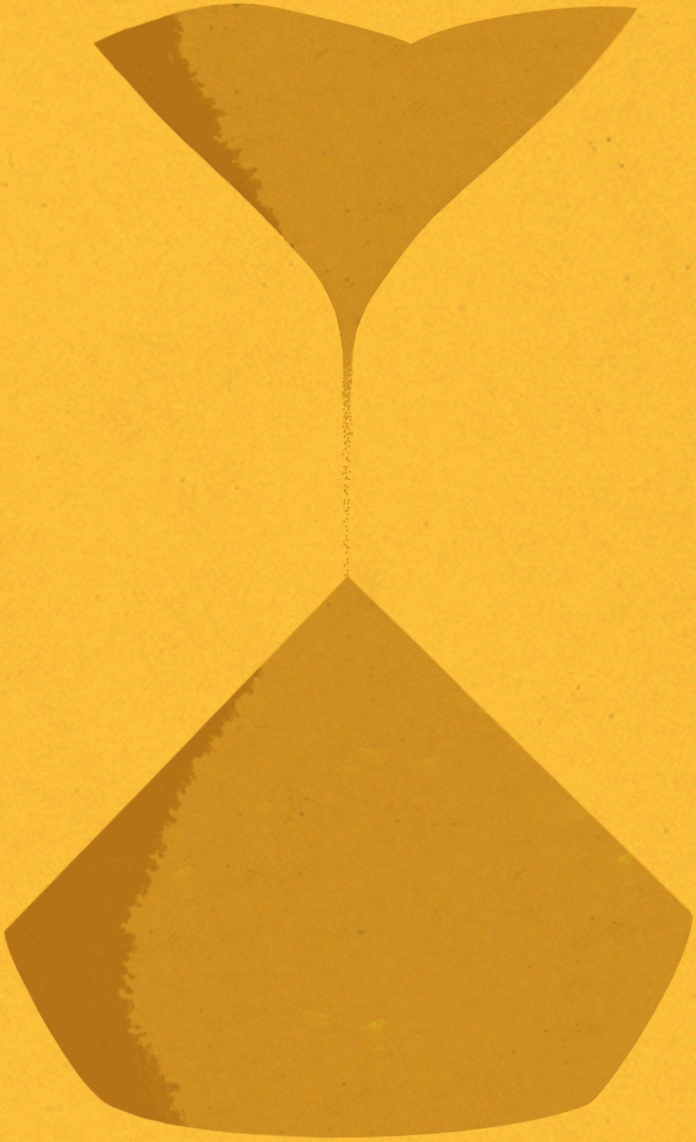
DUNG BEETLE TRAITS

a conceptual, experimental and biogeographical approach



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Programa de Doctorado
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Fundamental y de Sistemas

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A la paciencia,
kaikki valmistuu ajallaan

Publications

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Journal articles in this thesis

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I. deCastro-Arrazola, M. Moretti, F. Sánchez-Piñero, E. Nichols, E.M. Slade, N. Andrew, S.L. Chown, H.M. Griffiths and J. Hortal
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Ch.2. **Assessing the functional relationship between dung removal, burial and seedling emergence and dung beetle traits**
I. deCastro-Arrazola, J. Hortal, J.A. Noriega and F. Sánchez-Piñero
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Ch.3. **Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara desert**
I. deCastro-Arrazola, J. Hortal, M. Moretti and F. Sánchez-Piñero
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Ch.4. **Aridity favors small, flight-efficient, dwelling and saprophagous dung beetle species**
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Other publications developed during this thesis

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I. deCastro-Arrázola, F. Sánchez-Piñero, E. Cuesta, A. Davis, C. Moreno and J. Hortal
In preparation

Contribution à la connaissance des Histeridae du Maroc
Y. Gomy, I. deCastro-Arrazola, F. Sánchez-Piñero and H. Labrique
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Foraging specialization shapes assemblage structure of dung-inhabiting Histeridae along an aridity gradient in North Africa
F. Sánchez-Piñero, Y. Gomy, C. Domene, J. Hortal and I. deCastro-Arrazola
In preparation

Dung-insect community composition in contrasting seasons along a coastal-desert transect in North Africa
A. DeGea, A.X. González-Reyes, I. deCastro-Arrazola, J. Hortal and F. Sánchez-Piñero
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¿Cuál es el alcance de la crisis de la Taxonomía? Conflictos, retos y estrategias para la construcción de una Taxonomía renovada
J.A. Noriega, A.M.C. Santos, S.C. Aranda, J. Calatayud, I. deCastro-Arrazola, V.R. Espinoza, J.L. Hórreo, N.G. Medina, M.L. Peláez and J. Hortal
2015, *Revista IDE - SEA*, 9(1). 1–16

Fine-scale coexistence patterns along a productivity gradient in wet meadows: shifts from trait convergence to divergence
O. Mudrák, Š. Janeček, L. Götzenberger, N. Mason, J. Horník, I. deCastro-Arrazola, J. Doležal, K. Klimešová, and F. de Bello
2015, *Ecography*, 39. 338–348

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Resumen

Aunque la ecología funcional está considerablemente desarrollada en ecología de plantas, la ecología animal todavía necesita cubrir algunas lagunas y subsanar ciertos errores, por ejemplo, la asunción de funcionalidad de los rasgos. Así, hasta qué punto los rasgos son sustitutos válidos de las funciones y reflejan la respuesta de los organismos a la variabilidad ambiental (rasgos de respuesta) o sus efectos en las funciones ecosistémicas (rasgos de efecto) requiere un estudio detallado.

En el estudio de los escarabeidos coprófagos, como en muchos otros taxones, es frecuente el uso de rasgos sin un significado funcional claro. Una exhaustiva búsqueda bibliográfica nos llevó a concluir que la ecología funcional de los escarabeidos coprófagos aún no está bien desarrollada (Capítulo 1). A menudo no se miden los rasgos y, cuando se hace, falta una metodología estandarizada. Por un lado, la mayoría de los estudios sobre las *respuestas* de los rasgos a la variabilidad ambiental realmente analizan patrones de diversidad de rasgos, sin una interpretación funcional. Por otro lado, los estudios sobre el *efecto* de los rasgos no identifican rasgos de efecto individuales, sino que se engloban en el ámbito de la relación Biodiversidad~Funcionamiento Ecosistémico (BEF, por sus siglas en inglés). El rasgo más comúnmente usado es todavía la manera de utilización del excremento para su alimentación y nidificación, lo que lleva a un abuso del uso de la clasificación de los escarabeidos coprófagos en telecópridos, paracópridos, endocópridos y cleptocópridos. Además de este rasgo principal, el tamaño de cuerpo también ha sido usado para caracterizar comunidades, la eficiencia en la retirada de excremento, tanto en pastos como en algunos experimentos de laboratorio. En general, tanto para los rasgos de efecto como para los de respuesta, los rasgos relativos a fisiología, reproducción y dispersión están mayoritariamente inexplorados. Tan solo las funciones de retirada de excremento y dispersión secundaria de semillas han sido algo estudiadas. Finalmente, la respuesta de rasgos frente a importantes variables ambientales como disponibilidad de excremento, suelo, humedad y temperatura es totalmente desconocida.

Intentando encontrar rasgos que tienen un *efecto* en tres funciones ecosistémicas (retirada de excremento, enterramiento de excremento y dispersión secundaria de semillas), establecimos un experimento de mesocosmos en el laboratorio con parejas de ambos sexos de escarabeidos coprófagos y les ofrecimos excremento de oveja que contenía un número controlado de semillas (Capítulo 2). Encontramos que los rasgos morfológicos de tamaño corporal, tamaño del protórax y área de la protibia explicaban satisfactoriamente la eficien-

cia de desarrollo de dos funciones importantes: retirada de excremento y enterramiento de excremento. Sorprendentemente, ni el comportamiento (es decir, la estrategia de relocalización del excremento) ni la identidad de las especies mostraron un efecto significativo en la eficiencia de la retirada de excremento o el enterramiento del excremento. También encontramos un efecto negativo de algunos rasgos en la eficiencia cavadora: el alargamiento de las tibias anterior y posterior (relacionado con una morfología de telecóprido) y una forma del cuerpo relativamente más alargada (característica de los endocópridos). Finalmente, encontramos que hubo un efecto positivo de algunas especies con enterramiento somero en la emergencia de plántulas.

Para poder identificar rasgos de *respuesta* a constricciones ambientales o interacciones bióticas, buscamos y muestreamos un pronunciado gradiente de aridez que pudiera imponer un estrés diferencial en los escarabeidos coprófagos, modificando la composición taxonómica de las comunidades y la estructura funcional y filogenética. En el Capítulo 3 analizamos en detalle los patrones taxonómicos espaciales (a lo largo del gradiente de aridez) y temporales (entre estaciones y entre años) y encontramos dos composiciones taxonómicas completamente diferentes entre las comunidades previas y posteriores a la época lluviosa pero comunidades casi idénticas entre años consecutivos. Tras la época lluviosa, encontramos que la aridez promueve un recambio de especies (apoyado por un progresivo pero suave reemplazo filogenético) a lo largo del gradiente de aridez y que las comunidades en las zonas más áridas no son un subconjunto de las presentes en condiciones más suaves sino un conjunto único de especies.

Estos conjuntos únicos de especies demostraron tener características únicas que responden al severo filtro ambiental impuesto por la aridez (Capítulo 4). En efecto, el patrón de promedios de los valores de rasgos individuales de las comunidades locales a lo largo del gradiente de aridez mostró claramente un reemplazo de especies coprófagas y de alas pequeñas en las comunidades semi-áridas, por especies endocópridas de cuerpo pequeño, saprófagas facultativas y con alas significativamente más grandes en relación a su tamaño corporal. Esto es probablemente una respuesta a la distribución dispersa del recurso trófico (típicamente consistente en pequeñas deyecciones), condiciones atmosféricas extremas (alta temperatura, elevada desecación) y suelos duros típicos de zonas áridas. Concluimos que la aridez es un fuerte factor determinante del ensamblaje de comunidades via filtrado ambiental del *pool* regional de escarabeidos coprófagos para conformar comunidades locales tanto en la dimensión espacial como en la temporal.

Summary

Although functional ecology has been considerably developed in plant ecology, animal ecology still needs to cover some gaps and caveats, namely, the assumption of trait functionality. Thus, whether traits are valid proxies for ecological functions and reflect either the response of organisms to environmental variation (response traits) or its effect on ecosystem functions (effect traits) requires further reseach.

Within the taxa in which traits are used lacking a clear functional meaning, dung beetles are not an exception. An in-depth search of literature led us to conclude that functional ecology of dung beetles is still not well developed (Chapter 1). Often, traits are not measured and, when they are, there is a lack of standard methodology. On the one hand, most of the studies focusing on *responses* of traits to environmental variability actually analyze patterns of trait diversity, without a functional interpretation. On the other hand, studies focusing on the *effect* of traits do not identify individual effect traits, but rather use trait diversity within the context of Biodiversity~Ecosystem Functioning (BEF). The most commonly used trait is still the way dung beetles utilize the excrement to feed and nest, which leads to an excessive use of the classification in telecoprids, paracoprids, endocoprids and kleptocoprids. Besides this major trait, body size has also been used to further characterize communities, their efficiency in removing dung from pasturelands and in some laboratory experiments. In general, for both effect and response traits, physiology, reproduction and dispersal traits remain largely unexplored. Similarly, only functions such as dung removal and secondary seed dispersal have been fairly studied. Finally, the response of traits to important environmental variables such as dung availability, soil, humidity and temperature is totally unknown.

Trying to find traits that have an *effect* in the delivery of three ecosystem functions (dung removal, dung burial and secondary seed dispersal), we set up a mesocosm laboratory experiment with dung beetle sexual pairs provided with sheep dung containing a controlled set of seeds (Chapter 2). We found out that the mor-

phological traits body size, prothorax size and protibia area successfully explained the performance of dung beetles in the delivery of two important functions: dung removal and dung burial. Surprisingly, behavior (i.e. dung relocation strategy) did not show a significant effect on performance in either dung removal or burial, nor did species identity. We also found a negative effect of some traits in burrowing efficiency: elongation of fore and hind tibiae (related to a telecoprid morphology) and a relatively longer body shape (typical of endocoprids). Finally, we found that there is a positive effect of some shallow-burying species on seedling emergence.

To be able to identify traits *responding* to environmental constraints or biotic interactions, we searched and sampled a steep aridity gradient that would impose a differential stress on dung beetles, shaping taxonomic composition of communities and the functional and phylogenetic structure. In Chapter 3 we thoroughly analyzed the taxonomic patterns in space (along the aridity gradient) and time (between years and within years) and found two completely different taxonomic compositions in the communities before and after the rainy season, but nearly identical communities in consecutive years. After the rainy season, we found that aridity drives a species turnover (supported by a progressive but mild phylogenetic replacement) and that communities in the most arid areas are not a subset of species present in milder aridity conditions, but rather a unique set of species.

These unique sets of species proved to have specific features responding to the severe environmental filter imposed by aridity (Chapter 4). Indeed, the average single-trait values of the local communities along the aridity gradient clearly showed a pattern of replacement of the mainly coprophagous paracoprid and small-winged dung beetles in semiarid communities by small-bodied facultatively saprophagous endocoprid species with significantly larger wings compared to body size. This is probably a response to the sparse distribution of trophic resource (typically consistent of small droppings), extreme climatic conditions (high temperature and desiccation) and hard soils typical of arid areas. We conclude that aridity is a strong driver of community assembly via environmental filtering of the regional pool of dung beetles into local communities at the temporal and spatial dimensions.

Introduction

Functional ecology is currently at the cutting edge of ecological research. The promises of understanding how ecosystems are organized (patterns) and how they work (mechanisms) have led to a burst of studies focusing on the topic. While it has been considerably developed in plant ecology (Tilman et al. 2014), animal ecology has followed its path with major difficulties (Luck et al. 2012). The eagerness and urge to test the ecological theories proposed by plant functional ecologists has sometimes led to some gaps and caveats (Blaum et al. 2011). One of the major caveats is the assumption of trait functionality, that is, that traits are valid proxies for the functions under study (Mlambo 2014). The assumption of functionality for traits should be based on strong evidence that the chosen traits reflect either the response of organism to environmental variation (response of traits) or its effect on ecosystem functions (effect of traits) (Violle et al. 2007). Failing to do this leads to knowledge gaps and, consequently, serious caveats in interpretation of results (Perronne et al. 2017). This thesis aims to cover some of these gaps.

Classifying species according to their functions, through their response to the environment or their effect on it, has a long tradition (e.g. Blondel 2003; Reiss et al. 2009). Early classifications did not explicitly mention traits, but used them implicitly to create functional groups (Blaum et al. 2011). Often, the functionality of these traits was unknown and they were measured in a coarse-grain categorical way (traits with two categories being the coarsest). Later developments sought to measure traits in a continuous way, thus, a much finer grain and the functional meaning of traits was considered (Hillebrand & Matthiessen 2009; Reiss et al. 2009). Recent works in plant ecology mostly use continuous traits with known functionality (Pérez-Harguindeguy et al. 2013). On the contrary, animal ecologists still use few continuous traits and their functional meaning is largely unknown (Moretti et al. 2017; Wong et al. 2018). This thesis pays special attention to the selection of traits, measuring them continuously and testing their functional meaning.

Building evidence of the functionality of traits (that is, of their validity as response and/or effect traits) requires design and methodological soundness to enable a reliable use of such traits in future ecological research (Perronne et al. 2017). An appropriate research design is essential to detect patterns and enable finding a coherent explanation for them (Stephens et al. 2007), in both experimental and observational ecology. It requires careful choosing of the appropriate identity and quality of explanatory variables. That is, choosing the most suitable explanatory variable(s) and measuring them at sufficient range and grain size to detect a significant amount of effect. Another prerequisite for estimating these relationships with accuracy is to sample enough variation of the response variables. However, attaining the optimum sample coverage may be less obvious, since the response variables are the phenomena whose variability we seek to understand. Finally, an appropriate sample size is needed to ensure robustness of the findings (Stephens et al. 2007).

Finding which effect traits affect any particular ecosystem function of interest requires measuring the function and potentially explanatory traits at a fine-enough grain to detect the effect of trait variability instead of other side effects such as abundance-effects or variations in individual performance due to environmental conditions. Furthermore, finding response traits that determine the niche of species, their spatial and temporal distribution and, thus, the functional structure of communities, requires measuring a biologically meaningful environmental variable along a wide-enough range. It also requires selecting traits that can potentially respond to such environmental gradient and measuring them as continuous variables to allow for fine analysis of their covariation with environmental conditions. Thus, this thesis reveals the functionality of traits that have a manifest effect on ecosystem functions, and traits that respond to environmental variations.

Biologically meaningful and steep environmental gradients have a strong power to filter out trait values that impede survival or pose a great competitive disadvantage. Typically, studies focus on broad environmental gradients of spatially and temporally varying temperature, water, light intensity, resource availability, soil structure, etc., as well as the often-interchangeable altitudinal and latitudinal gradients that are combinations of the previous environmental factors. Among all these environmental variables, water stands out as an essential resource for the development of life and a driver of broad-scale diversity patterns (Hawkins et al. 2003). Therefore, biologically meaningful and steep gradients can be found in some regions. Desert edges, where aridity (i.e. water scarcity) becomes an important abiotic stress (Polis 1991), are appropriate ecotones to study trait-mediated species responses and assembly processes.

However, aridity gradients that are broad enough so as to characterize trait-based species responses with reliability are scarce. Suitable regions should host geographically explicit gradients, as opposed to those built from scattered sites with decreasing aridity. This will ensure the existence of few or no barriers to dispersal (Ricklefs 2015) and an homogeneous regional species pool (Cornell & Harrison 2014). In this sense, the essential nature of water implies a covariation of aridity with many other biotic and abiotic variables that can be also affecting the diversity patterns under study (O'Brien 2006). Therefore, for survey designs aiming to disentangle community responses to aridity it is crucial to keep stable the values of as many environmental variables as possible, except aridity. This allows studying the responses of diversity patterns such as turnover of species, phylogenetic lineages and combination of functional traits. This thesis presents a long, geographically explicit and steep aridity gradient, with little influence of other major geographical variables.

In order to study such trait variations along environmental gradients a suitable model taxonomic group should meet a number of criteria: 1) to have a wide geographic distribution and habitat requirements (as opposed to specialized in small habitat patches); 2) to be sensitive to the chosen environmental variable (aridity in this case); 3) to be fairly diverse taxonomically, phylogenetically and functionally; and last, but not least, 4) to be easy to sample, identify and to have easy to measure response traits.

Scarabaeidae dung beetles is such a group that combines large abundances, relatively easy-to-identify species, relative stable systematics and a wide distribution (geographically and across habitats) making them ideal to study spatial and temporal changes in community structure (Spector 2006). They are considered good bioindicators (Favila & Halffter 1997; Spector 2006; Bicknell et al. 2014) as they rapidly respond to changes in environmental conditions (normally associated to human perturbations). But they are also known to respond to large-scale environmental gradients (Nunes et al. 2016), in particular to variations in water availability (Haloti et al. 2006). Dung beetles are sensitive to aridity as they are thought to be constrained by both their physiological water economy (Chown et al. 2011) and the decrease in the availability and quality of trophic resources (Nichols et al. 2009). Further, Palearctic Scarabaeidae are well diversified in mesic and arid areas (Lumaret 1991) and the surrounding desert regions (Baraud 1985), making them a suitable model taxa to investigate biodiversity responses to aridity gradients. Dung beetles are used in this thesis to illustrate how traits can shed light on the mechanisms that produce diversity patterns along aridity gradients.

Dung beetles are also an ideal group to study the performance of traits involved in the delivery of ecosystem functions. They are easy to sample in the field, relatively simple to breed in the laboratory, easy to handle and it is feasible to set suitable conditions for their biological activity in the laboratory (Nervo et al. 2017). Moreover, they deliver well-known and measurable functions with an important role in ecosystem functioning (Nichols et al. 2008). This thesis uses dung beetles as a model organism and a worldwide significant actor in nutrient cycling and vegetation dynamics to establish solid links between traits and functions.

Overall, this thesis aims to contribute to the understanding of dung beetle response and effect functional ecology while bearing in mind design and methodological pitfalls. Ultimately, this dissertation seeks to make animal functional ecology an unmatched discipline to reveal the mechanisms of ecosystem functioning. We tackle this overarching aim through working in three different, though complementary, approaches: setting up the conceptual basis for a trait-based dung beetle functional ecology (Chapter 1); assessing the functional effects of dung beetle traits through mesocosm experiments (Chapter 2); and empirically studying the responses of dung beetle communities to aridity (Chapter 4).

Chapter 1: *A trait-based framework for dung beetle functional ecology* summarizes the state of the art of dung beetle trait ecology. In this chapter traits are compiled, defined and organized into categories according to the aspect of the biology of species they describe. This information is used to establish hypotheses of which traits allow dung beetles to respond to a set of major environmental variables, and how. Finally, it describes which traits determine the effect of dung beetles on ecosystem functions as a result of their activity, and how. This chapter identifies gaps in the current knowledge on dung beetle trait ecology and suggests hypotheses on how traits may allow dung beetles to respond and affect the environment.

In a next step, Chapter 2: *Assessing the functional relationship between dung removal, burial and seedling emergence and dung beetle traits* presents evidence for the effect traits that determine the efficiency of the delivery of some widely accepted functions of dung beetles. This is done by means of a laboratory experiment that validates the relationship between morphological and behavioral effect traits and three ecosystem functions related to their feeding and reproductive habits. This chapter addresses a severe gap in the knowledge of most plant and animal traits: the unknown functionality of effect traits.

Chapter 3: *Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara desert* studies biogeographical patterns of taxonomic diversity in space and time at two different scales (inter-annual and seasonal). The spatial dimension represents a gradient of varying aridity, trophic resource, soil structure and vegetation. This chapter sets a solid taxonomic base for the study of functional diversity patterns in Chapter 4.

Finally, Chapter 4: *Uncovering community assembly rules using taxonomic, phylogenetic and functional diversity: Dung beetle assemblage structure along an aridity gradient in space and time* identifies traits that respond to aridity, a strong environmental driver, and potential biotic interactions. These traits ultimately shape the functional structure of dung beetle communities. This chapter addresses the other severe gap in the knowledge of most plant and animal traits: the unknown functionality of response traits.

To conclude, a *General discussion* frames the contributions of this thesis in the particular context of dung beetle functional ecology, as well as in the general context of animal functional ecology. The ideas summarized in the *Conclusions* condense the contributions of this thesis attempting to improve our understanding of how nature works. Hopefully, this thesis serves as a stepping stone in this quest.

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Aims

General aim:

(1) To contribute to the understanding of dung beetle response and effect functional ecology while bearing in mind design and methodological pitfalls.

Specific aims:

(2) To set up the conceptual basis for a trait-based dung beetle functional ecology providing a set of measurable traits, their response to environmental drivers and their effect on ecosystem functions (Chapter 1).

(3) To asses the functional effects of dung beetle morphological and behavioral traits on the delivery of three important ecosystem functions: dung removal, dung burial and secondary seed dispersal (Chapter 2).

(4) To empirically study the responses of dung beetles to aridity and how these responses determine functional structure and the assembly of local communities from the regional species pool (Chapter 3 and Chapter 4).

General methodology

For development of this thesis, we performed a laboratory experiment and a series of field sampling campaigns along an aridity gradient.

Laboratory experiment

To analyze the relation between functional traits and three ecosystem functions (dung removal, dung burial and secondary seed dispersal) we designed a mesocosm experiment. Mesocosms consisted of large flowering pots (30 L) filled with compacted organic soil on whose surface we placed a sexual pair of dung beetles and a carefully weighed 100 gr dung pat. These sheep-dung pats included seeds of three plant species native to the Mediterranean semi-arid region and are very probably eaten by sheep while grazing. Thus, although laboratory conditions allowed controlled conditions and accurate measurement of dung removal and, especially, dung burial, details were kept as similar and realistic as possible. We used dung of a local sheep breed adapted to arid conditions, seeds of three typical Mediterranean species and a good representation of the local dung beetle community (pertaining to the three main dung relocation strategies and covering the whole body size range). (see Chapter 2 for a detailed description).

Aridity gradient

To analyze the effects of aridity on the three facets of diversity (taxonomic, functional and phylogenetic) we carried out an extensive sampling along an aridity gradient in northern Sahara. We chose this region because it offers a set of unique and appropriate features: a steep aridity gradient in a geographically explicit straight 400 km transect with homogeneous habitat. These features ensure minimal effect of dispersal barriers that may force a faunal replacement for reasons different than the variable of interest: aridity. The traditional and ongoing means of economic trade in the region based on sheep, goat and dromedar herding and the frequent use of donkeys and, in a lower frequency, horses and cows, ensures a significant presence of herbivores in the field which is key for the maintenance of abundant dung beetle populations. this is not the case in other regions in the northern coast of the Mediterranean where the abandonment of herding has lead to a severe decline in the populations of dung beetles. To obtain a precise representation of the dung beetle assemblages along the 400 km gradient, we estabished ten sampling sites (with two replicates each) every ca. 40 km (see Chapter 3 for a detailed description).

Dung beetle sampling

Exploitation of herbivore faeces, a specific discrete resource, by dung beetles makes them easily sampled by means of dung baited pitfall traps (Lobo et al. 1988; Veiga et al. 1989; Larsen & Forsyth 2005; Silva & Hernández 2015). Spatially, the distance from which they can detect a bait is probably highly variable and heavily dependent on vegetation structure (Silva & Hernández 2015) and air flow. Temporally, the time during which the bait releases volatile compounds and attracts dung beetles is also key and depends on the dessication rate at different atmospheric relative humidities (Lumaret 1995; Vliet et al. 2009; Enari et al. 2016). This is the case of Mediterranean and arid climates that impose strong atmospheric dryness (specially during long and warm summer droughts) and the typical little vegetation cover allows fair air flow that accelerates dessication of baits. These conditions require a careful placement of baits relative to the ground, trap and vegetation (Espinoza 2015). The trapping method used in this thesis is specially designed for drylands where baits loose up to 50% of their water content in less than 72h, thus, loosing all their attractive power.

The trap consisted of a 1 L plastic cup (11.5 cm diameter, 14 cm depth) covered by a 2 x 2 cm mesh on top of which 300 g fresh cow dung was laid as bait (see Lobo et al. 1988). It is very important to note that the bait was shaped into a natural-shaped cow pad that covers the plastic cup to the very edge. Covering the mouth of the cup with the bait ensures that no air can flow below the bait, significantly slowing down the dessication rate of the bait, and also to hide the trap to reduce trap losses by people in widely open areas. Moreover, the trap is filled with 300 ml of a soapy preservative water solution with chloral hydrate (10 gr/L) to prevent quick insect degradation due to high temperatures and fungi proliferation. Thus, there is a positive interaction between the lid-like bait and the water inside the cup. The bait helps slowing down water evaporation and the water keeps the under part of the bait moist during a longer period of time, ensuring at least 48h of attractive power. Last, but not least, the total coverage of the cups mouth makes entering the trap very difficult and unattractive for non dung-feeding animals, although in extremely dry regions, the water contained in the cup might spuriously attract some individuals.

This trap design has been successfully used to sample the dung beetles for the biogeographical community ecology study in Chapter 3 and Chapter 4. Indeed, this trap design has proved great effectiveness, as five traps per replicate have achieved sampling coverages over 98% in most of the sampling sites and campaigns.

Measurement of environmental variables

To analyse spatial and temporal variations of dung beetle assemblages along the aridity gradient, we measured a number of environmental variables. Aridity (AI = mean annual precipitation / mean annual evapotranspiration) was obtained and used as GIS layers from Trabucco & Zomer (2009). We gathered a set of other environmental variables from Hijmans et al. (2005): solar radiation, mean monthly temperature, annual and monthly precipitation and altitude.

During the sampling campaigns we also gathered data on naturally available resource, i.e. dung. We did not quantify other trophic resource types as the proportion of necrophagous species is negligible in the temperate faunas (Veiga 1985). Saprophagous dung beetles are abundant, but very little is known about the vegetation debris that is suitable for these species to use. Consequently, measuring naturally available trophic resource for saprophagous species is not feasible. Accordingly, we sampled naturally available dung by estimating the amount of five types of dung (sheep/goat, cow, horse/donkey, dromedary and carnivore droppings) present in each locality as a general proxy for the actual amount of fresh dung that is available for dung beetles. To do this, in each replicate of the four campaigns we conducted two perpendicular 250 m long and 2 m wide linear transects, each surveyed by one researcher following a standardized sampling protocol, covering a total of 1000 m^2 per replicate (similar to Lobo et al. 2006). In each transect the total mass of the five types of dung mentioned above was estimated based on dung volume, according to previous measurements of dung pats of different volume in the field (González-Megías & Sánchez-Piñero 2004).

Other environmental variables that determine dung beetle activity are essential descriptors of soil structure. Moreover, arid environments typically present increased soil compaction and Mediterranean areas are traditionally used for a variety of purposes that affect dung beetles probably via soil properties: agriculture (Campos & Hernández 2015), herding (Lobo et al. 2006; Ramos et al. 2010), logging (Slade et al. 2011), etc. To measure soil properties, we extracted three arbitrarily located soil cores (4 cm diameter and 30 cm depth) from each replicate. Soil samples were split into three depths (0-10 cm, 10-20 cm and 20-30 cm) and kept in separate air-tight plastic bags for further laboratory analyses. From these samples, seven soil variables were measured (Table C.6 in Appendices), accounting for structure (hardness, bulk density), water content (water field capacity) and particle size (percentage of gravel, sand, silt, and clay) (see Tovar 2015).

Finally, we measured a few variables regarding vegetation structure along the aridity gradient. As previously mentioned, arid environments present very scarce vegetation (in contrast with tropical or even temperate regions) and, when present, it hardly raises above 20-50 cm. Because of this, all sampled sites corresponded to open habitats. Vegetation height (cm) and vegetation percentage cover were estimated using the point-quarter method every 5 m along a 250 m x 2 m transect at each replicate and campaign to account for seasonal and yearly variations.

Trait measurement

Measurement of traits is the cornerstone of the studies presented in this thesis and its most valuable contribution to dung beetle ecology. Rigorous measurement of morphological traits and gathering of categorical traits from literature was carried out for the mesocosm experiment in Chapter 2, the thorough analysis of community assembly in Chapter 4 and the preparation of comparative research (not included in the thesis) of the community assembly processes in three warm deserts of the world.

Data on two non-morphological traits, adult diet and dung relocation strategy for feeding purposes (both qualitative traits), were obtained from the literature and our own field observations, allowing to successfully describe these behavioral aspects of the life-history of most species used in each chapter.

All morphological traits were measured with a Leica M165C microscope (similar to Griffiths et al. 2015), using Leica Application Suite LAS V4.0 with the Z-builder module to process the images and obtain the measurements. The procedure requires excellent preservation of specimens from the moment of the capture in the field, during transportation and the time till measurement. Specimens are pinned and appendages set in the appropriate position to ensure perpendicular photographs. Each measurement is best measured from a different point of view. While length and width of the main body tagmas are easily photographed perpendicularly from a dorsal point of view, appendages usually require specific pictures to ensure capturing whole protibias or metatibias in a single frame. Finally, measurement of wing length and area requires dissection and extremely delicate preparation of the wing in its total extension. In this thesis the wing was gently extended over the exterior flat surface of a petri dish with the help of a fine watercolor brush and some drops of water. Then the petri dish was fitted in its counter petri dish that had previously been lined with silver paper. The silver paper placed at ca. 1 cm below the extended wing reflects the light of the microscope and/or photographic camera, resulting in an all-angle illumination of the wing. With this procedure, even veins are depicted with great accuracy, enabling precise measurements and future use for other measurements.

Several other continuous measured traits correspond to weights: fresh and dry body weight and the experimental trait *elytrum weight*. These traits are easy to measure but great care is needed to prevent any damage on the specimen. Weighing elytrum weight of the smallest specimens requires a sensitive precision scale as many elytra weigh below 1 mg.

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1 A trait-based framework for dung beetle functional ecology

1.1 Introduction

Functional traits are phenotypic characteristics of the individuals that affect their fitness, the fitness of other individuals (of the same or other species) or, in general, ecosystem functioning through their effect on the flux of matter and energy (e.g. McGill et al. 2006; Violle et al. 2007 see below). Functional traits are behind all ecological processes, from broad scale biogeochemical cycles to ecosystem functions, ecosystem services or very specific interactions. Functional trait-based ecology is currently undergoing a large development, advancing in the understanding of the response of traits to the environment and the effects of traits on ecosystem processes. Therefore, the horizons and future directions in biodiversity and ecosystem functioning (BEF) research outlined by Reiss et al. (2009) are already being accomplished through the study of traits. But the purely taxonomic patterns of species distributions and co-occurrence in space and time provides very limited information on community assembly and ecosystem functioning. Besides the effects of long-term evolutionary processes (e.g. Wiens & Donoghue 2004; Ricklefs 2010), a mechanistic understanding of the ecological processes underlying these patterns requires the study of spatial and temporal variations in traits and functions (Díaz et al. 2013; Violle et al. 2014). Functional traits are used to understand the mechanisms behind interacting aspects of biodiversity (Arnan et al. 2016), the nature of species pools (Lewis et al. 2016), community assembly (Bello et al. 2012), population dynamics (Nichols et al. 2013), and ongoing evolutionary processes (Carroll et al. 2007), to mention a few examples. On the other hand, researchers also try to explain the mechanism behind ecosystem function delivery: which species and through which traits?

