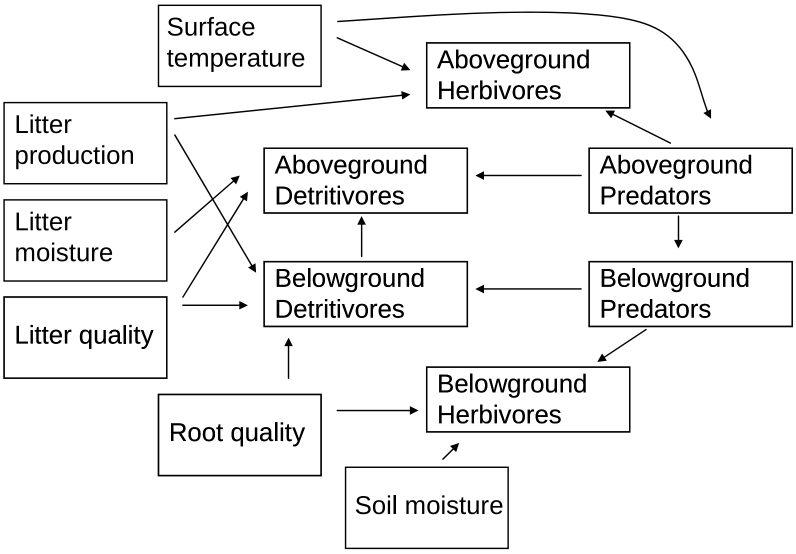
After elaboration of the more inclusive models, then we considered a number of alternative, competing nested models sharing the same causal structure as the basic model but eliminating some of the paths. These nested models were built by removing alternative non-significant variables from the previous covariance matrix (in the second model, some of the non-significant paths were part of intervening endogenous variables and we can not eliminate them since, otherwise, the model would become non-causal). To reject or accept a model, we used the best goodness of fit and three information criterion indices (Johnson and Omland 2004): Akaike Information Criterion (AIC), Schwarz's Bayesian Criterion (SBC), and Browne-Cudeck Cross Validation index (CVI). Due to the low number of samples, path coefficients (partial regression coefficients) were obtained using Monte Carlo distribution methods. Variables were log-transformed when necessary to normalize.

Figure 1. Alternative Structural Equation Models of the influence of different factors on the soil macroarthropod trophic assemblage at Baza. Basic models include all the variables and the potential relationships among them.

a) Consumers affect predators



b) Predators affect consumers



Results

1. Relationships among independent variables

All three humidity variables (precipitation, and litter and soil moisture) were positively correlated, but negatively correlated with temperature variables (surface and soil temperature), also positively correlated one to each other (Table 1). Also, root production was positively correlated with all humidity variables, and litter production showed significant correlations with litter and root quality (Table 1).

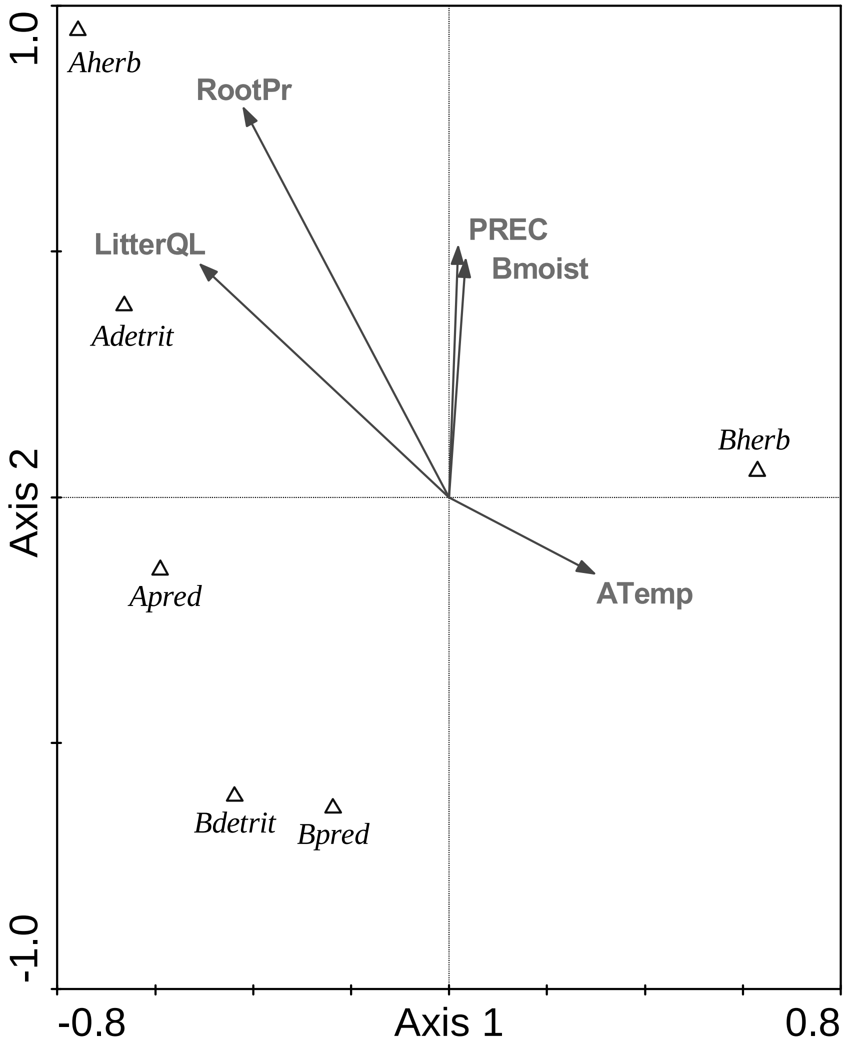
Table 1. Matrix of significant ($P < 0.05$, $n = 25$) linear correlation coefficients among environmental and biotic variables.

Variable	Precp.	Surf. temp.	Litter moist.	Soil temp.	Soil moist.	Litter prod.	Litter quality	Root prod.
Surface temperature	*-0.74*	1.00						
Litter moisture	*0.57*	*-0.71*	1.00					
Soil temperature	*-0.72*	*0.96*	*-0.81*	1.00				
Soil moisture	*0.42*	*-0.54*	*0.97*	*-0.67*	1.00			
Litter production						1.00		
Litter quality						*0.77*	1.00	
Root production	*0.53*		*0.50*		*0.51*			1.00
Root quality						*0.49*		

2. Ordination of trophic groups

CCA revealed three significant variables explaining the soil macroarthropod trophic group abundances (Fig. 2). A significant effect of soil moisture ($\lambda = 0.03$; $P < 0.01$), root production ($\lambda = 0.04$; $P < 0.05$) and surface temperature ($\lambda = 0.03$; $P < 0.05$) was found. Litter quality and precipitation were included in the analysis to improve the first axis eigenvalue (axis 1 = 0.101; axis 2 = 0.034). First ordination axis was significant ($P < 0.01$). Axes 1 and 2 accounted for 94% of trophic groups-variables relationship, with 44% of the total trophic groups variation explained. Aboveground groups were affected negatively by surface temperature, while belowground detritivores and predators showed an inverse relationship with moisture. Root production showed a positive influence on aboveground herbivores and detritivores.

Figure 2. Biplot of soil macroarthropod trophic groups (small open triangles; A = aboveground, B = belowground; detrit = detritivores, herb = herbivores, pred = predators) and environmental and resource variables (arrows) from canonical correspondence analysis. Soil moisture (Bmoist), root production (RootPr) and surface temperature (ATemp) were significant variables (*P* < 0.05), while litter quality (LitterQL) and precipitation (PREC) were not.



3. General Linear Models

The GLMs were significant only for aboveground herbivores (F = 5.68, $P < 0.01$, df = 4) and belowground detritivores (F = 3.37, $P < 0.05$, df = 6). For herbivores, litter production was the only significant variable of the model ($\beta = 0.59 \pm 0.28$, $P < 0.05$). For belowground detritivores, root quality ($\beta = 0.74 \pm 0.23$, $P < 0.01$), litter quality ($\beta = 0.84 \pm 0.33$, $P < 0.05$) and litter production ($\beta = 0.90 \pm 0.39$, $P < 0.05$) significantly explained the model.

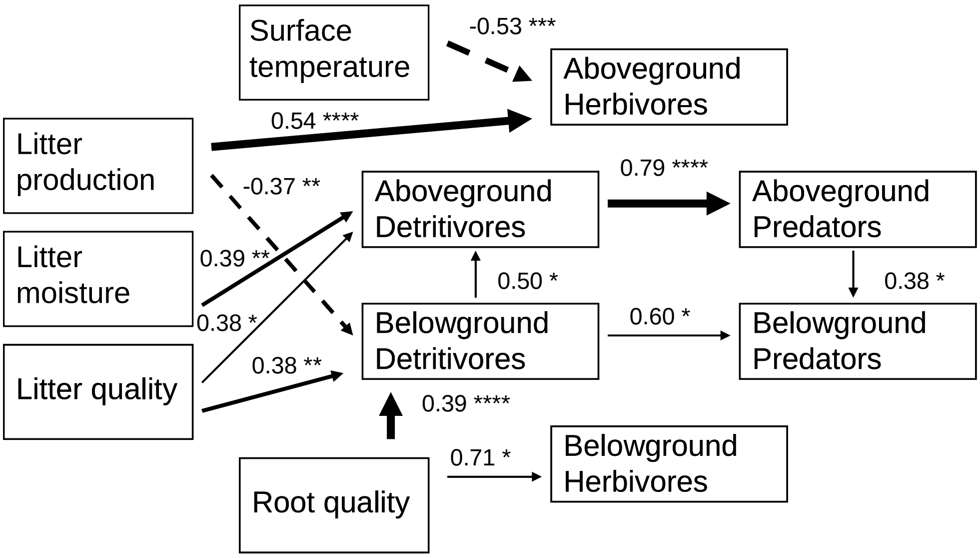
4. Structural Equation Models

From the first set of models, the most parsimonious one (see Appendix A) included surface temperature, litter moisture, litter production and quality, and root quality as significant exogenous variables (Fig. 3). Aboveground herbivores were affected by litter production and temperature meanwhile belowground herbivores were positively related to root quality. Aboveground detritivores where positively affected by litter moisture and quality, while belowground detritivores were negatively affected by litter production and positively by litter and root quality (Fig. 3). There were important connections between trophic groups: detritivores positively affected predators both above and belowground. Also there were significant connections between above- and belowground groups: belowground detritivores positively affected aboveground detritivores, and aboveground predators positively affected belowground predators (Fig. 3).

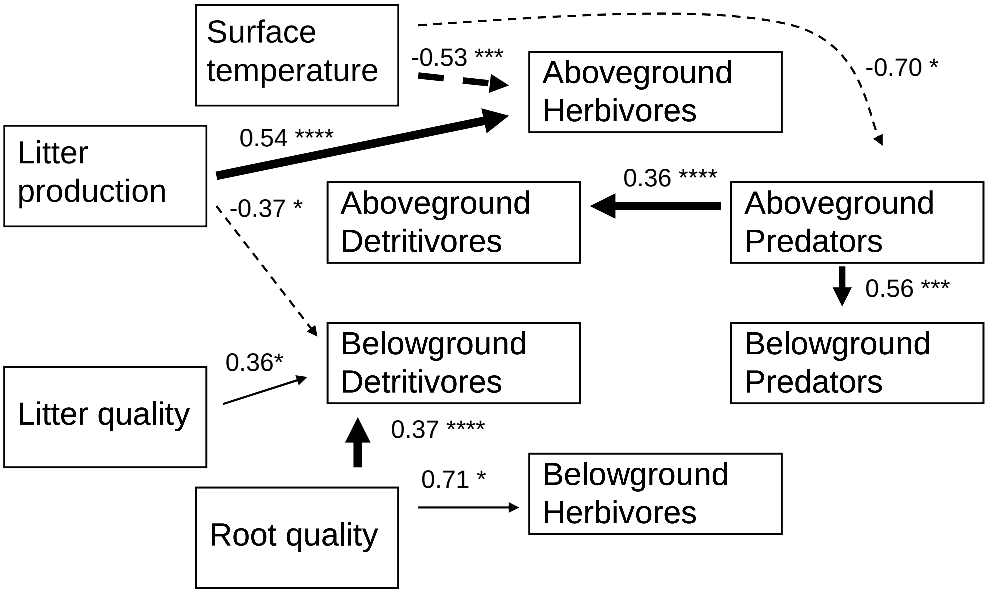
From the second set of models, the most parsimonious one (see Appendix A) included surface temperature, litter production and quality, and root quality as significant exogenous variables (Fig. 3). Most of the effects of the exogenous variables on trophic groups where the same than those obtained in the previous model, except that aboveground predators were negatively affected by surface temperature, and aboveground detritivores did not show any link with environmental or resource variables (Fig. 3). In contrast to the previous model, aboveground predators positively affected aboveground detritivores and, interestingly, also showed a positive influence on belowground predators (Fig. 3).