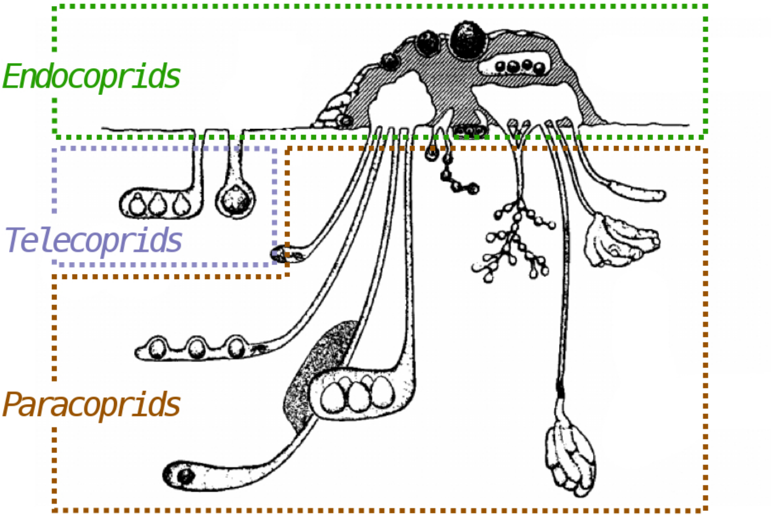
The theoretical basis of our current knowledge on functional ecology comes from vegetation science. Plant functional traits (*sensu* Violle et al. 2007) have been thoroughly studied and systematically described (Cornelissen et al. 2003; Pérez-

Harguindeguy et al. 2013), mainly from a response~effect perspective (Lavorel & Garnier 2002; Suding & Goldstein 2008; see below). In contrast, the study of animal traits has been traditionally approached from a descriptive perspective, where their morphology and physiology have been used to characterize their ecological and geographical responses rather than the contribution of their individuals to ecosystem functioning. Animal trait databases such as PanTHERIA (Jones et al. 2009) or EltonTraits (Wilman et al. 2014) thus contain information on morphology, diet, life history or even aspects of the geographic range of the species, but without any explicit link to their function. Only recently traits have been integrated in the study of interaction networks as a key element to understand community assembly and a number of key ecosystem functions, such as pollination, frugivory, herbivory or detritivory (Lavorel & Garnier 2002; Dehling et al. 2016; Noriega et al. 2018). Based on the success of plant functional ecology, animal ecologists have started to adopt similar theoretical concepts and methods, although without a deep conceptual thinking of the fundamental differences between the functional roles played by the two taxa, and the challenges associated to them (but see Moretti et al. 2017; Wong et al. 2018). At least for insects, the lack of experimental measurements and solid theoretical knowledge has led to assuming the validity of many traits as proxies for response and effect, without proper testing (Noriega et al. 2018).

Some problems arise from the measurement of the traits themselves. For example, the limited data on physiological traits is often compensated by deriving species' responses to the environment from their spatial distributions (see Hortal et al. 2015). However, species' geographic ranges are also affected by biotic interactions and dispersal limitations (Soberón 2007; Jiménez-Valverde et al. 2010), thus invalidating them as a mean to assess the species' fundamental niche and the associated potential responses to the environment (Hortal et al. 2012). The concerns raised by the limitations of current approaches and the lack of quantitative evidence on the relationships between traits have forced ecologists to rethink trait-based approaches in animal ecology (Luck et al. 2012; Fountain-Jones et al. 2014; Moretti et al. 2017). Here, it is key to develop standardized methods for the measurement of traits and their ecological functions. Indeed, recent approaches have developed general frameworks for measuring terrestrial invertebrate traits (Gallego et al. 2016; Moretti et al. 2017). However, extending these frameworks to specific taxa requires identifying key traits and developping protocols that account for the peculiarities of each particular functional or taxonomic study group.

Dung beetles of the superfamily Scarabaeoidea play a key role in many terrestrial ecosystems, for they are responsible for decomposing and recycling mammal feces, among many other functions (Hanski & Cambefort 1991; Nichols et al. 2008). *Dung beetles* is itself a term that defines a group of taxa as a functional group (Finn & Gittings 2003) based on a simple trophic trait, coprophagy. Dung beetles feed on dung in either or both adult and larval stages (although some of them present other primary trophic preferences, see Holter & Scholtz 2007; Scholtz et al. 2009). Dung beetles have long been studied from a functional point of view, and the way they utilize the excrement to feed and nest has been traditionally used to classify them (Halffter & Matthews 1966; Bornemissza 1969; Halffter 1977; Hanski & Cambefort 1991). According to their dung relocation strategy, dung beetles can be divided into four main functional groups: telecoprids, paracoprids, endocoprids and kleptocoprids (Figure 1.1). Besides this major trait, body size has also been used to further characterize the efficiency in dung removal performed by this group. So, a combination of body size and feeding behavior is commonly used to describe the functional diversity of dung beetle communities (Doube 1990). Other classifications use competitive ability for dung and space (Finn & Gittings 2003; Krell et al. 2003b) or extinction proneness (Larsen et al. 2008), although these have been rarely used (but see Horgan 2008).

Beyond this traditional functional categorical classification (Fountain-Jones et al. 2014), many other dung beetle traits have been studied in detail, so the main aspects of dung beetle morphology, life history, physiology, phenology and behavior are well known (reviewed in Scholtz et al. 2009; Simmons & Ridsdill-Smith 2011). Indeed, a number of studies use traits to describe many ecological and evolutionary aspects of this group, including community assembly rules, BiodiversityEcosystem Functioning (BEF, Tilman et al. 2014; e.g. Slade et al. 2007; Beynon et al. 2012), ecosystem service delivery (e.g. Nichols & Gomez 2014), global change effects (e.g. Nichols et al. 2007; Barragán et al. 2011), intraspecific competition (e.g. Hernández et al. 2011), functional effects of selective extinction (e.g. Dangles et al. 2012), biological control (e.g. Araújo et al. 2015), sexual selection (e.g. Emlen et al. 2007; Favila et al. 2012), gene expression (e.g. Moczek & Rose 2009) or phylogenetic patterns (e.g. Forgie et al. 2005; Cabrero-Sañudo 2007; Philips 2016). However, such wide use of traits has not been accompanied by the development of a conceptual framework in the same way it happened with plants. Comparatively little systematic research on dung beetle functional ecology has been done so far (but see e.g. Radtke & Williamson 2005; Nichols et al. 2008; Griffiths et al. 2016). Rather, successive trait-based approaches have reused already described



Trait: Dung relocation strategy	Behavior name	Common name
No relocation. Use dung for feeding or nesting only within the original source.	Endocoprids	Dwellers
Only vertical relocation. Bury a portion of dung by excavating a tunnel directly below the original source.	Paracoprids	Tunnelers
Horizontal and vertical relocation. Remove, and usually roll, a portion of dung away from the original source and bury it.	Telecoprids	Rollers
No relocation. Often facultative. Use of a dung brood mass that has already been buried by other dung beetle.	Kleptocoprids	Kleptoparasites

Figure 1.1: Traditional classification of dung beetles according to a single behavioral trait: dung relocation strategy. Table following Hanski & Cambefort (1991) and figure adapted from Doube (1990). Note that the figure does not include kleptocoprids because they do not make a burrow to be included in the diagram.

traits (sometimes renaming them) without either a clear hypothesis or a proper test of the response of traits to the environment, or their effect on ecological functions.

The main aim of this chapter is to develop a framework for the study of the functional ecology of dung beetles from a trait-based response-effect approach. To do this, we first outline a handful of running definitions for basic concepts in trait-based functional ecology and, then, present a survey of traits of functional significance and review current knowledge on both how traits respond to environmental factors and their effect on ecosystem functions. Based on this information, we provide specific hypotheses on the functional role played by dung beetles and how to evaluate the effects of trait variations in both effects and responses. We classify traits in different groups, according to whether they are morphological, trophic, reproductive, physiological, or related to the temporal segregation of activity or the movement of the individuals. Besides providing a useful tool for researchers seeking to select specific traits according to their questions, our review seeks to provide a starting point for the development of a collaborative framework to study the ecological significance of dung beetle traits.

Running definitions of basic concepts in trait-based functional ecology

Although several definitions of what a functional trait is have been proposed to date (Díaz & Cabido 2001; Violle et al. 2007; Díaz et al. 2013), so far we lack a consistent definition that applies to all the ecological functions provided by organisms. This is perhaps due to the initial focus of functional ecology on plant functioning, which left apart some ecological characteristics that are typical of animals, such as their movement (apart from dispersal) or their variety of responses to environmental and biotic effects (see Moretti et al. 2017). Therefore, here we update and extend former definitions to provide a more generalized interpretation of the meaning of *functional trait*. Functional traits are any phenotypic (morphological, physiological, phenological, behavioral) or movement-related features that determine or modify the ecological functions performed by an individual. They can be either raw direct measurements on the individual or the result of processes involving multiple features. Their ecological impact can occur both as an *effect* of trait variation on ecosystem functions (influencing the fitness of either the individual itself or individuals of the same or other species, or the abiotic characteristics of the environment); or as a *response* to external filters or drivers (such as environmental variations, abiotic gradients or the interaction with individuals of the same or other species).

The impact of raw traits (i.e. those that can be measured directly on the individual) on organismal fitness occurs through its effects on growth, reproduction and survival of the individual, affecting its ecological performance and, ultimately, the overall performance of the populations. Any ecological process carried out by an individual requires the interaction of several raw traits, and has itself an outcome that can be still considered a trait or a function. In this sense, here we define *performance traits* as an intermediate concept between *performance trait sensu* Violle et al. (2007) and *functional marker sensu* Garnier et al. (2004). These traits are typically expressed as process-related rates such as consumption rate, metabolic rate or burial rate, and resemble plant traits such as photosynthesis, stomatal conductance or respiration which are normally expressed as a rate over time and are the result of a process. All these traits may sometimes be considered the measure of the function itself. For example, photosynthesis (as defined in Pérez-Harguindeguy et al. 2013) can be both a trait of the plant individual or a measure of carbon fixation, which is directly an ecosystem function.

Trait-based functional ecology is full of classifications of trait types.

Effect vs response traits

We choose not to use the terms *effect* and *response* explicitly to classify traits, because specific traits can rarely be attributed to only one of these categories. Rather, we reflect this conceptual classification in two of the main sections of this review (i.e. Response of traits and Effect of traits), allowing traits to be classified in both categories (Suding & Goldstein 2008). Most, if not all, functional traits vary in response to the environment and have an effect on some ecological function (see the studied dung beetle traits below).

Similarly, we avoid classifying traits as either soft or hard. The degree to which a trait affects the fitness of the individual is part of a continuum, and trying to make it discrete by classifying traits into soft or hard is totally arbitrary, so these terms are already being deprecated by plant functional ecologists.

Finally, classifying traits into general categories according to the type of ecological function they relate to can lead to oversimplification, for the limits between these categories are often fuzzy. However, and although we avoid using the classifications above, for this review we have decided to use a simple classification of traits into morphological, feeding, reproductive, temporal, physiological, and movement, placing each trait only in one category for the sake of simplicity.

1.2 A general classification of dung beetle functional traits

In this section we seek to provide an overview of the most important traits that could be measured to assess the ecological functions performed by dung beetles, and their ecological performance. Certain traits can be regarded as raw traits of the individual or as performance traits that serve as proxies to measure the delivery of ecosystem functions (see above). For example, the traits describing dung burial are related to feeding and reproduction, and have at the same time a significant input into nutrient cycling. Deciding whether one aspect is more significant than the other is a matter of the purpose of each particular analysis using traits. Therefore, for the sake of generality we deliberately avoid making such categories in this document. Rather, we group traits in six main categories: morphological, feeding, reproductive, time of activity, physiological and movement. Below we provide general descriptions of the traits that may be relevant for these categories, together with an introduction to how they could be measured and their use in ecological and biogeographical research. We assigned over 60 traits to either of these categories (see brief descriptions in Table 1.1). Note that a number of traits can be assigned to more than one category; in these cases, we have assigned them to the category they may be most prominent in, but they can be equally important for others.

Morphology

Description

Dung beetle morphological traits of functional significance can be grouped in four general categories. General body features include several aspects of body size, as well as color, glossiness and iridescence, hair and cuticle texture traits. The functionally most-relevant limb traits are limited to characteristics of the tibia of the anterior and posterior legs (protibia and metatibia). Head-clypeus traits include the size and shape of the clypeus, as well as the presence and number of horns. Finally, morphological traits should include features of larval morphology. However, since many dung beetle larvae present different ecological roles to those of adults (Hanski & Cambefort 1991; Nichols et al. 2008) we do not include them into this review. Further, we have not include several morphological traits in this section because, despite being clearly part of the individual morphotype, their role is tightly related to other trait categories. This is the case of, e.g. subelytral cavity, which is included within the physiological traits (Duncan 2002), wing load (Gibb et al. 2006) that is included within movement traits, or mandible type (Hata & Edmonds 1983), which we list as part of the feeding traits.

Measurement

Morphology is the aspect of dung beetles which is easiest to measure. Morphological traits have been measured by many groups of researchers in many different ways and for different purposes, from species descriptions to the evaluation of evolutionary relationships, community ecology or ecoevolutionary studies (for references see e.g. reviews in Scholtz et al. 2009; Simmons & Ridsdill-Smith 2011; Nichols et al. 2013). This has resulted in a high diversity of ways of measuring different traits, and therefore in non-comparable measurements, where a trait is named the same but measured differently. A paradigmatic case is body size, which, to mention a few examples, has been measured as body length, body mass of individuals that are alive, freshly-dead or preserved in alcohol, and body volume (Radtke et al. 2006). Further, body length is the most popular way of measuring body size and several measurements can also be found in the literature: from clypeus to pygidium, from anterior margin of pronotum to pygidium, same as these two but without including the pygidium, and finally measuring head, thorax and elytra lengths separately and summing them up. However, we do not aim to provide a detailed measurement protocol (such as, e.g. Moretti et al. 2017) with detailed descriptions of landmarks to measure morphological traits (as in, e.g. Hernández et al. 2011; Pizzo et al. 2011; Buse et al. 2018). A brief description of most traits and some more additional information can be found in the references recorded for each trait in the traits section.

Use

Morphological traits are used as proxies for other traits which are more difficult to measure (internal morphology, physiology or even feeding, reproduction or behavior). However, they are often poor proxies, as a wide gap lies between the proxy and the trait, not only in the hypothesized relation but also in the quantitative correlation between desired trait and morphological proxy. This is especially true for physiological traits. However, some morphological traits have successfully been used to predict other morphological traits (Radtke & Williamson 2005; Radtke et al. 2006), or have been found to infer behavioral traits such as dung relocation strategy (Inward et al. 2011). For example, Slade et al. (pers. obs.) have found that a dung beetle species which was phylogenetically classified as a paracoprid can facultatively shift into a telecoprid behavior when subject to strong intraspecific competitive pressure at high population densities. These two facultative behaviors are reflected in the morphology of its hind legs, which is intermediate between that of paracoprids and telecoprids.

The use of dung beetle morphological traits in functional ecology is also hampered by other difficulties, in particular the fact that the knowledge of which morphology performs which function is still poor (see Hortal et al. 2015 for a general overview on insects). Similar morphologies might be responsible for different functions, and we are unaware of the functional role of infrequent/rare morphologies. Given the general absence of experimental evidence (see Noriega et al. 2018), this limits the amount of functional information that can be inferred from morphological traits (but see Chapter 2). Despite all these limitations most studies on trait-based dung beetle functional ecology include some or many morphological traits. The ease of measuring them and their potential as proxies for other traits of higher functional significance provide such clear advantages that it has been common to oversee their limitations.

Feeding

Description

This category includes traits that are involved in the feeding process in a wide sense. Feeding and reproductive behaviors are often very similar for dung beetles, as both involve handling dung, including dung relocation and burial for tunnelers and rollers. Because of this, many feeding traits also hold reproductive significance, and should be classified in both categories. However, some other traits are specific to feeding, including those related to feeding mechanism

	Trait	P	Description	Type	Suggested units
Feeding	Seed relocation	✓	Active seed relocation from dung, including final destination	B	no dispersal, surface, buried
	Adult diet	✓	Main type of diet of the adult	ZZ	(sapro/copro/necro/mico)-phagy
	Trophic preference		Use of different types of dung or other resources	ZZ	dung types, carrion, fungi, etc.
	Adult diet range	✓	Number of different resources that couled be used by the beetle	#	count data
	Burrow depth	✓	Depth of the brood masses	C	cm
	Burrow length	✓	Length of the tunnel that leads from surface to brood masses	C	cm
	Burrow ramification	✓	Degree of ramification of the burrow	F	no, some, many ramifications
	Number of brood balls	✓	Number of brood balls by a single couple of beetles	#	count data
	Dung burial	✓	Amount of dung taken away from original location and buried for eating or nesting	C	gr
	Dung burial rate	✓	Amount of dung buried per unit of time (from start of digging to end of dung burial)	C	gr / h
	Dung relocation distance	✓	Distance from original dung location to burrow across which a telecoprid rolls a dung mass	C	cm
	Dung relocation strategy	✓	Strategy for the relocation of brood balls/masses	F	(endo / para / tele)-coprid
	Feeding mechanism		Mechanism used for the ingestion, as associated to the morphology of mouthparts	B	filtering, grinding, other
	Ingested particle size		Maximum size of ingested particle	C	micrometers
	Larval diet	✓	Main type of diet of larvae	ZZ	(sapro/copro/necro/mico)-phagy
	Soil relocation	✓	Active relocation of soil from the burrow towards the surface	B	yes / no
Morphology	Body color		Color	C	HSL (Hue, Satur., Lightness)
	Body hairiness		Amount of hair (not spines, spikes, sensilia) per area unit	C	Number of hairs / mm^2
	Body size	✓	Body size: length, mass, volume	C	mm, mg, mm^3
	Clypeus size		Length and/or width of clypeus	C	mm, mm^2
	Clypeus shape		Length, width and depth, measures of circularity, or clypeus shapes	C/F	mm, shape indices, categories
	Cuticule toughness		Measures of toughness of elytra or other body parts, including texture, density, thickness	C	various
	Glossiness, iridiscence		Glossiness and iridiscence of pronotum, elytra, metasternum and/or abdominal sternites	C/F	reflectance or categories
	Larval body mass		Length and volume of larva are difficult to measure, but fresh/dry mass are easier	C	mg
	Metatibia length		From the junction with the mesotibia and the end of the tibial spur	C	mm
	Metatibia width		Width of metatibia at widest section including marginal teeth. Spicules and setae excluded	C	mm
	Metatibia curvature		Curvature index may be calculated from straight and curved lengths of metatibia	C	no units
	Protibia size		Protibia size can be measured in multiple ways, typically as length, width or area	C	mm, mm, mm^2
	Volume of prothorax		Volume of prothorax, excluding coxas	C	mm^3
Time related	Colonization moment	✓	Time at which the beetle individual arrives at the dung, counted as time since deposition	C	h
	Daily activity time	✓	Time of the day at which the individuals are most active	ZZ	dawn, midday, dusk, night
	Parity	✓	Number of times a female reproduces along its life	#	count data
	Yearly activity time	✓	When are the beetle individuals active along the year	ZZ	relative to rainy season
	Voltinism	✓	Number of generations of a species during a year	#	count data

	Trait	P	Description	Type	Suggested units
Physiology	Air sacs/subelytral cavity		Presence of empty cavities either closed or with possibility to exchange gases	B/C	Yes / no, volume estimates
	Hydric regulation	✓	Resistance to dehydration; can be measured in multiple ways	C	Seconds, rel. humidity degree
	Immersion resistance	✓	Time of underwater survival	C	Seconds under water
	Respiratory pattern		Differences in the respiratory system that result in different patterns of air flow	B	continuous / discontinuous
	Basal metabolic rate		Measured as the metabolic rate by a resting individual	C	ml CO2 emmitted
	Salinity tolerance	✓	Resistance to salinity measured in multiple ways	C	Seconds, salinity scale
	Soil acidity tolerance	✓	Resistance to acid conditions measured in multiple ways	C	Seconds, acidity scale
	Thermal regulation	✓	Resistance to changes in temperature. Thermal limit to movement and mortality	C	degrees C
	Olfactory ability	✓	Minimum quantity of molecule volume-flow that activates a sensorial or locomotory response	C	flow or air conc. units
Movement	Flight distance and time	✓	Flight ability, measured in multiple ways per time unit	C	m / day, h / day, etc.
	Escaping strategy	✓	Strategy used to escape from predators or any other threat	F	flying, thanatosis, burying, stridulation, etc.
Reproduction	Seed removal from dung	✓	Active seed relocation from dung, including final destination	F	no dispersal, surface, buried
	Antimicrob. in brood masses		Does the brood mass contain antimicrobial substances secreted by parentals?	B	yes / no
	Burrow depth	✓	Depth of the brood masses	C	cm
	Burrow length	✓	Length of the tunnel that leads from surface to brood masses	C	cm
	Burrow ramification	✓	Degree of ramification of the burrow	F	no, some, many ramifications
	Clutch size	✓	Number of eggs per reproductive event (in one burrow, no matter how many ramifications)	#	count data
	Cover burrow walls with dung	✓	Are the walls of the burrow covered with dung?	B	Yes / no
	Dung burial amount	✓	Amount of dung taken away from original location and buried to eat or nest	C	gr
	Dung burial distance	✓	Horizontal distance from original dung location to (telecoprid) burrow	C	cm
	Dung burial rate	✓	Amount of dung buried per unit of time (from start of digging to end of dung burial)	C	gr / h
	Dung relocation strategy	✓	Includes kleptocoprids, which do not relocate, but search for buried brood masses	F	(endo/para/tele/klepto)-coprid
	Egg length, volume, weight		Size of the laid egg measured in multiple ways	C	mm, mm^3, microgram
	Soil relocation	✓	Does the beetle actively relocate the soil from the burrow towards the surface?	B	yes / no

Table 1.1: Description of traits grouped into the category in which they are more prominent. Column *P* shows which traits are considered *performance traits* (see Section 1.1 Introduction). Column *Type* describes the suggested type of variable in which the trait should be measured: *F* = **F**actorial variable (i.e. measurement can only provide one of the suggested values), *B* = **B**inary (i.e. a two level factor), *ZZ* = fuzzy factorial variable (i.e. measurement of the trait can provide several categories in different proportions), # = count variable, *C* = **C**ontinuous variable. *Suggested units* includes both units and the factor levels which can be assigned to each trait.

(Holter & Scholtz 2011), adult and larvae diet (Holter & Scholtz 2007; Holter 2016) and ingested particle size (Holter & Scholtz 2005).

Diet is the most determinant feeding trait, as it determines the type of resource that the beetle has to process, and therefore can make the whole feeding process completely different from one species to another. Here we must note that the clades within the Scarabaeoidea that are referred to with the general term *dung beetles* (i.e. all species in the subfamilies Scarabaeinae, Aphodiinae and the family Geotrupidae) do not feed exclusively on dung. Many members of these subfamilies may either feed, reproduce or develop in other substrates, such as carrion, detritus, roots or fungi (Hanski 1987; Cambefort 1991; Scholtz et al. 2009), and in some rare cases even perform active predation (ants, Silveira et al. 2006; and millipedes, Larsen et al. 2009). These dietary habits can be anecdotal or minimal in some regions (e.g. necrophagy in temperate dung beetles; but see Veiga 1985), but can constitute a dominant trait in many regions and/or taxa, such as necrophagy in tropical Scarabaeinae or detritivory in many genera of Aphodiinae (in either adult or larval stage) inhabiting Mediterranean, other semiarid and arid systems. For those species that feed mainly on dung, the traditional groups based on their dung relocation strategy (see above) determine the traits that need to be measured to understand feeding behavior. Obviously, burial traits do not apply to strict endocoprids, and dung burial distance only applies to telecoprids.

Measurement

Traits related to feeding fall into three main categories, namely the characteristics of the ingested particles, dietary preferences, and the behavioral strategies related to feeding. There is a large variation in the size and hardness of the particles ingested by adult and larval dung beetles (Holter 2016), but a limited number of trait measures and standardized measurement protocols are already available in the literature (e.g. Holter et al. 2002; Verdú et al. 2004; Holter & Scholtz 2005; Holter & Scholtz 2007; Holter & Scholtz 2011). Dietary preferences in adults have been traditionally assessed through cafeteria experiments in the laboratory (Stavert et al. 2014), but diet contents can now be measured from dung beetle gut contents with recourse to genetic tools (Gómez & Kolokotronis 2016). Here note that larval diet is often determined by the material of the brood masses supplemented by the parents and/or the dung pats (Byrne et al. 2013; Holter 2016), except in the case of detritus- and root-feeding larvae. Measuring behavioral traits related to feeding, such as burial traits (see also Reproduction section) may require laboratory mesocosm experiments. In this case, extrapolation to field conditions has to be done with care as many factors such as temperature (affecting dung beetle behavior and dung desiccation), soil structure, compaction, humidity and stoniness can strongly influence the burrowing behavior (see Response of traits to the environment).

Use

As mentioned above, in the definition of *dung beetles* the majoritary diet of part of the Scarabaeoidea clade is used to define a group of species that in fact present diverse trophic habits. This term is also used to define communities as the species in the same trophic guild that feed upon mammal dung and interact, therefore competing for the same trophic resource. Here, mainly detritivorous species, such as many Aphodiinae, are facultative dung feeders, so they do not actually compete for the dung resource. But some of these species occur in such large numbers that they actually overcompete other ”dung specialist” species. Also, since we do not know whether dung may provide better quality resources for gravid females, competition for feeding (not nesting) on dung could actually be intense in these beetles. Therefore, under a strict definition of coprophagy, the detritivores that are very often captured in dung baited traps could be excluded from the dung beetle community, if the focus is determining the strength of the interactions in resource use. However, detritivore species are in fact coprophilous, as a significant part of their activity very often develops within the dung, and they do remove or, at least, disaggregate an important proportion of the dung pat. It follows that studies on the delivery and performance of dung beetle ecosystem functions should account for their role, despite being minoritary. To do this, it is important to take into account that not all species sampled by dung-baited traps might be using dung in the same manner, so they will differ in the delivery of the studied functions.

Reproduction

Description

As stated above, many reproduction traits are at the same time feeding traits. Here, traits related to dung relocation describe the provision of food for the development of the larvae by parents at each burrow to form brood balls. There are also a number of reproductive traits that are not related to feeding, such as clutch size, egg size, burrow ramification, covering burrow walls with dung, or presence of antimicrobial substances in brood masses (Bellés & Favila 1983; Favila et al.

2012; Cortez et al. 2015). Like in feeding, some of these traits are not present in all dung beetles, such as strict endocoprids lacking burial traits, and some dung beetle species not provisioning reproductive burrows with dung, but other trophic resources. Thus, traits regarding dung relocation should be understood in terms of provisioning of any trophic resource, not only dung, but also carrion or other materials for the development of the larvae.

Measurement

Besides some traits describing the number and size of brood masses or burrow ramification, obtaining field data from most reproductive traits would be particularly difficult. Mesocosm experiments are probably necessary to obtain an adequate sample size of reproduction traits while controlling for trophic resource and soil conditions. Although natural conditions in the field are almost impossible to achieve in the laboratory, working with gradients in the mesocosm conditions may help understand the way these traits respond in the field.

Use

Reproduction traits have a very direct relation with individual fitness. Indeed, these traits show strong responses to environmental filters or evolutionary drivers (Vessby 2001). At the same time, they are also responsible for the effects of dung beetles on ecosystem functioning. Thus, any study focused on assessing the effects of assembly processes and/or environmental gradients on dung beetle community structure should include reproduction traits as response traits, while studies on ecosystem functioning and its variation under altered global change conditions should account for reproduction traits as effect traits.

Temporal traits

Description

Temporal traits is a non-standard category that aims to group several traits that account for a very plastic aspect of behavior: dung beetle activity at different time scales i.e. within a year, within a day and along dung desiccation/succession process. Some of these traits are relatively well known. Although very plastic, yearly activity (phenology) and the closely related parity (i.e., number of generations of a species per year; Gittings & Giller 1997) have been traditionally studied in most biomes. Daily activity time and its relation with eye morphology are also well studied (Caveney et al. 1995; McIntyre & Caveney 1998; Byrne & Dacke 2011).

In contrast, despite its importance, colonization time has been seldom studied. This trait accounts for the gradient in the usefulness of the dung resource that diminishes from deposition to total dessication, resulting in the impossibility to be used by dung beetles, and has been often highlighted as an important factor determining competition for trophic resource (Doube 1990; Giller & Doube 1994).

Measurement

Given their nature, and their dependence on the response of dung beetle species to varying weather conditions, perhaps the only meaningful way to measure yearly activity time and colonization time is in the field. Yearly activity time is determined by the number of active individuals, both newly emerged and surviving individuals from former generations in long-living species. These processes are influenced by many environmental cues such as rainfall events, temperature variations, etc. The limited understanding of how these cues operate makes replicating them in mesocosm experiments a great challenge. It follows that understanding the processes determining temporal activity must rely on studying field emergence date patterns of yearly activity in populations. It should be noted that emergence is a significant time-flag for the whole life-cycle of dung beetles. Information on the periods corresponding to adult sexual maturation, reproduction and larval development would be critical. Variations of these traits are probably responsible for parity in different populations and species.

Daily activity time is partly determined by circadian rhythms and partly by conditions. This trait can be studied both in the field (Krell-Westerwalbesloh et al. 2004; Feer & Pincebourde 2005) and in the laboratory, which has allowed to link it with eye morphology (Byrne & Dacke 2011). Dung colonization time is dependent on distance, detection and movement abilities. Thus, it can only be measured in the field (Barth et al. 1994; Finn & Giller 2002), as distances needed to test dung detection abilities are surely in the order of hundreds of meters.

Use

Most biomes present considerable variations in environmental conditions both through the year and between years due to the effects of periodic eventes, as El Niño cycles, and climate change processes. The different outcomes of these processes generate regional differences in yearly temperature patterns from high thermal variations in temperate and cold biomes to the relatively stable tropical regions' rainfall seasonality including summer or winter rainfall, bimodal regimes, etc. and even herbivore activity patterns including changes in their main food source, dung quality, and migrations (Edwards 1991). Temporal traits are particularly important in harsh environments, where the strong environmental pressures can be partly avoided by varying the atmospheric conditions that adults and larvae have to face (Nylin & Gotthard 1998), thereby making emergence time and/or sesonal and diel activity period crucial for survival. This implies that studies describing the response of dung beetles to climate change should include assessments of the variations in yearly activity.

Nonetheless, researchers interested in the dynamics of dung or carrion communities should seek to determine the differences in colonization time across species. Further, studies on dung beetle services should take into account that the provision of some services requires the temporal coupling of dung beetle activity with herbivore grazing (and dung availability) and resource quality.

Physiology

Description

Physiological traits seek to describe the performance of the individual organism under different conditions, and comprise any measurement of respiration, metabolism and stress resistance. Respiration is largely unknown for most dung beetles, although some research groups have developed in-depth studies of the types and rates of respiration for several species (e.g. Duncan & Byrne 2005). Knowledge of dung beetle metabolism is similarly restricted to a few species for which metabolic rates have been thoroughly studied (e.g. Davis et al. 2000). In the same way, the tolerance or resistance to many types of stress faced by dung beetles can be measured. These include the extremes of key environmental variables, such as extremely high or low temperatures (e.g. Verdú et al. 2011; Gallego et al. 2016), but also drought and inundation resistance by larvae and pupae in burrows (e.g. Vessby 2001), high solar radiation, soil parameters (e.g. high salinity or extreme pH), or hypoxia (Whipple 2011).

Measurement

Physiological traits are among the most difficult traits to measure. This process typically involves simulating different environmental conditions in experimental conditions while obtaining measures of the physiological performance of the individuals and/or identifying lethal levels of different stressors thus sacrificing dung beetle individuals. This often requires maintaining relatively large numbers of live specimens in the laboratory, specialized equipment, fine-tuned techniques and protocols, and specialized training. Because of this, they are usually costly and therefore are difficult to afford by most research groups. Further, some legal and ethical issues may arise from policies on handling live specimens. Therefore, to raise the current capacity of providing measures of dung beetle physiological traits it is necessary to design simpler protocols and/or experiments that allow to either measure certain traits in the field or, at least, obtain acceptable proxies for them.

Use

Physiological traits are usually considered to have a direct relationship with individual fitness and to be mainly response traits to environmental variables (Diamond et al. 2012). However, in some cases traits such as metabolic rate can serve as proxies for the variations in certain performance traits such as feeding or burial rate that, in turn, have an effect on ecosystem functions (in this case, nutrient cycling). Therefore, physiological traits can prove useful not only to understand the effects of environmental filters on species distributions and/or community structure along environmental gradients, but also to assess changes in the provision of ecosystem services under changing conditions.

Movement

Description

Most dung beetles are relatively good fliers, so they mainly move by flying, but also by walking (here note that there are a number of flightless dung beetle species) and burying. The general aim of dung beetle movement is to reach dung pats for feeding and reproduction (Hanski 1980; Roslin 2000). Here note that dung does not only serve as food resource and material for nesting burrows, but also as a meeting place for sexual interactions.

Flying period during the day (i.e. diurnal, crepuscular, nocturnal) is many times considered as equivalent to activity period (see Temporal traits), disregarding the fact that dung beetles develop many activities in the dung pat and within burrows under the soil surface. However, flying period *per se* is a major component of dung beetle ecological performance, while requiring sight modifications to meet the light intensity conditions during flight (Byrne & Dacke 2011). Another set of traits that interact with movement, and in particular with flight capability, are thermal regulation traits. Flying muscles produce physiological heat while moving, hence requiring morphological and physiological temperature dissipation strategies (Bartholomew & Heinrich 1978; Verdú et al. 2006; Verdú & Lobo 2008).

These four sets of traits (i.e. flying, flight period, eye adaptations and thermal regulation) interact to allow each species to forage in an efficient manner, also facilitating the temporal partitioning of the arrival to the excrements. If the aim of a beetle is to find fresh dung for feeding, sexual interactions and reproduction, foraging flight period should optimally be coupled with herbivore defecating time patterns, and/or be fast enough to minimize the time between the detection of a fresh dung pat (through their olfactory system) and the arrival to it. These needs might critically shape the traits of certain dung beetle communities. Although anecdotal, some dung beetles have developed movement strategies that do not involve foraging flight for dung, but instead searching for the herbivore itself (see Ratcliffe 1980; Jacobs et al. 2008; Majumder & Datta 2012).

Finally, another purpose of dung beetle movement may be to escape predators and any other risk, such as avoiding herbivore trampling, intense solar radiation, flooding water, etc. Indeed, several escaping strategies can be observed in the field, such as flying, burying and staying still (i.e. immobility and/or thanatosis).

Measurement

There are two basic approaches to measuring dispersal and movement rates in insects: laboratory mill experiments and field capture-recapture sampling. Both present certain limitations. While laboratory mills can provide much data on several flight parameters, such as distance, time, speed, intervals of flight and rest, etc., their results should be interpreted with care, as lab conditions can greatly influence the results (Taylor et al. 2010). In contrast, the results of capture-recapture field experiments (Turchin & Thoeny 1993) are more directly interpretable, but they should be extrapolated to other systems with care, and provide much less data, as flight distance is the only variable that can be safely measured. New technologies can help improve field measurements (e.g. see Rink & Sinsch 2007 for an example with Lucanid beetles), but these are expensive and so far have seldom been employed.

It should be noted that movement, and thus the area at reach for an individual, determines the extent of both populations and communities. Therefore, sampling different aspects of movement in the field should be designed accordingly to avoid pseudo-replication (i.e. considering two samples as coming from different populations/communities when they are actually the same). This implies that the movement capabilities of the species measured should be taken into account to decide the distance between traps and replicates in movement studies (Larsen & Forsyth 2005; Silva & Hernández 2015).

A particular trait that may be easier to characterize is escaping strategy. Assessing variations in this trait should be done experimentally, exposing the individuals to different kinds of risk (e.g. terrestrial and aerial predators) and levels of threat/risk. Given the necessarily extreme and fast responses, whether these measures are done in the laboratory or in the field probably has little influence in our ability to characterize dung beetle responses to threats.

Use

When interpreting the relationship between dung beetle populations or communities and the spatial distribution of dung in the field (Roslin 2001), much care should be taken to estimate the potential foraging area of the species of interest. In open habitats such as deserts or grasslands, foraging areas might be much larger than those in closed habitats (Arellano et al. 2008), enabling dung beetles to thrive in dung-sparse environments. The same rationale may be applied when understanding the geographical scope of the gene flow of a population (see Roslin 2000).

Movement and habitat selection have been used simultaneously to investigate the conservation risk of species. Both habitat specialists and low dispersal species may not be able to reach suitable habitat patches in an increasingly fragmented world (Gibb et al. 2006). Here, species with high dispersal ability may in fact need wider patches of continuous habitat to sustain their populations, which makes small patches unsuitable for them (Gibb et al. 2006).

1.3 Response of traits to the environment

In this section we summarize and comment which and how dung beetle traits from the different categories may respond to the most common environmental gradients and stressors. Further details on which and how specific traits might respond to these factors can be found in Table A.1 (in Appendices). Only some of the relations are referenced, urging for serious testing in formal experiments (Sowig 1996) to provide evidence and avoid the eventual misattribution of responses to certain gradients that may result from field observations when the actual stressors are correlated with other environmental factors.

Functional traits may respond at several time scales, which are traditionally classified into long-term evolutionary scales and short-term ecological scales. However, both kinds of processes occur across a range of temporal scales, including short-term contemporary evolutionary processes (Carroll et al. 2007) as well as long-term ecological processes that shape up the distribution of species (Hortal et al. 2011). These processes are often inextricably interrelated, so trait responses to environmental factors may be either called *abiotic filters* or *evolutionary forces/drivers*, depending on the mechanism of interest. In the lack of a common framework that allows making an easy reference to processes studied in both types of focus, for simplicity we adopt a more ecological approach, but without leaving out references to evolutionary processes.

Temperature

Temperature varies along time and space, exhibiting annual and daily patterns, latitudinal and altitudinal gradients, and variations between microhabitats due to the effects of vegetation cover, surface water and soil depth. Temperature is probably a strong driver of trait selection, as it fosters multiple niche partitioning and has lethal effects on individuals living at their tolerance extremes, thus determining the distribution and activity of their populations. It is highly related to incidence of solar radiation (see below Other environmental stressors), so an effort to avoid mixing effects of temperature and solar radiation must be done while measuring responses in the field. This may be crucial in tropical areas, where dung beetle communities very often develop their activity under the vegetation cover provided by the canopy of forests and/or savanna shrubs, thus diminishing radiation while temperature can remain high.

Traits responding

Temperature affects all biological processes, from enzymatic reactions to behavior and phenology. Thus, all categories of traits are affected by temperature to a certain extent. The values of many morphological traits, such as body size and shape can be selected by temperature (e.g. Statzner et al. 2004). However, such responses are not universal for ectothermic invertebrates, being rather the outcome of the complex interaction of a series of processes that prevent them from being included in the general ecogeographical rules that link endotherm morphology with temperature (Vinarski 2014). Indeed, the processes by which certain traits drive insect responses to the environment may be radically different from those of the, better-studied, vertebrates. For example, although hairiness is known to be part of certain insect strategies against freezing, it provides protection against extreme temperatures in a fundamentally different from the way it does in vertebrates (Bale 2002; see further comments about radiation in the subsection Other environmental stressors below).

It is likely that dung beetle physiology itself responds to temperature variations, but little has been studied in this aspect beyond the strategies against overheating during flight discussed above (see Verdú & Lobo 2008). Rather, thermal resistance is the physiological trait that has been most used to account for dung beetle physiological responses to temperature. Indeed, dung beetles show a large range of variation in this trait, and their physiological responses even include achieving true endothermy through certain behaviors that include fast muscular movements (Bartholomew & Heinrich 1978; Gallego et al. 2016).

Several temporal traits also vary in response to varying temperature conditions, thus providing a stress-avoiding strategy (Hodkinson 2005; Traill et al. 2010). The relationship between temperature and dung beetle yearly activity has been widely studied in different biomes, although particularly in temperate environments (see e.g. chapters in Hanski & Cambefort 1991). Most dung beetle species avoid harsh temperatures by constraining their yearly activity periods to the mildest seasons, whereas a few others avoid competition for resources by being active during cold winters in the Holarctic or the dry season in the Neotropics. A similar temporal partitioning can be seen along the day, resulting in fully diurnal, crepuscular or nocturnal dung beetles. This change of daily activity patterns requires developing adaptations of eye morphology to the different light intensities of night and day (Byrne & Dacke 2011). Last, but not least, parity is related to longevity and maturation rates, which in turn are likely to be positively correlated with temperature, as high temperatures enable high metabolism and maturation rates (Gittings & Giller 1997).

Indeed, reproduction traits also respond to temperature, as higher temperatures can result in higher burial rates. But further, they may promote deeper burrows to buffer surface thermal variation (Rasa 1994), and shorter dung burial distances in telecoprids to avoid extreme temperature conditions while rolling the ball on hot soil surfaces (Smolka et al. 2012).

Use

Responses to temperature are particularly important to understand climate change effects (Traill et al. 2010), drivers of diversity gradients (e.g. Davis & Scholtz 2001; Lobo et al. 2002; Hortal et al. 2011), as well as determinants of species distributions and habitat selection (Roslin 2001).

Relative humidity

Although dung beetle diversity is often studied in relation to precipitation, this is because of its easier measurability. However, it is likely that dung beetles actually respond to relative humidity. Like temperature, relative humidity varies in both time (along the year and through the day) and space depending on the protection from solar radiation provided by hillside and vegetation cover, as well as the depth into the soil. Variations in relative humidity correlate with those of temperature and solar radiation. High temperatures and intense exposition to solar radiation promote water evaporation, and low temperatures also promote dessication (Sømme 1986; Block 1996). This makes difficult measuring the effects of humidity under varying temperatures and levels of exposure to solar radiations, so particular efforts may be needed to separate dung beetle responses to these three factors.

Traits responding

Probably the first response of dung beetles to variations in humidity is related to the time of the year in which they are active (Liberal et al. 2011). Besides that, dessication stress can be avoided by modifying the time spent above the ground. Whilst periods in the surface are essential for foraging, feeding and reproducing, they are also physiologically hard to endure. In contrast, the periods spent under the soil surface or within dung pats are much more stable thanks to the buffering effect of soil. However, the proportion of time spent either above or below ground is a hard to measure trait, so its importance can only be inferred from other related traits. Indeed, colonization moment is directly related to dung moisture and dung quality (Finn & Giller 2002), so the response of this trait to relative humidity is particularly important for both feeding and reproduction. In the same way, soil moisture affects reproduction success via invested time and burrow structure (Rougon & Rougon 1983; Sowig 1996) that directly affect offspring survival (Sowig 1995). As a result, changes in relative humidity can provoke changes in reproduction strategy (Hammond 1976; Rougon & Rougon 1980; 1983; Verdú & Galante 2004), morphological traits (Duncan 2002; Verdú & Galante 2004), and even ontogenetic development (Vessby 2001).

Use

Disentangling the effect relative humidity has under different types of habitats and/or different vegetation structures can be very challenging. However, this factor could be playing a major role in the responses of dung beetles to land use and climate changes. Its effects can be assessed through the use of dataloggers and sampling designs that include replicates of different habitats along strong environmental, altitudinal and/or latitudinal gradients, together with measurements of traits that may be responding to relative humidity (Lumaret 1995; Hawkins & Porter 2003).

Soil

Dung beetles spend most of their lives underground. The full development from egg to pupae state of paracoprid and telecoprid larvae occurs below the ground, and they only emerge as fully developed imagos. As adults, many dung beetles bury for feeding, reproducing and maybe even for resting and escaping from risks. Thus, many traits involved in all these life stages and activities will respond to soil parameters. Indeed, dung beetle diversity responds to basic soil conditions (e.g. Silva et al. 2015, Davis et al. 2016). Soil type and/or texture, soil profile structure and compaction in each layer can determine dung beetle presence in a local community or the whole species pool. Soil humidity is another soil parameter that can severely influence dung beetle activity and might explain their distribution. Finally, acidity, salinity (which is also tightly related to humidity of soil), organic matter content and cation exchange can affect dung beetle performance, although their responses to these factors are likely less significant than those of other soil organisms such as earthworms. Of course, endocoprids are probably much less affected by soil parameters and, thus, their traits may not respond so clearly to variations in soil conditions.

Traits responding

Burial traits are obvious candidates to respond to soil type, structure, compaction and texture (Fincher 1973; Sowig 1995). But several morphological traits involved in burial, such as the shape and area of the protibias and metatibias may respond to soil texture, to increase burial efficiency or in extreme cases just to enable burial in hard soils. Indeed, feeding and reproduction traits also involving burial will change along gradients in soil characteristics, including burrow depth and ramification, as well as the distance at which telecoprids roll the brood mass to find an appropriate burial site. On the other hand, physiological traits can respond to soil humidity or inundation as an extreme case of humidity, as well as to acidity and salinity of the soil.

Use

Certain groups of dung beetles can be very specific of certain soil types and/or structures. This makes traits responding to soil very useful to understand the factors behind variations in community composition. It follows that traits responding to soil structure are useful in studies of areas and/or land uses where the compaction of soils is suspected. Compaction can arise as a result of land use change (agriculture, over grazing, logging, etc. Brussaard & Faassen 1994; Vulinec 2000; Slade et al. 2007) and harsh climatic conditions (i.e. aridity Verdú et al. 2009). Indeed, climate change in expected to increase aridity in certain areas, and flood frequency in others. In this case inundation resistance traits are useful to understand local extinction proneness. Physiological traits responding to salinity and acidity will probably respond in heavily exploited agricultural lands where excess of watering leads to nutrient lixiviation, salinity and, depending on water source, acidification or increase in pH making soil alkaline.

Only a few publications studying dung beetle community ecology and species distributions have included soil patterns (Davis et al. 2008; Davis et al. 2010; Sullivan et al. 2016a) and soil evolution (Davis et al. 2016).

Trophic resources

The availability and quality of trophic resources (such as different types of dung, carrion, fungi or detritus) can drive the spatial and temporal responses of dung beetles, acting as a strong filter for certain traits related to dietary preferences. Here we focus exclusively on mammal dung because it is the main component of the diet of most dung beetles. But other trophic resources might be characterized in other ways, that is, their associated traits may respond differently.

Dung beetle traits can vary in response to the abundance, quality and distribution of dung. Dung availability regulates abundance and/or biomass of dung beetles in a community. A higher dung abundance allows higher numbers of individuals and thus lowering the strength of competitive processes (Finn & Gittings 2003). Moreover, some dung beetle species might need a minimum abundance of dung to form a single brood mass (Shafiei et al. 2001; Sullivan et al. 2016b), so they can be excluded from very dung-scarce systems.

Dung quality is related to palatability and capability to be manipulated by dung beetles. Mammal dung typically contains a high proportion of water and undigested fiber, together with a fraction that can be considered *dead and alive microbial biomass* (Holter 2016). These proportions vary greatly across different dung types, such as those provided by mammal herbivore ruminants and non-ruminants, carnivores, frugivore primates or other vertebrates (e.g. birds, reptiles, etc.) (Stavert et al. 2014). The size and shape of the deposition units in piles, pats, lumps, pellets, etc. of different volume can also modify dung dessication dynamics, considerably affecting the palatable life-time of dung. For example, pellets have a high surface-volume ratio, so they dry out faster than pats, which present low surface-volume ratio and can take several years to disintegrate completely in certain conditions (Milton & Dean 1996).

The spatial distribution of dung in the field is determined by the movement and deposition patterns of the dung producer (i.e., the so-called piosfera; Lange 1969). Wild and livestock animals follow tracks, have preferred watering and sleeping sites (Lobo et al. 2006; Du Toit et al. 2008) or even proper latrines (Krell et al. 2003a, Sánchez-Piñero et al. 2012). These habits result in a variety of spatial distributions of dung, from very sparse but recurrently localized (such as rabbit latrines in semiarid areas), to difficult to find randomly placed droppings in dense tropical forests. Again, they also result in dung units ranging from the big piles provided by large herbivores such as rhinoceros or elephants, to the groups of small pellets that are characteristic of sheep, goats or rodents.

Traits responding

Given that mammal dung is the most extended trophic resource both for adult and larvae dung beetles, it is reasonable to think that feeding and reproduction traits will respond to the dung parameters mentioned above. These include basic diet preferences and diet range (i.e. number of different trophic resources that a dung beetle individual can feed upon), but also dung burial amount and perhaps even burial rate, which can respond to variations in dung quality.

Also, when dung is not available nearby, dung beetles are capable of actively foraging for dung. This implies that they respond to dung distribution (not only presence of dung but also better quality or abundance) by means of the traits that determine their ability to reach dung resources in the right time and place (Finn & Giller 2002). This is probably achieved by emerging in the right season (yearly activity time, i.e. phenology), being active at the right time of the day (daily activity time, thermoregulation; Ybarrondo & Heinrich 1996), detecting the dung from large distances (olfactory traits; Dormont et al. 2010; Tribe & Burger 2011) and flying to it (flight-related traits).

Use

Traits related to resource use may be particularly useful to understand dung beetle responses to livestock intensification/extensification and the extinction of certain wildlife outside protected areas through hunting or other human impacts. Traits responding to dung parameters can be useful in some areas to estimate the impact of livestock intensification, where dung may increase in abundance coupled with high spatial concentration, but presumably with a decrease in dung quality. Protected Natural areas can also present increases in dung or even over-populations of wild herbivores, with the consequent increase in dung beetle populations. In contrast, the numbers of these wildlife mammals may decrease outside of these areas as a consequence or land use change or direct hunting, which can have negative effects on dung beetle communities (Nichols et al. 2009).

Other environmental stressors

Solar radiation

Solar radiation is directly correlated with latitude, although cloud cover, mountain slope, aspect and vegetation modify the radiation that reaches the surface of the earth. Radiation should be separated from temperature, as they can promote different responses on dung beetles, and they can also vary separately (e.g. radiation is high while temperature is low in cold deserts or mountains). Radiation has, however, a heating effect on organisms, also producing an oxidative damage. Dung beetles can respond to such radiation by avoiding being active during the day through the adoption of nocturnal habits, or through morphological traits such as iridescence, color or hairiness that diminish the potential impacts of radiation in their organisms (Shi et al. 2015). Studies carried out in environments exposed to high solar radiation should bear in mind the potential presence of special adaptations of dung beetles to this phenomenon, which could otherwise be difficult to explain.

Vegetation structure

Although dung beetles generally do not use vegetation directly, some tropical species might need vegetation to perch on. Other dung beetle species might need the protection of vegetation against solar radiation to prevent overheating and dessication (Nealis 1977). Increments in vegetation biomass can support larger herbivore communities and thus provide abundant dung that allows sustaining larger dung beetle populations and richer communities. In addition, soil conditions vary significantly along different types of habitats, from forests to grasslands or deserts. Thus, dung beetle traits might respond to vegetation structure in some ecosystems but be generally reflecting soil properties (Davis et al. 2010). These responses include variations in morphological traits such as color, glossiness and iridescence (that seem more frequent in tropical forests than in other biomes), to feeding or reproduction traits such as burial distance by telecoprids (due to the difficulty in finding an appropriate site to bury) or flight parameters (as complex and open aerial space require different flying skills). Studies on habitat fragmentation (especially on the transformation of forests or shrublands to pastures) should be enlightening on this topic as they allow comparing communities with the same climate regime and similar soil conditions, but different vegetation structures.

Predation risk

Dung beetles are subject to predation by birds, small carnivores, rodents (Sánchez-Piñero 2007; Larsen et al. 2008) and other insectivore and omnivore animals. Traits responding to such a lethal pressure are those involved in camouflage (color, glossiness, etc.), spending the least time on the surface (burial rate) and of course escaping strategy (flying, stasis and burying). However, predation risk can be challenging to measure, and to our knowledge, no studies have reported predation as a strong enough filter so as to actually explain functional differences across species or determine community structure.

	FILTERS or FORCES								**TRAITS**		**ECOSYSTEM FUNCTIONS**									
env.∼trait relations	**predation risk**	**competition for dung**	**Light / radiation**	**vegetation structure**	**dung distribution**	**soil**	**relative humidity**	**temperature**	**category**	**trait**	**removal amount**	**burial amount**	**cycling quality**	**bioturbation**	**second seed disp.**	**reg. Dung. Orgs.**	**Parasite reg.**	**pollination**	**predation**	**trait∼func. relations**
102	**5**	**19**	**5**	**6**	**12**	**14**	**21**	**20**			**16**	**17**	**16**	**15**	**23**	**10**	**9**	**8**	**4**	**118**
4		✓			✓		✓	✓	morphology	body length, volume, mass, density	✓	✓			✓	✓	✓	✓	✓	7
2		✓			✓					volume of prothorax		✓								1
2		✓				✓				metatibia width		✓								1
1						✓				protibia length, width, area	✓	✓			✓					3
2	✓		✓							body color								✓		1
2			✓					✓		body hairiness						✓	✓	✓		3
–										clypeus width, shape		✓							✓	2
1			✓							cuticule texture, density, thickness							✓	✓		2
3	✓		✓	✓						glossiness, iridiscence										–
–										larval body dry mass	✓	✓								2
1		✓								metatibia length	✓	✓			✓					3
4		✓			✓		✓	✓	time related	colonization moment	✓	✓	✓		✓	✓	✓			6
3		✓			✓			✓		yearly activity time			✓					✓		2
3		✓	✓					✓		daily activity time								✓		1
1								✓		parity	✓	✓		✓						3
1								✓		voltinism										–
3				✓	✓			✓	physiology	volatile detection ability	✓							✓	✓	3
2						✓	✓			inundation resistance										–
2						✓	✓			salinity tolerance										–
2						✓	✓			soil acidity tolerance										–
2							✓	✓		dessication resistance										–
2							✓	✓		respiratory pattern										–
1								✓		air sacs, subelytral cavity...										–
1								✓		resting metabolic rate	✓	✓								2
1								✓		thermal resistance				✓						1

3		✓			✓		✓		reproduction	dung relocation strategy	✓	✓	✓	✓	✓	✓				6
2		✓			✓					dung burial amount	✓	✓			✓	✓				4
4		✓				✓	✓	✓		burrow depth			✓	✓	✓		✓			4
2						✓	✓			covering burrow walls with dung	✓	✓		✓						3
2						✓	✓			soil relocation			✓	✓	✓					3
2						✓	✓			burrow ramification			✓	✓	✓					3
4		✓		✓		✓		✓		dung burial distance			✓	✓	✓					3
3		✓					✓	✓		antimicrobials in brood masses			✓		✓		✓			3
4	✓	✓					✓	✓		dung burial rate					✓	✓				2
1							✓			egg length, volume, weight										–
–										active seed removal from buried dung					✓					1
–										burrow length			✓	✓						2
1		✓								clutch size			✓		✓					2
4	✓			✓	✓	✓			movement	escaping strategy				✓						1
4		✓		✓	✓		✓			flight distance, time, etc.	✓				✓		✓	✓		4
3		✓			✓		✓		feeding	dung relocation strategy (includes klepto)	✓	✓	✓	✓	✓	✓				6
1					✓					adult diet	✓	✓		✓	✓				✓	5
1					✓					adult diet range										–
3						✓	✓	✓		burrow depth			✓							1
2						✓	✓			soil relocation			✓	✓	✓					3
4		✓		✓		✓		✓		dung burial distance			✓	✓	✓					3
4	✓	✓					✓	✓		dung burial rate					✓	✓				2
1							✓			feeding mechanism						✓	✓			2
–										active seed removal from buried dung					✓					1
–										burrow length			✓	✓						2
1		✓								dung burial amount	✓	✓			✓	✓				4
–										ingested particle size			✓		✓		✓			3
–										larval diet	✓	✓								2

Table 1.2: Relations of dung beetle traits (left) responding to filters and forces (right) affecting the delivery of ecosystem functions. Numbers in margins count checkmarks (✓) in each row or column. For full descriptions of each relationship see Appendix A.

1.4 Effects of traits on ecosystem functions

The ecosystem functions delivered by Scarabaeinae dung beetles were extensively reviewed by Nichols et al. (2008). Here we review also all other dung beetle groups feeding on dung, including Aphodiinae and Geotrupidae. We have revised and discussed the list provided by Nichols et al. (2008), renaming and collapsing some of the functions they propose. In this document we focus on the traits that deliver those functions. When we provide a brief description of functions, we focus on details that may change from the definition in Nichols et al. (2008). However, we refer to that publication for more extensive explanations and implications of each function.

During the last decades some effort has been done to study some dung beetle trait~function relationships in laboratory mesocosms (e.g.Nervo et al. 2014; Chapter 2), field mesocosms (e.g. Beynon et al. 2012; Nervo et al. 2014) and even in the field (e.g. Andresen 2002; Braga et al. 2013; Slade et al. 2016). This includes some assessments of global change effects on the delivery of functions (e.g. Slade et al. 2016), specifically under land use changes (e.g. Hingrat & Feer 2002; Braga et al. 2013; Nichols et al. 2013). Based on this information, here we provide an overview of the groups of traits that have an effect on each type of function. Further, we also provide detailed hypotheses of the traits affecting each function in Table A.2 (in Appendices). Only some of the relationships that we describe are supported by published references, evidencing the limited knowledge on the ecosystem functions and services provided by dung beetles (see Noriega et al. 2018). This urges for serious testing in formal experiments (Sowig 1996) to provide empirical evidence on these relationships and avoid the eventual assignment of correlated traits to the wrong functions as a result of field observations.

Nutrient cycling: dung removal, burial and cycling quality

Nutrient cycling by dung beetles consists in the transfer of freshly deposited dung below the soil surface, physically relocating nutrient-rich organic material and instigating micro-organismal and chemical changes in the upper soil layers (Nichols et al. 2008). This is a complex ecosystem function that can only be analyzed by subdividing it in at least three measurable functions: dung removal, dung burial and nutrient cycling quality.

Dung removal amount

Dung removal amount refers to the quantity of dung that *disappears* from the original dung pat or dropping by feeding or reproducing, independently of the dung relocation strategy. It thus applies to the removal performed by endocoprids, paracoprids and telecoprids. Kleptocoprids do not provide any significant removal, since their reproduction does not involve any removal of dung from the original dropping location but the use of dung already buried by a paracoprid or a telecoprid.

The traits that determine the amount of dung removed by an individual are spread over several types. Besides dung relocation, traits such as adult and larval diet (obviously, strictly necrophagous or saprophagous dung beetles do not remove dung) and body size (Nervo et al. 2014) coupled with metabolic rate determine the nutritional requirements and thus the amount of dung that the individual will utilize and therefore remove from the original dung pat. Other indirectly related traits are those that increase frequency of reproduction such as parity or competition ability, as well as those related to dung detection ability, flight and colonization moment (Tixier et al. 2015b).

Dung removal amount is a key measurement to understand the overall contribution of dung beetles to nutrient cycling in ecosystems. Dung removal from the surface is related to two other functions: secondary seed dispersal and reduction of seed predation in the pat (Beaune et al. 2012), and regulation of the populations of other dung-based organisms (see below). Dung removal has been widely studied (e.g. Bornemissza 1960; Mittal 1993; Anduaga 2004) and continues to be so, using progressively more developed experimental approaches (e.g. Wu & Sun 2010; Nervo et al. 2014; Tixier et al. 2015b; Slade & Roslin 2016).

Dung burial amount

Paracoprids have different tunnel morphologies when feeding or reproducing but during both processes they bury dung right below the original dung dropping location, so in this case the relocation is mainly vertical (Bang et al. 2005), although some ramification and/or diagonal tunnels may be found in nests. In contrast, telecoprids perform a horizontal relocation of dung on the soil surface through their rolling behavior, followed by a vertical dung burial. Although telecoprid tunnels for feeding and reproducing also differ in morphology, both require horizontal and vertical relocation of dung. Therefore, by redistributing some excrement outside the original dung pat, this behavioral functional group contributes significantly to the cycling of organic matter throughout the whole pasture (see below).

Dung burial amount is affected by several traits shared with the process of dung removal, as both processes are combined in paracoprids and telecoprids (but obviously not in endocoprids). Adult and larval diet and body size coupled with metabolic rate determine the nutritional requirements and thus the amount of dung that the individual will bury. Morphological traits such as the volume of the prothorax (that hosts digging muscles) and protibia robustness make digging and burying easier and can increase the amount of dung an individual is able to bury. Traits related to rolling capacity such as metatibia length can also increase the final amount of dung that an individual buries. Dung burial has sometimes been studied along with dung removal, but it is logistically more difficult to measure as feeding or reproduction nests have to be found and dug out, balls found, cleaned and finally weighed (Horgan 2001; Gregory et al. 2015; Chapter 2).

Nutrient cycling quality

Nutrient cycling quality refers to the decomposition conditions (and further enrichment of soil for vegetation) in which the removed or buried amount of dung is left after dung beetle activity. It can be mainly summarized by the horizontal and vertical distribution of dung, and the humidity conditions. Nutrients in dung are rapidly lost without the action of beetles (Gillard 1967), but many of these nutrients can remain in a mineral state if microbial activity is absent or very low as a result of unfavorable abiotic conditions at the soil surface (Milton & Dean 1996). Dung beetles relocate dung underground, where temperature is more stable and humidity greater, thus enhancing microbial processes (Tixier et al. 2015a). But dung buried too deep might end up surrounded by highly inorganic soil with low microbial activity. The horizontal distribution of dung also influences nutrient cycling quality, since the nutrients sequestered in the original dropping location enrich the soil below it, but nutrients spread in an area around the original dropping site may be more beneficial for vegetation and nutrient cycling.

Nutrient cycling quality is affected by dung beetle performance traits characterizing dung burial and, especially, the final location of dung. Feeding or reproductive burrow depth (related to body size Gregory et al. 2015), length, ramification, distance from the source and relocation of soil to the surface (bioturbating the soil and relocating microbiota) can highly improve dung decomposition, and, thus, nutrient cycling processes. Other traits related to the time of the year and the age of the dung pat (Tixier et al. 2015b) at which dung beetles actively process the dung may determine the humidity of the dung that is buried, increasing the possibility of microbial activity. Although endocoprid activity does not involve burying dung, it may also improve nutrient cycling, as endocoprid populations can be very large in some temperate ecosystems, spreading the dung pat across a wide area in the soil surface or even mixing it with the first centimeters of the top soil layer.

As far as we know, no studies have delved into the optimal location for dung decomposition, except perhaps Tixier et al. (2015a). This is probably due to the difficulty to detect and measure dung burial mentioned above. Some classic publications deal with the subsequent plant growth enhancement (Bornemissza 1960; Bornemissza & Williams 1970), but finer analyses to assess the eventual increase in nutrients in the soil and its consequences for plant growth have seldom been performed (Bang et al. 2005; Yamada et al. 2007; Santos-Heredia et al. 2016).

Bioturbation and plant growth enhancement

Bioturbation is the displacement and mixing of sediment particles by animals or plants often modifying the structure of the soil, and so, increasing permeability of air and water (Nichols et al. 2008). Bioturbation is linked to the three main aspects of plant performance: survival, growth and reproduction. The activity of dung beetles in the soil while burrowing (either for adult feeding or reproduction) has an effect on the permeability of the soil to air and/or water (Brown et al. 2010). It has been suggested that dung beetles affect the macrostructure of the soil in their tunnels making rooting easier, while smaller organisms (such as Annelida, Isopoda, Collembola, Fungi, etc.) affect the microstructure of the soil (Brussaard & Hijdra 1986). Therefore, it can be speculated that these organisms may benefit from some facilitation by dung beetles.

Traits affecting

Bioturbation will be affected by traits involved in burrowing. This includes reproduction performance traits such as reproductive strategy (here note that endocoprids may contribute to bioturbation as they use the interphase between dung and soil surface), as well as burrow depth, length, ramification, soil relocation to the entrance of the burrow or soil surface. Further, the frequency or total number of times an individual reproduces along its life multiplies its bioturbating effect on the ecosystem, so lifespan may become important for assessing ecosystem service provision. Some morphological traits such as prothorax volume which correlates with the development of digging muscles, along with protibia traits might serve as useful proxies when no data are available for those performance traits.

Use

Several studies have measured the bioturbation delivered by dung beetles to ecosystems (Brussaard & Hijdra 1986; Mittal 1993; Bang et al. 2005), as well as plant growth enhancement in both laboratory experiments and in the field (Bornemissza & Williams 1970; Yamada et al. 2007) and even nutrient content in plant tissues (Santos-Heredia et al. 2016; Nervo et al. 2017). A trait-based approach to the study of bioturbation is suggested in areas of compacted soils (Bang et al. 2005; see Soil in the Responses subsection above).

Secondary seed dispersal

Secondary seed dispersal by dung beetles consists of vertical and/or horizontal relocation of plant seeds from the original herbivore deposition location (Nichols et al. 2008). Seeds may benefit in several ways, including relocation to more suitable microhabitats (Pérez-Ramos et al. 2013; Griffiths et al. 2015), avoidance of pathogens and predation in the original dung pat (Beaune et al. 2012), increased seedling survival (but see D'hondt et al. 2008) and decreased competition for space and resources. In some systems, the importance of dung beetle activity on seed dispersal has been crucial in a broad temporal scale, driving seed evolution to mimic dung pellets and deceive dung beetles into burying them (Midgley et al. 2015). Researchers however, have mostly used plastic beads mimicking seeds (Feer et al. 2013; Griffiths et al. 2015), thus seed survival, seedling emergence and survival has yet to be studied in depth (but see D'hondt et al. 2008; Pérez-Ramos et al. 2013). Few studies have used real seeds and plastic mimics (Koike et al. 2012).

Traits affecting

Seeds are dispersed during the dung relocation process, so feeding and reproduction traits related to horizontal and vertical relocation of the dung are also determinant to understand the efficiency of secondary seed dispersal by dung beetles. Diet and dung relocation strategy are binomial factors that indicate which seeds are dispersed by each species. In a extreme case of diet preferences, strictly necrophagous beetles do not bury dung, and thus do not bury seeds either. Dung relocation strategy provides a second filtering trait that excludes some dung beetle species from secondary seed dispersal, because kleptocoprids and endocoprids do not relocate dung from the original deposition site. Then, dung burial amount, distance and rate may determine the amount of seeds buried; whereas the quality of the final seed location, is more influenced by the active removal of seeds before burial (Andresen & Levey 2004), burrow depth, ramification and antimicrobial substances in the dung ball (preventing fungi proliferation). When the measurement of these performance traits is difficult, some morphological traits may serve as proxies. Body size, protibia and metatibia shape and size can help inferring the potential role of individuals in seed dispersal: Large nocturnal beetles have already been related to high rates of secondary seed burial (Andresen 2002; Slade et al. 2007), although some of these seeds may end up being buried too deeply, as larger beetles dig deeper burrows (Gregory et al. 2015) making seedling emergence more difficult (Andresen & Levey 2004; Koike et al. 2012). However, these seeds that end up too deep to emerge (Koike et al. 2012) may enter the seed bank and emerge when the conditions of depth, humidity and temperature are more adequate. Indeed, soil relocation from deep layers to the surface by paracoprids and telecoprids (in the same manner any other burrowing animal would do) may help rising some seeds from the deeper layers of the seed bank to more appropriate conditions for their germination and/or emergence.

Use

The study of dung beetle traits related to seed dispersal may be particularly interesting to understand vegetation dynamics and habitat regeneration (Andresen & Feer 2005) under high or moderate herbivore pressure. Indeed, this dung beetle function may significantly interact with the performance of herbivore and frugivore vertebrates such as monkeys or bears as seed dispersers (Koike et al. 2012).

Regulation of other dung-based organisms

Dung beetle feeding and reproductive activity changes dung conditions, affecting the development of other organisms inhabiting, feeding on or reproducing in the excrement. Moreover, excrement manipulation by dung beetles very often leads directly to the destruction of eggs and immature stages of these other organisms, and the removal of dung entails an unbalanced competition for trophic resource

(Nichols et al. 2008). All these processes provide dung beetles with a major role in controlling the populations of many organisms.

Traits affecting

Each one of the three processes mentioned above are driven by different dung beetle traits, although some of them may overlap. Dung conditions are diversely altered by different dung relocation strategies. Therefore, each strategy exerts a different effect on the organisms living within the dung. Telecoprids remove a portion of dung and roll it away, leaving the rest of the dung pat undisturbed, whereas endocoprids feed and reproduce within the dung, thus altering its structure and allowing air, light and arthropod predators (such as Histeridae or Staphyllinidae species) to enter the dung pat more easily even after the superficial crust is formed. These effects of endocoprids will be more important at high densities of beetle individuals per pat, eventually destroying it completely. It follows, that gregarism may have important effects on the biological control services provided by dung beetles, disaggregation of the pat often occurs in this situation, leaving (in the case of herbivore dung) a widespread mass of vegetation fibers, several times larger than the initial dung pat area.

Indeed, the indirect destruction of eggs and immature stages of dung-based organisms is more likely to be driven by endocoprids, as they spend more time within the dung pat. However, larger dung beetles which are usually paracoprids or telecoprids may also be more effective in processing the dung. Here, competition for the common trophic resource dung is driven by the amount of dung needed by each individual to feed or reproduce. Thus, body size and dung burial amount are meaningful traits in this process. Further, hairiness and large body size may also increase chances of passive transport of mites which are known predators of flies.