Figure 3. Alternative Structural Equation Models of the influence of different factors on the soil macroarthropod trophic assemblage at Baza. Significant standardized path coefficients (* p < 0.05, ** p < 0.01, *** p < 0.001, **** p < 0.0001). Strength of associations between variables is represented by proportional weighted arrows.

a) First Model



b) Second Model



Discussion

Classic ideas emphasize the role of environmental conditions as the principal factors governing desert environments (Noy-Meir 1979/80; Whitford 1989), affecting the fauna directly and indirectly via abiotic factors effects on productivity (Noy-Meir 1985; Ludwig 1987; Wisdom 1991). In the study area, temperature and moisture influenced distribution of soil macroinvertebrates above- and belowground. Additionally, moisture affected root production (as reported in deserts by Peek et al. 2005) and root production influenced the distribution of all macrofauna. Therefore, abiotic factors in the study system showed direct and indirect effects on faunal distribution; however, consumers are limited by more than abiotic factors and their effects in the amount of resources, and it is important to consider other factors as resource quality (Polis 1991). In the study system the soil macrofauna aggregates in the shrub species (Doblas-Miranda et al. *submitted*), which show lower temperature, higher moisture and higher root production than the surroundings (similar shrub effects on nematode populations have been assessed by Pen-Mouratov et al. 2004), but there are shrubs with low production of high quality roots and vice versa (unpublished data). Therefore, root production did not affect the densities of each trophic group separately, but root quality strongly affected both belowground detritivores and herbivores, confirming that both groups are not only restricted by abiotic factors or the availability of their food resources (Crawford 1991; Wisdom 1991; Wardle and Lavelle 1997).

Litter detritus effects on macrofaunal distribution also suggest than resource factors are as crucial as environmental conditions in arid ecosystems. Litter is a recognised habitat that modifies moisture, light, temperature and even wind flow velocity (Moore et al. 2004). In effect, aboveground herbivores were positively influenced by litter production, since litter dwelling herbivores may look for shelter or annual plants into the litter accumulations. Alternatively, litter quality effects were more important than litter production influence on detritivorous consumers, as reported for root resources. In summer occurs a combination of maximum litter production but minimum litter quality in mostly all shrubs in the study area (unpublished data) that could explain the negative effect of litter production on belowground detritivores. In addition, we can hypothesize a reduction of competitive interactions among predators, that provoke an impact increase on their shared prey (Finke and Denno 2002), but controlled experiments would be necessary to analyze these mechanisms. However, litter quality clearly affected the distribution of above- and belowground detritivores. The more abundant detritivores in the study site, Tenebrionidae beetle larvae, could use both the surface litter and the root detritus deeper in the soil (Doblas-Miranda et al. *submitted*). In winter or spring, when detritus are more humid (the edibility of detritus depends on moisture; Olear and Seastedt 1994), they probably feed in the surface (in fact, aboveground detritivores were also affected by litter moisture), and in summer, when the litter is dry, they possibly feed mainly on dead roots. Therefore, resource and abiotic factors affected together the spatiotemporal distribution of desert macrofauna.

This study showed that macrofaunal distribution was not only affected by abiotic factors and resource availability and quality but also by macro-arthropod interactions. These interactions were more evident between detritivores and predators, but inexistent between herbivores and other trophic groups. Litter macro-herbivores were a small group which only seeks for refuge or annuals growing in litter under the shrubs (we did not study shrub canopy insects), and belowground macro-herbivores seems not to suffer predation (their natural enemies in belowground food webs are probably pathogens, such as bacteria, fungi or nematodes; Brown and Gange 1990). However, predators have the possibility to feed on both herbivores and detritivores (Polis and Strong 1996), and in the second model of the present study, predators positively influence the densities of detritivores aboveground. We can argue about intra-guild predation effects (Holt and Polis 1997), because most predators in the study site are arachnids (Doblas-Miranda et al. *in press*), whose species show predation in younger stages of the same group (Wagner and Wise 1996). Also, interaction among endothermic and ectothermic predators could release macro-detritivores from predation (Ayal 2007). In fact, in the Baza Basin, litter dwelling arthropods are important components in the diet of predators not accounted in our study as lizards and shrikes (Hódar et al. 1996; Hódar 2006). In any case, controlled experiments would be crucial to analyze these mechanisms. Some authors consider predation as an important factor determining the distribution of animals in desert habitats (Polis et al. 1998; Groner and Ayal 2001; Ayal 2007), however, it has been argued that predators do not play important roles in the determination of abundances of animals in deserts (Noy-Meir 1985). Previous manipulative experiments of resource addition in soil food webs have proved to affect detritivorous macroarthropods elevating their populations, but also increasing the densities of predatory macrofauna, indicating a strong bottom-up control of these organisms (Chen and Wise 1999; Wardle et al. 1999). In agreement, the first model suggests a bottom-up control derived from the positive effect of detritivores on predators, both above and belowground. Taking into account the crucial influence of resource factors on detritivorous macrofauna, it suggests the importance of resource indirect effects in trophic group interactions.

Interestingly, in the first model we found also indirect effects of belowground detritivores on aboveground predators via interactions with aboveground detritivores, showing very important connections between above- and belowground systems. In agreement, most subterranean larvae could perform vertical migrations and feed on the litter level (Doblas-Miranda et al. *submitted*) or can emerge as surface dwelling adults (Crawford 1991). In both cases, they could become prey of aboveground generalist predators, confirming the role of detritivorous and predatory macrofauna in the connection of both levels (Scheu 2001; Miyashita et al. 2003). Moreover, the connection of belowground detritivores with aboveground, together with the effect of surface litter on belowground detritivores, demonstrate that subterranean detritivorous macrofauna could affect the patterns of surface litter decomposition, with important consequences in the cycles of matter and energy between above- and belowground systems (González-Megías et al. *submitted*).

In contrast to classic ideas of arid ecosystems, moisture and temperature were not the only factors affecting fauna, and litter production and resource quality were revealed as important factors controlling soil macrofaunal distribution. Trophic groups interactions were also a key factor controlling the faunal densities and suggested different possibilities of ecosystem functioning, with above- belowground links. We thus conclude that desert ecosystems, and especially the soil macrofauna living there, are complex, offering the possibility of study essential ecological processes and showing new important ideas for future research.

Bibliography

Arhonditsis, G. B., C. A. Stow, L. J. Steinberg, M. A. Kenney, R. C. Lathrop, S. J. McBride, and K. H. Reckhow. 2006. Exploring ecological patterns with structural equation modeling and Bayesian analysis. Ecological Modelling **192**:385-409.

Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. Journal of Arid Environments **68**:171-187.

Begon, M., J. L. Harper, and C. R. Townsend. 1987. Ecology: Individuals, populations and communities. Blackwell Scientific Publications, Oxford.

Bell, S. S., E. D. McCoy, and H. R. Mushinsky. 1991. Habitat Structure. The Physical Arrangement of Objects in Space. Chapman and Hall, London.

Brown, V. K., and A. C. Gange. 1990. Insect herbivory below ground. Advances in Ecological Research **20**:1-58.

Caldwell, M. M., and R. A. Virginia. 1989. Root systems. Pages 367-398 *in* R. W. Pearey, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant physiological ecology: field methods and instrumentation. Chapman and Hall, London.

Castillo-Requena, J. M. 1989. El clima de Andalucía: clasificación y análisis regional de los tipos de tiempo. Instituto de Estudios Almerienses, Almería.

Chen, B., and D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology **80**:761-772.

Christensen, R. 1997. Log-Linear Models and Logistic Regression, second edition. Springer, New York.

Coleman, D. C. 1996. Energetics of detritivory and microbivory in soil in theory and practice. Pages 39-50 *in* G. A. Polis, and K. O. Winemiller, editors. Food Webs: Integration of patterns and dynamics. Chapman and Hall, New York.

Crawford, C. S. 1991. The community ecology of macroarthropod detritivores. Pages 89-112 *in* G. A. Polis, editor. The Ecology of Desert Communities. University of Arizona Press, Tucson.

Decaëns, T., T. Dutoit, D. Alard, and P. Lavelle. 1998. Factors influencing soil macrofaunal communities in post-pastoral succesions of western France. Applied Soil Ecology **9**:361-367.

Di Castri, F., and V. V. Di Castri. 1981. Soil fauna of Mediterranean-climate regions. Pages 445-478 *in* F. Di Castri, D. W. Goodall, and R. L. Specht, editors. Ecosystems of the World. 11. Mediterranean type shrublands. Elsevier, Amsterdam.

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. TRENDS in Ecology & Evolution **17**:177-183.

Ettema, C. H., D. C. Coleman, G. Vellidis, R. Lowrance, and S. L. Rathbun. 1998. Spatiotemporal distributions of bacteriovorous nematodes and soil resources in a restored riparian wetland. Ecology **79**:2721-2732.

Ettema, C. H., S. L. Rathbun, and D. C. Coleman. 2000. On spatiotemporal patchiness and the coexistence of five species of Chronogaster (Nematoda: Chronogasteridae) in a riparian wetland. Oecologia **125**:444-452.

Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. Ecology **83**:643-652.

Flower-Ellis, J. G. K., and H. Persson. 1980. Investigation of structural properties and dynamics of Scot pine stands. Pages 125-138 *in* T. Persson, editor. Structure and Function of Northern Coniferous Forest: an Ecosystem Study. Ecological Bulletins 32, Stockholm.

Fralish, J. S. 2002. Community-based ordination: the problem of data handling and interpretation. Bulletin of the Ecological Society of America **83**:77-81.

Garner, W., and Y. Steinberger. 1989. A proposed mechanism for the formation of fertile islands in the desert ecosystem. Journal of Arid Environments **16**:257-262.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature **405**:220-227.

Gongalsky, K. B., F. A. Savin, A. D. Pokarzhevskii, and Z. V. Filimonova. 2005. Spatial distribution of isopods in an oak–beech forest. European Journal of Soil Biology **41**:117-122.

Görres J. H., M. J. Dichiaro, J. B. Lyons, and J. A. Amador. 1998. Spatial and temporal patterns of soil biological activity in a forest and an old field. Soil Biology and Biochemistry **30**:219-230.

Groner, E., and Y. Ayal. 2001. The interaction between bird predation and plant cover in determining habitat occupancy of darkling beetles. Oikos **93**:22-31.

Gutierrez J. R., and W. G. Whitford. 1987. Chihuahuan desert annuals: Importance of water and nitrogen. Ecology **68**:2032-2045.

Hernández, P., M. Gutiérrez, M. Ramajo, D. Trigo, and D. J. D. Cosín. 2003. Horizontal distribution of an earthworm community at El Molar, Madrid (Spain). Pedobiologia **47**:1-6.

Hódar, J. A., F. Campos, and B. A. Rosales. 1996. Trophic ecology of the Ocellated Lizard *Lacerta lepida* in an arid zone of southern Spain: relationships with availability and daily activity of prey. Journal of Arid Environments **33**:95-107.

Hódar, J. A. 2006. Diet composition and prey choice of the southern grey shrike *Lanius meridionalis* L. in South-eastern Spain: the importance of vertebrates in the diet. Ardeola **53**:237-249.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149**:745-764.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. TRENDS in Ecology & Evolution **19**:101-108.

Laiho, R., N. Silvan, H. Cárcamo, and H. Vasander. 2001. Effects of water level and nutrients on spatial distribution of soil mesofauna in peatlands drained for forestry in Finland. Applied Soil Ecology **16**:1-9.

Lavelle, P. 1997. Faunal activities and soil processes: Adaptative strategies that determine ecosystem function. Advances in Ecological Research **27**:93-132.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659-1673.

Ludwig, J. 1987. Primary productivity in arid lands: myths and realities. Journal of Arid Environments **13**:1-7.

Margerie, P., T. Decaëns, F. Bureau, and D. Alard. 2001. Spatial distribution of earthworm species assemblages in a chalky slope of the Seine Valley (Normandy, France). European Journal of Soil Biology **37**:291-296.

Maudsley, M., B. Seeley, and O. Lewis. 2002. Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables. Agriculture, Ecosystems and Environment **89**:77-89.

Miyashita, T., M. Takada, and A. Shimazaki. 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. Oikos **103**:31-36.

Moore, J. C., D. E. Walter, and H. W. Hunt. 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annual Review of Entomology **33**:419-439.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, D. Quan, A. Hastings, N. Collins Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni, and D. H. Wall Freckman. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters **7**:584-600.

Noy-Meir, I. 1979/80. Structure and function of desert ecosystems. Israel Journal of Botany **28**:1-19.

Noy-Meir, I. 1985. Desert ecosystem structure and function. Pages 93-103 *in* M. Evenary, editor. Hot Deserts and Arid Shrublands. Elsevier, Amsterdam.

Olear H. A., and T. R. Seastedt. 1994. Landscape patterns of litter decomposition in alpine tundra. Oecologia **99**:95-101.

Peek, M. S., A. J. Leffler, C. Y. Ivans, R. J. Ryel, and M. M. Caldwell. 2005. Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. New Phytologist **165**:171-180.

Pen-Mouratov, S., M. Rakhimbaev, G. Barness, and Y. Steinberger. 2004. Spatial and temporal dynamics of nematode populations under *Zygophyllum dumosum* in arid environments. European Journal of Soil Biology **40**:31-46.

Polis, G. A. 1991. Desert communities: an overview of patterns and processes. Pages 1-26 *in* G. A. Polis, editor. The Ecology of Desert Communities. University of Arizona Press, Tucson.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist **147**:813-846.