Colonization period can also have an important effect on biological control. Early dung beetle colonizers arrive at the early stages of development of other dung based organisms, which are normally extremely early colonizers too. Therefore, their effect may be stronger than late dung beetle colonizers. These arrive at more mature stages of development of dung-dwelling organisms and perform a softer manipulation of the dung pat, which is often drier and might even have a superficial crust, making its destruction more difficult. This degradation of dung pat conditions might be a reason why telecoprids, which need to remove a relatively large portion of dung, are normally early colonizers so they can profit from fresher and easier to manipulate excrement.

Use

Dung-dwelling organisms are commonly related to livestock and human diseases, thus making biological control a key dung beetle ecosystem service. Flies that feed on mammal blood and enteric parasites (such nematodes, protozoa or helminths) present challenging health and economic issues. Therefore, their control should be an integral part of medical and veterinary governmental policies, and extreme outbreaks of these organisms become action priorities for local administrations. It follows that our understanding of the effects of livestock intensification and the management of pasturelands within inhabited rural areas will benefit from an in-depth characterization of the interaction between dung beetles and other dung-bdwelling organism, as well as the influence of traits on the regulating effects of dung beetles.

Dung beetle regulation of parasite transmission

Dung beetles interact with a wide diversity of parasitic species with fecal-oral transmission through the consumption, manipulation and relocation of vertebrate feces during feeding and reproduction. Some dung beetle~parasite interactions suppress the probability of successful parasite survival and transmission (i.e. direct and indirect mechanical interference) while other dung beetle~parasite interactions maintain or amplify successful transmission (i.e. indirect mechanical facilitation, direct biological facilitation and direct transport facilitation; Nichols & Gomez 2014).

Traits affecting

The outcome of a given dung beetle~parasite interaction is strongly influenced by dung relocation strategy, body size and immune function. For example, direct mechanical interference occurs when dung beetles directly damage and kill parasite eggs during feeding and nesting activities (Miller et al. 1961), including during passage through the beetles' masticatory and gastrointestinal systems (Mathison & Ditrich 1999; Ryan et al. 2011). Such direct mechanical effects may be most common for larger bodied dung beetles, which are capable of consuming relatively larger food particles (Holter et al. 2002; Holter 2016). Indirect mechanical interference occurs when dung beetles damage and kill parasite eggs and larvae indirectly, by altering abiotic conditions in fecal pats in ways that are unsuitable for parasite development or survival (Mfitilodze & Hutchinson 1988; Stromberg 1997). Endocoprid beetle activity appears to have a particularly strong impact on dung pat microclimate (see above), and may be associated with both positive and negative influences on parasite emergence rates over time (Chirico et al. 2003; Sands & Wall 2016).

In contrast, dung beetles also facilitate parasite survival and transmission rates through indirect mechanical, direct biological and direct transport mechanisms. While little empirical evidence supports this, the shallow burial of infected feces by small-bodied paracoprid and telocoprid species may theoretically enhance parasite survival and development within the soil, by creating an oxygenated environment that is buffered from both solar radiation and temperature extremes (Bryan 1976; Houston et al. 1984; Chirico et al. 2003; Coldham 2011). Dung beetles may additionally maintain infection in wild vertebrates by acting as intermediate hosts for parasites with indirect life-cycles (Anderson 2000). These wildlife parasites have a life cycle that requires the sequential ingestion, infection and development within the adult beetle followed by consumption of infected beetles by the definitive host (Gottlieb et al. 2011; Du Toit et al. 2012). Infection intensity and prevalence varies widely across beetle genera, with greater infection intensity biased towards larger-bodied species (Gregory et al. 2015). These differences in infection patterns likely stem from a combination of exposure to infection (e.g. diet breadth, and feeding volume, which may positively scale with body size) and infection susceptibility (i.e. immune function). Finally, dung beetles may positively contribute to parasite transmission success by transporting parasite eggs or larvae on beetle exoskeletons or within their gastrointestinal systems. While empirical data on this relationship is scarce, larger-bodied beetles may have a higher capacity for such transport activities.

Use

Dung beetle-mediated parasite transmission suppression may have positive public health and veterinary impacts by reducing environmental reservoirs of viable soil-transmitted helminth (STH) eggs and helminths of veterinary importance. Similarly, interactions between dung beetles and parasites that maintain infection rates in wild animals also play a key role in the maintenance of ecosystem structure and function, and evolutionary processes in wild animals.

Other effects

Although anecdotal at a global scale, dung beetles may deliver an important function in certain ecosystems by pollinating flowers and actively regulating populations of free-living organisms, beyond their role in the regulation of dung-based organisms.

Pollination

Dung beetles are the most important, and often obligate, pollinators of decay-scented flowers from a number of species of the Araceae and Lowiaceae families (Sakai & Inoue 1999). This pollination requires a mutualistic adaptation process of dung beetle traits. Certain volatile detection ability is required by dung beetles for the pollination of decay-scented flowers. But other flowers with no decay-scent are also pollinated by dung beetles. In these cases, other traits such as body color may need to mimic that of the pollinated flowers, so that dung beetle males are attracted to the flower, as it happens with other insect groups (e.g. bees and orchids of the *Ophrys* genus). Indeed, as in other pollinators, phenological and diel activity coupling with flowers, flight ability, and traits related to pollen attachment to dung beelte bodies (cuticle texture, hairiness, etc) are likely relevant features related to their role as pollinators.

Predation

At least two cases of predation by dung beetles have been reported. *Canthon virens* predates on the leafcutter ant *Atta laevigata* (Silveira et al. 2006), with an intensity that may even be used as a biological control agent for this species (Araújo et al. 2015). Further, another Neotropical dung beetle species, *Deltochilum valgum*, has also been recorded to predate on millipedes (Larsen et al. 2009), a predation behavior that may be related to the attraction of dung beetle species to volatiles from already dead millipedes (Schmitt et al. 2004). In both cases, the clypeus of the dung beetles present shape modifications that allow using them as weapons to kill the prey. Although these cases may be anecdotal at a global scale, this function can have an important effect on prey population regulation in the ecosystems where it occurs. Future records of predation by dung beetles will probably be related to traits of specialized detection of volatiles emitted by preys, and perhaps the development of particular *weaponized* clypeus shapes (as in the case described in Silveira et al. 2006 for ants, and Larsen et al. 2009 for millipedes).

Use

Both functions are anecdotal and we do not expect that many new cases are found. Therefore, we make no specific recommendations to use these traits in any study, as probably these special behaviors are detected much earlier through observation than the study of morphology or other traits, and can be coded as presence of either pollination and predation behavior, as well as with the identity of the species or genera that are predated or pollinated.

1.5 Relationships between traits, responses and effects

To assess which dung beetle traits and functions have been most studied, we conducted a literature survey and two specific workshops in the dung beetle research groups at the University of Pretoria (South Africa) and the Universidad Autónoma del Estado de Hidalgo (Mexico), and complemented the survey with several personal communications with other dung beetle researchers. Further, we used the information in these surveys to identify the known relationships between traits, responses, and effects, as a proxy for the relevance of each trait and function. Our review produced a total of 96 trait~response and 97 trait~effect relationships, respectively (Table A.1 and Table A.2 in Appendices). Based on this information and our knowledge of dung beetle ecology, we constructed a tripartite network that describes the relationships between the main groups of traits, responses, and effects, using the number of traits involved in each relationship (Table 1.2) to characterize the strength of such relationship. Perhaps the most striking result of this literature survey is the high interconnection between traits and functions; almost all responses and effects are mediated by traits of at least five out of the six categories we studied (Figure 1.2).

Among environmental factors, competition for dung, relative humidity and temperature are the drivers that involve the documented responses of more traits (Figure 1.2). The large number of traits involved in these responses may be related to importance of these three environmental factors for essential biological processes and may produce an organismic response. Indeed, many of these traits are reproductive and, in the case of humidity and temperature, physiological traits. Here, soil appears to exert also some influence on trait-mediated reproductive responses, while relative humidity also produces responses in several feeding traits. These three groups of traits seem to be under strong pressure from several

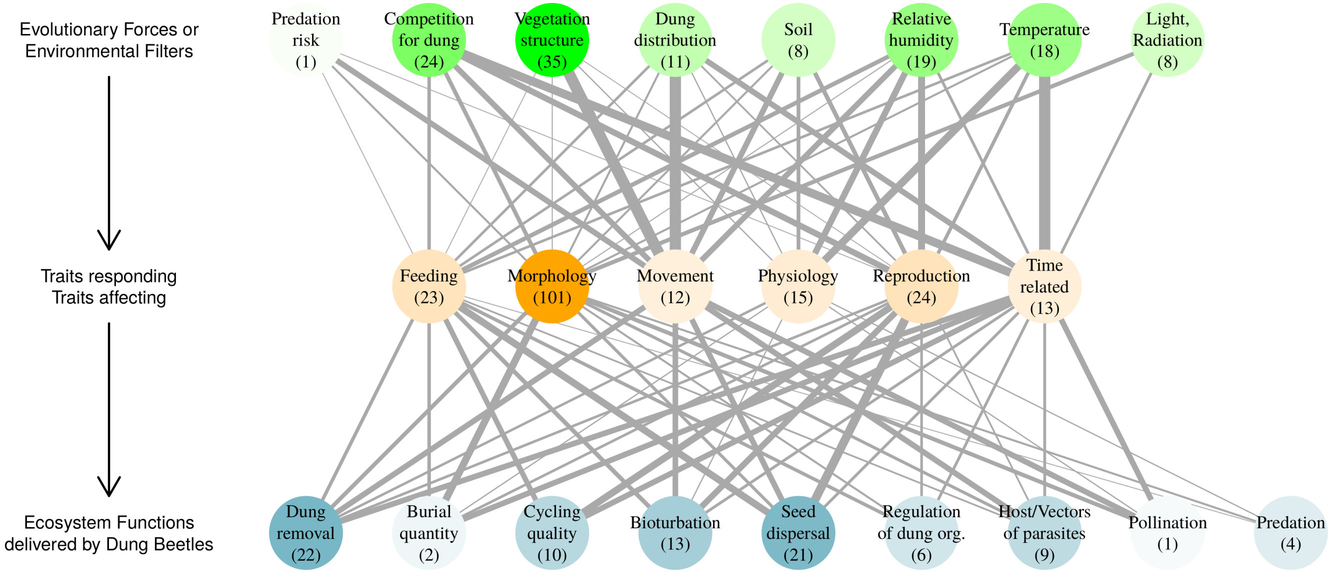


Figure 1.2: Representation of how dung beetle traits *may* respond to evolutionary forces and/or environmental filters and how these same traits *may* allow dung beetles to deliver ecosystem functions. Line widths represent number of traits involved in the link (see Table 1.2). There are three types of nodes: 1) *Evolutionary forces or Environmental filters* (hereon called *forces*), 2) Groups of traits (hereon called *traits*) and 3) *Ecosystem Functions* (hereon called *functions*). Node labels include in brackets the number of publications studying each force, trait or function. Color intensity of nodes represents the number of publications in brackets standardized (0-1) among each type of node (i.e. forces, traits or functions). That is, the node with most publications in each type of node (*veg.struct* in forces, *morphology* in traits and *dung.rem* in functions) take the darkest colors and the rest of nodes take lighter colors according to the publication support.

environmental factors, which makes trait selection and evolution along environmental gradients a complex intertwined phenomenon that poses a challenge to dung beetle ecologists. In contrast, only a few morphological traits are involved in the responses to each of these environmental gradients, thus simplifying the study of their responses. Nonetheless, while vegetation cover has been the most extensively studied environmental stressor, it seems to exert a widespread influence only on movement-related traits (Figure 1.2), so we may be relatively near to reaching a comprehensive understanding of dung beetle responses to habitat change.

With regard to effects, the groups of traits with greatest number of connections are Feeding and Reproduction (Figure 1.2). If we assume that the amount of traits documented to deliver ecological functions can be used as a proxy for which biological processes most affect the ecosystem, this indicates that dung burial is the dung beetle activity with the highest ecological impact. First, during this action they relocate dung (which is, in fact, a large piece of nutrient-rich organic matter) into a more suitable compartment for decomposition. This promotes a high diversity of macro- and microdecomposers that will thrive in the stable and appropriate underground conditions. Further, this allows secondary seed dispersal, where seeds that have passed through mammal digestive systems are buried together with a nutrient-rich substrate. Further, the associated tunneling and soil aeration makes dung beetles ecosystem engineers, playing a significant role in bioturbation. This view is supported by the extensive literature on dung beetle ecology, where most connected functions are secondary seed dispersal, nutrient cycling quality, dung burial quantity and bioturbation. However, very few articles have been devoted to study other dung beetle functions (Figure 1.2). Therefore, we cannot rule out that this result may be, in part, the outcome of the insufficient knowledge on the relationships between traits related to feeding mode and serving as hosts/vectors of parasites, and other ecosystem functions.

1.6 Discussion

Current knowledge on the ecology of dung beetles provides a solid foundation for the development of a trait-based approach to their functional ecology. We have identified ca. 60 traits that have been already measured and related to at least one ecological function (Table 1.1). In fact, there is a fairly good level of knowledge of their behavior (e.g. Halffter & Edmonds 1982), population and community ecology (e.g. Hanski & Cambefort 1991), and evolution (e.g. Scholtz et al.

2009), as well as of the evolutionary ecology of a number of Scarabaeinae species, including their physiology, ontogeny, development and sexual selection (see e.g. Simmons & Ridsdill-Smith 2011). In fact, the level of knowledge of certain model species, such as *Onthophagus taurus* (see e.g. Casasa et al. 2017), may allow facing the study of their functional ecology from an organismic point of view. However, our review puts into evidence that there are large gaps in the knowledge of many functional traits beyond nesting behavior and morphological characteristics. Moreover, there is a dearth of studies on most dung beetle ecological functions beside responses to vegetation structure, and perhaps a limited understanding of trait-mediated responses to the competition for dung, temperature and humidity as well as a valuable knowledge of the effects on dung removal and seed dispersal. From this review it is clear that, despite the large number of studies on dung beetle ecology, our knowledge of the functional ecology of this group is still scarce and biased towards certain traits and functions, as well as to certain taxa and regions.

This document seeks to establish the foundations of a comprehensive framework for the development of a quantitative trait-based functional ecology for dung beetles, which allows integrating the study of traits, responses and effects. Functional ecology should bare in mind the true ecological meaning of all measured variables for each taxon and system, regardless of the spatial, temporal or organizational scale. Ideally, working on functional ecology should imply measuring functions, either responses to environmental factors or effects on ecosystems. However, this poses a serious challenge for most functions, which can be at least partially circumvented through the use of trait variations as proxies for the delivery and/or efficiency of these functions. Indeed, traits have been increasingly used in dung beetle ecology over the last decades. Despite the utility of this approach, the use of particular traits has not always been accompanied by well-developed hypotheses on their functional meaning. Further, the actual significance of traits for the delivery of specific functions, whether effects or responses, has been seldom assessed, particularly in laboratory conditions. This has led to approach a *trait ecology* rather than to a true *functional ecology*. Reverting this undesirable trend in the discipline implies i) recognizing the limitations of traits as simplifications of natural variation in the ecological performance of individuals, and ii) contextualizing their use within the broader scope of a comprehensive functional ecology that relates traits with the study of their role on the individual responses to environmental gradients and the effects of these individuals on ecosystem functions.

Simplifying the complexity of the real world

Interpreting the complexity of real world necessarily means simplifying it. This implies making continuous variations discrete by placing boundaries between related phenomena to create understandable classifications. These boundaries between classes or groups are almost unavoidably arbitrary, following the mere convenience of researchers for either analytical or communication issues. We have deliberately avoided following the formulation of universal functional groups (as e.g. Doube 1990). It could be argued that the development of *ad-hoc* functional group classifications may be particularly useful for the study of specific ecological systems. Here, novel quantitative methods that allow defining functional groups in any system can provide a standardized way of assessing community structure through easy-to-interpret classifications (e.g. Carmona et al. 2016). However, although these methods can be independent to some extent from the criteria of particular researchers, the functional group classifications will depend on the total perceived variation of the system, and thus on the selection of traits and the detail at which they are measured. Due to this, the value of these classifications is limited to the system under study; extrapolations should be avoided, thus, resulting in many functional group classifications that, despite capturing the essence of continuous variation in nature, are of little use for researchers working in different systems.

Thus, direct comparison between systems should be done through the quantification of trait data (or function data) at the individual level. That said, we must note that this fundamental limitation of classifications applies to all levels of classification, from categorical trait values or the identification of (sub)traits, to the classification of traits between cause and effects in environment~trait and trait~function relations. The limits between all these classes are naturally fuzzy. Further, the definitions of what we call *trait* and what we call *function* are unavoidably imperfect.

At the most basic level, some traits are commonly assigned categorical values. This may reflect a natural break between two reproductive modes (endocoprids vs. telecoprids) or between two diet preferences (coprophages vs. necrophages). In a given instant, there is no possible intermediate between these. There are, however, species that perform two (or more) of these modes in different reproductive/feeding events, thus researchers call them *facultative endocoprids* or *facultative necrophages*. When possible, this information should be stored in a quantitative way, recording the observed frequency of each class (e.g. 90% coprophagous and 10% necrophagous diet), although such frequencies are likely to be context-dependent. In the ideal case, where the information is available at the individual level, the count of events for each reproductive mode observed for the individual will provide a true measure of trait variation in the study conditions.

Further, there are traits with a real continuous variation that researchers try to fit into discrete categories that are easily recorded, instead of tediously measuring continuous variables. This assignment into ordinal or categorical values was the norm in the past, but current practice in functional ecology is becoming more and more quantitative. For example, while body size was merely described as either big, intermediate or small, nowadays accurate measurements can be found throughout the literature. In this document we have avoided describing trait measurements as categorical whenever possible (see Table 1.1). There are, however, several traits for which classes are still more operative than seeking to obtain continuous measurements. These include: Glossiness/iridescence, Soil relocation, Covering burrow walls with dung, Feeding mechanism, Presence of antimicrobial substances in brood masses, Active removal of seeds from buried dung, and some others. These are mostly traits for which no quantitative work has been done to date, and we can hardly imagine either the methods or the benefits of having continuous data for them. That said, we must encourage researchers to quantitatively measure as many traits as possible. This may be particularly important when the focus of the research is on the functions performed by these traits, such as, e.g., in the expression of glossiness/iridiscence as a response to solar radiation.

Another aspect of the classification of traits is whether some of the traits that are commonly measured (and that we include in Table 1.1) can be considered subtraits of or proxies for other more general and/or difficult-to-measure traits that hold a more direct functional significance (i.e. hard traits). This is again a problem of making arbitrary classifications out of a continuous reality. Distinguishing between hard and soft traits is indeed complex and potentially misleading, for all trait measurements are in fact soft traits used as proxies to estimate an ecological process. To decide which traits to select, and which to leave aside, in this document we have considered, first, whether they are mere measurements that help calculate the really ecologically meaningful traits, but also if there is a practical way of measuring the functionally most significant trait. When the latter traits were difficult and/or impractical to measure we have included the soft trait on our list.

Nonetheless, there is a more interesting point to make. Traits are not isolated entities but features of a single individual. This means that values of traits of the same individual are necessarily correlated, because they are part of the organism's integrated phenotype. Therefore, not all combinations of trait values are possible, as general constraints apply to groups of traits that covary to some extent. This means that, in a certain population or region, the traits shown by the individuals of a given species can be highly correlated with each other following some apparently universal rule. This might not be the case when several species are considered (e.g. within communities, or with the arrival of exotic species to the study unit), but trait covariations are to be expected for individuals subject to similar selection pressures and pertaining to phylogenetically-related species. Indeed, this level of covariation can be influenced by the detail at which traits are measured, and which traits are actually measured and/or selected for analyses. The more important intraspecific variation is for the questions tackled, the more important it becomes to perform detailed measurements and assess trait variation.

The classification of traits into groups of similar functional meaning is also subject to the limitations of categorizing complex natural variations. Many traits may be included in two or more groups (e.g. ingested particle size in either feeding or morphology). Also, some groups may lack cohesion, such as time-related traits, which span across several scales. Some groups may even be used as proxies for other groups; for example, morphology as a proxy for the more difficult-to-measure physiology. Again, traits are not isolated entities, they are part of an individual that performs all its biological processes with a finite number of traits. It follows that, most if not all, traits perform and/or participate in several of those processes. A good example is given by prothorax volume, a single and very specific morphological trait that is a proxy for muscle volume (morphological) which is related to walking (movement), and also involved in dung and soil manipulation during burial (feeding and reproduction), as well as in temperature regulation via heat production and dissipation (physiological). A practical consequence of this complexity is that trait assignation into categories should be fuzzy, allowing each trait to be included in different classes.

Disentangling the environmental forces causing trait-mediated responses from the effects of these responses to the functional activity of individuals may also be difficult. The limits between variables taken as causes and those taken as effects are sometimes fuzzy. Most functions are delivered as a complex result of the synergy between several traits. Similarly, the response of an individual to an environmental force is generally an organism-wide response, which implies responding with modifications in several traits at the same time (especially those traits that are tightly related). This unavoidably results in a cascade of effects that may, and often does change the functional effects of the individuals. A couple of examples may illustrate how these organismic response/effect clusters operate (see Figure 1.2). Climate change-driven increases in environmental temperature may cause the responses of multiple physiological, time-related and feeding/reproduction traits, for individuals can modify their metabolism, become crepuscular or nocturnal to avoid the hottest time of the day, change their phenology to avoid the hottest days of the season, or dig deeper burrows to avoid the effects of extreme surface temperatures on larval development. This has obvious consequences on the functions delivered by these individuals, from *when* they deliver them, to their effects on soil aeration and the depth at which they bury the seeds embedded in the excrement. Another example is given by the ecosystem function of being hosts and/or vectors, which is delivered thanks to a variety of traits regarded as feeding (feeding mechanism and ingested particle size determine which parasites can use the host/vector), reproduction (burrow depth and, more importantly, antimicrobials in brood masses may inhibit parasites using individuals/species as hosts/vectors), morphological (size and external surfaces determine suitability as hosts/vectors) and even time related (colonization moment determines possibility of interacting with the right infective phase of parasites), and movement (a key feature of vectors) traits. This evidences the complexity of the functional responses and effects induced by environmental and biotic stressors. Indeed, it calls for an integrative study of traits and functions in which both responses and effects are considered altogether, using trait variations at the individual level as the connecting link between them.

1.7 Concluding remarks

We hope this document establishes foundations on which to build a solid quantitative trait-based functional ecology for dung beetles. Functional ecology regardless of spatial, temporal, or organizational scale should bear in mind the meaning of all measured variables in their taxa and system. Ideally, working on functional ecology should imply measuring functions (response to environmental factors or effects on ecosystems). However, this is seriously challenging in most cases. The use of traits as proxies for functions makes it much easier. In the last decades, the use of traits of dung beetles has spread over the ecological literature to better understand distributional patterns of dung beetles, giving birth to the new discipline of functional ecology. It seems that the original aim of *functional ecology* is sometimes forgotten and another kind of ecology is done, i.e. *trait ecology*.

This document summarizes the traits that have been most used to date in the literature on dung beetle ecology. But further, we add several new traits that, altogether, provide a comprehensive framework for a trait-based dung beetle functional ecology. This framework allows hypothesizing the relationships between traits and both the environmental factors to which they respond, and the ecosystem functions they might deliver. However, many of these relationships are speculative, as there is a dearth of literature on the effects of traits on the functional performance of dung beetles. Thus, there is a strong need to experimentally test each of these speculative hypotheses and transform them into already-evaluated knowledge, building up the theoretical body of the future trait-based dung beetle functional ecology. These problems are not exclusive of dung beetles (see e.g. Moretti et al. 2017), so we encourage experts in other groups to do a similar exercise, designing specific frameworks that match the ecological roles and characteristics played by their taxa of interest.

We believe that the framework we provide has the potential to constitute a cornerstone in the understanding of the ecological role played by dung beetles. Functional ecology comprises a wide scope of spatial, temporal and organizational scales. From very localized to planetary, from static patterns of diversity to macroevolutionary ecology and from trait heritability along lineages to regional pools of species. A comprehensive framework for the study of dung beetle traits should be useful for these three dimensions and all the relevant scales. However, in this document there might be a bias towards regional spatial scales, yearly temporal scales, and community scale in terms of organization, mainly due to the orientation of the authors' research interests. We encourage ecologists working in smaller (sexual selection, population biology, etc.) or larger scales (biogeography, macroevolution, etc.) to help complete a potential extended version of this framework.

On a more general perspective, the development of functional ecology is key to understanding the effects of global change on ecosystem service delivery. The knowledge on these services is limited and biased for all insect groups, being commonly based on proxies and empirical field studies (Noriega et al. 2018). We therefore encourage ecologists and land managers to bear in mind the available information on traits and their meaning as proxies, but also the quality of such information, and the eventual existence of experimental evidence for the functional significance of each trait. If the aim is to assess changes in the functionality provided by any particular group, traits should not be used without a clear idea of their functional meaning, including their relationship with environmental factors and/or their effects on ecosystem functioning. For this purpose, dung beetle researchers should include functional traits in their analyses on community structure and ecosystem functioning, but also progressively test their response to environmental factors and their effect on ecosystem functions. Only through this slow and tedious, but also thorough, process will dung beetle functional ecology reach the high levels of understanding that are now being reached by plant ecologists. The framework presented here may constitute a platform where to place all such information in an ordered way, allowing to both identify gaps in knowledge and construct a solid body of theory for the ecology and evolutionary biology of dung beetles.

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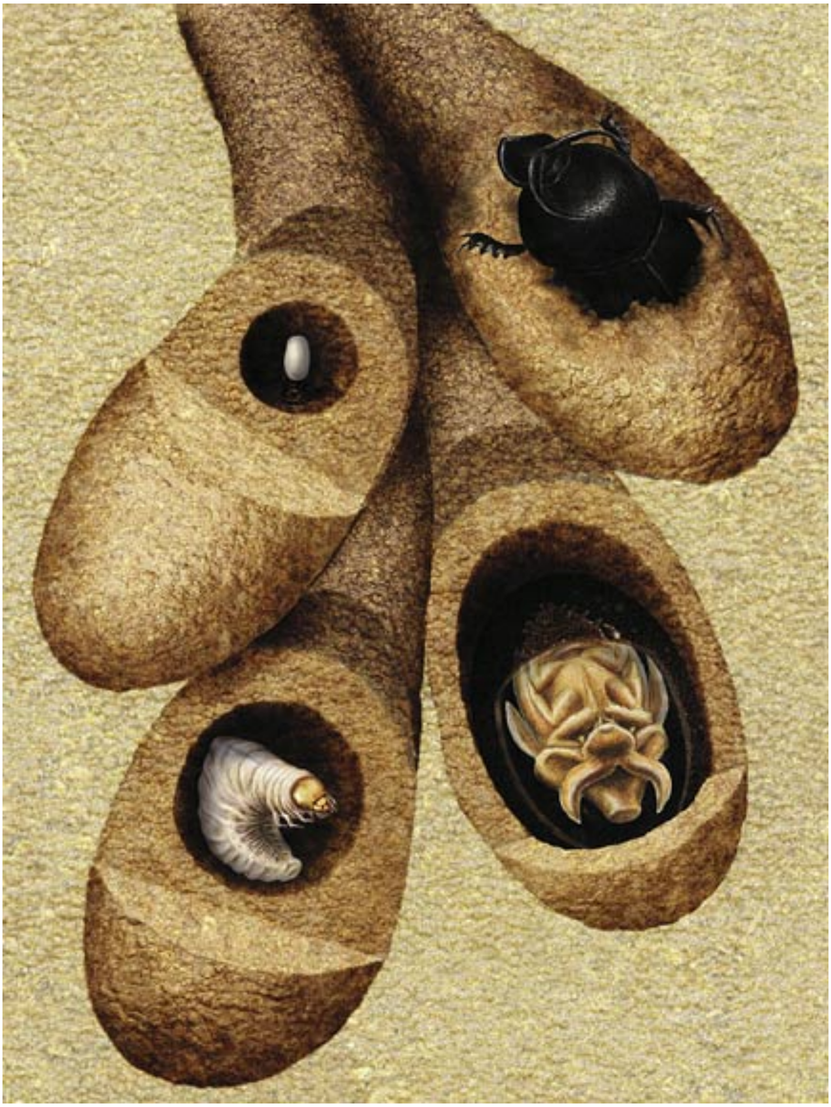

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2 Assessing the functional relationship between dung removal, burial and seedling emergence and dung beetle traits

2.1 Introduction

Understanding the role of biological diversity in ecosystem functioning is a major endeavor of ecology in the current scenario of global change and high biodiversity loss (Hooper et al. 2005). In recent decades, functional diversity has been increasingly included in studies on ecology, evolution, and conservation (Noriega et al. 2018). Functional diversity relies on the value and range of traits of species and individuals that influence ecosystem functioning (Tilman 2001), and requires the measurement of ecologically meaningful traits (Petchey & Gaston 2006). Although some researchers have opted to measure simple functions directly avoiding the use of traits (Gollan et al. 2013), most have measured traits as proxies for functions (Violle et al. 2007). Whereas in some studies groups of traits have been used to analyze whether functional diversity is related to a given function (Griffiths et al. 2015; Griffiths et al. 2016) but without testing the relationship between the selected traits and function. However, it is essential to bear in mind that in these latter cases the trait~function relationship is only a working hypothesis. To confidently use a selection of traits as proxies for some functions of interest it is necessary to test if these function~trait(s) relationships actually exist (Mlambo 2014; Nervo et al. 2014) and the extent to which these relationships apply throughout all the individuals performing these functions.

Decomposition of organic matter is a key ecological process, essential for both carbon and nitrogen cycles (Swift et al. 1979; Bardgett 2005; Nervo et al. 2017). Herbivore dung is a nitrogen-rich form of organic matter dropped on the soil surface, where decomposition can be slow. The relocation of organic matter from the surface into deeper layers of the soil usually enhances decomposition, as decomposing organisms very often require humidity (but see Gliksman et al. 2016), stable conditions and darkness. Moreover, herbivore dung also contains variable amounts of viable seeds. That is, seeds that have survived herbivore digestion and are still able to germinate (Wessels & Schwabe 2008) if conditions are favorable (Wicklow & Zak 1983; Chambers & MacMahon 1994). Dung beetles play an essential role in the degradation and relocation of herbivore dung, as well as in secondary seed dispersal by relocating seeds found in the dung, preventing surface predation by rodents, ants and other organisms (Shepherd & Chapman 1998; McConkey 2005; Beaune et al. 2012; Nichols et al. 2008). These functions can ultimately affect plant populations, vegetation and community dynamics (Andresen 2003; Verdú et al. 2009; Griffiths et al. 2016).

Dung beetles of the superfamily Scarabaeoidea (mainly Geotrupidae, Scarabaeinae and Aphodiinae) are a highly diverse and widely distributed group (Scholtz et al. 2009) that exploits faeces, mainly from large herbivores (Hanski & Cambefort 1991; Scholtz et al. 2009). According to their feeding and/or nesting behavior, three main dung beetle functional groups have been traditionally established (Hanski & Cambefort 1991): endocoprids (dung dwellers), which feed and nest directly in the dung pat; paracoprids (tunnelers), which bury the dung in the soil below the dung pat; and telecoprids (rollers), which construct and roll away dung balls, burying them at some distance from the dung pat. These different food/nest-provisioning relocation strategies are a likely consequence of intense competition in dung beetle communities, and determine where dung, and the seeds embedded in it, are relocated.

Because of their different strategies to exploit the dung, dung degradation may be due to direct consumption of the dung pat (carried out mainly by endocoprids, but telecoprids and paracoprids in many instances also feed directly on the dung pat) or due to dung pat disaggregation on the ground surface (Verdú et al. 2018). In addition, paracoprid and telecoprid beetles bury dung masses for feeding and nest-provisioning at different depths in the soil depending on species and environmental conditions (Halffter & Edmonds 1982; Sowig 1995; 1996; Macagno et al. 2016). In addition, seeds contained in the dung are also dispersed by the activity of dung beetles, potentially favoring seed germination and emergence by soil bioturbation, dung disaggregation, and dung burial, providing more favorable microhabitats and reducing seed predation (Feer 1999; Culot et al. 2011; Beaune et al. 2012; Griffiths et al. 2015). In contrast, dung burial at some depths has been reported to negatively affect seed emergence (Andresen & Levey 2004; D'hondt & Hoffmann 2011; Griffiths et al. 2016).

Several morphological features have been traditionally regarded as adaptations of dung beetles to coprophagy and, especially, dung burial (Halffter & Matthews 1966; Edmonds 1972; Halffter & Edmonds 1982): stronger and toothed front tibiae for scrapping and moving soil, increase of dorsal surface area of the head to work like a shovel, enlargement of prothorax to accommodate the increase in muscle tissue responsible for head and foreleg movement for dung manipulation and digging. In addition, short and stout hind tibiae would provide higher traction during excavation and help in dirt removal (Martín-Piera 2000). In telecoprids, these adaptations are considered as much less pronounced in return for specializations in ball construction and rolling (Halffter & Edmonds 1982). Also, hind legs increase in length and curvature, forming an elliptical form better suited for ball construction and enhancing pulling of balls (Martín-Piera 2000). Finally, some general traits, such as body shape and size, are also considered as important functional traits in dung beetles. Thus, an elongated body shape has been also related to poor burrowing capabilities (Halffter & Edmonds 1982). Further, another trait usually considered as an important factor structuring dung beetle assemblages is body size or body mass (Doube 1991; Hernández et al. 2011; Piccini et al. 2018). Diverse measures related to the abovementioned traits have been recently used to analyze the functional structure of assemblages based on morphology (Inward et al. 2011) and to analyze the relationship of functional diversity with ecosystem functions (Griffiths et al. 2015; Griffiths et al. 2016).

Few papers have experimentally analyzed the relationship of these morphological traits with the performance of their ecological functions (i.e. dung removal and dung burial). Nervo et al. (2014) experimentally demonstrated that body mass is related to a higher dung removal efficiency. Also, the shape of protibiae has been experimentally shown to be related to differences in dung burial depth among populations of *Onthophagus taurus* and *O. illyricus* (Macagno et al. 2016). Similarly, although several observational and experimental works have been carried out to uncover the role of dung beetles as secondary seed dispersers (Feer 1999; Laverde et al. 2002; D'hondt et al. 2008; Culot et al. 2011; Iannuzzi et al. 2013; Griffiths et al. 2015), few studies have analyzed the effect of dung beetle activity, such as dung burial and burial depth, on seedling emergence (Andresen & Levey 2004; D'hondt et al. 2008; Griffiths et al. 2016).

In this study we experimentally evaluate the relationships between the outcome of two ecosystem functions delivered by dung beetles (dung removal and dung burial) and morphological traits regarded as being related to these functional outcomes in dung beetles. Also, we analyzed the outcome of a third function, secondary seed dispersal, by looking at the effects of dung removal, dung burial and depth of buried dung on seedling emergence. To do this, we set up a mesocosm laboratory experiment with sexual pairs (the minimal functionally meaningful unit in dung beetles) of nine species (three endocoprids, four paracoprids and two telecoprids) provided with sheep dung containing a controlled set of seeds. Sixteen simple morphological traits related to head, prothorax, fore and hind legs, as well as total body length, weight and volume were selected as measurements of the morphological features regarded as associated to dung removal and dung burial. Specifically, we aim to answer the following questions: 1) Are morphological traits regarded as adaptations for dung processing and digging actually related to the functional outcomes of dung removal and dung burial?; 2) Which traits can be used as effective, simple functional proxies for these functions?; 3) Is relocation behavior also an explanatory variable related to the functional outcome, i.e. the amount of dung removed and buried?; and 4) Do dung beetles enhance seedling emergence through their activity on dung removal and dung burial?

2.2 Materials and methods

Collection of dung beetles

We collected 8-10 pairs of ten species including endocoprid (*Acrossus luridus*, *Aphodius foetidus*, *Euorodalus tersus*), paracoprid (*Bubas bubalus*,*Onitis ion*, *Onthophagus vacca*, *O. vacca*, *O. ruficapillus*) and telecoprid dung beetles (*Scarabaeus sacer*, *S. puncticollis*) and ranging in size from the smallest (*E. tersus*, 3.4-3.7 mm body length) to the largest (*S. sacer*, 22.0-29.0 mm body length) species inhabiting arid areas of SE Iberian Peninsula. Dung beetles were collected by means of dung baited pitfall traps and hand collecting from natural dung pads in the Guadix-Baza Basin (Granada, Spain) during April 2015. In this experiment, *Onthophagus merdarius*, a dominant species in the area in the 1990s (Sánchez-Piñero & Ávila 2004; González-Megías & Sánchez-Piñero 2003) could not be used because of the very low number of individuals collected, as a consequence of livestock breeding abandonment in the region (F. Sánchez-Piñero and E. Murciano, unpublished data). Instead, we used pairs of *O. vacca*, a species similar in size, which was abundant in one of the sites surveyed. After collection, beetles were sexed and kept for 1-3 days in laboratory conditions until placed in the mesocosms.

Seeds and dung preparation

In order to test whether dung beetle activity affected seedling emergence, we used dung containing seeds of three plant species: *Hordeum vulgare*, *Anthyllis cytisoides*, and *Cistus albidus*. Seeds of these plant species were selected because: 1) they are able to grow in the pH 7 soil used in the experiment (see below); 2) are edible by sheep; 3) differ in size (ca. 6 mm, 2 mm and 0.5 mm for *H. vulgare*, *A. cytisoides* and *C. albidus*, respectively); and 4) pertain to different families (Poaceae, Fabaceae and Cistaceae, respectively), with broadly different dispersal/reproductive strategies (endozoochory, barochory and pyrophyte, respectively). In addition, the seeds used in the experiment are also commercially available, as they are commonly used for land restoration, which ensured the availability of seeds for the experiment.

To obtain dung containing seeds of the above plant species, we were allowed to supplement the diet of 21 housed sheep with the seeds at Finca los Morales (part of Rodríguez-Peñalva Foundation, Granada, Spain), a research center devoted to the preservation and development of the local *Segureña* sheep breed adapted to semiarid conditions. Sheep feeding and sanitary conditions at Finca los Morales are strictly organic, and veterinary medical products, such as ivermectin, were administered to sheep 6 months before dung was collected. We fed the 21 sheep with 1.5 kg of *A. cytisoides* and 1 kg of *C. albidus* seeds mixed with their typical diet including *Hordeum* grain (ca. 10 kg) for 2 consecutive days. We checked germination success of seeds before passing through sheep gut, as some seeds used for animal feeding are UV treated to prevent germination when stored for long periods of time.

Dung produced by the sheep after being fed with the mixture of seeds was hand collected during three days to ensure we collected most of the seeds (Ramos-Font et al. 2015). Dung contained an average 19.00 ± 4.44 *H. vulgare*, 49.50 ± 9.84 *A. cytisoides* and 273.10 ± 17.27 *C. albidus* seeds per 50 grams of dung. To prevent dung desiccation and preserve it in adequate conditions for the experiment, dung was stored in sealed buckets in a refrigerator at a mild 10°C (to prevent seed damage). Since part of the dung produced by the sheep were small pellets, we added some water to homogenize the dung used in the experiment. We also checked germination viability of seeds after passing through sheep gut.

Experimental design

A mesocosm experiment was performed during April and May 2015 in laboratory conditions with constant temperature 22.68 ± 0.98°C and humidity conditions 58.02 ± 8.98%, and natural light regime. A total of 108 mesocosms were built with flowering pots 28 cm diameter x 30 cm height to which we cut the base to allow plunger-like extraction of the soil after the experiment. We filled and slightly compacted each pot with sieved pH 7 organic-farming soil up to 25 cm height. Surface of the soil in each mesocosm was smoothly levelled to allow detection of dung beetle galleries and clean retrieval of dung remains after the experiment. Each mesocosm was closed with a 1 mm mesh to prevent dung beetles from escaping.

In each mesocosm we placed exactly 100 g of fresh dung and a sexual pair of dung beetles, except for 10 pots used as control to measure seedling emergence in the absence of beetle activity. We used sexual pairs because dung removal and dung burial are largely performed by nesting pairs. All pots were closed with mesh after beetles were introduced. After 7 days the dung was dry and we assumed that no feeding or reproduction had taken place (Ryan et al. 2011; González-Megías and Sánchez-Piñero, pers. obs.) and dung beetles were retrieved by careful inspection of the soil surface for beetles trying to leave mesocosms. Beetles were individually preserved in ethanol to ensure the match between measured traits on dung beetles and measured functions in each mesocosm. Mesocosms in which dung beetles remained inactive (e.g. buried just near the walls of the pot or walking encircling the pot without using the dung) were not considered in the analyses. Thus, we discarded 29 out of the 98 pairs of beetles placed in mesocosms. Ten of these mesocosms corresponded to *Onitis ion*, as none of the pairs buried dung (see also González-Megías & Sánchez-Piñero 2003) and barely removed any dung from the dung pad. Thus, our final data comprise a total of nine species (after removal of *Onitis ion*) and 69 mesocosms. In addition, since it was not possible to accurately measure the depth of buried dung in seven mesocosms (due to burrow collapsing or to the fact that the beetles ate all the buried dung), the number of mesocosms used to analyse seedling emergence was 62.

After dung beetle retrieval mesocosms were lightly watered to ensure soil moisture and allow seed germination. Emerged seedlings were identified, counted and removed every five days until the end of the experiment, 30 days from the starting date (the day dung and dung beetles were placed). We then uncovered the mesocosms, retrieved the dung remains from the soil surface and individually dried them in an oven at 80°C for three days. The soil in each mesocosm was searched sequentially in 1 cm layers and buried dung was retrieved, noting down the depth at which each individual dung mass (feeding or brood ball) was found. Dung balls were then measured in their maximum and minimum diameters, and dried following the same procedure used for surface dung remains.

Measurement of functions

We measured three functions related to dung beetle activity (see definitions in Table B.1 in Appendices): dung removal, dung burial, and seedling emergence (as a consequence of relocation of seeds, *successful seed dispersal*). Dung removal was measured as the difference between the dry weight of a 100 g dung pat (estimated from ten dung pats made with the same dung used in the mesocosms, mean dry weight 19.9 ± 0.1 g) and the dry weight of dung remaining in the soil surface. Dried dung (see above) was weighed on a precision scale (± 0.1 g).

To measure dung burial we estimated the dry weight of dung masses buried in the soil. Buried dung masses were oven dried at 80°C and weighed on a precision scale ± 0.1 mg. Length (maximum diameter) and width (minimum diameter) of buried dung masses were measured with a calliper ± 0.1 mm before drying in the oven, and their volume mm^3 estimated as an ellipsoid. Depth of buried dung was also measured considering the depth (in cm) at which the middle of each dung mass was found.

The number of emerged seedlings was visually counted in each mesocosm. Because sometimes it was difficult to distinguish among species, a conservative attitude was adopted and seedling species were pooled for data analysis, eliminating any bias due to misidentification.

Measurement of traits

We selected 16 morphological traits (see Table B.2 in Appendices) that can be related to dung beetle species performance in the three abovementioned functions. Thus, selected traits might serve as proxies for the measured functions, evaluating hypotheses on the relationship between traits and functions. Most traits were measured with image analysis tools using a Leica M165C microscope and Leica Application Suite LAS V4.0 with the Z-builder module in all dung beetle individuals used in the experiment, this is both males and females. All traits measured with image analysis tools have an accuracy of ± 0.001 mm for distances and ± 0.001 mm^2 for areas. All measurements were done on images taken perpendicularly to the distance of interest, that is, maximizing the distance or area to measure. Further, we estimated head area, pronotum volume, total body length, and body volume based on the direct measurements above (Table B.2 in Appendices). Dry weight of beetles was obtaining by weighing specimens in a precision scale (± 0.1 mg) after drying for 72 h in an oven at 70°C.

Because relevant functional aspects of dung beetle behavior may not be entirely considered with the measured morphological traits (Inward et al. 2011; Griffiths et al. 2015), we also considered the dung relocation strategy (i.e. endocoprid, paracoprid or telocoprid) of the different species based on natural history information of the species (Gonzalez-Megías 1999; González-Megías & Sánchez-Piñero 2003; González-Megías & Sánchez-Piñero 2004). For example, although *E. tersus* is a brood-parasite in nests of paracoprid beetles in arid systems of the Guadix-Baza Basin, it behaves as an endocoprid in laboratory conditions (González-Megías & Sánchez-Piñero 2003) and it is at least partially endocoprid in more mesic habitats in SW Spain (Sánchez-Piñero, pers. obs.).

Statistical analyses

To analyse the relationship between morphological traits and dung removal and burial, measurements of traits for each mesocosm corresponded to the average values of the two individuals of each pair (male and female) in a pot, since it was not possible to determine the specific contribution of each individual in dung removal and dung burial. To find the combination of morphological traits related to dung removal and dung burial, partial least squares generalized lineal regressions (PLS-GLR; Bastien et al. 2005). This method allows analysing data characterized by a large number of multicollinear predictor variables (such as morphological traits) by extracting a set of orthogonal components (or latent vectors) considering not only the structure of predictor variables (as provided by a PCA) but also their relationship with the response variable. Once the components were computed, a GLM with Gaussian function and identity link of the response variable on the PLS components was carried out in order to test for the significance of the components and the whole model. To carry out the analyses, measurements of morphological traits were log transformed. Dung removal data were square root-transformed and dung burial log10-transformed to meet assumptions of homoscedasticity and normality of model residuals. Cross-validation and Akaike Information Criterion (AIC) were used to select among models including different number of components. The weights of the different explanatory variables in each component were obtained, and variables which squared values were greater than 1/number of variables (0.063) were considered as the most important predictors of the response variable (Carrascal et al. 2009). Also, the standardized coefficients and significance of each predictor in the final PLS-GLR model were obtained by bootstrapping (1000 iterations). PLS-GLR analyses were conducted using the ℝ package `plsRglm` (Bertrand et al. 2014).

We included endocoprids (which do not bury dung) in the analysis of dung burial as *non-burial control* of traits. In the analysis we used individual mesocosms as sample unit, in order to account for both individual and species variations in traits and performance (Albert et al. 2012; Griffiths et al. 2016), as individuals of different species usually overlap in size (e.g. the largest individuals of *O. opacicollis* usually overlap with the smallest individuals of *O. vacca*).

We also analyzed the relationship between functions delivered by dung beetles (dung removal, dung burial, depth of buried dung) and seedling emergence by means of PLS-GLR, because of collinearity among predictor variables. Because seedling emergence is a count variable, a PLS-GLR model with Poisson function and log link was performed.

To find whether dung relocation strategy (i.e. endocoprid, paracoprid and telecoprid) and species also affected the three functions measured and added explanatory power to the models, we used generalized linear mixed models. We used the selected components of the PLS analysis above and dung relocation strategy (= functional group: categorical, 3 levels) as fixed effects. Functional group was included as a fixed effect since we selected species of each of the three main dung beetle functional groups. As interactions between PLS components and functional group was not significant in any analysis (not shown), these were not included in the results (Section B.0.1). Species (categorical, 9 levels) was included as a random effect since different species may not only differ behaviorally but also be affected in different ways by laboratory conditions. A Gaussian function and log link were used to model square root-transformed dung removal and log10-transformed dung burial, but a Poisson function and log link were used to model untransformed count of emerged seedlings. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. We used package `lme4` to conduct generalized lineal mixed model analyses. P-values for continuous fixed effects and levels within categorical values were obtained with `lmerTest` package. All analysis were performed in ℝ v.3.2.2. Selection of models considering Akaike information criterion AIC values and model comparison by means of ANOVA tests are shown in Section B.0.1.

Differences in seedling emergence among the control treatment and the different species were analyzed by means of a generalized lineal model (GLM) with Poisson function and log link. Due to deviations from homoscedasticity of the residuals across the predictions of the GLM, we used the heteroscedasticity-corrected coefficient covariance matrix to obtain the proper significance between the control treatment and the diverse species included in the experiment. The HC4m estimator (Cribari-Neto 2004) was used to further improve the performance in significance estimations due to departure from normality of the residuals due to the presence of influential observations under small sample sizes. The GLM analysis was carried out using the ℝ package `lme4` version 1.1-17 (Bates et al. 2015) and the HC4m estimator was used by means of the ℝ package `sandwich` (Zeileis 2004).

2.3 Results

Dung removal

The final GLMM model selected included the two PLSR components explaining 57.3% of the variability in dung removal (Table 2.2). Neither species (as a random factor) nor behavioral functional group (endocoprid, paracoprid, telecoprid; p = 0.494) provided additional explanatory power to the model (subsection B.0.1 in Appendices). The two PLSR components included in the model indicate that two groups of morphological traits conform different *trait syndromes* (Table 2.1, Figure 2.1). Most traits showed square weights higher than 0.063 (i.e. 1/number of explanatory variables) in PLSR component 1, and included variables positively related to dung removal. The majority of measured traits were included in this first component (mainly related to pronotum traits, head area and width, protibia area and size of the first tooth of the protibia, total volume, weight and total body length). The second component, in contrast, was mainly associated to a group of traits negatively related to dung removal. All these traits were associated with the length of structures used for dung manipulation and burrowing, such as head, protibia and metatibia (Table 2.1, Figure 2.1). As suggested by Figure 2.1, this second component was mainly related to the fact that the smaller species *Euorodalus tersus*, with comparatively shorter legs and head, removed more dung than expected based solely in PLSR component 1. In contrast, *Scarabaeus* species removed a proportionally smaller amount of dung.

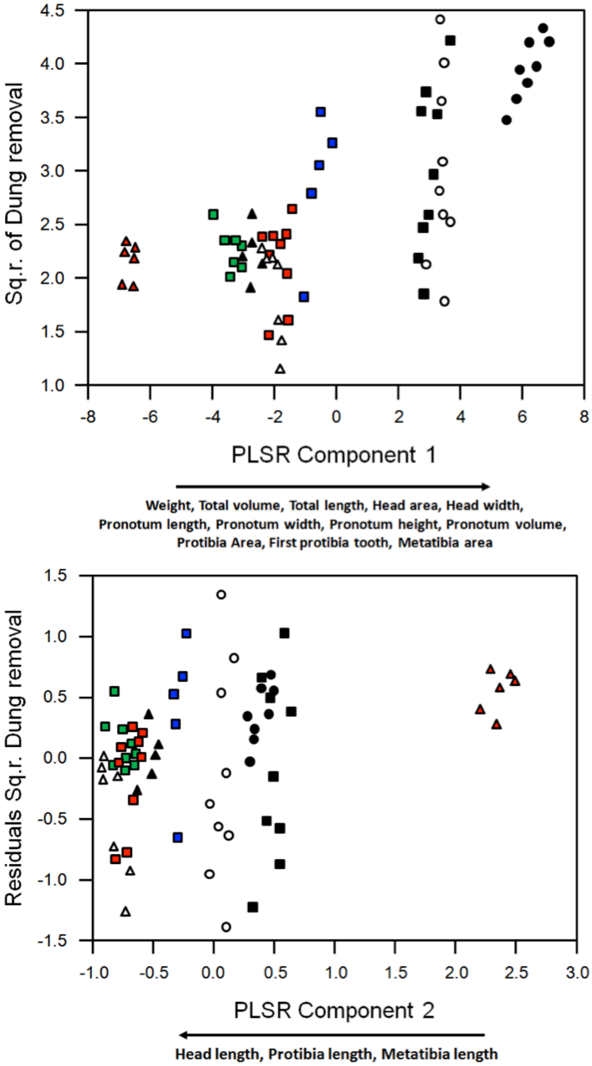


Figure 2.1: Correlations between PLSR components and dung removal by pairs of dung beetles of nine different species. Arrows below the PLSR components indicate the morphological traits related to each component and whether they are positively or negatively related to the response variable. Triangles (endocoprids): white = *Acrossus luridus*; black: *Aphodius foetidus*; red: *Euorodalus tersus*. Squares (paracoprids): green: *Onthophagus ruficapillus*; red: *O. opacicollis*; blue: *O. vacca*; black: *Bubas bubalus*. Circles (telecoprids): white: *Scarabaeus puncticollis*; black: *S. sacer*.

Variable	Standardized coefficient (Mean ± S.E.)	t	p	w Comp1	w Comp2
Head length	***-0.109 ± 0.029***	***-2.019***	***0.0003***	***0.185***	***-0.532***
Head width	***0.072 ± 0.020***	***-1.986***	***0.0007***	***0.262***	***0.063***
Head area	***0.072 ± 0.020***	***1.520***	***0.0007***	***0.262***	***0.063***
Pronotum length	***0.085 ± 0.019***	***5.604***	***<0.0001***	***0.266***	***0.100***
Pronotum width	***0.079 ± 0.009***	***4.408***	***<0.0001***	***0.265***	***0.083***
Prothorax height	***0.111 ± 0.025***	***-4.099***	***<0.0001***	***0.269***	***0.187***
Prothorax volume	***0.091 ± 0.016***	***3.874***	***<0.0001***	***0.268***	***0.123***
Protibia length	***-0.076 ± 0.019***	***2.554***	***0.0001***	***0.209***	***-0.427***
Probitia first tooth length	***0.098 ± 0.038***	***3.568***	***0.0133***	***0.260***	***0.176***
Protibia area	***0.126 ± 0.032***	***-3.818***	***0.0003***	***0.270***	***0.240***
Metatibia length (straight)	***-0.072 ± 0.036***	***3.568***	***0.0481***	***0.206***	***-0.415***
Metatibia length (curved)	-0.071 ± 0.036	4.563	0.0517	0.207	−0.411
Metatibia area	0.061 ± 0.040	8.771	0.1340	0.257	0.050
Total body length	***0.077 ± 0.026***	***3.004***	***0.0039***	***0.261***	***0.089***
Total body volume	***0.095 ± 0.015***	***6.456***	***<0.0001***	***0.268***	***0.137***
Dry weight	***0.065 ± 0.012***	***5.236***	***<0.0001***	***0.262***	***0.040***
R^2				0.518	0.573
Eigenvalues				14.82	0.79

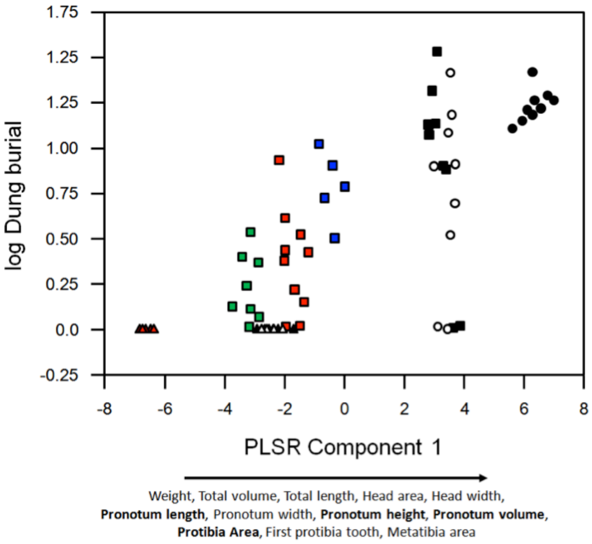
Table 2.1: Standardized coefficients (Mean ± S.E.), Student t, significance ($p < 0.05$) and weights of the different components of the PLSR model for the explanatory variables (log transformed) on dung removal (square root transformed). PLSR weights whose squares are > 0.063 (> 1/number of variables) are shown in bold; variables with significant ($p < 0.05$) standardized coefficients are shown in italics.

	Estimate	S.E.	t	p
Intercept	2.608	0.066	39.31	< 0.0001
Comp1	0.155	0.017	8.95	< 0.0001
Comp2	0.219	0.075	2.92	0.0048

Table 2.2: Results of the final GLM model (Gaussian function, log link) relating the two PLSR components with dung removal.

Dung burial

The final GLMM model selected included only the three PLSR components explaining 64.5% of the variability in dung burial (Table 2.4). As in the case of dung removal, neither species nor behavioral functional group (endocoprid, paracoprid, telecoprid; p = 0.304) provided additional explanatory power to the model. The PLSR model showed that only prothorax volume, pronotum length, pronotum width and protibia area appeared as significant explanatory variables (Table 2.3). However, variable weights in each component indicate the occurrence of *trait syndromes* related to dung burial. As in the case of dung removal, PLSR component 1 included a set of traits positively related to dung burial (Table 2.3, Figure 2.2): in addition to prothorax volume, pronotum length and width, and protibia area indicated above, body weight, body volume, total length, head area and width, and size of first protibia tooth, and metatibia area appeared as important variables (square weight > 0.063) in this component. PLSR components 2 and 3 combine variables with positive and negative relationships with dung burial. PLSR component 2 reinforces the positive relationship with dung burial of some of the variables in PLSR component 1 (especially protibia area). Also, PLSR component 2 includes traits with negative relationship with dung burial (the same variables negatively related to the abovementioned dung removal). The third component is mainly related to a negative relationship of dung burial with total body length, indicating that beetles with proportionally longer bodies bury smaller amounts of dung (Figure 2.2).



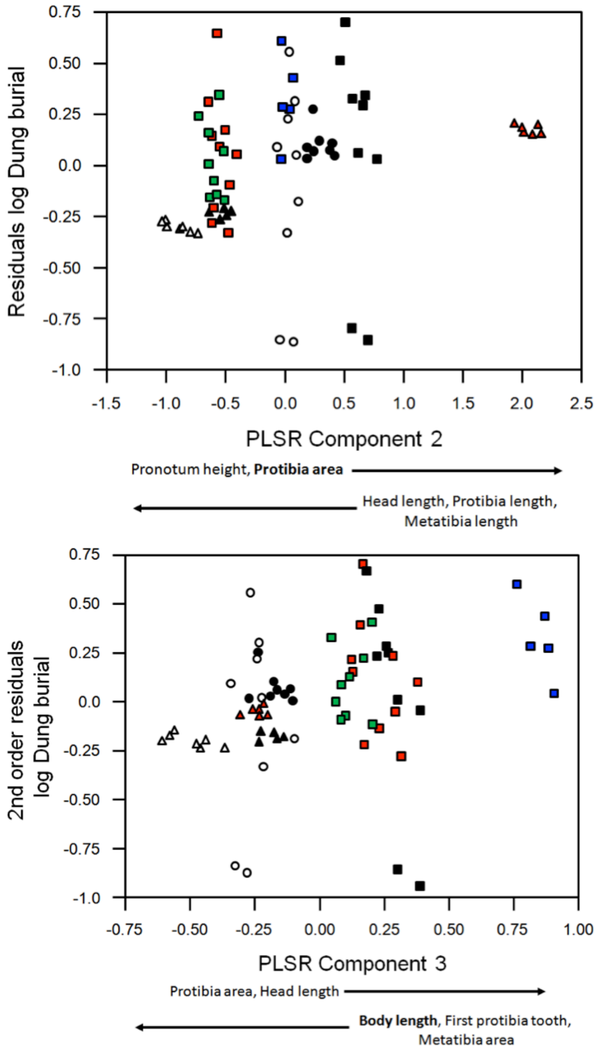


Figure 2.2: Correlations between PLSR components and dung burial by pairs of dung beetles of nine different species. Arrows below the PLSR components indicate the morphological traits related to the component and whether they are positively or negatively related to the response variable. Symbols as in Figure 2.1.

Variable	**Standardized coefficient (Mean ± S.E.)**	**t**	**p**	**w Comp1**	**w Comp2**	**w Comp3**
Head length	0.062 ± 0.189	0.33	0.7439	0.209	**-0.355**	**0.387**
Head width	-0.064 ± 0.137	-0.47	0.6397	**0.255**	-0.035	-0.203
Head area	-0.064 ± 0.137	-0.47	0.6397	**0.255**	-0.035	-0.203
Pronotum length	***0.238 ± 0.106***	***2.24***	***0.0288***	***0.265***	0.167	0.159
Pronotum width	***0.187 ± 0.069***	***2.70***	***0.0092***	***0.264***	0.117	0.086
Prothorax height	0.312 ± 0.158	1.98	0.0526	**0.266**	**0.260**	0.219
Prothorax volume	***0.245 ± 0.078***	***3.15***	***0.0026***	***0.266***	0.180	0.153
Protibia length	0.011 ± 0.064	0.17	0.8640	0.226	**-0.325**	0.219
Probitia first tooth length	-0.158 ± 0.2122	-0.75	0.4596	0.250	0.099	**-0.417**
Protibia area	***0.510 ± 0.242***	***2.11***	***0.0396***	***0.269***	***0.394***	***0.329***
Metatibia length (straight)	-0.166 ± 0.126	-1.32	0.1932	0.216	**-0.470**	0.037
Metatibia length (curved)	-0.139 ± 0.129	-1.07	0.2876	0.218	**-0.451**	0.062
Metatibia area	-0.092 ± 0.176	-0.52	0.6034	**0.255**	0.071	**-0.292**
Total body length	***-0.331 ± 0.160***	***-2.07***	***0.0431***	0.248	-0.106	***-0.491***
Total body volume	0.094 ± 0.089	1.06	0.2948	**0.262**	0.111	-0.028
Dry weight	0.107 ± 0.069	1.54	0.1284	**0.262**	0.081	0.024
R^2				0.574	0.603	0.645
Eigenvalues				14.88	0.63	0.12

Table 2.3: Standardized coeffients (Mean ± S.E.), Student t, signification ($p < 0.05$) and weights of the different components of the PLSR model for the explanatory variables (log transformed) on dung burial (log transformed). PLSR weights whose squares are > 0.063 (> 1/number of variables) are shown in bold; variables with significant ($p < 0.05$) standardized coefficients are shown in italics.

	Estimate	**S.E.**	**t**	**p**
Intercept	0.504	0.038	13.33	< 0.0001
Comp1	0.101	0.010	10.24	< 0.0001
Comp2	0.109	0.048	2.29	0.0254
Comp3	0.302	0.110	2.75	0.0076

Table 2.4: Results of the final GLM model (Gaussian function, log link) relating the three PLSR components with dung burial.

Seedling emergence

There were differences in seedling emergence between the control treatment and the different species (LRT = 220.72, d.f.= 1,9, p < 0.0001; Figure 2.3). *Aphodius foetidus*, *Bubas bubalus*, *Onthophagus vacca*, *Scarabaeus puncticollis* and *S. sacer* showed no differences in seedling emergence with respect to the control treatment, while *E. tersus*, *A. luridus*, *O. ruficapillus* and *O. vacca* significantly increased seedling emergence (Figure 2.3).

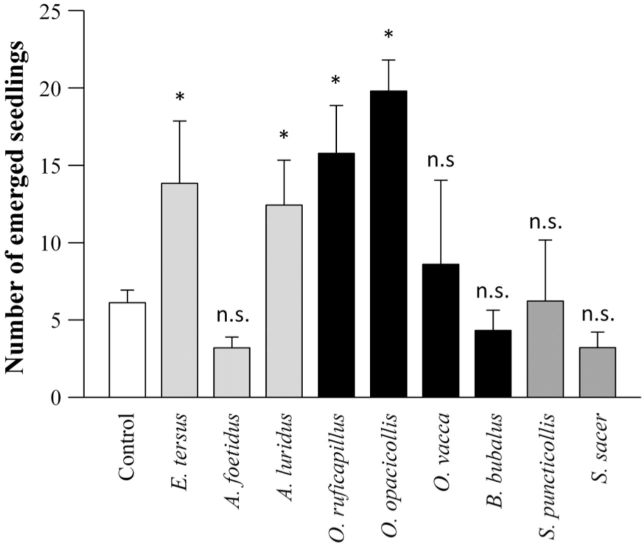


Figure 2.3: Mean number of emerged seedlings in control pots and in pots with different dung beetle species. Asterisks indicate significance of comparisons between the control treatment and each species. n.s. = not significant; * p < 0.0001.

Variable	**Standardized coefficient (Mean ± S.E.)**	**t**	**p**	**w Comp 1**
Dung Removal	**-0.114 ± 0.049**	-2.32	0.0238	-0.485
Dung burial	***-0.148 ± 0.035***	***-4.27***	***0.0001***	***-0.598***
Depth of buried dung	***-0.153 ± 0.038***	***-4.01***	***0.0001***	***-0.637***
R^2				0.127
Eigenvalues				3.701

Table 2.5: Standardized coeffients (Mean ± S.E.), Student t, signification (p < 0.05) and weights of the different components of the PLSR model for the effect of square root of dung removal, log dung burial and log depth of buried dung on seedling emergence.

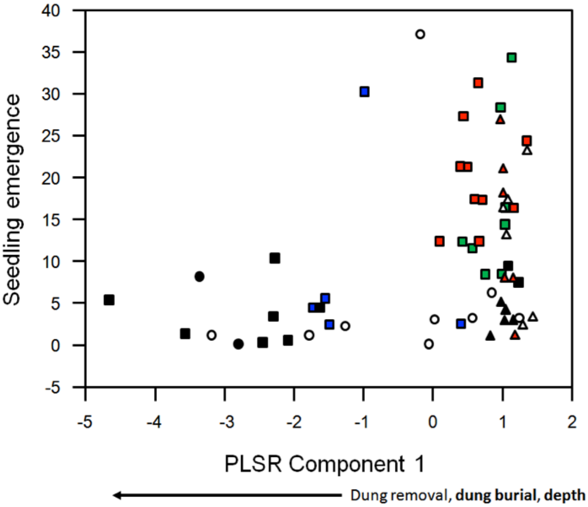


Figure 2.4: Correlations between PLSR components and seedling emergence. Arrows below the PLSR components indicate the functions (dung removal, dung burial and depth of buried dung) related to the component and whether they are positively or negatively related to the response variable. Symbols as in Figure 2.1.

Random effects:				
Variable	**Name**	**Variance**	**S.D.**	
sp	Intercept	0.245	0.495	
Fixed effects:				
	Estimate	**S.E.**	**z**	**p**
Intercept	2.149	0.174	12.34	< 0.0001
Comp1	0.190	0.053	3.55	0.0004

Table 2.6: Results of the final GLMM model (Poisson function, log link) including species as a random intercept and the single significant PLSR component as explanatory variables for seedling emergence.

The finally selected GLMM model indicated that species had a significant effect on seedling emergence. The species differ in the intercept with respect to the single component resulting from the PLSR analysis relating seedling emergence to dung removal, burial and depth of buried dung (Figure 2.4). Relocation strategy had no significant effect on seedling emergence. The PLSR component indicates that the three variables considered (dung removal, dung burial, and mean depth of buried dung) are highly correlated and conform a syndrome related to dung beetle activity. Depth of buried dung and dung burial were the most important variables in the single significant component of the PLSR analysis (Table 2.5, Figure 2.4).

2.4 Discussion

The results of our experiment reveal an actual relationship between morphological traits generally regarded as involved in dung removal and dung burial, and the delivery of these ecological functions by dung beetles. In addition, we found that these morphological traits indirectly affected seedling emergence through the ecological functions above (i.e. dung removal and dung burial), as well as a burial depth. It is worth noting that there are large variations in performance among individual pairs of the same species, especially regarding dung removal and dung burial. However, we believe that these variations represent the actual ranges of dung use in natural conditions. That is, dung beetles in the field may colonize a dung pat only for feeding, resulting in lower rates of dung removal and very low or no dung burial for nesting in paracoprid and telecoprid beetles. Indeed, in a field experiment carried out in the Guadix-Baza Basin, nesting occurred only in about half of the dung pats with 2-3 individuals (Gonzalez-Megías 1999). In addition, nests in the field showed a large variation in the number and size of brood masses, which ranged from 1 to 9 in the dominant *Onthophagus merdarius*, and from 1 to 3 brood balls in *Scarabaeus puncticollis* (Gonzalez-Megías 1999; González-Megías & Sánchez-Piñero 2003). In the case of *Scarabaeus* species, dung balls showed also large size variations and only 1/4 of them were brood balls (Gonzalez-Megías 1999; Sanchez-Piñero, unpublished data). Further, field experiments in the Doñana National Park also showed that a large number of beetles fed but did not nest in experimental dung pats (Verdú et al. 2018). Thus, we believe that dung beetle performance in the experiment represents the range of dung use in nature.

This experiment has some limitations regarding the extrapolation of its results. Methodologically, it was challenging to combine the analysis of the three ecosystem functions (dung removal, dung burial and seedling emergence) because they differ in the time needed for delivery and measurement. Dung removal and dung burial are delivered by dung beetles in a short period of time (although variable between behaviors and species). In contrast, seedling emergence requires nearly double the time. Thus, the experimental mesocosms could not be dismantled immediately after dung removal and burial was completed. The only option was to remove the dung beetles and leave the mesocosm untouched for the seeds to germinate and the seedlings to emerge. The removal of dung beetles was done after a minimum of seven days. But in order to keep the mesocosms unaltered, only visible dung beetles on the soil surface could be retrieved. Thus, dung beetle activity could potentially continue for different time lengths between species and even within pairs of the same species. Nonetheless, previous observations on the behavior of these species in the laboratory indicate that beetles use the dung only before it becomes too dry, after a week. Thus, although we are uncertain about the exact rate of dung removal and burial in the different species, we believe that our data provide a quite accurate estimation of the dung processed by the beetles.