Polis, G. A., R. D. Holt, B. A. Menge, and K. O. Winemiller. 1996. Time, space, and life history: influences on food webs. Pages 435-460 *In* G. A. Polis, and K. O. Winemiller, editors. Food Webs: Integration of patterns and dynamics. Chapman and Hall, London.

Polis, G. A., J. D. Barnes, M. K. Seely, J. R. Henschel, and M. M. Enders. 1998. Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. Ecology **79**:2560-2566.

Ponge, J. F. 2000. Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. Biology and Fertility of Soils **32**:508-522.

Pugesek, B. H., A. Tomer, and A. Von Eye. 2003. Structural Ecuation Modeling: Applications in Ecological and Evolutionary Biology. Cambridge University Press, Cambridge.

Quinn, G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Rae, D. A., W. S. Armbruster, M. E. Edwards, and M. Svengård-Barre. 2006. Influence of microclimate and species interactions on the composition of plant and invertebrate communities in alpine northern Norway. Acta Oecologica **29**:266-282.

Ricklefs, R., and D. Schluter. 1993. Species diversity in ecological communities. Historical and geographical perspectives. University of Chicago Press, Chicago.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, New York.

Rossi, J.-P., P. Lavelle, and A. Albrecht. 1997. Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity. Soil Biology and Biochemistry **29**:485-488.

Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. Basic and Applied Ecology **2**:3-13.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364-374.

Shipley, B. 2000. Cause and Correlation in Biology. Cambridge University Press, Cambridge.

Sierra, C., E. Ortega, J. Quirantes, J. Lozano, and J. Martínez. 1990. Proyecto LUCDEME. Mapa de suelos. Baza-994. M.A.P.A.-ICONA.

Sokal, R. R., and F. J. Rohlf. 2003. Biometry: the principles and practice of statistics in biological research, third edition. W. H. Freeman and company, New York.

Stanton, N. L., and V. J. Tepedino. 1977. Island habitats in soil communities. Pages 514-515 *in* U. Lohm and T. Persson, editors. Soil Organisms as Components of Ecosystems. Swedish Natural Science Research Council, Stockholm.

Stoyan, H., H. De-Polli, S. Böhm, G. P. Robertson, and E. A. Paul. 2000. Spatial heterogeneity of soil respiration and related properties at the plant scale. Plant and Soil **222**:203-214.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167-1179.

Ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariante methods in aquatic ecology. Acuatic Science **57**:255-289.

Ter Braak, C. J. F., and P. Smilauer. 2002. Canoco reference manual and user guide to Canoco for Windows: software for canonical community ordination, version 4.5. Microcomputer Power, Ithaca, NY.

Verschoor, B. C., R. G. M. de Goede, J.-W. de Hoop, and F. W. de Vries. 2001. Seasonal dynamics and vertical distribution of plant-feeding nematode communities in grasslands. Pedobiologia **45**:213-233.

Wagner, D., and J. B. Jones. 2006. The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biology and Biochemistry **38**:2593-2601.

Wagner, D., M. J. F. Brown, and D. M. Gordon. 1997. Harvester ant nests, soil biota and soil chemistry. Oecologia **112**:232-236.

Wagner, J. D., and D. H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology **77**:639-652.

Wallwork, J.A. 1982. Desert soil fauna. Praeger Publishers, New York.

Wardle, D. A. 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton & Oxford.

Wardle, D. A., and P. Lavelle. 1997. Linkages between soil biota, plant litter quality and decomposition. Pages 107-124 *in* K. E. Giller, and G. Cadisch, editors. Driven by Nature-Plant Litter Quality and Decomposition. CAB International, Wallingford.

Wardle, D. A., K. S. Nicholson, K. I. Bonner, and G. W. Yeates. 1999. Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity and temporal variability over a seven-year period. Soil Biology and Biochemistry **31**:1691-1706.

Whittaker, R. J., K. J. Willis, and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography **28**:453–470.

Whitford, W. G. 1989. Abiotic controls on the functional structure of soil food webs. Biology and Fertility of Soils **8**:1-6.

Whitford, W. G. 2000. Keystone arthropods as webmasters in desert ecosystems. Pages 25-41 *in* D. C. Coleman, and P. F. Hendrix, editors. Invertebrates as Webmasters in Ecosystems. CABI Publishing (CAB International), Wallingford.

Wisdom, C. S. 1991. Patterns of heterogeneity in desert herbivorous insect communities. Pages 151-179 *in* G. A. Polis, editor. The Ecology of Desert Communities. University of Arizona Press, Tucson.

Wolters, V. 2000. Invertebrate control of soil organic matter stability. Biology and Fertility of Soils **31**:1-19.

Wright, S. 1921. Correlation and causation. Journal of Agricultural Research **10**:557-585.

WRBSR, FAO. 1998. World Reference Base for Soil Resources. FAO-ISRIC-ISSS. Rome.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, New York.

Zimmer, M., H.-J. Brauckmann, G. Broll, and W. Topp. 2000. Correspondence analytical evaluation of factors that influence soil macro-arthropod distribution in abandoned grassland. Pedobiologia **44**:695-704.

Appendix A. Results of alternative structural equation models for each hypothesis. Basic models (M1) are the most inclusive (see Methods; Fig 2). The nested models are simplified ones (i.e., indicate the previous model minus the variable or the path between two variables). Highlighted models indicate the selected causal model for each hypothesis. AIC (Akaike Information Criterion), SBC (Schwarz's Bayesian Criterion), and CVI (and Browne-Cudeck Cross Validation index) are the three information criterion indices.

Models	**df**	**X^2**	**P**	**AIC**	**SBC**	**CVI**
Consumers affect predators						
Model 1	35	39.39	0.38	1.27	2.40	1.40
Model 2 [M1 – (BHerb-BPred)]	36	39.29	0.39	1.25	2.35	1.37
Model 3 [M2 – (AHerb-APred)]	37	39.79	0.42	1.23	2.31	1.35
Model 4 [M3 – (STemp-APred)]	38	40.80	0.39	1.22	2.27	1.34
Model 5 [M4 – (SMoist-BHerb)]	**33**	**33.25**	**0.49**	**1.00**	**1.87**	**1.09**
Predators affect consumers						
Model 1	35	38.58	0.39	1.26	2.39	1.39
Model 2 [M1 – (BPred-BHerb)]	36	38.71	0.39	1.24	2.34	1.37
Model 3 [M2 – (APred-AHerb)]	37	38.58	0.45	1.22	2.30	1.34
Model 4 [M3 – (LitterQL-ADetr)]	38	40.60	0.42	1.22	2.27	1.34
Model 5 [M4 – (LMoist-ADetr)]	33	36.28	0.38	1.03	1.90	1.13
Model 6 [M5 – (SMoist-BHerb)]	**28**	**29.23**	**0.46**	**0.84**	**1.55**	**0.91**

SEGUNDA PARTE:

EFECTOS DIRECTOS DE LOS MACROINVERTEBRADOS EN LOS PROCESOS DEL SUELO

Capitulo 5

Above- and belowground litter decomposition in an arid system: effects of belowground decomposers on surface litter.

Resumen

La descomposición de la hojarasca, tanto en el medio epigeo como en el medio hipogeo, es un aspecto fundamental del funcionamiento de los ecosistemas terrestres. Este proceso está dirigido por tres factores no excluyentes (la calidad de la hojarasca, el ambiente físico-químico, y la composición de la comunidad de descomponedores) cuya importancia relativa depende de las condiciones ambientales. Aunque existen evidencias del papel que juegan las asociaciones de descomponedores epigeos e hipogeos en los procesos de descomposición en muchos sistemas, no existe una evidencia empírica del papel que juegan los descomponedores hipogeos en la descomposición de la hojarasca superficial. En este trabajo, se evalúa el proceso de descomposición de la hojarasca y de las raíces, con diferentes calidades, en los medios epigeos o hipogeo, en un sistema árido europeo, así como el papel que juega la fauna descomponedora en los procesos de descomposición. Se llevó a cabo lo que consideramos el primer estudio experimental para discernir el papel que juegan los descomponedores hipogeos en la descomposición de la hojarasca del medio epigeo. La calidad de la hojarasca y las raíces fue uno de los principales factores que controlaron la descomposición en todos los experimentos, aunque las tasas de descomposición fueron mayores en el medio hipogeo para ambos tipos de calidad de recurso. Además, la presencia de micro- y macroartrópodos aceleró la tasa de descomposición. Uno de los resultados más sorprendentes de este estudio es el mayor porcentaje de masa perdida en el medio epigeo debido a la fauna hipogea. Por lo tanto, una de las mayores implicaciones del estudio es que los modelos de funcionamiento de los ecosistemas deberían tener en cuenta las interacciones complejas entre los descomponedores epigeos e hipogeos para poder predecir la descomposición de la hojarasca.

Abstract

Decomposition of above and belowground litter is a fundamental aspect on ecosystems function, and it is driven by three non-exclusive factors, litter quality, physicochemical environment, and the composition of the decomposer community. The relative importance of each factor on litter decomposition both above and belowground depends on the environmental conditions**.** Although there are evidences of the role of above- and belowground decomposers in above- and belowground decomposition processes in many systems, there is no empirical evidence of the role of belowground decomposers on aboveground decomposition. In this paper, we evaluated decomposition process of litter and root of different qualities in an arid European area, above and belowground, and the role of decomposers on decomposition. We carry out what we believe to be the first experimental study trying to discern the role of belowground decomposer on above ground litter decomposition. We found that litter/root quality appeared as one of the main factors controlling decomposition in all the experiments, although decomposition rates were higher below than aboveground for both type of litter. Moreover, the presence of micro- and macroarthropod accelerated decomposition rate, and one of the most surprising results of this study is the higher percentage of mass loss aboveground due to belowground fauna. Therefore, one of the major implications of our study is that ecosystem models need to include complex interaction between above and belowground decomposers to accurately predict litter decomposition.

Key words:

Decomposition process; above and belowground decomposers; litter and root quality; desert ecosystems**;** above and belowground interactions.

Introduction

Decomposition is a fundamental aspect in ecosystem functioning (Wardle 2002, Bardgett 2005, Hättenschwiler et al. 2005) as most net primary productivity is returned to the soil as litter and dead roots. Since the decomposition process governs nutrient and carbon cycling, a thorough understanding of this process is essential to comprehend the structure and functioning of terrestrial ecosystems (Wardle 2002). Although a large amount of information have been devoted to analyse decomposition processes (see Hättenschwiler et a. 2005 for a review), recent studies have emphasized that to fully understand decomposition, it is necessary to learn about how this process occurs at both above- and belowground levels (Moretto & Distel 2003, Gholz et al. 2000, Vivanco & Austin 2006).

The decomposition process is driven mainly by three non-exclusive factors: litter quality, physicochemical environment, and composition of the decomposer community (see Hättenschwiler et al. 2005 for a review). Although in general decomposition of plant litter results in a series of predictable chemical changes in the decomposing material as a result of carbon and nitrogen utilization by heterotrophic microbial and animal populations (Berg & Staff 1981, McClaugherty et al. 1982; Berg et al. 1984), the relative importance of each factor on litter decomposition depends on the environmental conditions (Coûteaux et al. 1995, González & Seastedt 2001). Thus, climate is considered the main factor involved in the decomposition process under unfavourable conditions, meanwhile litter quality seems to be the main governing factor under favourable ones (Coûteaux et al. 1995, González & Seastedt 2001). Different microclimatic conditions of surface and belowground levels appear to be one of the main reasons accounting for the different decomposition rates found aboveground and belowground (Coûteaux et al. 1995, González & Seastedt 2001).

Although there are evidences of the role of above- and belowground decomposers in above- and belowground decomposition processes in many systems (Santos et al. 1981, Whitford et al. 1988, Herlitzius 1983, Maraun & Scheu 1996, Ouédrago et al. 2003, Vivanco

& Austin 2006), there is no empirical evidence of the role of belowground decomposers on aboveground decomposition. In this paper, we carry out what we believe to be the first experimental study trying to discern the role of belowground decomposers on aboveground litter decomposition. Moreover, we analyse decomposition rate above- and belowground using litter and roots of different qualities.

In general, macro- and microinvertebrates play an important role in terrestrial ecosystem processes (Santos et al. 1981, Herlitzius 1983, Maraun & Scheu 1996, Bardgett 2005). Invertebrates contribute to decomposition by litter fragmentation, grazing on microflora, inoculation of litter with microflora, and preying on grazers of primary decomposers (Santos et al. 1981, Herlitzius 1983, Maraun & Scheu 1996, Bardgett 2005). However, the role of the decomposer community in decomposition rate is also controversial, varying between different environments, litter types, and even in latitude (Whitford et al. 1982, Schaefer et al. 1985, González & Seastedt 2001, Vivanco & Austin 2006). For example, the biological regulation of decomposition seems to be more important in wet areas than in dry systems (González & Seastedt 2001).