Our results confirm that the measured morphological traits were related to dung beetle performance in dung removal and burial, as proposed by Halffter & Matthews (1966); Halffter & Edmonds (1982). In the case of dung removal, most traits were positively related to the performance of dung beetle pairs in the first PLS component. This result can be interpreted as the occurrence of a general morphological syndrome shared by Scarabaeidae dung beetles related to dung manipulation (piercing of the dung or tunnelling within the dung) and a general fossorial capability of dung beetles (Halffter & Matthews 1966; Halffter & Edmonds 1982; Cambefort 1991). Thus, although many endocoprid species do not bury dung, they are still able to dig in the soil to hide or move in the soil-dung interface.

Among the most important traits positively related to dung removal in the first PLS component were body mass and body size. These traits are generally identified as relevant in functional diversity studies (Nervo et al. 2014; Piccini et al. 2018). However, traits related to prothorax characterictics (prothorax height, volume, pronotum length and pronotum width) and protibial area are indicated as equally important and significant traits in the first PLS component. Protibia area has been shown to be related to differences in the depth of burrows in *Onthophagus* both between species and populations (Macagno et al. 2016). Indeed, Griffiths et al. (2015); Griffiths et al. (2016) also used prothorax and leg traits to analyse functional diversity in Neotropical dung beetle communities.

Interestingly, the second PLSR component indicated that length of digging-related structures (mainly head and protibia, but also metatibia) were negatively related to dung removal. This component could be interpreted as a lower performance in telecoprid dung beetles, as well as higher residuals in the species with shorter and stouter head and legs, *Euorodalus tersus*. A lower performance of dung burial from telecoprids compared to that of paracoprids has been already pointed out (Halffter & Matthews 1966; Halffter & Edmonds 1982; Martín-Piera 2000; see below). Higher performance of *E. tersus* could be related to the ability of this species to use dung for a longer time (i.e. drier) than other species, however it usually occurs in fresh dung in field conditions (Dellacasa 1983; FSP, pers. obs.). Further, smaller Aphodiinae species appear to use a larger amount of dung than larger species (30-70 times the volume of the beetles in small species vs. 25-30 times in larger species; Dellacasa 1983). Although larvae (8-22 larvae) were found in some dung pats, the amount of dung removed did not differ between dung with and without larvae (3.5-5.2 mg vs. 4.7-4.9 mg of dung removed, respectively), indicating that, although larvae could have increased dung removal for this species, our results still reflect a higher removal efficiency by the adults. Differences among Aphodiinae species in dung removal efficiency have been also obtained by Nervo et al. (2014). Thus, although species was not a significant factor to explain the amount of dung removed by the beetles, this result suggests that species-specific behavior could be important to account for differences in the delivery of ecological functions (Nervo et al. 2014; Griffiths et al. 2016).

In contrast to dung removal, only a subset of traits were significantly related to dung burial, either positively or negatively. Features of prothorax (prothorax volume, pronotum length and pronotum width) and area of protibia were the only traits significantly and positively related to the amount of dung buried. The prothorax is known to accommodate the large extrinsic muscles responsible for leg movement (Edmonds 1972), and the area and shape of the protibia are related to burrow depth in *Onthophagus taurus* and *O. illirycus* (Macagno et al. 2016). Interestingly, body length was negatively related to dung burial in the third PLSR component, indicating that proportionally longer beetles (as this component is based on residuals of the response variable) actually bury a smaller amount of dung. This is in agreement with the statement that the longer body shape of Aphodiinae (mainly endocoprids) denotes poor burrowing ability (Halffter & Edmonds 1982; Cambefort 1991). This result is also in agreement with the relevance of body shape characteristics as important factors determining the functional structure of dung beetle assemblages (Hernández et al. 2011). However, our data also showed that the two *Scarabaeus* species have slightly longer body shapes than *Onthophagus* species. In addition, the second PLSR component also indicated that length of head, protibia and metatibia (also related to telecoprid dung beetles) were negatively related to dung burial, which corroborates the statement that telecoprids have a lower burrowing ability than paracoprids (Halffter & Matthews 1966; Halffter & Edmonds 1982; Martín-Piera 2000). However, no accurate data on dung burial rates in our experiment requires further testing to corroborate this result. All in all, our results indicate that a combination of traits related to prothorax size (especially volume of prothorax), area of protibia, length of head and pro- and metatibia, and total body length are better predictors of dung burial than behavior. Therefore, although body mass has usually been considered as a proxy related to dung burial, the use of additional traits could provide better estimates of dung utilization (see also Nervo et al. 2014).

Strikingly, our results were unable to detect any significant effect of behavioral traits on performance in either dung removal and dung burial. However, these behavioral traits consider the main strategies of dung exploitation (i.e. endocoprid, paracoprid and telecoprid; Halffter & Matthews 1966), and are usually used as functional groups in studies of dung beetle functional diversity. Two main factors could explain this contrasting and relatively unexpected result. First, the lack of explanatory power of behavioral strategies maybe related to the fact that we have included an array of morphological traits that, altogether, were able to account for the differences in the body design of the species performing each one of the three major behavioral strategies (e.g. longer appendages in telecoprid beetles or longer body shape in endocoprids). Thus, the measured traits agreed with the differences in efficiency in the dung burial between telecoprids and paracoprids, as ball construction and rolling appears to be related to a lower efficiency as dung burrowers (but allowing to avoid competition in the dung pat as well as to find more suitable microhabitats for nesting; Halffter & Edmonds 1982). Second, this result could also be due to the small number of species included in the experiment (three endocoprids, four paracoprids and two telecoprids) and the large variability of performance in dung beetles (with no dung buried even in some of the largest species). Third, the species used in the experiment included two endocoprids (*A. foetidus* and *A. luridus*) that are as large as three of the selected paracoprids (*O. ruficapillus*, *O. vacca*, *O. vacca*) as well as one paracoprid and one telecoprid species of similar size (*B. bubalus* and *S. puncticollis*). However, lack of telecoprids as small as the medium or small paracoprids and endocoprids and large endocoprids may cause a bias in the analyses (Huston 1997). Nonetheless, this body length gradient between dung relocation strategies is common in dung beetle assemblages of the Palearctic region, and represents the size structure occurring in arid areas of SE Spain (Sánchez-Piñero & Ávila 2004). Disentangling the effect of morphology from the effect of behavior (i.e. dung relocation strategy) on dung burial requires that future studies include species with different behaviors but similar body size.

Seedling emergence was negatively affected by dung burial and burial depth in our experiment. A negative effect of burial depth on seedling emergence was also reported by Andresen & Levey (2004) and D'hondt et al. (2008). Griffiths et al. (2016) also found that several community parameters such as total biomass (related to the occurrence of larger dung beetle species), species richness and burial depth decreased the probability of seedling emergence but increased seedling recruitment and survival. The effects of shallow nests on seedling emergence seem to be context dependent; while *Catharsius* 5 cm deep burrows increased emergence in Congo rainforests (Beaune et al. 2012), Feer (1999) reported low germination success of seeds buried 5-10 cm deep. Despite the similarity of our results with previous findings, the explanatory power of dung removal, dung burial and burial depth, explaining only 12% of the variability in seedling emergence, while species identity accounted for an additional 26% of the variation. Thus, our results emphasize the differential effect of species regarding seedling emergence. This result strongly suggests that behavioral differences among species are also involved in the final outcome of dung beetle activity on seedling emergence. Differences in species activity in the soil-dung interface influencing soil surface properties has been proposed as a potential factor to explain the positive effect of endocoprids and shallow nesting species in seedling emergence (Griffiths et al. 2016). For example, soil bioturbation by dung beetles in sandy areas provoked lower soil compaction, higher aeration and higher water infiltration (Brussaard & Hijdra 1986), likely promoting seedling emergence. In addition, scarab larvae have been shown to enhance water infiltration (Romero-López et al. 2015), suggesting that the Aphodiinae adult and larvae that are active in the soil-dung surface (such as the larvae of *Acrossus* species) may increase germination and seedling success.

2.5 Concluding remarks

In conclusion, the results of our experiment demonstrate that there is a relationship between the morphological traits of structures generally considered as related to dung manipulation and digging with dung removal and dung burial, two important functions provided by dung beetles. They also point to a negative effect of the elongation of certain structures (as length of fore and hind tibiae) and a relatively longer body shape (as in endocoprid Aphodiinae beetles) in burrowing efficiency. These structures should be used in studies on functional diversity not only as proxies for the performance of dung removal or burial, but also for further analyses to understand the functional role of dung beetles. Further studies including higher number of species and comparing similar gradients of body size among dung exploitation strategies, as well as comparing among similar species, will be necessary to uncover the relationship between functional traits and their performance.

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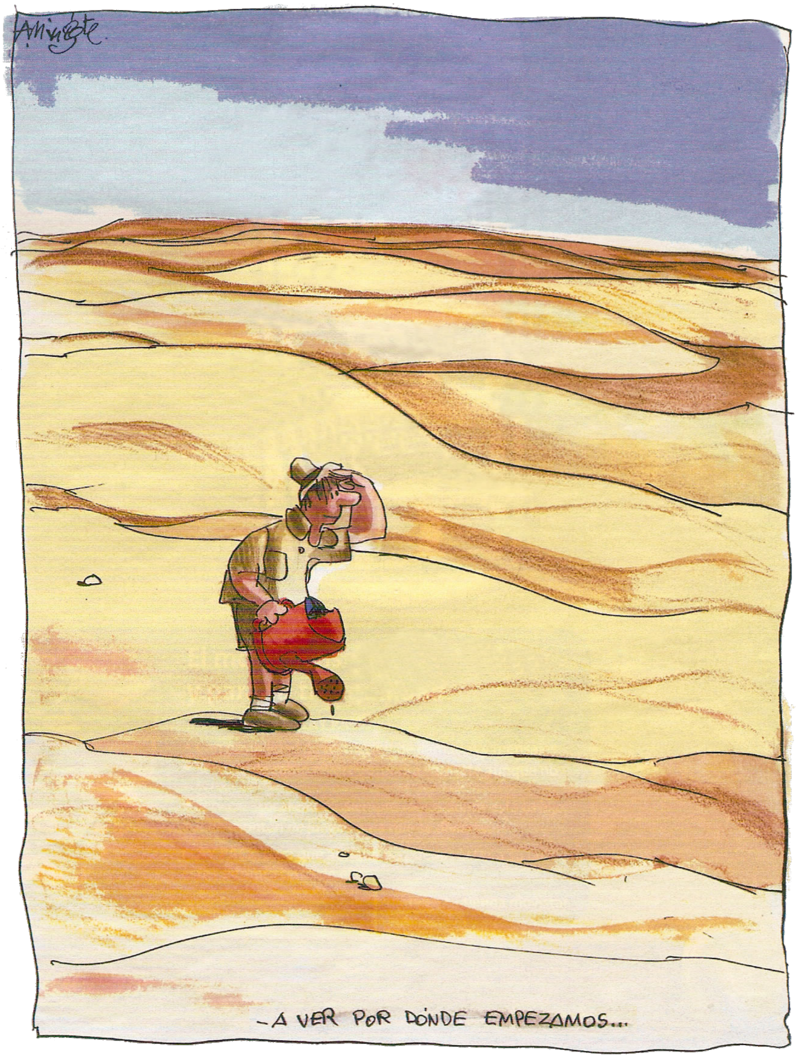

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3 Spatial and temporal variations of aridity shape dung beetle assemblages towards the Sahara desert

3.1 Introduction

Understanding the processes behind the geographical patterns of diversity is one of the central questions of ecology. Spatial gradients have long served as natural experiments to understand general principles in the ecology of animals, through the study of how changes in environmental factors, such as climate, influence the ecological and evolutionary processes that determine biodiversity variations from local to global scales (e.g. Pianka 1966; Willig et al. 2003; Sanders & Rahbek 2012). Aridity gradients emphasizing changes in water availability, a key abiotic factor, are especially important to understand geographical variations in biodiversity in warm temperate and tropical systems (Hawkins et al. 2003; Hawkins & Porter 2003). However, the effects of aridity on diversity remain unclear (Rohde 1992; Willig et al. 2003) because the response depends on taxa and geographic regions (Polis 1991; Wiens et al. 2013). For example, scorpion and bird diversity increase with aridity in North America, but decrease in Australia (Polis 1991). On the contrary, in ants there is a negative relationship of aridity with diversity in North America but the relationship is positive in Australian deserts (Polis 1991) and there is no relationship in Australian savannas (Andersen et al. 2015). Understanding biodiversity patterns across aridity gradients is also relevant because drylands currently occupy more than 40% of the land on Earth and their extent is expected to increase in the next decades in response to climate change (Huang et al. 2016).

Strikingly, temporal variations of diversity patterns along environmental gradients have received scarce attention (Bishop et al. 2014) despite their importance in shaping community assemblages and large-scale diversity patterns (Pianka 1966; Willis & Whittaker 2002; White et al. 2010; Gouveia et al. 2013). However, both intra-annual (seasonality) and inter-annual environmental variations play a significant role in the origin of diversity patterns and the variations of local species pools (Pianka 1966; Tonkin et al. 2017). Temporal variations are particularly important in Mediterranean (Agoglitta et al. 2012; Seager et al. 2014) and subtropical (Belda et al. 2014) climates, where the spatially uneven distribution of water at fine and broad scales is coupled with large variations in water availability within and between years (i.e. seasonal and interannual variations).

Mediterranean areas typically host strong spatial gradients of water availability, often ranging from warm-temperate to desert conditions (Safriel et al. 2018). Mediterranean climate is highly seasonal, with dry hot summers and wet cool winters that result in large differences in water availability throughout the year. Importantly, besides this overall seasonal regime, arid environments show large unpredictable variations in rainfall between seasons and years, which can sometimes be larger than the typical within-year fluctuations (Ward 2009). These differences may result in differing diversity patterns between seasons, in particular along aridity gradients, where their extremes show distinct seasonal variations – from abundant rains in winter and scarce precipitations in summer at the more humid places to scarce rains throughout the year in the desert. Drylands respond differently to extreme precipitations and seasonal rainfall than mesic biomes, with highly variable and temporally-limited increases in plant productivity (Zeppel et al. 2014). Such extreme variations in water and resource availability drive the phenology of desert animals (Polis 1991), and may produce strong oscillations in their communities (Tonkin et al. 2017). Despite the striking changes in community composition and structure caused by these variations in biologically available water (Seely & Louw 1980; Polis et al. 1997; Holmgren et al. 2001), the spatial and temporal effects of aridity on the diversity of invertebrates and trophic interactions have been seldom studied (Labidi et al. 2012; Tshikae et al. 2013c).

Dung beetles of the family Scarabaeidae feed and nest on the faeces of diverse animals, especially mammalian herbivores, showing diverse dung-exploitation strategies (Hanski & Cambefort 1991). In the Mediterranean, species in the Aphodiinae subfamily are mainly endocoprids that feed and breed within the dung pat (although many species are known to be kleptocoprids, saprophages and root feeders Christensen & Dobson 1976; González-Megías & Sánchez-Piñero 2003; Dellacasa & Dellacasa 2006), whereas the Scarabaeinae subfamily includes paracoprid and telecoprid species that feed and breed directly below or away from the dung pat respectively (Hanski & Cambefort 1991). The large abundances, relatively easy-to-identify species, relative stable systematics and wide distribution of dung beetles, makes them ideal to study spatial and temporal changes in community structure (Spector 2006). Moreover, the diversity of this group is known to respond to large-scale environmental gradients (Hortal-Muñoz et al. 2000; Nunes et al. 2016), in particular to variations in water availability (Haloti et al. 2006; Labidi et al. 2012; Tshikae et al. 2013c; Abdel-Dayem et al. 2016). In dry areas dung beetles are thought to be constrained by both their physiological water economy (Sowig 1996; Chown et al. 2011) and the decrease in the availability and quality of trophic resources (Lumaret 1995; Nichols et al. 2009). Further, Palearctic Scarabaeidae are well diversified in mesic and arid Mediterranean areas (Lumaret 1991; Sánchez-Piñero & Ávila 2004) and surrounding desert regions (Baraud 1985), making them a suitable model taxa to investigate biodiversity responses to aridity gradients.

Here we study the temporal and spatial variations of dung beetle communities along a water availability gradient in Eastern Morocco, spanning 400 km from coastal Mediterranean to desert Saharan conditions. We aim to answer three specific questions: (Q1) Are dung beetle communities of desert areas reduced subsets of communities living in less arid areas? (Q2) Are community variations along the aridity gradient stable within and between years? (Q3) Do climatic factors, soil features and resource availability contribute to shape the diversity and composition of communities along the aridity gradient? According to the water-energy hypothesis (Hawkins et al. 2003), we expect a decrease in dung beetle diversity with increasing aridity. Progressively dryer conditions will filter out the most sensitive species while selecting for highly adapted species able to cope with a harsher climate and limited resource availability, thus promoting high spatial species turnover and locally distinct species assemblages (Arakaki et al. 2011; Sánchez-Piñero et al. 2011). In addition, we expect temporal shifts in the relationship between dung beetle diversity and aridity, due to the strong variations in precipitation patterns. While in Mediterranean areas the higher water availability during the wet season will cause a stronger diversity-aridity relationship than in the dry season, desert environments will show lower seasonal species turnover but higher inter-annual shifts in assemblage composition because the temporally stochastic nature of their precipitations limits the adaptation to cope with seasonal environmental shifts (Tonkin et al. 2017).

Question Q1 was investigated by analysing species richness, abundance, evenness and community composition along the aridity gradient. To answer question

Q2 we analysed variations in community composition at seasonal (between wet and dry seasons) and annual (between years) temporal scales. Finally, we assessed question Q3 by analysing the effects of climate, soil, vegetation and dung availability on dung beetle assemblages.

3.2 Materials and methods

General design

Study area

We surveyed a linear transect spanning approximately 400 km in east Morocco, parallel to the Algerian border (Figure 3.1). The transect was placed along a strong aridity gradient, from a semiarid region at the Mediterranean coast (near Saïdia, 35°5’59” N, 2°17’15” W) towards the hyperarid Sahara desert (near Figuig, 32°6’33” N, 1°13’47” W) (Table C.1 in Appendices), with a threefold annual rainfall gradient (from ca. 350 mm at the coastal semiarid area to 100 mm at the nearly hyperarid Saharan end of the gradient) and a Mediterranean precipitation regime characterized by summer drought and rainy season in November-March (Belda et al. 2014). The difference in rainfall between the wet and dry seasons (as exemplified by the precipitation in April, the wettest month, and September, the driest month) ranged from 45 to 19 mm at the semiarid end, and showed no difference at the desert end (i.e. 13 mm in both months). However, during the dry season, the greatest rainfall (22 mm) was not registered in the coast, but in the middle of the gradient.

Livestock breeding is the main economic activity along the whole gradient. Sheep occur along the entire transect, while cattle appears mainly in the semiarid end of the gradient towards the Mediterranean coast. Donkeys also occur along the whole transect and dromedary herds appear in the Saharan areas, but both are scarce. The transect is dominated by a single soil type (Petric Calcisols) except the coastal area near Sa”idia. This area shows coastal Gleyic Solonchak soil that differ from the dominant Petric Calcisol because of a thicker silt layer ($\geq$ 50cm depth) and higher salt concentration (Jones et al. 2013). The northern part of the transect mainly corresponds to agricultural land, with forest areas restricted to mountain ranges, while the middle and the southern parts are dominated by grazing rangelands with shrub vegetation (20-30% cover, 25 ± 13 cm heightmean ± SD).

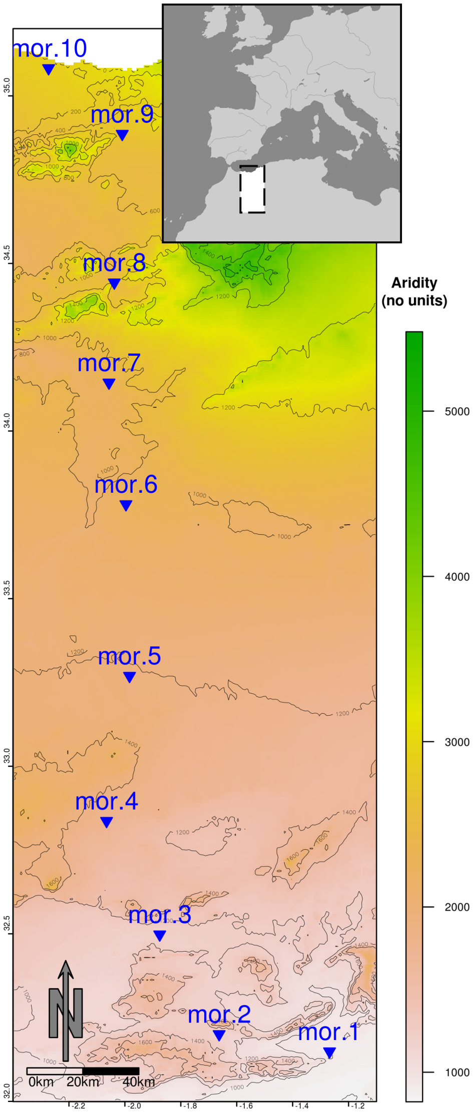

Figure 3.1: Map of the ca. 400 km transect from a semiarid zone (mor.10, Mediterranean coast) to the desert area (mor.1, Sahara desert). The map is constructed by overlapping an aridity (Trabucco & Zomer 2009) and an altitude layer (Hijmans et al. 2005) converted into elevation isolines (spaced 200 m).

Sampling design

Dung beetles were sampled during four campaigns held in two consecutive years: two in the wet season (April 2013 and 2014) and two in the dry season (September 2013 and 2014). These months were chosen to include the two peaks of dung beetle species richness and abundance in the Mediterranean region (as recommended by Hortal & Lobo 2005). In each campaign we surveyed 10 sampling sites along the Moroccan road N17 from the Sahara towards the Mediterranean, separated by an interval of around 40 km (Figure 3.1). Sampling and beetle collection were carried out under research permits Reference Numbers 01/2013 HCEFLCD/DLCDPN/DPRN/CFF and 01/2014 HCEFLCD/DLCDPN/DPRN/CFF issued by the *Haut Commisariat aux Eaux et Forêts et ʻa Lutte Contre la D'esertification* (Morocco). All sampling sites were placed at least 100 m away from the road margin. Annual precipitation was similar in both years at the three places with available meteorological stations (Saïdia and Oujda in the north and Figuig in the south; www.worldweatheronline.com), although it was about 20% higher in 2012-2013 than in 2013-2014 in all three stations.

Each sampling site was replicated twice. Replicates were placed 1 km apart, and consisted of five baited pitfall traps (thus, 100 traps per sampling campaign) separated 20 m one from another following a straight line (thus, 80 m from trap 1 to trap 5). Each pitfall trap consisted of a 1 l plastic cup (11.5 cm diameter, 14 cm depth) covered by a 2 cm x 2 cm mesh on top of which 300 g fresh cow dung was laid as bait (see Lobo et al. 1988). To avoid any spurious effects due to differences in dung composition, fresh organic-farming cow dung was harvested from a single farm (Colmenar Viejo, central Spain) and well-mixed to obtain a homogeneous dung mass, adding water and mixing right before placing the traps to ensure adequate dung moisture levels. All traps were filled with 300 ml of a soapy preservative water solution with chloral hydrate (10 g/l) to prevent quick insect degradation due to high temperatures and fungi proliferation. Traps were active for a standard period of 72 h (Labidi et al. 2012; Amraoui et al. 2016). All captures were immediately transferred to 96% ethanol in the field and transported to the laboratory where individuals were sorted and identified to species level.

During the sampling campaigns we gathered data on resource availability, vegetation and soil characteristics (Table C.6 in Appendices). GIS data on annual aridity (AI = mean annual precipitation / mean annual evapotranspiration) and solar radiation were obtained from Trabucco & Zomer (2009), and mean monthly temperature, annual and monthly precipitation and altitude from Hijmans et al. (2005). Resource availability was estimated using the amount of five types of dung (sheep/goat, cow, horse/donkey, dromedary and carnivore droppings) present in the locality as a general proxy for the actual amount of fresh dung that is available for dung beetles. To do this, in each replicate in the four campaigns we conducted two perpendicular 250 m long and 2 m wide linear transects, each surveyed by one researcher following a standardized sampling protocol, covering a total of 1000 m^2 per replicate (similar to Lobo et al. 2006). In each transect the total mass of the five types of dung mentioned above was estimated based on dung volume, according to previous measurements of dung pats of different volume in the field (González-Megías & Sánchez-Piñero 2004). Dung availability included "cow dung" and "sheep + other dung" (all expressed in g/100 m^2). Vegetation height (cm) and vegetation percentage cover were estimated using the point-quarter method every 5 m along a 250 m x 2 m transect at each replicate and campaign to account for seasonal and yearly variations. Finally, we extracted three arbitrarily located soil cores (4 cm diameter and 30 cm depth) from each replicate. Soil samples were split into three depths (0-10 cm, 10-20 cm and 20-30 cm) and kept in separate air-tight plastic bags for further laboratory analyses. From these samples, seven soil variables were measured (Table C.6 in Appendices) accounting for structure (hardness, bulk density), water content (water field capacity) and particle size (percentage of gravel, sand, silt, and clay) (see Tovar 2015).

Statistical analyses

We assessed inventory completeness for each sampling site at each campaign using Sample Coverage (Chao & Jost 2012) as implemented in iNEXT ℝ package (Hsieh et al. 2016). Average sample coverage was 99.18%, with a minimum of 91.50% for the site located at the semiarid end of the gradient in the wet season of 2014. For this reason, species richness (S) was measured as the total number of species recorded in each sampling site at each sampling campaign. Evenness (J′) was measured using Pielou's index, i.e. Shannon H′ / ln(S) (Magurran 2004).

Variations of species richness, abundance, and evenness along the aridity gradient

We analysed the relationship between aridity and species richness, abundance (mean number of individuals/trap) and evenness (question Q1) through a multivariate general linear regression (GLM) with restricted sigma parameterization. We considered aridity and its interactions with both season and year as factors, to assess their eventual influence on the relationship between community descriptors and aridity. The *Aridity*Season*Year* interaction was also included to assess whether these relationships show different seasonal patterns in the two study years. Significance levels were Bonferroni-corrected, since the same analysis was carried out for three different response variables (species richness, abundance and evenness).

Variations in community composition

To assess variations in community composition (questions Q1 and Q2) we used non-metric multidimensional scaling (NMDS; Quinn & Keough 2002), based on the Bray-Curtis similarity index. Abundance was Hellinger standardized prior to the similarity analyses, to balance relative abundances of species and minimize the double-zero problem typical of community samples (Legendre & Gallagher 2001). Pairwise differences in Bray-Curtis similarity at each site between years, seasons and their interaction (independent of aridity) were analyzed by means of a Permutational Analysis of Variance (PERMANOVA) (9999 iterations) using PAST 3.15 statistical package (Hammer et al. 2001).

In addition, we used a beta diversity partitioning framework based on both presence-absence data using Sørensen's dissimilarity index and abundance data using Bray-Curtis dissimilarity index. First, Sørensen dissimilarity was partitioned into its *true species turnover* (i.e. species replacement) and *nestedness* (i.e. species loss) components (Baselga & Orme 2012). This partitioning of dissimilarity only accounts for presence-absence variations in the data (Baselga et al. 2013), so to consider also species abundances we followed a similar procedure. We calculated abundance-based Bray-Curtis dissimilarity index (herein B-C dissimilarities for short), partitioning it into *balanced* (i.e. substitution of individuals of one species in one site by the same number of individuals of different species in another site) and *gradient* (i.e. loss of individuals from one site to another) components (Baselga 2013). Multiple site dissimilarity was used to calculate overall beta diversity partitioning in the turnover/nestedness and balanced/gradient components of Sørensen and B-C dissimilarities, respectively, for each season in each year (i.e., for each one of the four campaigns). To analyze whether turnover/nestedness and balanced/gradient components of Sørensen and B-C dissimilarities varied along the aridity gradient, we carried out non-parametric Spearman-rank correlations between pairwise dissimilarities and the differences in aridity between each pair of sites. We used Sperman-rank correlations because residuals from GLM models did not fit a normal distribution and were heteroscedastic. All Sørensen and B-C dissimilarities calculations were done using the R package Betapart 1.5.0 (Baselga et al. 2013). In addition, we identified the most representative species of three sections of the transect representing the semi-arid end, the intermediate zone and the arid end for each year and season using the Indicator Value Index (IndVal), calculated with the R package indicspecies (De Cáceres & Legendre 2009). Due to small sample size, a Wilcoxon signed rank test was carried out to test whether the Scarabaeinae/Aphodiinae abundance ratios were lower in the dry than in the wet season, using the R package stats.

We also used Sørensen's and B-C dissimilarities to analyse variations in community composition between seasons (wet vs. dry) and between years (2013 vs. 2014) for each one of the ten points along the transect. Then, to analyse whether these site similarities between seasons and between years were related to (continuous) variations in aridity we carried out a multivariate GLM with restricted sigma parameterization considering aridity and its interactions with both season and year.

Relationship of environmental variables with diversity and composition of communities

We evaluated the relationships of species richness, abundance and evenness with climate, soil, vegetation and dung availability (question Q3) through partial least squares generalized lineal regressions (PLS-GLR; Bastien et al. 2005). This method allows analysing data characterized by a large number of multicollinear predictor variables by extracting a set of orthogonal components (or latent vectors) considering not only the structure of predictor variables (as provided by a PCA) but also their relationship with the response variable. Once the components were computed, a GLM with Gaussian function and identity link of the response variable on the PLS components was carried out in order to test for the significance of the components and the whole model. Abundance data were log10-transformed to meet assumptions of homoscedasticity and normality of model residuals. Because communities differed mainly between seasons (see Results below), four PLS-GLR analyses were conducted (2 descriptor variables x 2 seasons) and the critical significance level of the models was set by Bonferroni correction ($p < 0.0125$). Cross-validation and corrected Akaike Information Criterion (AICc), due to low sample size were used to select among models including different number of components. When a model component coefficient was not significant ($p > 0.0125$), the next optimal model indicated by cross-validation and AICc was chosen. To identify the importance of each predictor in the model, the standardized coefficients of the final PLS-GLR model were obtained by bootstrapping (1000 iterations).

We assessed the best combination of environmental variables explaining variations in species composition (question Q3) through multivariate RDA-based variation partitioning (Borcard et al. 2011) (Figure C.1 in Appendices). Further, we used distance-based RDA (dbRDA) to assess the best predictors of Sørensen's and Bray-Curtis dissimilarities between all sites in each campaign. In both cases (RDA and dbRDA) we previously forward selected environmental and spatial predictors (Moran's Eigenvector Maps; MEMs) applying the two-step procedure proposed by Blanchet et al. (2008) to select significant predictor variables. We calculated the amount of variation of the different biodiversity metrics explained by the different groups of predictors (climate, space, soil and dung, as found in Table C.6 in Appendices) and evaluated the significance of the pure fractions (for each group of variables accounting for the variance explained by all other factors) using partial RDA for species composition and partial dbRDA for Sørensen and B-C dissimilarities.

We performed a spatial autocorrelation analysis to account for any spatially-structured unexplained variability. We did this by including the vectors obtained from a Moran's Eigenvector Map, MEMs (Borcard et al. 2004; Borcard et al. 2011) into the analyses. These vectors were calculated using R packages spdep (Bivand & Piras 2015) and spacemakeR (Dray 2013). PLS-GLR analyses were conducted using the R package plsRglm (Bertrand et al. 2014), and the multivariate variation partitioning analyses with the function varpart of R package vegan (Oksanen et al. 2016).

3.3 Results

We captured 70,326 individuals of 61 dung beetle species in the four sampling campaigns (9,627 individuals of 29 Scarabaeinae species and 60,699 individuals of 32 Aphodiinae species; see Table C.5 in Appendices). Overall, dung beetle abundance and richness were slightly higher in 2014 compared to 2013 for both seasons (Figure 3.2).

Variations in species richness, abundance and evenness

There was a significant pattern of decreasing species richness along the gradient, but neither abundance nor evenness showed a significant relationship with aridity (Figure 3.2, Table 3.1). The relationship between species richness and aridity strongly varied seasonally, with a higher slope of the *Season*Aridity* interaction in

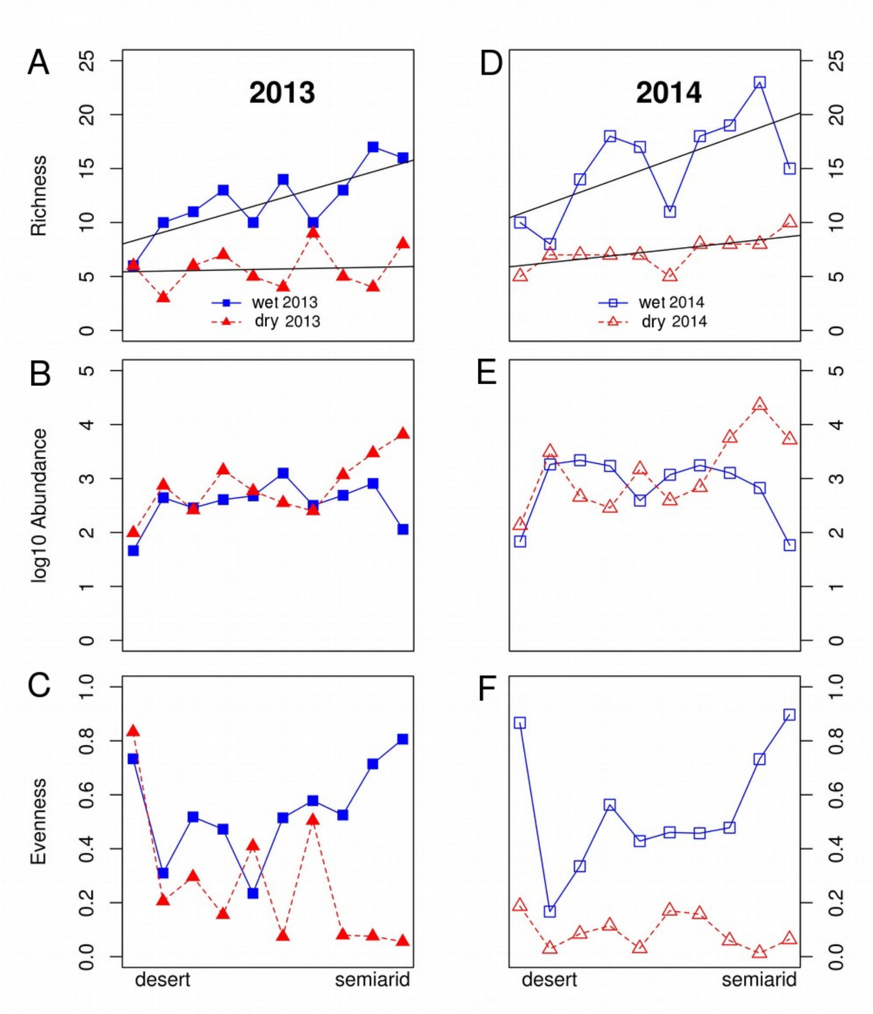

Figure 3.2: Variations in dung beetle community descriptors along an aridity gradient from a semiarid zone to the Sahara desert during the wet and dry seasons in 2013 and 2014. Variations in species (A, D) species richness, (B, E) log abundance and (C, F) evenness along an aridity gradient from a semiarid zone (350 mm mean annual rainfall) to the Sahara desert (100 mm) during the wet (April, blue lines) and dry (September, red lines) seasons in 2013 (A-C) and 2014 (D-F). The straight lines in the figures for species richness show the regression lines for the wet and dry season each year. Abundance and evenness did not show either linear nor unimodal fits to aridity. The range of Y axis was standardized to allow easier comparison between years.

the wet than in the dry season. The significant *Year*Aridity* interaction indicates that the relationship between species richness and aridity varied between years, 2014 showing a steeper slope than 2013 due to the higher number of species in the semiarid end of the transect, but not in the desert areas (Table 3.1, Figure 3.2). In fact, species richness showed a clear change only during the wet season, from low values (5-10 species) in the desert to the highest richness (15-20 species) in the semiarid zone (Figure 3.2). During the dry season, species richness hardly increased from the desert to semiarid areas in 2013, although a slight increase appeared near the semiarid end of the gradient, particularly in 2014.

Total abundance did not show a significant relationship with aridity and was very similar along the gradient in both sampling seasons (Table 3.1, Figure 3.2). The wet season showed relatively small variations of abundances throughout the gradient, with a decrease at both ends, while there was a striking increase in abundance in the semiarid end of the gradient in the dry season (Figure 3.2). Although evenness was not directly related to aridity, there was a significant *Season*Aridity* interaction (Table 3.1), indicating that evenness patterns change throughout the year along the gradient, especially because of the contrasting evenness values between the wet and the dry seasons at the semiarid end of the transect (Figure 3.2).

Variations in community composition

Although there were no significant relationships between total abundance and aridity, there were large seasonal differences in the relative abundance at the subfamily level. Communities in the wet season were dominated by Scarabaeinae, which accounted for 60-90% of total abundance in most sites. This contrasts with the dry season, when the communities were almost dominated by Aphodiinae, which accounted for more than 97% of abundance in most sites. Thus, the ratio of Scarabaeinae/Aphodiinae abundances significantly differed between seasons (2013: χ^2 = 10632.53, $p < 0.001$; 2014; χ^2 = 22483.74, $p < 0.001$). However, these differences did not hold for richness, which showed approximately a 1:1 ratio in the number of species in both seasons.

Community composition along the aridity gradient showed a strong seasonal structure. The communities during the wet and dry seasons were clearly different, except in the most arid extreme of the gradient (especially sites 2 and 3), as shown by NMDS ordination (Figure 3.3). While NMDS shows a clear spatial structure in community composition along the gradient in the wet season, in the dry season only the semiarid end of the transect (sites 8-10) shows a marked dif-

Effect	Richness F (1, 35)	log10 Abundance F (1, 35)	log10 Evenness F (1,35)
Aridity	15.17 **	6.39	1.43
Season*Aridity	67.07 **	2.72	38.75 **
Year*Aridity	7.57 *	2.48	5.16
Year*Season*Aridity	1.11	0.02	4.27

Table 3.1: Multivariate GLM on the effects of temporal (seasonal and interannual) variations of aridity over species richness, abundance and evenness. Significance levels after Bonferroni correction: * $p < 0.016$; ** $p < 0.0003$.

Effect	**Coeff. ± S.E.**	**Sørensen F (1,17)**	**Coeff. ± S.E.**	**Bray-Curtis F (1,17)**
Seasonal				
Aridity	-1.974 ± 0.406	23.63 **	-3.473 ± 0.458	57.58 **
Year*Aridity	0.019 ± 0.032	0.33	0.064 ± 0.036	3.14
Interannual				
Aridity	0.184 ± 0.529	0.12	1.468 ± 0.424	12.00 *
Season*Aridity	0.008 ± 0.042	0.04	0.109 ± 0.034	10.49 *

Table 3.2: Variation of seasonal (wet-dry) and interannual (2013-2014) dissimilarity for species occurence (Sørensen) and abundances (Bray-Curtis) in relation to aridity and its interaction with year and season. Sørensen dissimilarity for interannual comparison and Bray-Curtis dissimilarity for both seasonal and interannual comparisons were arcsin transformed. Statistical significance levels after Bonferroni correction: * $p < 0.0125$; ** $p < 0.00025$.

ference with all the other sites (Figure 3.3). PERMANOVA results corroborate that community composition significantly differed seasonally ($pseudoF$ = 8.255, $p < 0.0001$, $d.f.$ = 1.36) while showing similar patterns in both sampling years ($pseudoF$ = 1.341, p = 0.1968, $d.f.$ = 1.36), with no significant interaction between both factors ($pseudoF$ = 0.604, p = 0.805, $d.f.$ = 1.36). Changes in community composition between years were indeed small, with total Sørensen values of 0.2 and 0.3 for the wet and dry season respectively (Figure 3.5a), and total B-C of 0.3 in the wet season and 0.2 in the dry season (Figure 3.5b). Indeed, the indicator species of communities (IndVal analyses) sampled were the same in 2013 and 2014 (see Table C.6 in Appendices). In contrast, three Aphodiinae species were indicators of communities sampled during the dry season (IndVal > 0.95), while

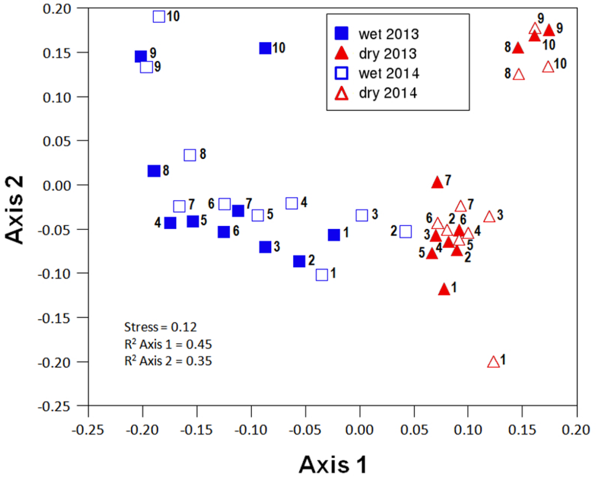

Figure 3.3: Non-metric multi-dimensional scaling (NMDS) ordination (stress = 0.12) of community composition for the different sites in the wet and the dry season of the two sampled years (2013 and 2014).

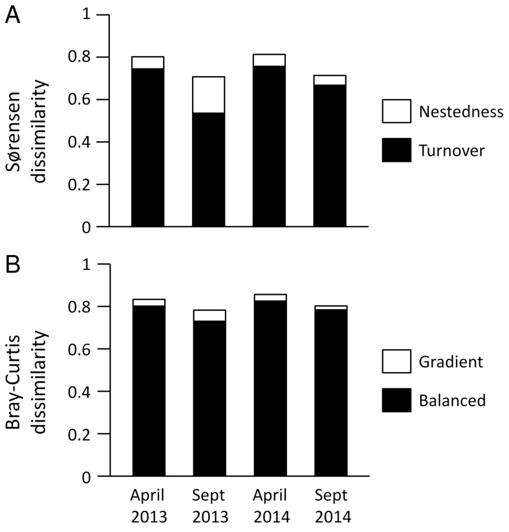

Figure 3.4: Multiple site dissimilarity of dung beetle communities along the aridity gradient based on species occurrence (Sørensen) and considering species abundances (Bray-Curtis). Multiple site dissimilarity partitioning into turnover/nestedness or balanced/gradient components of dung beetle communities along the aridity gradient for the different seasons and years sampled based on (A) species occurrence (Sørensen) and (B) considering species abundances (Bray-Curtis).

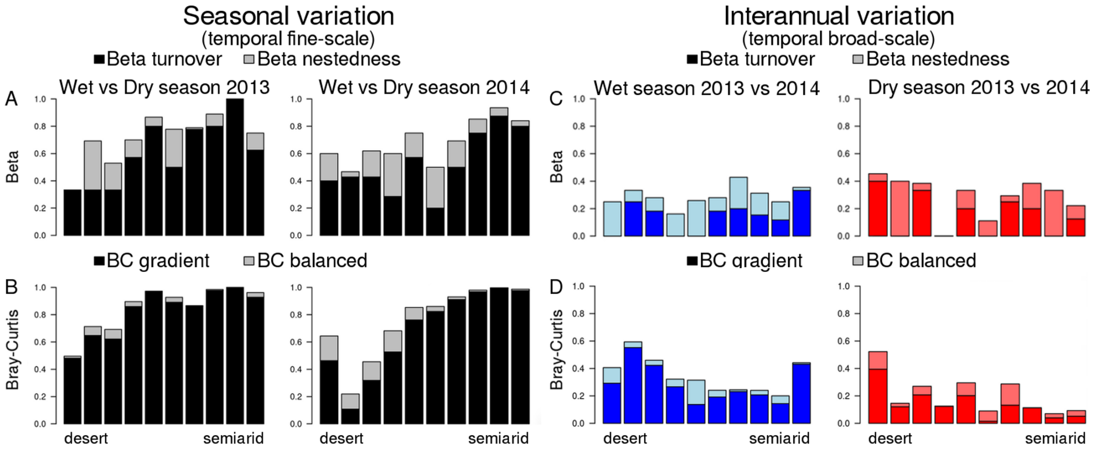

Figure 3.5: Temporal beta diversity (Sørensen coefficient) and Bray-Curtis dissimilarities of dung beetle communities along the aridity gradient. (A-B) Seasonal beta diversity and Bray-Curtis dissimilarities respectively; each bar compares communities for the same site in the wet and the dry seasons. (C-D) Interannual beta diversity and Bray-Curtis dissimilarities respectively; each bar compares communities for the same site in the two years included in this study. Beta diversity is partitioned in two components: beta turnover (dark colors) and beta nestedness (light colors). Bray-Curtis dissimilarities are also partitioned in two components: B-C gradient (dark colors) and B-C balanced (light colors). The range of Y axis (showing all possible variation of beta diversity or B-C, 0-1) was standardized in all plots to allow easier comparison.

seven Scarabaeinae and seven Aphodiinae species were indicators of wet season communities (see Table C.3 in Appendices).

Variations in community dissimilarities in space and time

Dissimilarity between wet and dry season communities (both Sørensen and B-C) significantly decreased with aridity (Figure 3.5), and there was no interaction with year (Table 3.2). In contrast, Sørensen dissimilarity between 2013 and 2014 communities was not affected by aridity (Figure 3.5), although B-C dissimilarity significantly increased with aridity with an interaction with season due to the stronger pattern occurring in the dry season (Table 3.2, Figure 3.5). Hence, total B-C dissimilarity was low between seasons in the most arid sites, but very high towards the semiarid end of the gradient (Figure 3.5b).

Multisite Beta diversity-partitioning showed that Sørensen dissimilarity among sites was mainly due to species turnover along the gradient in both seasons, although nestedness increases in importance in the dry season (Figure 3.4a). In contrast, according to B-C dissimilarity analyses balanced changes in abundance were prevalent in both seasons, with some gradient in the wet season (Figure 3.4b). This pattern was similar in both years. Interestingly, both pairwise Sørensen and B-C dissimilarities showed similar relationships with pairwise differences in aridity. The turnover and balanced components increased in relation to differences in aridity between sites, while nestedness and gradient components did not change significantly with differences in aridity (Table 3.2).

Relationships of environmental variables with the diversity and composition of communities

The PLS-GLR analysis shows that the relationship between environmental variables and species richness and abundance along the gradient largely differed between seasons. Results for evenness are not shown as data did not meet the premises of neither normality nor homocedasticity for the wet season and were not significant for the dry season. PLS components were only significantly related to species richness variations in the wet season and to abundance variations in the dry season (Table C.3 in Appendices). PLS standardized coefficients indicate that variations of species richness in the wet season were positively related to precipitation (both monthly and annual rainfall) and negatively related to radiation (Figure 3.6a). Differences of abundance in the dry season appeared positively related to cow dung availability (Figure 3.6b).

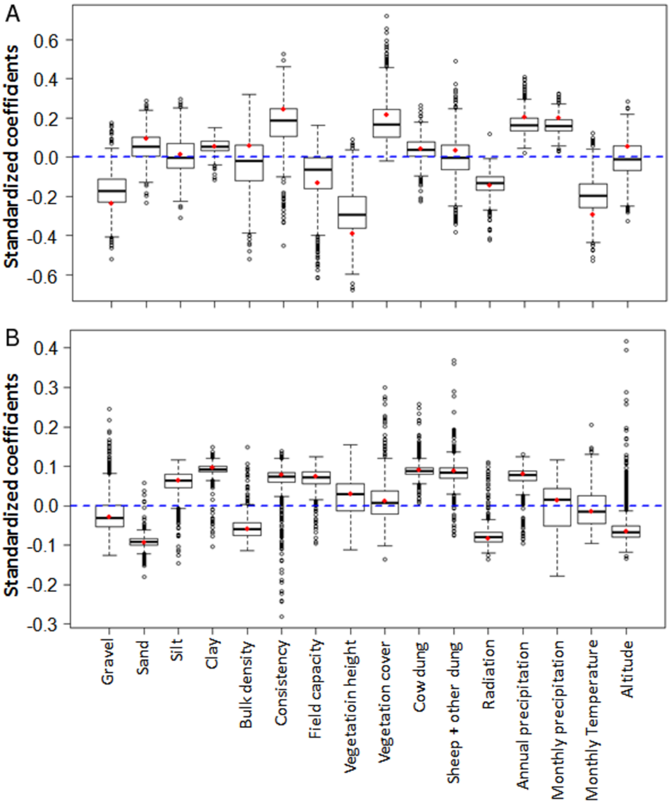

Figure 3.6: Distribution of standardized coefficients of PLS-GLR models for richness and abundance using all available environmental variables. Boxplots show standardized coefficients of PLS-GLR models for species richness in the wet season (A) and abundance in the dry season (B) of dung beetle communities along an aridity gradient from a semiarid zone (350 mm mean annual rainfall) to the Sahara desert (100 mm). Standardized coefficients were obtained by bootstrap (1000 iterations) to identify the importance of predictor variables in the models. Significant predictor variables differ from 0.

		Sørensen		Bray-Curtis	
Year	Season	Turnover	Nestedness	Balanced	Gradient
2013	Wet	0.429	-0.022	0.593 ***	-0.135
	Dry	0.493 **	-0.210	0.487 *	-0.331
2014	Wet	0.536 **	-0.208	0.683 ***	-0.402
	Dry	0.590 ***	0.116	0.479 *	-0.308

Table 3.3: Spearman rank correlation coefficients for the relationship between pairwise difference in aridity between sites and the components of the partitioning of Sørensen and Bray-Curtis dissimilarities. We used species presence/absence dissimilarity (turnover and nestedness components of Sørensen index) and abundance-based dissimilarity (balanced and gradient components of Bray-Curtis index) for the different surveys. Significance values after Bonferroni correction: ms = marginally significant; * $p < 0.003$; ** $p < 0.0006$; *** $p < 0.00006$.

Variation partitioning of multivariate data identified significant relationships of Sørensen and B-C dissimilarities and raw community composition with climate, space, soil and dung availability (Figure C.1 in Appendices). As expected, space and climate explained a large proportion of the variance in all cases, although in a few cases this latter factor only rendered significant results in partial dbRDAs. Dung availability and soil variables explained a relatively small proportion of the variance in B-C dissimilarities and community composition, mainly in both seasons of 2013. Variation of Sørensen dissimilarity in all campaigns was irregularly explained (and rarely significantly, see Figure C.1 in Appendices) solely by climate and space (from 71% to only 23%), with the only exception of the dry season of 2013, where dung availability also explained a marginal 4%.

3.4 Discussion

Although our results support the general expectation that water availability is a major factor structuring the diversity of communities in semiarid environments, they provide novel insights on how such relationship affects community structure through time. Even though dung beetle species richness shows a clear decrease with increasing aridity, contrary to our expectations abundance and evenness did not change along the gradient. And importantly, aridity fosters a gradual replacement of species, so the most arid areas are inhabited by distinct assemblages of dung beetle species adapted to the dry and resource-poor desert conditions, rather than poor subsets of the less arid areas (question Q1). But perhaps the most striking of our results is that diversity-aridity relationships show marked seasonal differences (question Q2). And further, these changes may be consistent between years, rather than stochastic. This, together with the somehow unexpected lack of predictive power of resource (dung) availability (question Q3) points to a strong environmental filtering as the major process behind not only of the distribution of dung beetles along the studied gradient, but also of their phenology.

Low water availability and/or precipitation is known to limit the diversity of many organisms (e.g. Sommer et al. 2010; Maestre et al. 2015), including dung beetles (e.g. Hortal et al. 2001; Tshikae et al. 2013a,b). Such negative relationship is however inexistent or even reversed in other organisms and/or systems (Polis 1991; Polis et al. 1997; Delsinne et al. 2010; Andersen et al. 2015). Water availability may determine species richness through two main mechanisms: physiological constraints (Chown et al. 2011) – thus following the water-energy hypothesis (Hawkins et al. 2003) and resource availability (Nichols et al. 2009; Tshikae et al. 2013b) – following the species-energy hypothesis (Wright 1983). While precipitation was directly related to species richness in our analysis, supporting the prediction of the water-energy hypothesis, dung availability did not correlate with species richness in our study. This is consistent with the claims that many other factors not directly related to resource availability may determine large-scale diversity gradients (e.g. Currie et al. 2004; Hurlbert & Jetz 2010). In the case of our gradient, the higher dung beetle richness at the semiarid end near the coast may be sustained by the increase in diversity of dung types provided by the appearance of cow herds (Lobo et al. 2006; Tshikae et al. 2013a). Further, some Aphodiinae species are generalist saprophages (Christensen & Dobson 1976; Dellacasa & Dellacasa 2006; Holter et al. 2009), so the higher availability of detritus resources (not quantified in this study) such as leaf litter in this area of higher plant production may be also promoting a higher richness.

Further, neither dung beetle abundance nor evenness showed any significant relationship with increasing aridity towards the Sahara. This result is also in contradiction with the species-energy hypothesis, and the general argument that greater productivity can maintain more individuals and therefore viable populations of a larger number of species (Hutchinson 1959; Brown 1981; Wright 1983). Instead, we found an unexpected decline in abundance at the semiarid end of the gradient in the wet season. This area was, by far, the one with higher availability of cattle dung (Table C.1 in Appendices), the richest resource present in the whole gradient, so it is unlikely that such low numbers are due to limited resource availability. Rather, the lower abundance of dung beetles in the coastal site may be partly explained by both land use intensification caused by cropland and urban spread (Davis et al. 2012; Nichols et al. 2013) and/or the higher salinity of the deep and superficial layers of the soil –that may deter burying dung beetle species to nest. Further, the large increase of beetle abundance at this area during the dry season was due to a single species, the aphodiid Anomius baeticus. This saprophagous beetle feeds on plant detritus (Sánchez-Piñero & Ávila 2004; Verdú & Galante 2004), which enables it to have massive population outbreaks in the dry season.

Strikingly, changes in community composition along the gradient follow an ordered replacement with aridity rather than a mere loss of species, although the rate of such replacement is progressively lower towards the Sahara. Most variation in composition was due to a balanced turnover in all surveys, with both Sørensen and B-C dissimilarities increasing towards the Mediterranean coast. Despite the decrease in species richness with increasing aridity, nestedness and gradient compositional changes were much smaller, remaining constant throughout the whole gradient. Such pre-eminence of species replacement indicates that the strong filtering imposed by aridity is not limited to the progressive inability of the species adapted to Mediterranean conditions to inhabit desert areas. Rather, there is a distinct pool of dung beetle species adapted to arid Saharan conditions (e.g. *Onthophagus transcaspicus*, *Scarabaeus aegyptiacus*, *Mendidius palmenticola* or *Calamosternus lucidus*; Baraud 1985), which progressively substitutes the semiarid elements of the communities. These species are seemingly adapted to the low -and stochastic- availability of resources, and form distinct communities compared to neighbouring areas with more mesic environments (Sánchez-Piñero et al. 2011). Extreme arid conditions determine the occurrence of a highly adapted biota in desert ecosystems (Arakaki et al. 2011), usually including a high proportion of endemics (LeHouérou 2001). Whether this pattern of pre-eminence of species replacement with increasing aridity is common in desert communities needs further investigation since no other studies partitioned beta diversity along aridity gradients before.

Importantly, although the general pattern of decrease in richness and balanced turnover along the gradient holds on for all surveys, our results also show important temporal variations. Indeed, the significance of the interactions of season and year with aridity evidence that the effect of water availability on species richness changes in time. Dung beetle faunas showed strong seasonal changes, with a steeper decline of richness with aridity in the wet season. In arid and semiarid environments this season is not only characterized by milder climate, but also by the higher abundance and quality of trophic resources (Hanski 1987). Further, the richness-precipitation relationship was weaker in 2013 than in 2014 −with no significant changes in species richness across the gradient in the dry season of the former year. These differences may be related to temporal changes in precipitation, as this factor was an important predictor of richness in spring but not in the dry season. The marked precipitation gradient along the transect in spring contrasts with the scarce difference in the amount of rain along the gradient at the end of the summer-early fall (from 46 to 13 and 22 to 13 mm of monthly precipitation, respectively). Spring precipitations allow a higher plant productivity that in turn results in more hydrated dung of better quality for nesting (Lumaret 1995), and ultimately higher reproductive success and the emergence of larger populations in the next generation. Indeed, annual precipitation was higher in 2013 than in 2012, allowing a higher abundance of dung beetles emerging the year after because of the higher reproductive success in 2013. Long-term data would be strongly needed to analyse these temporal changes in species richness and precipitation.

The spatial structure of dung beetle assemblages along the transect also varied in time. During the favourable conditions of the wet season species composition followed a structured sequence of replacement from the semiarid sites to the desert. This structure was disassembled in the harsher dry season, when assemblages were largely homogeneous, particularly in the arid and nearly hyperarid areas, and only the three sites in the semiarid end of the gradient showed compositional differences. Importantly, the temporal changes in composition at each site also varied in relation to aridity. Seasonal variations in species dissimilarity were lower as aridity increased, regardless of the relative effects of abundance. Similar findings have been reported for ant assemblages along an elevational gradient (Bishop et al. 2014), and corroborate the prediction that seasonal variations in assemblage composition are lower in habitats with more unpredictable climatic conditions (Hawkins et al. 2003). Hence, our results may indicate that desert communities inhabiting highly unpredictable arid habitats show a higher seasonal similarity than more mesic sites. This is likely due to the ability of some species to cope with the harsh desert conditions regardless of the season (Pierre 1958; Noy-Meir 1974; Heatwole 1996; Ghabbour & Mikhail 1997).

In contrast, these highly unpredictable arid habitats showed higher inter-annual compositional variations. However, these inter-annual differences were only significant when accounting for species abundances through the use of Bray-Curtis dissimilarities. This indicates that species composition at each season remains relatively constant from one year to another, and community structure only changes according to the variations in abundance. This is particularly true in the dry season, as revealed by the importance of the *Season*Aridity* interaction when analysing inter-annual variations in B-C dissimilarity. Differences in assemblage composition between two consecutive years in arid areas of SE Spain were mainly due to the differences in abundance of a single species, *Anomius baeticus*, whose abundance differed one order of magnitude between the two years (Sánchez-Piñero et al. 2011). Large differences between consecutive years in the abundance of particular species are characteristic of Mediterranean arid systems (Noy-Meir 1974; Sánchez-Piñero et al. 2011). Our results are consistent with the predictions that inter-annual variations in assemblage composition will be higher in more unpredictable habitats (Tonkin et al. 2017), although studies considering a greater number of years will be necessary, especially in the more unpredictable desert sites (Polis 1991).

Interestingly, changes in aridity through space and time also promote a spatio-temporal shift in the dominance of the two dung beetle subfamilies, Scarabaeinae and Aphodiinae. Aphodiinae are more abundant in the desert communities during the wet season (see also Abdel-Dayem et al. 2016), a change that may be related to a spatial shift in dung use strategies forced by environmental conditions. While all Mediterranean Scarabaeinae species are either paracoprids or telecoprids, the Aphodiinae include endocoprid, saprophagous and kleptocoprid species (Sánchez-Piñero 1994; González-Megías & Sánchez-Piñero 2003). Hence, the observed changes in relative abundance of Aphodiinae in the desert communities in the wet season, also reported in previous studies (Labidi et al. 2012; Abdel-Dayem et al. 2016), result in a functional shift from para- and telecoprid beetles to endocoprids and more generalist saprophagous species. Such shift also occurs in time, for Aphodiinae dominate in abundance during the dry season throughout the whole gradient (totalling > 95% of individuals in all local communities), a pattern also found in other Mediterranean dung beetle assemblages (e.g. Sánchez-Piñero & Ávila 2004; Sullivan et al. 2016). In fact, our results suggest that the ability of many Aphodiinae species to use different resources for feeding and nesting may allow them to maintain populations in more limiting dry conditions (both in more arid areas as well as in drier seasons), and their relative abundance will diminish when and where milder conditions allow Scarabaeinae to thrive and hold large populations and species-rich communities. Whether this is merely an effect of differences in environmental filtering between the two groups or by the eventual displacement of Scarabaeinae species by the superior competitive ability in dry conditions of the copro-saprophagous Aphodiinae remains an open question.

3.5 Concluding remarks

To summarize, climate-driven environmental filtering is the main process shaping the structure of dung beetle communities along the aridity gradient studied here. However, such filtering may be partly related to the availability of high-quality resources for feeding and nesting. In fact, the diversity-aridity relationship changes through time, determined by the highly variable seasonal and inter-annual patterns of precipitation, which in turn affect the quality and quantity of mammal dung. This results in a ordered replacement of functionally-different species in space and time, as generalist and saprophagous dung beetles become dominant in desert conditions and dryer seasons and years. That is, desert communities are not impoverished subsets of species from species-rich communities from milder climatic conditions, but unique combinations of species adapted to such conditions. Whether this pattern of pre-eminence of species replacement with increasing aridity is common in desert communities needs further investigation since no other studies partitioned beta diversity along aridity gradients before. The limited temporal extent of our study does not allow assessing the effects of large inter-annual changes in precipitation either, but it can however be expected that semiarid dung beetle faunas respond to the climate change-driven progressive aridification of East Mediterranean with large functional changes in community structure (see Tonkin et al. 2017). The loss of spatial structure of the dung beetle communities in the dry season for most of the gradient points to a reduction of richness and a higher homogeneity of assemblages if drought becomes a pervasive factor. Indeed, the expected lower seasonal changes in precipitation in progressively more arid conditions is likely to result in a generalized loss of diversity with climate change. But beyond these general patterns of change, the exact nature behind dung beetle responses to aridity remains elusive. Data on functional traits, physiological responses to aridity and long-term community variations are needed to understand the complex mechanisms behind it.

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4 Uncovering community assembly rules using taxonomic, phylogenetic and functional diversity: Dung beetle assemblage structure along an aridity gradient in space and time

4.1 Introduction

Taxonomic diversity is not sufficient to explain biogeographical diversity patterns (Villéger et al. 2013). Functional diversity is essential to reveal the mechanisms behind those patterns (Violle et al. 2014, but see Cadotte & Tucker 2017). However, functional approaches are still unevenly used among different taxa, mainly due to a lack of adequate trait data (Moretti et al. 2017). When available, phylogenetic data can shed light on evolutionary history, another of the factors affecting these biogeographical diversity patterns (Beck et al. 2012; Diniz-Filho et al. 2013; but see Díaz et al. 2013). These broad-scale patterns emerge from the process of differential filtering of the regional pool into local communities (Cornell & Harrison 2014). This filtering process is a complex balance between two major community assembly rules: limiting similarity (driven by biotic interactions) and environmental filtering (driven by abiotic stresses) (Guisan & Rahbek 2011; Hortal et al. 2012, but see Perronne et al. 2017). Most probably, these two rules act across taxonomic levels (species, genera, families) and spatial and temporal scales (Perronne et al. 2017). Yet, which one prevails at each scale depends on the intensity of their drivers.

Limiting similarity is the mechanism by which the competition for a limiting resource selects coexisting individuals (and species) with differing niches (i.e. different combination of trait values), as a result of the competitive exclusion among species (Mason et al. 2013 and references therein). On the other hand, environmental filtering is a mechanism where abiotic variables impose a stress (i.e. reduction of fitness) that selects individuals according to their niches, slowing down the pace of competition and allowing for the co-existence of functionally similar species (Mason et al. 2013). In this manner, the greater the abiotic stress along an environmental gradient, the stronger the selection (i.e. abiotic filtering) of species with trait values that allow them to thrive around the environmental optima (Mason et al. 2013 and references therein). This makes abiotic stress gradients (either spatial or temporal) perfect to test the relative importance of these two community assembly rules. In fact, all other factors being equal (i.e. same regional pool and no significant limitations to dispersal) a stress gradient provides a natural experiment (Sundqvist et al. 2013) to test if local communities are assembled mainly due to abiotic filtering (narrowing the distribution of community trait values around an optimum) or biotic interactions (leading to an overdispersion of trait values to avoid overlap and competition) (Pausas & Verdú 2010; Shevtsov et al. 2013).

Biologically meaningful and steep gradients have a strong power to disentangle the effects of limiting similarity and environmental filtering processes (Lavorel & Garnier 2002). Among many other environmental gradients, such as temperature, latitude (a combination of temperature, precipitation and light intensity and temporal distribution), altitude (a similar combination to that of latitude, Rahbek 1995), trophic resource availability, etc., water stands out as an essential resource for the development of life. Thus, water stands out as an axial ecological factor, especially in warm temperate and tropical regions (Hawkins et al. 2003). Desert edges, where water scarcity (aridity) becomes an important abiotic stress (Polis 1991), are therefore particularly appropriate ecotones to study community assembly processes.

Species traits are key to understand the relative importance of community assembly rules. Functional traits can be divided into effect and response traits (Lavorel & Garnier 2002; Violle et al. 2007). Effect traits determine how a species modifies its environment, including individuals of the same species, other species and its whole ecosystem. Response traits are the reflection of the evolutionary forces and environmental drivers (including biotic interactions) that shape the potential niche of each species. These traits shape species niches, determine their suitable habitat, geographic distributions (weighted by dispersal) and, thus, their presence (and abundance) in local communities. Therefore, response traits are essential to understand the structure and assembly of local communities. Unfortunately our knowledge of which traits respond to environment and how is very poor, especially for certain taxonomic groups such as invertebrates (Moretti et al. 2017). Because of this, it is suggested that phylogenetic relatedness can be used to infer trait similarity, assuming enough phylogenetic trait conservatism (Bello et al. 2017; but see Díaz et al. 2013).

Indeed, the covariation of taxonomy (a phylogenetic hypothesis), phylogeny and multi-trait similarity between species is yet to be examined in most taxa, regions and time scales. There is a strong and growing interest in quantifying the complementarity of results obtained with these three sources of information for three reasons (Arnan et al. 2016): a) maximizing conservation of known and unknown diversity, b) better understanding ecosystem productivity and stability and c) providing insights into the importance of deterministic or stochastic processes in community assembly. Moreover, the methodological possibility of using any of them as proxies for the rest when they are missing is very promising, but their reliability should be tested in each study system. For most taxa, taxonomic information is available, phylogenetic relations are being developed and trait information is still rarely available (not to mention their functional meaning, see Chapter 1).

Scarabaeidae dung beetles are one of the many taxonomic groups for which knolewdge on traits and functional responses to environmental drivers are poorly known (Buse et al. 2018). On the other hand, it is a suitable group for biogeographical studies as their taxonomy is relatively stable and well-developed, their phylogeny is well known in certain regions, and efforts are being done towards a better understanding of which traits respond to environment and how (Buse et al. 2018). However, rather than response traits, dung beetle effect traits are more widely studied, having been related to their impact in grassland management (Nervo et al. 2017), their possible contribution to climate change amelioration (Slade et al. 2016 and references therein), secondary seed dispersal (Griffiths et al. 2015) and several other ecosystem functions (Nichols et al. 2008).

Here we study the temporal and spatial variations in functional (i.e. trait) and phylogenetic diversity of dung beetle communities along a steep water availability gradient (i.e. aridity, and other associated variables: dung availability, vegetation cover and height and soil structure variables; see Chapter 3) in Eastern

Morocco, spanning 400 km from coastal Mediterranean to desert Saharan conditions.

The high species turnover along this gradient found elsewhere (see Chapter 3) leads to *a priori* discard the existence a phylogenetically nested pattern along it. Indeed, the replacement between species of two distinct subfamilies (Scarabaeinae and Aphodiinae) indicates that a phylogenetic turnover of deeply rooted lineages will also occur. On the other hand, the functional structure of the communities may either remain identical with increasing aridity, or loose intermediate response strategies but keeping the main functional strategies to deal with increasing aridity. Both patterns lead to high functional nestedness but different niche splitting, which we account for in question Q3. Two communities with similar overall functional strategies (i.e. same multi-trait functional volume) but different species richness will differ in the trait distance between nearest species, as the species from the poor community will leave gaps in the functional space that are occupied by intermediate species in the species-rich community. Theory predicts that increasingly stressful environments (through both space and time) will filter out most potential colonizers, so the resulting local communities will be composed by species with more similar response traits than expected from a random subset of species from the regional pool (e.g. Kluge & Kessler 2011; Mudrák et al. 2016). In contrast, a more relaxed environment will allow a greater relative importance of biotic interactions in the assembly of local communities, so under the traditional focus on competition, limited similarity processes will select response traits that are more dissimilar between species than it would be expected from a random subset of the regional pool (but see Pavoine & Bonsall 2011; Cadotte & Tucker 2017).