Arid systems are ideal environments to answer these questions because aboveground litter is patchily distributed and form a thin layer in the ground surface. Additionally, dead roots are the most reliable source of recalcitrant compounds that contribute to the soil organic matter pool in arid systems (Parker et al. 1984). Previous studies predict higher decomposition rates in buried litter belowground (see Gholz et al. 2000), and differential decomposition rates and decomposer fauna depending on litter quality in arid systems (Whitford et al. 1982, Schaefer et al. 1985). Therefore, our predictions are: 1) decomposition rate is higher in high quality litter, 2) decomposition rate belowground is higher than aboveground, 3) differential role of detritivores above- and belowground, being decomposition due to macro-invertebrates more evident belowground (better environmental conditions), and 4) no net effect of belowground decomposers on aboveground decomposition would be expected if belowground decomposers feed mainly on underground detritus.

Methods

Study system

The study was conducted at Barranco del Espartal, a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain). Potential evapo-transpiration exceeds three times the amount of annual rainfall (250-300 mm). Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40ºC to -14ºC), and highly seasonal.

The soil is characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. As a general trait of arid soils, most ground surface is devoid of litter (58%), which only occurs under shrubs and in ant-nest mounds. The vegetation is an arid open shrubsteppe dominated by *Artemisia herba-alba* Asso and *A. barrelieri* Bess and *Salsola oppositifolia* Desf. shrubs, tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.) and *Retama sphaerocarpa* L. brushes. Open areas inside the Ramblas have been traditionally used to cultivate bot barley (*Hordeum vulgare*). For a more detailed description of the study systems see Doblas-Miranda et al. (in press).

The dominant groups of the soil macroinvertebrate assemblage at the study are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae, Cebrionidae and Carabidae), Hemiptera (*Dimargarodes mediterraneus* Silvestri, 1908), Embioptera (*Haploembia palaui* Stefani, 1955), Araneae, Isopoda (*Porcelio sp.*), Julida (*Julus sp.*), Geophilomorpha, and Thysanura (Doblas-Miranda et al., in press). Microarthropods occur principally at the litter level, and therefore, under shrubs and in ant nest mounds. They are mainly predators, but an important 30% of the total abundance corresponds to detritivores (Gómez-Ross et al., personal comm.)

Litter bag experiments

In April 2005, we established three simultaneous experiments using litter bags filled with the aboveground portion of two plant species (*Stipa tenacissima* and *Hordeum vulgare*), and roots from two species (*Stipa tenacissima* and *Daucus carota*). Surface litter and roots were obtained from living plants directly from the field, except for carrots. Litter was oven-dried at 40º during 48 h to obtain the initial dry weight (2.82 ± 0.02 gr/bag). Plant species differed in quality according to the C/N ratio. We collected aboveground material (C/N rate = 31.27 ± 5.11) and roots (C/N = 43.25 ± 2.22) of *Stipa tenacissima*. For high quality treatments, we also collected aboveground material of bot barley (*Hordeum vulgare;* C/N = 13.46 ± 0.46), similar in quality to the detritus found under this shrub (C/N= 16.28 ± 0.81). As high quality roots we used carrots (*Daucus carota;* C/N = 22.71 ± 0.69) instead of *Salsola oppositifolia* (C/N= 22.64 ± 1.27) or bot barley roots. In one hand, we did not use *Salsola* roots because to obtain the amount or roots necessary for the experiments required the destruction of a high number of shrubs. In the other hand, desiccated carrots were more similar in size and structure to *Salsola oppositifolia* roots than the small and superficial roots of bot barley. Because we were interested in decomposition rates between low and high quality litter more than the exact decomposition rate of a particular plant litter, litter and root procedence did not really affect the results. Moreover, bot barley and carrot litter were placed in the filed under (in the surface or buried) *Salsola* shrubs. *Salsola* shoots and leaves are easily broken in tiny pieces, being very difficult to measure their decomposition rate in the field.

Litter bags of different mesh size have been widely used for excluding decomposers of different sizes in many experiments. A previous experiment in the study site showed that bags of smaller mesh sizes concentrated humidity provoking an increase of the decomposition rate in those bags, therefore altering decomposition rate between treatments. To avoid this problem, we designed a new method using cylinders of 20 cm of diameter built with two different mesh sizes (1 cm and 1mm mesh size), placing standard 10 x 10 cm litter bags of 1 cm mesh size inside this cylinder. To manipulate access of aboveground and belowground animals to the litter bags, cylinders were placed aboveground and belowground. Aboveground, mesh cylinders (buitl with 1 cm or 1 mm mesh size fiber glass, depending on the treatments; see below) were 20 cm diameter and 15 cm height. The bottom of the cylinder was buried 1 cm into the ground and fixed by nails. The top of these cylinders was closed by a cover (1 cm mesh size, irrespective of the treatments) to prevent, as much as possible, disturbance of the litter bag by large animals and to allow transpiration. Litter bags were located in the centre of the cylinder on the ground surface. Belowground cylinders (30 cm high x 20 cm diameter) constructed with fiberglass mesh of different sizes (1cm and 1mm mesh size) were filled with gypsum substrate from the study site in which macroarthropods were removed. These cylinders were then buried such that the upper surface was flush with the ground. Root bags were buried inside the cylinder at approximately 15 cm depth. To test this methodology, an experiment was set in the field at the beginning of the winter season using all types of cylinders. After two months, detritus mass-loss in the litter-bags and soil moisture were compared among the different cylinder types corresponding to the different treatments in the three experiments to test whether this method prevented the problems associated to moisture accumulation by the mesh. We did not find any significant difference between treatments both in mass-loss or soil moisture.

Experiment 1

The experiment was performed to test the agents responsible of litter decomposition aboveground. We established an experiment with 3 treatments: 1) Substrate quality, with two levels, 1.1) low quality, litter bags filled with tussock-grass litter and, 1.2) high quality, bags filled wit bot barley litter; 2) Decomposer organisms, with three levels, 2.1) Control, allowing access to all (macro- and microfauna, microorganisms) decomposers: cylinders of 1 cm of mesh size, 2.2) Macrofauna exclusion: cylinders of 1 mm mesh size, 2.3) Macro- and microfauna exclusion (thereafter Faunal exclusion): cylinders of 1 mm mesh size and naphthalene included in the litter bags (litter bags were checked every two weeks, and when necessary naphthalene added to them); and 3) Time, with 3 levels: 3.1) 6 months, removing a set of bags from the study site after 6 months, 3.2) 10 months, and 3.3) 14 months.

The 90 cylinders (10 replicates x 3 decomposer treatments x 3 time periods) containing litter bags corresponding to the low quality treatment were placed under the canopy of tussock-grass individual plants, and the 90 cylinders for the high quality litter treatment were placed under *Salsola* shrubs (for a total of 180 cylinders). At each time interval, 10 cylinders of each treatment were randomly removed from the field, and the litter bags were carried to the laboratory. Litter was oven-dried at 40º to establish mass loss and C and N concentrations. Dried material was carefully cleaned with a small brush to remove soil particles and re-weighted. Decomposition rate was calculated as the percentage of dry mass remaining in each bag. Finally, litter C and N concentrations were determined in three samples of each treatment using a CHN Elemental Analyzer (Centro de Instrumentación Científica, Universidad de Granada). We measured mass loss (organism comsumption + physicochemical degradation), C:N ratio and %N (as two measures of detritus quality).

Experiment 2

The experiment was carried out to test the agents responsible of root litter decomposition belowground. We established an experiment with the same three treatments than in Experiment 1 but filling the litter bags with roots instead of surface litter. Every two weeks, naphthalene was checked and replaced if necessary for the first months. Thereafter, naphthalene, due to their lower degradation in the soil, was checked and replaced once a month.

90 cylinders (10 replicates x 3 decomposer treatments x 3 time periods) were buried under tussock-grass individual plants for low quality root bags, and another 90 cylinders of

each treatment under *Salsola* shrubs for high quality root bags (180 cylinders total). At each time interval, 10 cylinders of each treatment were randomly removed from the field, and the root bags were carried to the laboratory for weighting and chemical analyses (see above).

Experiment 3

We established an experiment to test the effects of above- and belowground decomposers on aboveground litter decomposition including three factors: 1) Litter quality, with two levels (see above); 2) Above-/belowground macroinvertebrate effects, with three levels: 2.1) Total access to above and belowground consumers, placing a cylinder of 1 cm mesh-size aboveground and, beneath it, another 1 cm mesh-size cylinder belowground. A litter bag was placed at the ground surface and an additional bag with root material was buried inside the cylinder, to avoid a higher consumption of aboveground material due to the scarcity of resources belowground. 2.2) Exclusion of belowground macroinvertebrate consumers (thereafter belowground exclusion), as in 2.1 but a cylinder of 1 cm mesh size was placed aboveground and, beneath, a 1 mm mesh-size cylinder buried belowground. And 2.3) Exclusion of aboveground macroinvertebrates (thereafter aboveground exclusion), as in 2.1 but a cylinder of 1 mm mesh-size placed aboveground and, beneath, a 1 cm mesh-size cylinder belowground; and 3) Time, as described in experiment 1.

90 cylinders (10 replicates x 3 macroinvertebrate treatments x 3 time periods) were placed under tussock-grass individual plants with low quality litter bags, and another 90 cylinders were placed under *Salsola* shrubs with high quality litter bags (180 cylinders total). At each time interval, 10 cylinders of each litter quality and faunal exclusion treatment were removed randomly from the field, and the litter bags were carried to the laboratory for weighting and chemical analyses (see above).

Statistical analysis

We used full factorial general linear models to test for differences in decomposition rates in litter bags. Time, type of bags and litter/root type were used as independent fixed factors, and mass loss was included as the dependent factor. Differences within factors were tested using the post-hoc Tukey HSD test.

The used of traditional ANOVA models, or any parametrical model, is not recommended when sample sizes are low, mainly due to the absence of normality in the data. Therefore, we used the permutational multivariate analysis of variance (PERMANOVA, Anderson and Legendre, 1999, McArdle and Anderson 2001) to test C/N rate and % of N models. This method analyses the variance of univariate or multivariate data explained by a set of explanatory factors on the basis of any distance or dissimilarity measure of choice. The method provides P-values by permutations, so that effects linked to each factor or interaction between factors may be tested in generally thought to be best suited because it provides the best statistical power and the most accurate Type I error (Anderson and Legendre, 1999). To perform the PERMANOVA, the FORTRAN computer program PERMANOVA was used (Anderson 2005). Each term in the model was tested through permutation tests based on 9999 permutations of residuals under a reduced model to obtain P-values.

The decomposition rate constant (k) was calculated using the negative exponential decay model from Olson (1963): $X/X0 = e^{-kt}$, where X=mass remaining at time t, $X0$=original weight and k is the decomposition constant (yr^{-1}).

Results

Experiment 1

Decomposition rate was almost 10 times higher in high quality litter at the study site (Table 1). Decomposition rate was also higher, for both types of litter, in the control bags than in the other two treatments (macro- and microinvertebrate exclusion), although these differences were more evident for bot barley.

Table 1. Decomposition rate (k, see methods) for each type of litter and bags in Experiments 1 and 2.

	High quality			**Low quality**		
	Control	Macroarthropod exclusion	Total exclusion	Control	Macroarthropod exclusion	Total exclusion
Aboveground	1.03	0.95	0.74	0.11	0.09	0.09
Belowground	3.81	2.62	2.64	0.17	0.21	0.21

Aboveground litter mass loss was mainly affected by litter quality and time of exposure (R^2= 0.77, df= 17, 162, F= 35.87, p= 0.0001; Table 2). Bot barley litter decomposed 4 times quicker than tussock grass litter, losing more than 80% of the weight at the end of the experiment. In addition, the significant interaction term between time of exposure and litter quality indicated that mass loss of litter from the two plants behaved in different manner across time (Table 2): While bot barley mass loss increased over time, mass loss rates in tussock grass were almost identical in the 10 and 14 month treatments. However, there was no effect of bag type on litter mass loss, and none of the other interaction terms were significant.

Separated analysis for mass loss after 14 months for bot barley showed that decomposition on total exclusion bags was significantly smaller (less than 60%) than decomposition in control and macroarthropod exclusion litter bags (more than 70%; R^2 = 0.31, df = 2, 27, F = 7.09, p = 0.003). This analysis was non significant for tussock-grass ($p > 0.05$).

Table 2. Results obtained for the models testing variability in decomposition rate (weight loss), C/N rate and percentage of N in A) Experiment 2, and B) Experiment 3. (Weight loss values were obtained from GLM, and chemical models values from PERMANOVAs, see Methods).

		Weight loss		**C/N rate**		**%N**	
	df	F	p	F	p	F	p
1) Aboveground							
Bag type (B)	2	0.21	0.81	0.73	0.49	4.39	**0.02**
Litter type (L)	1	416.81	**0.0001**	132.12	**0.0001**	183.26	**0.0001**
B x L	2	0.08	0.92	0.73	0.49	1.67	0.20
Time	2	70.87	**0.0001**	0.18	0.84	0.70	0.51
Time x B	4	1.54	0.19	0.22	0.31	2.59	0.06
Time x R	2	21.60	**0.0001**	0.21	0.81	3.12	0.06
Time x B x L	4	0.82	0.51	0.68	0.61	0.51	0.72
2) Belowground							
Bag type (B)	2	4.57	**0.01**	1.14	0.33	0.85	0.44
Root type (R)	1	1019.47	**0.0001**	296.94	**0.0001**	**70.77**	**0.0001**
B x R	2	7.27	**0.0001**	0.96	0.39	4.84	**0.02**
Time	2	10.96	**0.0001**	2.06	0.14	14.17	**0.002**
Time x B	4	0.19	0.94	0.65	0.64	1.59	0.19
Time x R	2	5.23	**0.006**	2.99	0.06	15.87	**0.0001**
Time x B x R	4	0.69	0.59	0.69	0.60	1.57	0.20

The model for C/N ratio only showed significant differences between litter types (Table 2). On the contrary, %N varied both between litter types and bag types (Table 2). Percentage of N was higher in bot barley than in Tussock-grass, and Total exclusion treatment showed in general higher %N than the other two treatments. Although only marginally significant, %N changed through time in a different way depending of the bag type treatment. In this case, %N decreased through time in the total exclusion treatment, meanwhile in the other two treatments %N increased through time. The interaction term Time x Litter type was also marginally significant (Table 2). In this case, in bot barley %N increased through time, meanwhile in tussock grass it first decreased and then remained constant.

Experiment 2

Belowground, decomposition rate was more than13 times higher in high quality carrot roots than in low quality *Stipa* roots (Table 1). Decomposition rate was also higher in the control bags than in the other two treatments (microinvertebrate exclusion and micro + macroinvertebrate exclusion), but only for carrot (Table 1).

Belowground root mass loss was affected by bag type, root type, and removal time ($R^2 = 0.86$, df = 17, 162, F = 63.47, p = 0.0001; Table 2). Root mass loss in the faunal exclusion was lower than in the other treatments. Moreover, tussock-grass roots decomposed much slower than carrots. The model also showed a significant interaction between decomposer organism and substrate quality treatments (Table 2), the differences between decomposer organism treatment being significant for carrots but not for tussock grass roots. Substrate quality treatment differed in the pattern of mass loss through time (Table 2): carrot decomposition increased over time, meanwhile the highest loss rate for tussock-grass roots was found after 10 months. None of the other interaction terms were significant (Table 2).

C/N rate only varied between root types (Table 2). Neither time nor decomposer organism treatments showed any significant variation in C/N rate. On the contrary, %N varied between treatments (Table 2). There were significant differences in %N between substrate quality and Time (Table 2). Carrot showed higher %N concentration, and %N increased through time. However, as indicated by the significant interaction term, %N varied between decomposer organism treatment levels. The percentage of N was significantly higher in the control than in macrofauna exclusion and faunal exclusion treatments in carrot, meanwhile there was no difference among treatments for Tussock-grass. Different substrate quality bags also varied in a different way in %N concentration through time (Table 2). Percentage of N increased in carrot through time, but it remained almost identical in Tussock-grass.

Experiment 3

Decomposition rate was not significantly different among decomposer treatments for low quality litter (k between 0.12 y 0.14 in all treatments); however, for high quality litter, decomposition rate was higher when aboveground decomposers where excluded (k = 1.56) compared with the completely open (1.03) and belowground exclusion (1.03) treatments.

There was a significant effect of the decomposer treatments in litter mass loss (R^2= 0.74, df= 17, 162, F= 30.33, p= 0.0001; Table 3). Litter decomposed faster in treatments in which belowground fauna was allowed, although only the belowground fauna exclusion treatment and aboveground fauna exclusion treatment were significantly different. Mass loss in litter bags open to both types of decomposers was intermediate to mass loss in the other two treatments. There was also a significant difference in decomposition rates between litter types, barley litter decomposing faster than tussock-grass litter. Time was an important factor determining mass loss but, as showed by the significant interaction terms, both types of litter decomposed in a different way through time, as described in experiments 1 and 2 (Table 3).

C/N rate and %N also varied among treatments (Table 3). Again, the only significant factor accounting for the differences was litter type, and neither time nor the exclusion of belowground or aboveground decomposers seems to affect these two dependent variables (Table 3).

Table 3. Results obtained for the models testing variability in decomposition rate (weight loss), C/N rate and percentage of N in Experiment 4. (Weight loss values were obtained from GLM, and chemical models values from PERMANOVAs, see Methods).

		Weight loss		**C/N rate**		**%N**	
	df	F	p	F	p	F	p
Bag type (B)	2	3.32	**0.03**	0.01	0.99	0.76	0.48
Litter type (L)	1	262.85	**0.0001**	145.31	**0.0001**	9.80	**0.0001**
Litter x bag type	2	2.54	0.08	0.46	0.63	1.88	0.88
Time	2	88.27	**0.001**	0.63	0.54	0.82	0.44
Time x B	4	0.60	0.65	0.12	0.97	0.13	0.96
Time x L	2	29.98	**0.0001**	0.56	0.59	2.04	0.14
Time x L x B	4	0.53	0.71	0.08	0.98	0.38	0.81

Discussion

Litter/root quality appeared as one of the main factors controlling decomposition in all the experiments. High quality litter decomposed up to four times faster than poor quality litter in some of the treatments. Many authors suggest that decomposition rate is related to the initial concentration of N (Berg and Staaf, 1987, Mun & Whitford 1998, Vivanco & Austtin 2006), which is recognized as the main factor limiting the growth of decomposer populations (Berg and Staaf, 1987, Wardle et al. 2003). Decomposer organisms utilize N to breakdown C substrates and, therefore, litter with high total N and narrow C:N ratios decompose faster.

However, variations in decomposition rates among litter of different plant species can also be a consequence of the preferences of animals for different types of litter (González & Seastedt 2001). Both non-exclusive mechanisms probably contributed to the decomposition rates obtained in the Baza basin, where soil faunal assemblages under different shrubs differ considerably not only in the number of individuals but also in species composition (Doblas-Miranda et al. submitted a) and resource (litter and root) quality appears as a significant factor determining the abundance of detritivores (Doblas et al., submitted b).

As expected, differences in decomposition rate due to litter quality were also evident below- and aboveground, but additionally, decomposition rates for both types of litter were higher belowground. Although many authors have found a higher decomposition rate below- than aboveground in arid systems (Elkins & Whitford 1982, Moorhead & Reynolds 1989a,b, Moretto et al. 2003), the opposite result has also been obtained (Kemp et al. 2003), suggesting that the degree of lignification of the root litter is a potential factor reducing decomposition rates belowground. Gholz et al. (2000), in an extensive study including many ecosystem types, found that belowground decomposition rates exceed aboveground decomposition in desert ecosystems, grassland, and tropical dry forest. Higher decomposition rate belowground has been explained because of the better environmental conditions belowground than in the surface, with lower solar radiation levels and temperature and higher humidity most of the year (Vivanco & Austin 2006, Gholz et al. 2000). Thus, the differences between the decomposition of leaf and root litter may be buffered due to the compensatory effects of more suitable micro-environmental conditions of belowground decomposition in spite of lower litter quality for roots (Gholz et al. 2000, Vivanco & Austin 2006).

In general, the dominant processes responsible of mass-loss processes seem to shift from biotic ones in temperate areas to abiotic ones in arid biomes (Coûteaux et al. 1995). As aridity increases, unfavourable climatic conditions and the concentration of litter in discrete patches hinder the development of the surface decomposer community (Elkins & Whitford

1982, Montaña et al. 1988, Moorhead & Reynolds 1989a, Coûteaux et al. 1995). However, some authors found that most root turnover in arid and semi-arid systems is due to macroarthropod activity, in particular to termites in some studies (Santos & Whitford 1981, Whitford et al. 1988, Schaefer et al. 1985, Ouédrago et al. 2003), even though termite effects seem to be negligible in wet years where moisture seems to be the determinant factor (Steinberger et al. 1995, Kemp et al. 2003). Surprisingly, other experiments on decomposition of buried litter in the same arid system showed little effect of abiotic factor in the decomposition process (Moorhead & Reynolds 1989). In our system, the exclusion of micro- and macroarthropods had a significant effect on decomposition rate, but only in high quality litter. Mass loss after 6 months in the total exclusion treatment seems to indicate that a high proportion of the decomposition belowground was due to abiotic factors + bacterial/fungal agents. Despite the considerable amount of mass loss in the total exclusion treatment, carrot decomposed faster in treatments with micro- and macroarthropods, losing after 6 months more than 83% of mass in both treatments compared with the 67% of the total exclusion treatment. Therefore, the presence of micro- and macroarthropod accelerated decomposition rate by 1.23 times. Interestingly, the effect macrofauna on mass loss was only evident aboveground in high quality litter at the end of the experiment, although decomposition rate was also higher in the presence of macroarthopods. This reinforces the idea that decomposition occurred at lower rate above- than belowground, but also evidences that the effects of macroarthropods on decomposition are important aboveground in the Baza basin, like in other arid, semi-arid, and temperate areas (Herlitzius 1983, Setälä et al. 1996, González & Seastedt 2001, Bradford et al. 2002, Smith & Bradford 2003).

At the Baza basin, N dynamics varied according to litter quality both above- and belowground, but also between treatments. This result is consistent with other studies in arid systems, where nitrogen immobilization in litter of annual plants occurred faster than in litter of shrubs (Mun & Whitford 1998). We should not expect a significant change in %N through time if the agents involved in decomposition were mainly physical agents (Moorhead & Reynolds 1989b). This occurred because decomposers provoke the immobilisation of N during decay (Parker et al. 1984, Mun & Whitford 1998). Indeed, in the presence of micro- and macroarthropods, nitrogen immobilisation occurred faster, despite the fact that some authors have found that the use of naphthalene to exclude microarthropods can stimulate microbial activity, provoking an enhanced immobilisation of soil inorganic N (Blair et al. 1989, González & Seastedt 2001), something that did not occur in our system. Other authors also found an increment in %N through time in arid systems in surface and/or root litter (Moorhead & Reynolds 1991, Mun & Whitford 1998, Kemp et al. 2003).

One of the most surprising results of this study is the higher percentage of mass loss in litter bags due to belowground fauna. In this study, we carry out what we believe to be the first such analysis for above-belowground decomposition processes. This result is very important because most studies on above and belowground interaction processes have focused on plant mediated interactions (Wardle 2002, Poveda et al. 2004), but no experimental studies have focused on direct interactions between decomposers. Some authors have found that in arid systems belowground detritivores feed on aboveground litter, such as in the Chihuahuan desert, where subterranean termites feed on surface litter (Ettershank et al. 1980). However, no specific experimental studies have been done excluding above- and belowground fauna at the same time. Our results support the observations obtained through the analysis of the vertical distribution of macroarthropods in the study area, where some groups appear exclusively as belowground dwellers, other groups only as surface litter dwellers, and only some groups are equally abundant in litter and, at least, the first 10 cm in the soil (Doblas-Miranda et al. submitted). Moreover, seasonal vertical migrations of some macroarthropod detritivores (tenebrionid larvae), indicate that these detritivores moved to the upper soil levels and the litter when litter is more humid, migrating belowground (20-30 cm deep) in drier seasons (Doblas-Miranda et al. submitted). We believe that our results can be extrapolated to most arid and semi-arid systems, where aboveground litter is patchily distributed (mainly under shrubs and ant-nest mounds) and usually forming a thin, distinct layer in the soil surface.

Interestingly, the direct interactions between above- and belowground macroarthropods at the Baza basin is not a mere sharing of the resources provided by surface litter between epigeal and endogeous detritivores. A puzzling result is that decomposition rate was higher in the absence of aboveground detritivores. One of the possible mechanism is reduction of larval predation in the aboveground macroarthropod exclusion treatment, which not only excluded detritivores, but also a number of potential predators of tenebrionid larvae and Embioptera, as ants, spiders and carabid beetles (Hodar and Sánchez-Piñero 2002; authors, pers. obs.). Predation of aboveground predators on soil biota has been found in others systems where salamanders and shrews ingested a high proportion of soil biota (Wyman 1998, Shvarts et al. 1997). In addition, competition with aboveground detritivores may also result in a reduction of decomposition rates. Interestingly, adult tenebrionid beetles (the main aboveground detritivores in our system) predate on tenebrionid larvae when these are at or near the surface (authors pers.obs.), provoking a combination of competitive and predatory interactions, which may reduce decomposition rates.

In desert ecosystems macrofauna can play an important role in the decomposition of above and belowground litter independently of litter quality. In this case, the relative time necessary to decompose litter is determinant to discriminate between the differential effects of the factors involved on decomposition. One of the major implications of our study is that ecosystem models need to include complex interaction between above and belowground decomposers to accurately predict litter decomposition.

Bibliography

Anderson, M.J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.

Anderson, M.J. & Legendre P. 1999. An empirical comparison of permutation methods for tests of partial regresión coefficients in a linear model. Journal of Statistical Computation and Simulation 62: 271-303.

Berg, B., and Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Ecological Bulletins 33, 163–178.

Blair J.M., D.A. Crossley Jr., & Rider S. 1989. Effects of naphthalene on microbial activity and nitrogen pools in soil-litter microcosms. Soil Biology & Biochemistry 21: 507-510.

Coûteaux M-M, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Trends Ecol Evol 10:63–66.

Doblas-Miranda, E., Sánchez-Piñero, F. and González-Megías, A. Soil macroinvertebrate fauna of a Mediterranean arid system: composition and temporal changes in the assemblage. - Soil Biology and Biochemistry, In press.

Elkins, N.Z. & Whitford, W.G. (1982). The role of microarthropods and nematodes in decomposition in semi-arid ecosystems. Oecologia 53: 303–310.

Ettershank G., J.A. Ettershank, M Bryant & W.G. Whitford 1980. Effects of nitrogen fertilisation on primary production in a Chihuhuan desert ecosystem. Journal of Arid Environment 1: 135-139.

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6:751–765

González G. & Seastedt T. R. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 84: 955-964.

Hättenschwiler S., A. V. Tiunov & P. Gasser 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36:191–218.

Herlitzius H. 1983. Biological decomposition efficiency in different woodland soils. Oecologia 57: 78-97.

Hódar, J. A. 2006. Diet composition and prey choice of the southern grey shrike Lanius meridionalis L. in South-eastern Spain: the importance of vertebrates in the diet. - Ardeola 53: 237-249.

Hódar, J. A. and Sánchez-Piñero, F. 2002. Feeding habits of the blackwidow spider Latrodectus lilianae (Araneae: Theridiidae) in an arid zone of south-east Spain. - Journal of Zoology: 101-109.

Hódar, J. A., Campos, F. and Rosales, B. A. 1996. Trophic ecology of the Ocellated Lizard Lacerta lepida in an arid zone of southern Spain: relationships with availability and daily activity of prey. - Journal of Arid Environments 33: 95-107.

Kemp P.R., JF Reynolds, RA Virginia, & WG Whitford 2003. Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. Journal of Arid Environment 53: 21-39.

Maraun M. & S. Scheu 1996. Chnages in microbial biomass, respiration and nutrient status of beech (Fagus selvatica) leaf litter processes by millipedes (Glomeris marginata). Oecologia 107: 131-140.

McArdle, B.H. & Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance based redundancy analysis. Ecology 82: 290-297.

Montaña C., Ezcurra E., A. Carrillo & Delhoume J.P. 1988. The decompostion rate of litter grasslands of northern Mexico: a comparison between arid and non-arid environments. J. Arid. Environ. 14: 55-60.

Moorhead D.L.& Reynolds J.F. 1989. The contribution of abiotic processes to buried litter decomposition in the northern Chihuhuan Desert. Oecologia 79: 133-135.

Moorhead D.L.& Reynolds J.F.1989b. Mechanism of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation. Journal of Arid Environment 16: 157-163.

Moorhead D.L.& Reynolds J.F. 1991. A general model of litter decomposition in the northern Chihuahuan desert. Ecological Modelling 56: 197-219.

Moretto A. S., & R. A. Distel 2003. Decomposition of and nutrient dynamics in a leaf litter and roots of Poa ligularis and Stipa gyneroides. Journal of Arid Environment 55: 503-514.

Mun H.T. & Whitford W.G. 1998. Changes in mass and chemistry of plants roots during long-term decomposition on a Chihuahuan Desert watershed. Biology and Fertility of Soils 26: 16-22.

Ouédrago E., A. Mando, & L. Brussaard. 2003 Soil macrofaunal-mediated organic resource disappearance in semi-arid West Africa. Applied Soil Ecology 27: 259-267

Olson J.S. 1963. Energy storage and the balance of producers and decomposers

in ecological systems. Ecology 44:322–331

Parker LW, Santos FP, Phillips J, Whitford WG (1984) Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual, Lepidium lasiocarpum. Ecol Monogr 54:339–360.

Poveda K., I. Steffan-Dewenter, S. Scheu & T. Tscharntke. Effects of below- and above-ground herbivores on plant growth, flower visitation and seed set. Oecologia 135: 601-605.

Santos PF, Whitford WG (1981) The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. Ecology 62:654–663

Santos PF, Philipps J & Whitford WG (1981) The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62:664–669.

Schaefer D., Steinberger Y., & W.G. Whitford 1985. The failure of nitrogen and lignin control of decomposition in a North American desert. Oecologia 65: 382-386

Smith & Bradford 2003 Applied Soil ecology 24,197

Steinberger Y., R. Degani & Barness G. 1995. Decomposition of root litter and related microbial population dynamics of a Negev Desert shrub, Zygophyllum dumosum. Journal of Arid Environment 31: 383-399.

Shvarts E.A., N.V. Chernyshev & Popov I.Y. 1997. Do shrews have an impact on soil invertebrates in Eurasian forests? Ecoscience 4:158-162.

Torreta & Takeda 1999. Carbon and Nitrogen dynamic of decomposing leaf litter in a tropical hill evergreen forest. Eur.J.Soil.Biol. 35:57-63.

Vivanco L. & A. T. Austin 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America

Oecologia 150: 97-107.

Wardle, D. A. 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. - Princeton Univ. Press.

Wardle, D. A., Nilsson, M.-C., Zackrisson, O, & Gallet, C. (2003) Determinants of litter mixing effects in a Swedish boreal forest. Soil Biology and Biochemistry 35: 827-835.

Whitford W.G., Steinberger Y. & G. Ettershank 1982. Contributions of Subterranean Termites to the "Economy” of Chihuahuan Desert Ecosystems. Oecologia 55: 298-302.

Wyman R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation 7: 641-650.

DISCUSIÓN GENERAL

Discusión

La comunidad de macroinvertebrados edáficos está dominada por artrópodos. Esta característica la diferencia de otras comunidades de hábitats templados y tropicales, mucho más estudiadas, donde las lombrices son, en general, el grupo dominante (e.g., Decaëns et al., 1998; Barros et al., 2002). Sin embargo, aunque menos estudiadas, parece ser un rasgo común de otras comunidades desérticas y mediterráneas, donde encontramos gran abundancia de formícidos y coleópteros (Ghabbour y Shakir, 1980; Legakis, 1994; Sánchez-Piñero, 1994). Por otro lado, en esta comunidad destaca la abundancia de herbívoros subterráneos. La herbivoría bajo suelo es un tema al que se le ha dedicado poca atención (e.g., Blossey y Hunt-Joshi, 2003), a pesar de que la producción primaria subterránea suele exceder a la epigea, especialmente en desiertos (e.g., Eissenstat y Yanai, 1997). Sin embargo, en nuestro sistema, la gran biomasa de herbívoros sugiere que la herbivoría parece ser tan importante como la detritivoría o la omnivoría, consideradas las vías tróficas más comunes de ecosistemas áridos (Seely y Louw, 1980; Polis, 1991).

Toda esta comunidad demostró una gran variación entre los distintos periodos de muestreo. Es cierto que la estacionalidad es una característica de muchos ecosistemas (e.g., Wolda, 1988) y especialmente los desérticos, donde las fluctuaciones de temperatura y precipitación provocan marcados pulsos de productividad y actividad (Noy-Meir, 1979/80; Blondel y Aronson, 1999), pero en los resultados destacan dos características interesantes dentro de la variación temporal. Por un lado las variaciones en la comunidad de macroartrópodos fueron más destacadas en la hojarasca que bajo suelo, ya que las fluctuaciones de temperatura y humedad son más pronunciadas también en el exterior que en el medio subterráneo (Di Castri y Di Castri, 1981). Por otra parte, también existieron fuertes diferencias entre años en el patrón estacional, algo común en sistemas impredecibles (Seely y Louw, 1980; Mooney, 1981), pero siempre interesante de registrar, debido a las diferentes reacciones que puede provocar en los distintos taxones (Sánchez-Piñero y Ávila, 2004).

La variabilidad temporal tendría importantes implicaciones en la estructura de la comunidad, ya que los cambios en la composición de especies y la estructura trófica de los macroinvertebrados podrían afectar a las interacciones entre especies y a la dinámica y estructura de la red trófica en el sistema. Consecuentemente, dado el marcado carácter de las variaciones estacionales, éstas afectaron a los patrones de distribución espaciales, tanto horizontal como vertical, de la comunidad edáfica.

Para conocer la distribución horizontal de la macrofauna de la Hoya de Baza, el factor clave son las islas de fertilidad. Se consideran como tales los microambientes generados por arbustos, hormigueros, etc. que proporcionan un microclima más suave, mayor disponibilidad de recursos y cobertura en ambientes áridos (Schlesinger et al., 1996; Bochet et al., 1999; Cammeraat et al., 2002; Wagner y Jones, 2006). Los diferentes arbustos estudiados y los cúmulos de detritus de los hormigueros muestran la característica distribución parcheada de recursos, capaz de generar la agregación de la fauna del suelo (Ettema et al., 1998), así que los macroinvertebrados mostraron una gran abundancia, biomasa y riqueza en los arbustos y los hormigueros, comparados con la matriz de suelo desnudo. Pero las comunidades de macrofauna de los distintos "microhábitats isla" también mostraron importantes diferencias entre sí en biomasa, abundancia y riqueza, ya que dichos microhábitats poseen características diferentes, como la calidad del recurso que acumulan (Wardle, 2002) o la cobertura que ofrecen (Bochet et al., 1999). Algo muy interesante ya que las diferencias en la distribución de macrofauna del suelo dentro de un mismo ecosistema han sido pobremente estudiadas (Peterson et al., 2001). Aún más, las diferencias fueron taxonómicas y tróficas, con lo que podrían generar variaciones espaciales en la red trófica del sistema. Por último, como se mencionó en el párrafo anterior, el patrón espacial resulta ser dinámico en el tiempo, variando la distribución de la macrofauna por microhábitat según la estación de muestreo, algo documentado en muy pocos estudios (Sinclair et al., 2001).

La distribución espacial de la fauna edáfica también posee una componente vertical, que en la zona de estudio mostró un claro patrón, y constante para todos los microhábitats, de disminución gradual en la abundancia, la biomasa y la riqueza de los macroinvertebrados con la profundidad, en concordancia con otros estudios (Berg et al., 1998; Sadaka y Ponge, 2003). Sin embargo, la característica diferenciación entre la comunidad de la hojarasca y la del medio subterráneo en los ecosistemas mediterráneos (Di Castri y Di Castri, 1981) se reflejó en la distribución de las especies y en la de los grupos tróficos, pues los depredadores son principalmente habitantes de la hojarasca y los herbívoros edáficos aparecieron en el medio subterráneo, donde pueden alimentarse (Sadaka y Ponge, 2003). Pero al mismo tiempo, a pesar de las diferencias taxonómicas y tróficas, hubo taxones que mostraron una proporción parecida en ambos medios, como *Geophilomorpha*, *Tenebrionidae* y *Embioptera*. Asimismo, el grupo trófico de los detritívoros mostró su capacidad de encontrar recursos en ambos medios, la hojarasca en la superficie y el detritus de las raíces bajo suelo (Sadaka y Ponge, 2003). Por lo tanto, ambas comunidades no reflejan compartimentación debido a unos pocos, pero dominantes (Capítulo 1), grupos de macrofauna con una primordial labor conectiva. Dentro de ellos destacan los tenebriónidos, los cuales mostraron una conexión de intensidad variable en el tiempo entre la hojarasca y niveles más subterráneos, a través de migraciones estacionales, demostrando de nuevo la importancia de la variación temporal en el sistema estudiado. Aunque es cierto que la migración vertical ha sido registrada en diferentes especies de fauna del suelo (e.g. Briones et al., 1998; Jiménez y Decaëns, 2000; Frouz et al., 2004) y, efectivamente, parece depender de cambios estacionales, los detritívoros *Tenebrionidae* demuestran que los macroinvertebrados pueden participar más directamente a través del transporte de energía entre los compartimentos epigeo e hipogeo (Wardle, 2002). Así, los tenebriónidos podrían participar en esta conexión al consumir hojarasca superficial principalmente en invierno y primavera, cuando es más comestible por la humedad (Olear y Seastedt, 1994), y el detritus de las raíces en verano, especialmente.

Es sabido que la comunidad de fauna edáfica tiene considerables efectos en el crecimiento vegetal, ya que los invertebrados del suelo forman parte de los ciclos que unen C, N, las comunidades microbianas y las plantas (Lavelle, 1997; Wardle, 1999; Ehrenfeld et al., 2005). Así que los microhábitats isla en ecosistemas áridos, donde la macrofauna edáfica muestra agregación, podrían estar potencialmente mantenidos por las uniones complejas que implican a los macroinvertebrados que allí habitan. De esta manera, la acción conectiva de las larvas de *Tenebrionidae* podría tener implicaciones en el consumo de detritus superficial, lo que sugiere importantes consecuencias para los ciclos de materia y energía entre los medios epigeo e hipogeo (Capítulo 5).

La importancia de los microhábitats afectando a la distribución de la fauna se debe a que estas zonas poseen unas condiciones ambientales y disponibilidad de recursos características. Curiosamente, en contra de la idea clásica de que las condiciones medioambientales son el factor principal que gobierna los ecosistemas desérticos (Noy-Mair, 1979/80; Whitford, 1989), los recursos influyeron notablemente en las densidades de fauna. Aún cuando la producción primaria depende principalmente de los factores abióticos, los consumidores están restringidos por algo más que la energía disponible, y es importante considerar otros factores como la calidad del recurso (Polis, 1991). En el sistema de estudio hay plantas de gran calidad pero baja producción y viceversa (manuscrito no publicado), con lo que la producción de raíces no afectó la densidad de los grupos tróficos por separado. Sin embargo la calidad de las raíces si afectó mucho a los detritívoros y herbívoros edáficos, confirmando que ambos grupos no sólo están restringidos por la disponibilidad de su alimento (Crawford, 1991; Wisdom, 1991; Wardle y Lavelle, 1997). Es más, en el caso de la hojarasca, ésta no sólo es útil como alimento, sino que posee una reconocida eficiencia como hábitat, ya que modifica la humedad, la luz, la temperatura y hasta la velocidad del viento (Moore et al., 2004), lo que explicaría su influencia sobre la distribución de los macroherbívoros superficiales. Para los detritívoros, consumidores directos, la calidad de la hojarasca jugó un papel principal. De hecho, la relación negativa entre cantidad de hojarasca y los detritívoros subterráneos podría quedar explicada por una mayor producción de hojarasca combinada con una menor calidad de la misma en verano (manuscrito no publicado). Los efectos de la hojarasca superficial sobre los detritívoros tanto epigeos como hipogeos apoyan los resultados obtenidos sobre su papel conector y las variaciones estacionales en su intensidad (Capítulo 3).

Pero los factores externos no son los únicos que explican la distribución de la fauna, y las interrelaciones de los propios grupos tróficos mostraron interesantes efectos en la densidad de la fauna edáfica. Únicamente los herbívoros edáficos no mostraron interrelaciones con otros grupos en ninguno de los dos modelos: los herbívoros asociados a la hojarasca, como ya se ha comentado, buscan en ésta refugio, y los macro-herbívoros hipogeos parecen no sufrir depredación, ya que sus enemigos naturales son principalmente patógenos (Brown y Gange, 1990). No obstante, los depredadores no sólo se alimentan de herbívoros (Polis y Strong, 1996) y de hecho las relaciones más interesantes se produjeron entre depredadores y detritívoros, representando un sistema dominado por los recursos. Experimentos de adición de recursos en redes tróficas edáficas han probado afectar a los macroartrópodos detritívoros aumentando sus poblaciones, pero también incrementando la densidad de la macrofauna depredadora, lo cual indica un fuerte control por recurso en estos organismos (Chen y Wise, 1999; Wardle et al., 1999). Se ha argumentado que los depredadores no juegan un papel importante en el control de las densidades animales en desiertos (Noy-Meir, 1985), pero sin embargo hay estudios que demuestran lo contrario, considerando a los depredadores como un factor principal en la distribución de animales de superficie en hábitats desérticos (Polis et al., 1998; Groner y Ayal, 2001; Ayal, 2007). Sobre la influencia positiva de los depredadores sobre los detritívoros se puede hipotetizar acerca de depredación dentro de gremio, ya que muchos depredadores son arácnidos, que suelen depredar sobre estadios juveniles del mismo grupo (Holt and Polis 1997; Wagner and Wise 1996). Además, hay depredadores que no han sido tenidos en cuenta en este estudio, como lagartos o pájaros, que podrían afectar a los artrópodos depredadores del suelo liberando a los macro-detritívoros de la depredación (Ayal 2007). De todas maneras, la realización de experimentos controlados sería crucial para analizar estos mecanismos.

Entre las relaciones tróficas destacan especialmente las que conectan los medios epigeo e hipogeo: Los macro-detritívoros hipogeos afectaron positivamente a los macro-detritívoros epigeos, y estos, a su vez, a los macro-depredadores epigeos. Efectivamente, las larvas subterráneas pueden realizar migraciones verticales y alimentarse en el nivel superficial (Capítulo 3) o pueden emerger como adultos de vida epigea (Crawford, 1991), y en ambos casos pueden alimentar a depredadores epigeos generalistas, confirmando el papel de la macrofauna detritívora y depredadora en la conexión de ambos niveles (Scheu, 2001; Miyashita et al., 2003). Lo que de nuevo nos llevaría, además, a considerar la importancia de los detritívoros en la conexión de los medios epigeo e hipogeo por medio del consumo del detritus superficial.

La descomposición del detritus en la zona de estudio está fuertemente influenciada por la calidad del substrato. Esto puede deberse a dos factores no exclusivos, por una parte debido a la concentración inicial de Nitrógeno (Berg y Staaf, 1987; Mun y Whitford, 1998; Wardle et al., 2003; Vivanco y Austtin, 2006), ya que los organismos descomponedores usan el N para romper el substrato de Carbono. Por el otro lado, estas diferencias podrían basarse en las preferencias de los propios descomponedores en su alimentación (González y Seastedt, 2001). Igualmente, estas diferencias se mantienen tanto a nivel superficial como subterráneo, siendo la descomposición de las raíces más evidente que la de la hojarasca. Este hecho ha sido comprobado en otros sistemas áridos (Elkins y Whitford, 1982; Moorhead y Reynolds, 1989; Moretto y Distel, 2003), y es probablemente debido a las mejores condiciones ambientales edáficas, en oposición a la alta temperatura y baja humedad en la superficie (Gholz et al. 2000; Vivanco y Austin, 2006). Sin embargo, la descomposición es también importante en la superficie, especialmente para los macroartrópodos, como en otros sistemas (Herlitzius, 1983;

Setälä et al., 1996; González y Seastedt, 2001; Bradford et al., 2002; Smith y Bradford, 2003). La fauna jugó un papel importante en la degradación en general (tasa de descomposición 1,23 veces más alta en presencia de micro- y macro-artrópodos), al igual que en otros sistemas áridos y semi-áridos (Santos y Whitford, 1981; Whitford et al., 1982; Schaefer et al., 1985; Ouédraogo et al., 2003), a pesar de que los procesos dominantes en la pérdida de masa del detritus en biomas áridos se consideran principalmente abióticos (Coûteaux et al., 1995).

Pero los resultados más importantes, como ya se ha mencionado anteriormente, son los relacionados con el consumo del detritus superficial a través de la macrofauna subterránea, algo que ha sido observado en termitas (Ettershank et al., 1980), pero nunca experimentado específicamente. Este efecto prueba una vez más lo sugerido en el Capítulo 3, basándonos en las migraciones verticales de las larvas de Tenebriónido, y en el Capítulo 4, donde se analizan los factores que afectan a la distribución de los grupos tróficos en el estudio, y se sugería la importancia de la hojarasca superficial para los detritívoros epigeos e hipogeos, además de la propia influencia de los detritívoros edáficos sobre los superficiales al desplazarse hacia la superficie en busca de alimento.

Los macroinvertebrados edáficos de la Hoya de Baza, un ecosistema mediterráneo árido, se distribuyen de forma parcheada, concentrados en los microhábitats que les ofrecen condiciones ambientales más favorables que la matriz de suelo, y principalmente al ser donde se concentran los recursos. Son las diferencias en producción y especialmente en la calidad de los recursos entre los distintos microhábitats las que provocan una gran heterogeneidad espacial, que a su vez se combina con la alta variabilidad temporal del sistema. Como resultado, la comunidad varía en el tiempo y en el espacio, con importantes consecuencias en los ciclos de materia y energía. Así, las larvas de Tenebriónido, un grupo dominante de fauna subterránea, realizan migraciones verticales en busca del mejor alimento, contribuyendo a la interacción entre la hojarasca superficial y el medio subterráneo, y participando en la degradación del detritus superficial, uno de los procesos ecológicos más importantes en los ecosistemas terrestres.

Bibliografía

Ayal, Y. 2007. Trophic structure and the role of predation in shaping hot desert communities. Journal of Arid Environments 68: 171-187.

Barros, E., B. Pashanasi, R. Constantino y P. Lavelle. 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biology and Fertility of Soils 35: 338-347.

Berg, B. y H. Staaf. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Ecological Bulletins 33: 163-178.

Berg, M. P., J. P. Kniese, J. J. M. Bedaux y H. A. Verhoef. 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. Biology and Fertility of Soils 26: 268-284.

Blondel, J. y J. Aronson. 1999. Biology and wildlife of the Mediterranean Region. Oxford University Press, Oxford, 328 pp.

Blossey, B. y T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: Influence on plants and aboveground herbivores. Annual Review of Entomology 48: 521-547.

Bochet, E., J. L. Rubio y J. Poesen. 1999. Modified topsoil islands within patchy Mediterranean vegetation in SE Spain. Catena 38: 23-44.

Bradford, M. A., G. M. Tordoff, T. Eggers, T. H. Jones y J. E. Newington. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos 99: 317-323.

Briones, M. J. I., P. Ineson y J. Poskitt. 1998. Climate change and *Cognettia sphagnetorum*: effects on carbon dynamics in organic soils. Functional Ecology 12: 528-535.

Brown, V. K. y A. C. Gange. 1990. Insect herbivory below ground. Advances in Ecological Research 20: 1-58.

Cammeraat, L. H., S. J. Willott, S. G. Compton y L. D. Incoll. 2002. The effects of ants' nests on the physical, chemical and hydrological properties of a rangeland soil in semi-arid Spain. Geoderma 105: 1-20.

Chen, B. y D. H. Wise. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80: 761-772.

Crawford, C. S. 1991. The community ecology of macroarthropod detritivores. En: Polis, G. A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 89-112.

Coûteaux, M.-M., P. Bottner y B. Berg. 1995. Litter decomposition, climate and litter quality. Trends in Ecology and Evolution 10: 63-66.

Decaëns, T., T. Dutoit, D. Alard y P. Lavelle. 1998. Factors influencing soil macrofaunal communities in post-pastoral successions of western France. Applied Soil Ecology 9: 361-367.

Di Castri, F. y V. V. Di Castri. 1981. Soil fauna of Mediterranean-climate regions. En: Di Castri, F., D. W. Goodall y R. L. Specht (Eds.), Ecosystems of the World. 11. Mediterranean type shrublands. Elsevier, Amsterdam, pp. 445-478.

Ehrenfeld, J. G., B. Ravit y K. Elgersma. 2005. Feedback in the plant-soil system. Annual Review of Environmental Resources 30: 75-115.

Eissenstat, D. M. y R. D. Yanai. 1997. The ecology of root life-span. Advances in Ecological Research 27: 1-60.

Elkins, N. Z. y W. G. Whitford. 1982. The role of microarthropods and nematodes in decomposition in semi-arid ecosystems. Oecologia 53: 303-310.

Ettema, C. H., D. C. Coleman, G. Vellidis, R. Lowrance y S. L. Rathbun. 1998. Spatiotemporal distributions of bacterivorous nematodes and soil resources in a restored riparian wetland. Ecology 79: 2721-2734.

Ettershank, G., J. A. Ettershank, M. Bryant y W. G. Whitford. 1980. Effects of nitrogen fertilisation on primary production in a Chihuhuan desert ecosystem. Journal of Arid Environment 1: 135-139.

Frouz, J., A. Ali, J. Frouzova y R. Lobinske. 2004. Horizontal and vertical distribution of soil macroarthropods along a spatio-temporal moisture gradient in subtropical Central Florida. Environmental Entomology 33: 1282-1295.

Ghabbour, S. I. y S. H. Shakir. 1980. Ecology of soil fauna of Mediterranean desert ecosystem in Egypt. III. Analysis of Thymelaea mesofauna populations at the Mariut frontal plain. Revue D'écologie et de Biologie du Sol 17 (3): 327-352.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon y W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6: 751-765.

González, G. y T. R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 84: 955-964.

Groner, E. y Y. Ayal. 2001. The interaction between bird predation and plant cover in determining habitat occupancy of darkling beetles. Oikos 93: 22-31.

Herlitzius, H. 1983. Biological decomposition efficiency in different woodland soils. Oecologia 57: 78-97.

Holt, R. D. y G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149: 745-764.

Jiménez Jaen, J. J. y T. Decaëns. 2000. Vertical distribution of earthworms in grassland soils of the Colombia Llanos. Biology and Fertility of Soils 32: 463-473.

Lavelle, P. 1997. Faunal activities and soil processes: Adaptative strategies that determine ecosystem function. Advances in Ecological Research 27: 93-132.

Legakis, A. 1994. Community structure and species richness in the Mediterranean-type soil fauna. En: Arianoursou, M. y R. H. Groves (Eds.), Plant-Animal Interactions in Mediterranean-Type Ecosystems. Kluwer Academic Publishers, Netherlands, pp. 37-45.

Miyashita, T., M. Takada y A. Shimazaki. 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. Oikos 103: 31-36.

Mooney, H. A. 1981. Primary production in Mediterranean-climate regions. En: Di Castri, F., D. W. Goodall y R. L. Specht (Eds.), Ecosystems of the world, Vol. 11: Mediterranean-type shrublands. Elsevier, Amsterdam, pp. 249-255.

Moore, J. C., E. L. Berlow, D. C. Coleman, P. C. de Ruiter, D. Quan, A. Hastings, N. Collins Johnson, K. S. McCann, K. Melville, P. J. Morin, K. Nadelhoffer, A. D. Rosemond, D. M. Post, J. L. Sabo, K. M. Scow, M. J. Vanni y D. H. Wall Freckman. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7: 584-600.

Moorhead, D. L. y J. F. Reynolds. 1989. Mechanism of surface litter mass loss in the northern Chihuahuan desert: a reinterpretation. Journal of Arid Environment 16: 157-163.

Moretto, A. S. y R. A. Distel. 2003. Decomposition of and nutrient dynamics in a leaf litter and roots of *Poa ligularis* and *Stipa gyneroides*. Journal of Arid Environment 55: 503-514.

Mun, H. T. y W. G. Whitford. 1998. Changes in mass and chemistry of plants roots during long-term decomposition on a Chihuahuan Desert watershed. Biology and Fertility of Soils 26: 16-22.

Noy-Meir, I. 1979/80. Structure and function of desert ecosystems. Israel Journal of Botany 28: 1-19.

Noy-Meir, I. 1985. Desert ecosystem structure and function. En: Evenary, M. (Ed.), Hot Deserts and Arid Shrublands. Elsevier, Amsterdam, pp. 93-103.

Olear, H. A. y T. R. Seastedt. 1994. Landscape patterns of litter decomposition in alpine tundra. Oecologia 99 (1-2): 95-101.

Ouédraogo, E., A. Mando y L. Brussaard. 2004. Soil macrofaunal-mediated organic resource disappearance in semi-arid West Africa. Applied Soil Ecology 27: 259-267.

Peterson, A. C., P. F. Hendrix, C. Haydu, R. C. Graham y S. A. Quideau. 2001. Single- shrub influence on earthworms and soil macroarthropods in the southern California chaparral. Pedobiologia 45: 509-522.

Polis, G. A. 1991. The Ecology of Desert Communities. University of Arizona Press, Tucson, 456 pp.

Polis, G. A., y D. R. Strong. 1996. Food web complexity and community dynamics. The American Naturalist 147: 813-846.

Polis, G. A., J. D. Barnes, M. K. Seely, J. R. Henschel y M. M. Enders. 1998. Predation as a major cost of reproduction in Namib Desert tenebrionid beetles. Ecology 79: 2560-2566.

Sadaka, N. y J. F. Ponge. 2003. Soil animal communities in holm oak forests: influence of horizon, altitude and year. European Journal of Soil Biology 39: 197-207.

Sánchez-Piñero, F. 1994. Ecología de las comunidades de coleopteros en zonas áridas de la depresión de Guadix-Baza (Sureste de la Península Ibérica). Universidad de Granada, Granada.

Sánchez-Piñero, F. y J. M. Avila. 2004. Dung-insect community composition in arid zones of south-eastern Spain. Journal of Arid Environments 56: 303-327.

Santos, P. F. y W. G. Whitford. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. Ecology 62: 654-663.

Schaefer, D., Y. Steinberger y W. G. Whitford. 1985. The failure of nitrogen and lignin control of decomposition in a North American desert. Oecologia 65: 382-386

Scheu, S. 2001. Plants and generalist predators as links between the below-ground and above-ground system. Basic and Applied Ecology 2: 3-13.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley y A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77: 364-374.

Seely, M. K. y G. N. Louw. 1980. First approximation of the effect of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. Journal of Arid Environments 14: 131-143.

Setälä, H., V. Marshall y T. Trofymow. 1996. Influence of body size of soil fauna on litter decomposition and 15N uptake by poplar in a pot trial. Soil Biology and Biochemistry 28: 1661-1675.

Sinclair, B. J., J. M. Lord y C. M. Thompson. 2001. Microhabitat selection and seasonality of alpine invertebrates. Pedobiologia 45: 107-120.

Smith, V. C. y M. A. Bradford. 2003. Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Applied Soil Ecology 24: 197-203.

Vivanco, L. y A. T. Austin. 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from North and South America. Oecologia 150: 97-107.

Wagner, D. y J. B. Jones. 2006. The impact of harvester ants on decomposition, N mineralization, litter quality, and the availability of N to plants in the Mojave Desert. Soil Biology and Biochemistry 38: 2593-2601.

Wagner, J. D. y D. H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. Ecology 77: 639-652.

Wardle, D. A. 1999. How soil food webs make plants grow. Trends in Ecology & Evolution 14: 418-420.

Wardle, D. A. 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton & Oxford.

Wardle, D. A. y P. Lavelle. 1997. Linkages between soil biota, plant litter quality and decomposition. En: Giller, K. E. y G. Cadisch (Eds.), Driven by Nature-Plant Litter Quality and Decomposition. CAB International, Wallingford, pp. 107-124.

Wardle, D. A., K. S. Nicholson, K. I. Bonner y G. W. Yeates. 1999. Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity and temporal variability over a seven-year period. Soil Biology and Biochemistry 31: 1691-1706.

Wardle, D. A., M.-C. Nilsson, O. Zackrisson y C. Gallet. 2003. Determinants of litter mixing effects in a Swedish boreal forest. Soil Biology and Biochemistry 35: 827-835.

Whitford, W. G. 1989. Abiotic controls on the functional structure of soil food webs. Biology and Fertility of Soils 8: 1-6.

Whitford, W. G., Y. Steinberger y G. Ettershank. 1982. Contributions of subterranean termites to the "economy" of Chihuahuan Desert ecosystems. Oecologia 55: 298-302.

Wisdom, C. S. 1991. Patterns of heterogeneity in desert herbivorous insect communities. En: Polis, G. A. (Ed.), The Ecology of Desert Communities. University of Arizona Press, Tucson, pp. 151-179.

Wolda, H. 1988. Insect seasonality: Why? Annual Review of Ecology and Systematics 19: 1-18.

CONCLUSIONES

Conclusiones

1) La comunidad de macrofauna del suelo en la Hoya de Baza está compuesta casi exclusivamente por artrópodos, tanto en términos de abundancia como de biomasa. Los órdenes más destacados fueron Hymenoptera (Formicidae), Coleoptera (en especial las familias Tenebrionidae y Cebrionidae), Hemiptera (Margarodidae) y Embioptera (Oligotomidae). Los herbívoros edáficos comprenden una importante proporción de los macroinvertebrados de suelo en el área de estudio, lo que sugiere que la herbivoría subterránea podría ser tan importante como la detritivoría o la omnivoría en los ecosistemas desérticos.
2) La comunidad de macrofauna sufrió importantes variaciones estacionales tanto en composición como en abundancia o biomasa, que fueron más marcadas para la fauna que habita en la hojarasca que para la subterránea. Además, dicho patrón de variación estacional fue diferente para cada uno de los dos años de estudio. Esta variabilidad temporal tendría importantes implicaciones en la estructura de la comunidad, ya que los cambios en la composición de especies y la estructura trófica de los macroinvertebrados podrían afectar a las interacciones entre especies y a la dinámica de la red trófica del sistema.
3) La distribución de macroinvertebrados fue afectada por las islas de fertilidad (las principales especies de arbustos del área y los cúmulos de detritus de hormiguero), mostrando grandes diferencias en riqueza, abundancia y biomasa entre éstas y la matriz de suelo desnudo. Las comunidades asociadas a los distintos “microhábitat isla” de la zona de estudio mostraron también importantes diferencias entre ellas, diferencias a su vez afectadas por la variabilidad temporal.

4) Los microhábitat isla en los ecosistemas áridos estarían potencialmente mantenidos por las complejas interacciones que implican a los macroinvertebrados del suelo, los cuales viven allí agregados.
5) La comunidad de macrofauna de la Hoya de Baza mostró un claro patrón de distribución vertical, en el que la riqueza, abundancia y biomasa de la comunidad de macrofauna decrecieron gradualmente con la profundidad.
6) Hubo diferencias de diversidad y riqueza entre la hojarasca y el medio subterráneo. Algunos taxones, principalmente depredadores, aparecieron asociados a la hojarasca (como Araneae y Carabidae) mientras que otros, generalmente herbívoros, aparecieron exclusivamente en el medio subterráneo (como Margarodidae y los estadios larvarios de Cebrionidae y Melolonthidae).
7) Ambos sistemas están unidos directamente por algunos grupos de macroartrópodos dominantes en el sistema, tanto detritívoros (Embioptera y larvas de Tenebrionidae) como depredadores (Geophilomorpha), que habitan en la hojarasca y el suelo. Por medio de migraciones verticales, las larvas de tenebriónido aparecen con mayor proporción en la superficie en invierno y primavera, y en el medio subterráneo en verano, demostrando la importancia de considerar las variaciones temporales al establecer las interconexiones entre los medios epigeo e hipogeo.
8) Aunque las comunidades faunísticas de la hojarasca y el medio subterráneo mostraron ciertas diferencias, existen grupos que comparten ambos hábitat, indicando que se trataría de medios interconectados, con posibles consecuencias directas en las dinámicas de materia y energía entre los medios epigeo e hipogeo.
9) Aunque las condiciones abióticas tuvieron efectos sobre algunas variables, la calidad de los recursos (hojarasca, raíces) afectó de manera destacada a la distribución de la macrofauna edáfica. Efectos directos e indirectos de los recursos sobre las abundancias de detritívoros y predadores sugieren la importancia de las interacciones

entre estos grupos tróficos, con implicaciones en la conexión entre la comunidad epigea e hipogea.

10) La descomposición en la zona de estudio está fuertemente influenciada por la calidad del substrato. Esta influencia se mantiene tanto en la superficie como en el medio subterráneo, siendo la descomposición hipogea más evidente que la epigea. Pese a que la descomposición en los ecosistemas áridos se considera principalmente controlada por los factores abióticos, micro- y macro-artrópodos demostraron su importancia en la degradación.
11) La fauna subterránea detritívora participa activamente en la degradación de la hojarasca superficial, siendo su contribución mayor que la de los detritívoros epigeos de la zona de estudio.
12) Los macroinvertebrados edáficos de la Hoya de Baza se distribuyen de forma parcheada, concentrados en los microhábitat donde se concentran los recursos, y que les ofrecen condiciones ambientales más favorables. Las diferencias en la calidad de los recursos provocan una gran heterogeneidad espacial, que a su vez se combina con la alta variabilidad temporal del sistema afectando a la distribución espacio-temporal de la fauna. Así, las larvas de Tenebriónido realizan migraciones verticales en busca del mejor alimento, contribuyendo a la interacción entre la hojarasca y el medio subterráneo, y participando en la degradación del detritus superficial, con importantes consecuencias en los ciclos de materia y energía.

Conclusions

1) The macrofaunal assemblage at the Baza Basin was dominated mainly by arthropods both in terms of abundance and biomass. The most important groups were Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae and Cebrionidae), Hemiptera (Margarodidae) and Embioptera (Oligotomidae). In the study system subterranean herbivores represent an important proportion of soil macroinvertebrates, suggesting that belowground herbivory is potentially as important as detritivory or omnivory in arid ecosystems.
2) There were important seasonal variations in the macrofaunal community composition, abundance and biomass that were more marked in litter than belowground. Also, the pattern of seasonal variation showed important differences between the two years considered in this study. This temporal variability has potentially important implications on the community ecology in the study system, since the changes in species composition and trophic structure of soil invertebrate assemblages may affect species interactions and food web dynamics over time.
3) Macroinvertebrate distribution was affected by the fertile islands in the study site (the principal shrubs species and ant nest mounds), and the differences in richness, abundance and biomass between these microhabitats and the bare soil matrix were high. Also, macrofaunal communities of the distinct “island microhabitats” showed important differences among them, and were also affected by temporal variavility.
4) Island microhabitats in arid ecosystems, where soil fauna showed aggregation, are potentially maintained by complex links that involve the soil macroinvertebrates living within.

5) The macrofaunal assemblage at the Baza Basin showed a clear pattern of vertical distribution where richness, abundance and biomass decreased gradually with soil depth.
6) There were great differences in diversity and richness between the litter layer and the underground profile. Some taxa appear mainly associated to the litter (such as Araneae and Carabidae, both predators) or belowground (e.g. Cebrionidae and Melolonthidae larvae and Margarodidae, all herbivores).
7) Both subsystems are linked directly through some important macroinvertebrates in the system: Detritivorous Tenebrionidae and Embioptera and Geophilomorpha predators, which are both, litter and soil dwellers. By mean of vertical migrations, tenebrionid larvae are found mainly in the surface litter in winter or spring, and deeper in the soil in summer, showing the importance of consider temporal variability in the connection of above- and belowground habitats.
8) Therefore, although the faunal assemblages of the litter layer and belowground habitat showed differences, there were faunal groups that share both profiles, showing that both habitats are interconnected, which could have potential direct consequences in the soil dynamics of matter and energy between above and belowground.
9) Although abiotic conditions showed to affect some variables, resource quality (litter and roots) were revealed as important factors controlling soil macrofaunal distribution. Resource direct and indirect effects on the abundance of detritivores and predators suggest the importance of interactions among both trophic groups, with implications in the connection among above- and belowground communities.
10) Decomposition at the study site is strongly influenced by substrate quality. Differences in decomposition between poor and rich substrate occur in the soil surface and the subterranean habitat, being belowground decomposition more evident than in the surface. In spite of decomposition in arid ecosystems is considered to be controlled

principally by abiotic factors, micro- and macro-arthropods showed their importance in decomposition processes.

11) Detritivore belowground fauna actively takes part in surface litter degradation, and their contribution to this process is higher that from aboveground detritivores in the study site.
12) Soil macroinvertebrates in the Baza Basin show a patched distribution, aggregated on microhabitats where they found resources and milder environmental conditions. Differences in resource quality provoke a great spatial heterogeneity that, in combination with the high spatial variability of the system, affect the faunal spatio-temporal distribution. Tenebrionid larvae perform vertical migrations looking for better food, contributing in the interaction among litter and belowground, and taking place in surface litter degradation, with important consequences in the cycles of matter and energy.