We aim to answer four specific questions: (Q1) Does increasing aridity filter trait values and/or lineages resulting in a functional and/or phylogenetic nested pattern of communities? (Q2) Do taxonomic, phylogenetic and functional patterns covary along the gradient? (Q3) Are dung beetle communities structured by either environmental filtering, limiting similarity, or both? (Q4) Does increasing aridity create a directional change in certain traits?

Question Q1 was investigated by analyzing functional and phylogenetic beta diversity and their partition in turnover and nestedness components between consecutive pairs of sites along the aridity gradient. To complement Q1, in Q2 we investigate the covariation of taxonomic, functional and phylogenetic beta diversity. To answer question Q3 we analyzed patterns of functional and phylogenetic Standard Effect Sizes of Mean Pairwise Distance and Mean Nearest Taxon Distance. The analysis of the patterns in Q1 and Q2 and mechanisms in Q3 are based on analysis using all traits together and the ultimate biological origin of these patterns is difficult to perceive. Thus in Q4 we assess variations in trait values through the Community Weighted Mean, to identify any response trait subject to environmental filtering that allows species to thrive in the harsh desert conditions. Should we identify any trait following such pattern, we will assess their contribution to the patterns found in Q1 and Q2.

4.2 Materials and methods

Study area

We surveyed a ca. 400 km linear transect following a strong aridity gradient parallel to the Morocco-Algerian border from the semiarid Mediterranean coast towards the hyperarid Sahara desert (see Chapter 3, for more details). This aridity gradient is characterized by a threefold difference in annual rainfall (from ca. 350 mm at the coastal semiarid area to 100 mm at the nearly hyperarid Saharan end of the gradient). The gradient is under a Mediterranean precipitation regime with a typical dry season (summer drought) and a rainy season in November-March (Belda et al. 2014). For details on the availability of different types of livestock, grazing intensity, soil type and vegetation type, height and cover along the gradient see Chapter 3.

Taxonomic data

Dung beetles were collected during four survey campaigns: two in the wet season (April 2013 and 2014) and two in the dry season (September 2013 and 2014). These two seasons represent the two peaks of dung beetle richness and abundance in the Mediterranean region (Hortal & Lobo 2005). Annual precipitation was about a negligible 20% higher in the wet season of 2012–2013 than in 2013–2014. In each campaign we surveyed 10 sampling sites, located every ca. 40 km along the transect (Figure 3.1 in Chapter 3). Dung beetle collection was carried out under research permits Reference Numbers 01/2013 HCEFLCD/DLCDPN/DPRN/CFF and 01/2014 HCEFLCD/DLCDPN/DPRN/CFF issued by the Haut Commisariat aux Eaux et Forêts et à Lutte Contre la Désertification (Morocco). Each sampling site consisted in two replicates, placed 1 km apart. Each replicate consisted of five baited pitfall traps baited with fresh cow dung (thus, 100 traps per sampling campaign) separated 20 m one from another (see details of trap design and bait in Chapter 3). Traps were active for a standard period of 72 h (Labidi et al.

2012; Amraoui et al. 2016) and collected insects were immediately transferred to 96% ethanol in the field and transported to the lab for identification (following Baraud 1985), DNA extraction if previously not available (see details below) and trait measurement (see details below).

Phylogenetic data

Phylogenetic information come from a phylogenetic inference of 202 Scarabaeidae species inhabiting the Palearctic (J. Calatayud, J.E. Uribe, N. Guil, I. deCastro-Arrazola, R. Zardoya, J. Hortal et al., unpublished). Briefly, this phylogenetic reconstruction is based on one nuclear (28S) and two mitochondrial (COI and COII) makers that were used to conduct a Bayesian inference. Molecular dating was based on five fossil calibration points according to Ahrens et al. (2014). To have into account phylogenetic uncertainties we randomly selected 1000 phylogenetic trees from the posterior distribution after the burn-in period. These phylogenetic hypotheses contained 42 species out of a total of 61 species found in the surveys (69%). Missing species (19 species, 31%) were included in the phylogenetic trees using the SUNPLIN software (Martins et al. 2013). Here, the species are randomly inserted in tree below the most derived clade where they can be unequivocally assigned based on taxonomic information (Rangel et al. 2015). These random insertions were done 1000 times for each molecular tree. Thus, we obtained 10^6 trees from which we randomly selected 100 trees to use in subsequent analyses.

Functional data

We selected several dung beetle traits that could potentially present responses to aridity based on the hypotheses described in Chapter 1. Here, although the response of dung beetles to aridity is unknown, it is possible to identify traits that could respond to it by decomposing it into simpler variables. Aridity is defined as the ratio between precipitation and evapotranspiration (Trabucco & Zomer 2009). Evapotranspiration in turn depends on temperature, radiation, wind, vegetation cover etc. Therefore, ideally traits reflecting the functional response of dung beetles to increasing aridity should encompass the following aspects of their biology: physiology (i.e. thermoregulation, water balance traits), trophic habit (fast drying dung can promote trophic generalism, including the ability to process dry dung and saprophagy), dispersal (fast drying dung can promote traits related to a fast and/or distant arrival at fresh dung), reproduction (a short season with suitable atmospheric conditions can promote fast gonadal development, but other strategies have been reported; i.e. *Scarabaeus puncticollis* may develop its gonads during adult activity in September-October, emerging the next spring as a nearly mature adult; González-Megías & Sánchez-Piñero, unpublished data) and phenology (harsh atmospheric conditions can promote a shift in seasonality, and modify the diurnal/nocturnal activity patterns).

In total, we selected 23 traits (see Table 4.1) that were either measured or gathered from the literature. All morphological traits were measured with a Leica M165C microscope, using Leica Application Suite LAS V4.0 with the Z-builder module to process the images and obtain the measurements. Not all traits could be measured in all 61 species. Adult trophic habits and dung relocation strategy for feeding purposes (both qualitative traits) were obtained from the literature and our own field observations. We did not consider reproductive dung relocation strategy because there is a wide diversity of behaviors, especially among Aphodiinae species, whose larvae can develop in simple nests in the dung pad, in the dung-soil interphase, as kleptocoprid larvae and even with a soil dwelling saprophagous habit. For these categorical traits values could be assigned with some confidence to all species. However, some quantitative morphological traits could not be measured in a few very rare species, with 1-2 captured individuals in all campaigns (*Mendidaphodius sitifoides*, *Pleurophorus pannonicus*, *Rhyssemus sp nova*, *R. bedeli* and *R. vaulogeri*), because of their use for obtaining molecular data, their destination in a reference collection, their bad conservation or their minute size, which was under the detection threshold of the tools used in some measurements.

Uneven distribution of missing traits across taxa could lead to biases in results and their interpretation (Plas et al. 2017). As mentioned, rare species had missing traits, but have little effect (compared to species with hundreds or thousands of individuals) on abundance weighted metrics (MPD, MNTD and CWM explained below). However, they could potentially have an effect on incidence-based metrics like Sorensen beta diversity (Perronne et al. 2017; Violle et al. 2017). Therefore, traits with available measured values for less than 80% of the total collected species were discarded as they would not allow computing functional metrics in several communities with low taxonomic richness (Pakeman 2014). Among the traits that were finally discarded perhaps the most interesting were: dung relocation strategy for reproduction, larval trophic traits and, above all, diel activity (diurnal/crepuscular/nocturnal).

In total, 92% of species had values for all traits and 93.33% of them had values for most quantitative traits. We aimed at measuring 10 individuals per species (Bolnick et al. 2011) and finally 80% of species had measures for 5 or more individid-

Trait	Category	Unit	Measurement description or factor levels
Feeding relocation strategy	Feeding	Qualitative, fuzzy coded	Endocoprid, paracoprid and/or telecoprid
Adult trophic preference	Feeding	Qualitative, fuzzy coded	Saprophagous, coprophagous, micophagous and/or necrophagous
Dry biomass	Morphological	Quantitative	Weight of whole individual after drying in oven at 60°C for 72h
Fresh weight	Morphological	Quantitative	Weight of whole individual directly from alcohol storage, gently dried on the outside with a paper tissue
Body length	only used for calculations		Sum of Head length + Pronotum length + Elytra length
Head length	Morphological	Quantitative	Distance from clypeus to vertex (no horns included)
Head width	Morphological	Quantitative	Maximum head width, normally at genas
Pronotum height	Morphological	Quantitative	Maximum distance between pronotum discus to point between protibia coxas
Pronotum length	Morphological	Quantitative	Distance along the individuals longitudinal axis
Pronotum width	Morphological	Quantitative	Maximum pronotum width
Abdomen height	Morphological	Quantitative	Maximum abdomen height
Elytrum area	Morphological	Quantitative	Area measured with polyline tool to outline the whole elytrum
Elytra length	Morphological	Quantitative	Distance along the longitudinal axis, from insertion (scutellum included) to apex (pygidium not included)
Elytra width	Morphological	Quantitative	Maximum elytra width, normally at the callus humeralis
Elytrum weight	Morphological	Quantitative	Weight of single elytrum (cut off from joint) after drying in oven at 60°C for 72h
Protibia area	Reproduction	Quantitative	Area measured with polyline tool to outline the whole protibia
Protibia length	Reproduction	Quantitative	Distance from joint with profemur to insertion of tarsi
Protibia tooth length	Reproduction	Quantitative	Distance from insertion of spine to apex of first tooth of protibia
Metatibia area	Reproduction	Quantitative	Area measured with polyline tool to outline the whole metatibia
Metatibia length straight	Reproduction	Quantitative	Distance from insertion with metafemur to insertion of tarsi in a straight line
Metatibia length curved	Reproduction	Quantitative	Distance from insertion with metafemur to insertion of tarsi following the curvature of metatibia
Wing area	Dispersal	Quantitative	Wing (cut off from joint) area measured with polyline tool to outline the whole wing
Wing length	Dispersal	Quantitative	Maximum distance from joint to wing apex
Wing load	Dispersal	Quantitative	Wing area / dry biomass

Table 4.1: Description of trait measurements. Categorization as *reproduction* traits is just a hypothesis. Fuzzy coding of qualitative traits allows to reflect intraspecific variability/plasticity with porcentual assignment of several categories to a single species (ie. *Anomius baeticus* 40% coprophagous and 60% saprophagous). All quantitative traits were measured on pictures (see text for more details).

uals due to the limited numbers of individuals that were gathered (Bishop et al. 2015, but see Griffiths et al. 2016). The individuals measured for each species were chosen from as much localities as possible, depending on their distribution along the gradient.

Analyses

Analyses can be divided into two parts: phylogenetic and functional metrics (Figure 4.1). Both follow the same background structure although they differ in some steps due to the different nature of the data (trees for phylogenetic data and matrices for functional trait data) and the limitations of the complex algebra enabling the calculation of multi-trait functional beta diversity. We defined our species pool as all species sampled in a season (dry vs wet), thus, we consider two species pools and all metrics were calculated based on these pools. This allows for a finer analysis within each season, as seasons have completely different faunas (Chapter 3). Having only one pool would blur any within-season functional or phylogenetic pattern when comparing observed communities to randomly assembled communities from a species pool that is too widely defined.

Decoupling phylogenetic and functional variations

Phylogenetic differences have been suggested as appropriate data to cover missing functional trait data in community ecology (but see Díaz et al. 2013), especially in studies focusing on environmental gradients and trying to disentangle community assembly rules (see references in Bello et al. 2017). However, these two sources of information simultaneously describe distances among species, leading to partially redundant results when using the same information both as functional and phylogenetic distance. To avoid this partial redundancy and, thus, to obtain non-overlapping results from phylogenetic and functional data, we performed a procedure that provides independent separation of functional and phylogenetic distances among species using the ℝ function decouple (Bello et al. 2017). As suggested by Bello et al. 2017 we checked whether the shared functional and phylogenetic distance (jointFPdist) was small (11-12% in our communities). We accordingly chose splitting the distance between species in communities in the whole fraction contributed by phylogenetic relations (Phylogenetic distance, Pdist) and the pure fraction of functional distances contributed by traits (decoupled Functional distance, dcFdist). All distance matrices obtained in the decoupling process and all other analysis steps were Euclidean.

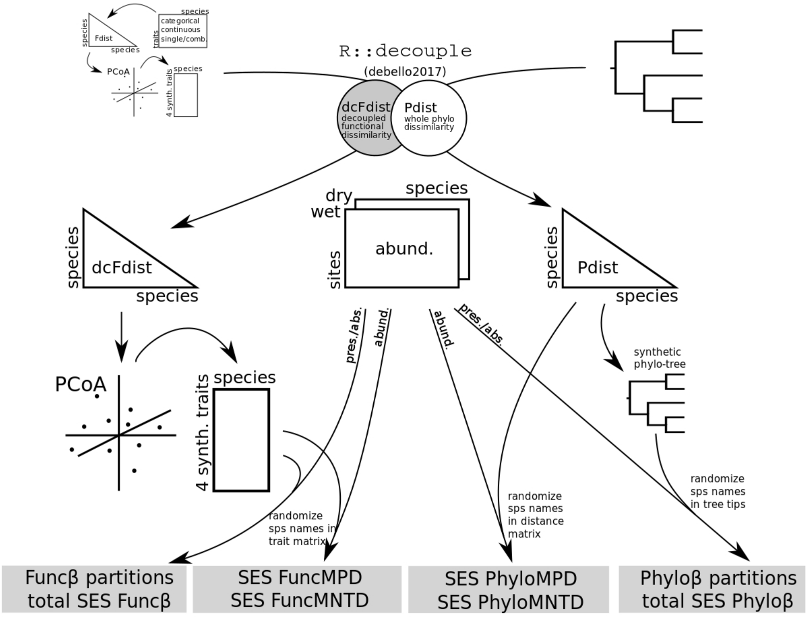

Figure 4.1: Diagram showing the data used and the analysis steps to obtain the different functional and phylogenetic metrics.

Metrics of phylogenetic and functional diversity

We used Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD) to describe both the phylogenetic and functional diversity of each community. These are two commonly used phylogenetic and functional metrics that describe the average distance between all pairs of species in the community and nearest species respectively (Kembel et al. 2010). When weighted by abundance, MPD describes the average distance between pairs of individuals taken at random from the community and MNTD describes the average distance between nearest individuals. Although these two metrics may correlate to some degree, phylogenetic MPD is appropriate to answer questions regarding communities with species related through deep nodes in the phylogenetic tree (our two subfamilies Scarabaeinae and Aphodiinae), while phylogenetic MNTD helps with phylogenetic diversity represented by terminal branching of the trees (congeneric species in the same community) (Kembel et al. 2010). A parallel explanation applies to functional MPD and MNTD, when considering distances between species in a multi-trait space. We used the pure phylogenetic distances (Pdist) to calculate phylogenetic MDP and phylogenetic MNTD and the dcFdist to calculate functional MPD and functional MNTD (Figure 4.1) using the available R package picante (Kembel et al. 2010). The four metrics were abundance weighted as very different proportions of the same species occur in different communities along the gradient, especially during the dry season (Chapter 3).

Assessing changes in community structure along the gradient

To calculate the overlap between pairs of communities we used functional beta diversity and phylogenetic beta diversity using the R package betapart (Baselga et al. 2017). To calculate phylogenetic beta we backtransformed the Pdist triangular matrix into a synthetic phylogenetic tree that resembles the original tree and combined it with the species incidence matrices. On the functional side, we applied a Principal Coordinates Analysis (PCoA) and used its first eigenvectors as *orthogonal synthetic traits*. For each campaign (season and year) we selected the appropriate number of synthetic traits limited by the maximum number of dimensions to compute hypervolume overlap. This is, algebraic limitations (max dimensions = 4) and the minimum number of species in any of the compared sites (max dimensions = richness − 1) (Villéger et al. 2013; Baselga et al. 2017).

We partitioned total beta diversity (both functional and phylogenetic) into its turnover and nested components (Villéger et al. 2013) and calculate the standard effect size (see details below) for total diversity and each of the partitions. In order to present relevant comparisons of the ten sites along the aridity gradient for each campaign we calculated mean pairwise beta diversity of each site with all others in the gradient (thus, ten mean pairwise beta diversities) and show the selected values of total and partitions of beta diversity between consecutive pairs of sites (thus, nine consecutive beta diversities).

Null models

For both functional and phylogenetic aspects of diversity and each species pool (i.e. species sampled in each campaign, as explained above) we applied the following null models to build virtual communities under stochastic community assemblage rules.

To calculate the expected values of functional metrics we used a *random traits* null model that responds to *what would the functional diversity be if the species had different trait values?*. To do this, we randomized trait values (within each trait) among the species in the species pool and then used it in combination with the observed incidence or abundance in the species × sites matrix. This method ensures that observed and virtual communities have identical taxonomic richness and abundance distributions, although it may potentially assign trait values of dominant species to rare ones (Perronne et al. 2017).

To calculate the expected values of phylogenetic metrics we used a *random tip labels* null model that responds to *what would the phylogenetic diversity be if the species were differently related to each other?.* To do this, we randomized tip names within the tree of the species pool and then used it in combination with the original and unaltered incidence or abundance *species × sites* matrix. This method also ensures that species richness and abundance distribution remain unchanged between observed and virtual communities.

All null models were run 100 times, thus obtaining 100 expected values for each functional and phylogenetic metric, from which we calculated avgExp and sdExp, and finally the SES.

Assessing standardized effect size

We calculated the standard effect size (SES) to evaluate whether of the observed functional and phylogenetic diversity metrics depart from what would be expected by a stochastic community assemblage process (see null model details below). The use of SES also removes the effect of richness on functional or phylogenetic diversity indices, in particular MPD and MNTD.

$$\mathrm{SES} = (\mathrm{Obs} - \mathrm{avgExp})/\mathrm{sdExp} \tag{4.1}$$

where

Obs	observed values of the given metric
avgExp	average of expected values of the same diversity metric for communities built under a null community assembly model
sdExp	standard deviation of expected values

Complementary analyses

Correlations between the three aspects of beta diversity (taxonomic, functional and phylogenetic) were calculated using Mantel tests. Whole triangular distance matrices were used separately for the three partitions of beta diversity (total, turnover and nestedness partitions).

Finally, Community Weighted Mean (CWM) was computed for all traits and all sites during all four campaigns. In order to find cues of investigate the mechanism of environmental filtering on species response traits, correlations between CWMs and aridity were examined to find any significant trend with increasing environmental filter pressure.

4.3 Results

We captured 70,326 individuals of 61 dung beetle species in the four sampling campaigns (9,627 individuals of 29 Scarabaeinae species and 60,699 individuals of 32 Aphodiinae species; see Table C.5 in Appendices). Overall, dung beetle abundance and richness were slightly higher in 2014 compared to 2013 for both seasons (Figure 3.2, in Chapter 3). We measured 23 traits on 347 individuals (average 5.7 individuals per species, Bishop et al. 2015) leading to a total of more than 7000 measurements, complemented with further categorical traits gathered from literature or our own observations in the field (Table D.1 in Appendices).

(Q1) Does increasing aridity filter trait values and/or lineages resulting in a functional and/or phylogenetic nested pattern of communities?

Both dry seasons show about two thirds of the phylogenetic beta diversity (Figure 4.2a,b) between pairs of consecutive sites in the wet season (Figure 4.2c,d) indicating an overall clustering of lineages during the harsher summer conditions. Moreover, in the dry season of 2013 most of the total phylogenetic beta diversity between consecutive sites was due to nestedness (Figure 4.2a), which points out to the presence of few lineages along the whole gradient. On the other hand, during the rest of the campaigns phylogenetic beta diversity presents a much larger proportion of turnover (ca. 75%). Surprisingly, phylogenetic beta diversity between sites 7 and 8 in the wet season of 2013 (Figure 4.2c) shows large total beta and turnover proportions (80-90%), evidencing a replacement of lineages. The same comparison between these two consecutive sites during the wet 2014

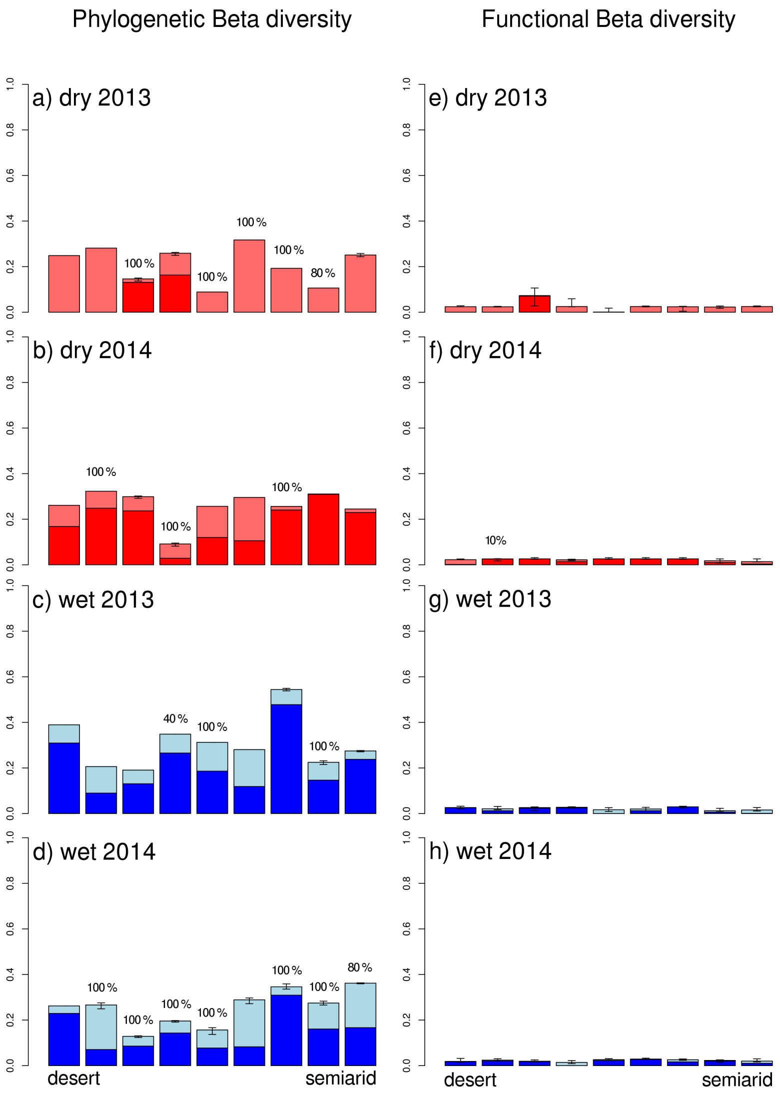

Figure 4.2: Functional beta diversity for dung beetle communities in the wet and dry seasons during two consecutive years along an aridity gradient from the Mediterranean sea to the Sahara desert. Turnover (dark colors) and nestedness (light colors) partitions of beta diversity are shown. Error bars represent the standard error of results due to phylogenetic uncertainty (more than one phylogenetic tree used) which affects functional results via the decoupling process. Consequently, each total beta diversity value (bar height) has more than one significance values, here expressed as percentage of significant results ($p - \text{value} < 0.05$).

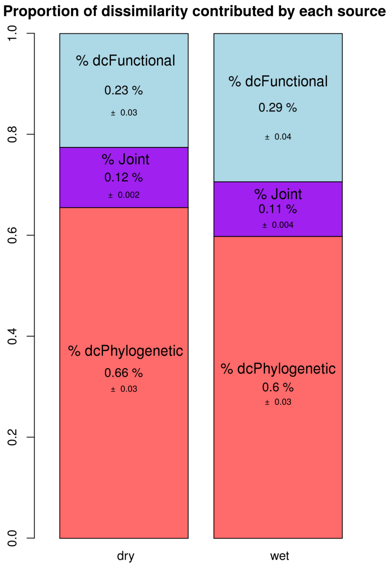

Figure 4.3: Proportions of the different sources of functional and phylogenetic distance between species of dung beetles in two regional pools (wet and dry season) along a threefold aridity gradient from the Mediterranean sea to the Sahara desert. Standard error of results due to phylogenetic uncertainty (more than one phylogenetic tree used) are shown under the percentage of each portion.

Beta	Campaign	Taxonomic vs. Phylogenetic		Taxonomic vs. Functional		Phylogenetic vs. Functional	
total	*dry2013*	0.945	***	0.466	**	0.548	***
	dry2014	0.893	***	0.489	**	0.419	**
	wet2013	0.972	***	0.732	***	0.777	***
	wet2014	0.925	***	0.634	***	0.588	**
nestedness	*dry2013*	0.956	***	0.678	***	0.757	***
	dry2014	0.672	***	0.165	ns	-0.113	ns
	wet2013	0.798	***	-0.103	ns	-0.265	ns
	wet2014	0.690	***	-0.003	ns	-0.219	ns
turnover	*dry2013*	0.973	***	0.739	***	0.768	***
	dry2014	0.774	***	0.524	***	0.453	**
	wet2013	0.929	***	0.717	**	0.612	**
	wet2014	0.940	***	0.569	***	0.483	**

Table 4.2: Mantel correlations and p-values for beta diversities taken by pairs of taxonomic, functional and phylogenetic aspects of diversity for dung beetle communities in the wet and dry seasons during two consecutive years along a threefold aridity gradient from the Mediterranean sea to the Sahara desert. Total beta diversity and its nestedness and turnover partitions are shown.

campaign (Figure 4.2d) shows an even higher (and highly significant) turnover proportion, although the total beta diversity is more similar to the rest of the pairwise comparisons in the gradient. These high turnover rates between sites 7 and 8 are probably due to a fast replacement of Aphodiinae species in site 7 to a Scarabaeinae-dominated community in site 8, with a strong turnover of lineages between those consecutive sites (Figure D.2 in Appendices).

Functional beta diversity (Figure 4.2e-h) is negligible compared to phylogenetic beta diversity (Figure 4.2a-d). None of the four campaigns reach 0.1 values, about a fourth or a fifth of phylogenetic beta diversity, indicating a high similarity in the trait space occupied by consecutive sites along the aridity gradient. The proportions of turnover and nestedness are similar to that of phylogenetic beta diversity. That is, the dry 2013 campaign (Figure 4.2e) has the highest nestedness and the rest of the campaigns are dominated by turnover.

(Q2) Do taxonomic, phylogenetic and functional patterns covary along the gradient?

While phylogeny contributes with up to 66% of dissimilarity between species, trait information contributes with a maximum of 29%. Finally a mere 11-12% of species dissimilarity is jointly explained by traits and phylogeny in both seasons, indicating that using both sources of information together may be appropriate (see Bello et al. 2017 for a warning on combining functional and phylogenetic data when overlap is very large). Regarding seasons, phylogenetic information contributes to a slightly higher proportion of species dissimilarities in the dry (66%) than in the wet season (60%). In contrast, dissimilarities among species in the regional pool are slightly better explained by functional information during the wet (29%) than the dry season (23%).

Taxonomic and phylogenetic beta diversities were highly correlated in all campaigns (Table 4.2) as expected from a well-established taxonomy that follows a phylogenetic hypothesis (but see Arnan et al. 2016). This is especially true for total beta diversity and the turnover component where covariation showed highly significant Mantel R values, well over 0.9 (the dry 2014 campaign being the only one with slightly lower values). The nestedness component of beta diversity had lower covariation, not only between taxonomic and phylogenetic beta diversities but with any of the two with functional beta diversity, in which most values were in the -0.3 to 0.3 range (and accordingly not significant). Again, the nestedness component was exceptionally high during the dry 2013 campaign, in which covariation of the three facets of diversity (taxonomic, functional and phylogenetic) was indeed high (Table 4.2). In general, the covariation of any two facets of beta diversity was higher for 2013 than for the slightly more species rich and individual abundant campaigns of 2014.

(Q3) Which community assembly mechanism drives dung beetle community structure in arid areas, environmental filtering or limiting similarity?

SES phylogenetic MPD

The four campaigns have most of their SES phylogenetic MPD values below 0, thus indicating a trend for phylogenetic clustering (only few lineages are present in each site). However, few communities have significant values (see percentages of significance in Figure 4.4a). There is a general trend in the dry season to be stable at a lower than expected value of phylogenetic MPD with an increase towards zero (random selection of lineages) approaching the semiarid end of the gradient. Surprisingly, there is a significant clustering in site 8 during the wet season, indicating a filtering-out of lineages that can be partly explained by a great dominance of Scarabaeinae species and a lack of Aphodiinae species, which is supported by the power of MPD to detect changes in deep nodes of phylogenetic trees.

SES phylogenetic MNTD

Phylogenetic MNTD shows patterns of both clustering and overdispersion in the tips of the trees. This can help understand why the dry season has values very near random selection (Figure 4.4b). During this season communities at the semiarid end of the aridity gradient show positive values (i.e. mean phylogenetic distance between nearest species is bigger than expected) indicating that species in these semiarid communities during the dry period are composed by single species in each genus. On the contrary, the wet season has stable low values, indicating that more congeneric species (clustering at tree tips) appear in the same community, negative SES MNTD values become significant for some of the trees used (see percentages in Figure 4.4b).

SES functional MPD

Functional MPD (Figure 4.4c) shows clear different patterns for the dry and the wet season, but strikingly similar patterns for the two years. The dry season has stable and significant negative values (less trait diversity than expected by chance) indicating a strong environmental filtering of similar traits in the communities. The surprising drop from the positive values in the desert to intermediate sites is probably an artifact due to the low number of species in the desert communities. In contrast, the wet season has positive values in sites 4, 5 and 9 that approach significance (although not significant when applying the rank method used by SES MPD; Kembel et al. 2010).

SES functional MNTD

The pattern of functional MNTD (Figure 4.4d) is similar to that of functional MPD (Figure 4.4c). However, the unstable values of the wet season show even greater fluctuations. In other words, in some of the sites during the wet season, the trait volume is kept (similar MPD) but intermediate trait values are lost (lower MNTD) leaving gaps, lowering the density of the trait volume.

(Q4) Does increasing aridity create a directional change in certain traits?

Very few quantitative traits had clear and significant directional patterns along the aridity gradient (Figure D.1 in Appendices). Community Weighted Mean of wing loading (wing area / dry mass of the individual) had a clear interaction with aridity both in time (seasons) and space (along the aridity gradient). During the dry season wing load was low (large wings relative to dry mass) except for the most arid site (Figure 4.5). On the other hand, during the wet season, wing load had a declining pattern from high CWM values (small wings) to low values (big wings) in the driest sites (Pearson correlation r -0.73 and -0.85 for wet season of years 2013 and 2014 respectively). That is, in average, the individuals of communities in dry sites and season had larger wings (relative to dry mass) than those of the wet season and the less arid sites. This holds true for both Scarabaeinae and Aphodiinae species, which show very similar patterns (Figure 4.5).

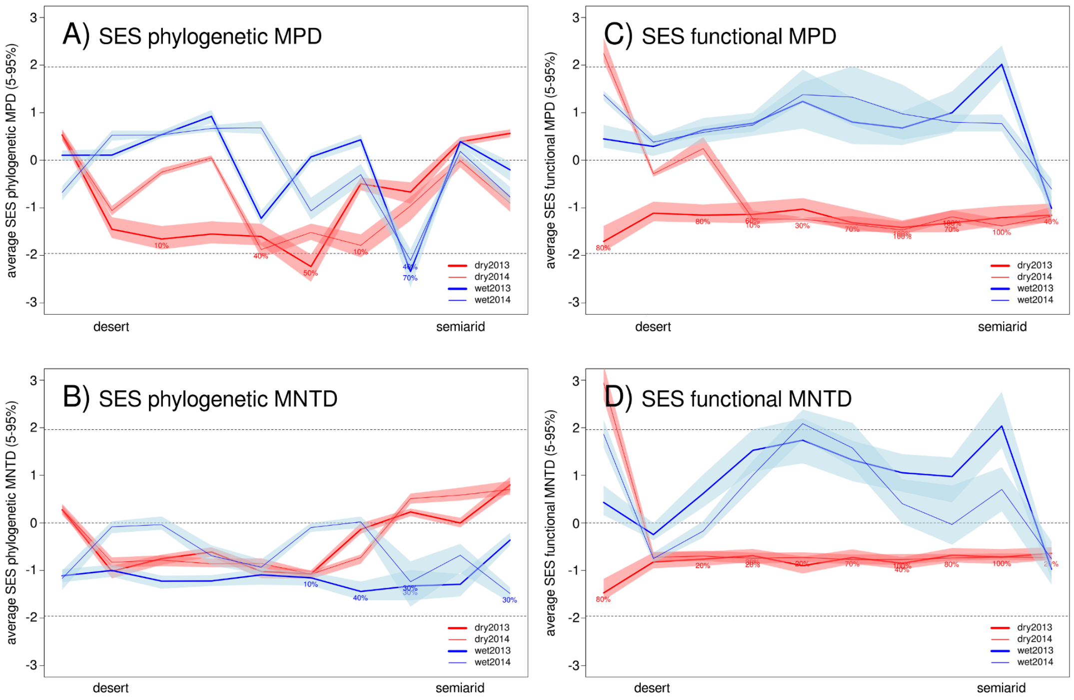

Figure 4.4: Phylogenetic and Functional MPD and MNTD for dung beetle communities in the wet and dry seasons during two consecutive years along a threefold aridity gradient from the Mediterranean sea to the Sahara desert. Confident intervals (5-95%) represent the variation of results due to phylogenetic uncertainty (more than one phylogenetic tree used) which affects functional results via the decoupling process. Consecuently, each point has more than one significance values, here expressed as percentage of significant results $(p - \text{value} < 0.05)$.

Community weighted means of qualitative traits regarding dung relocation strategy and adult trophic habit showed evident patterns but few significant correlations with aridity. Alike wing loading, aridity favored similar functional types in the most arid conditions of the dry season and the desert sites (Figure 4.5). Saprophagy had a strikingly stable and large representation (up to 50%, y-axis is interpretable as proportion of individuals of each strategy) in communities affected by severe aridity. Coprophagous individuals show complementary proportions along the gradient, dominating absolutely the semiarid sites during the wet season (80-100%), but decreasing steadily with increasing aridity down to 50% in the driest sites (Pearson correlation $r = -0.94$ and -0.89 for 2013 and 2014 respectively although only significant at $p\text{-value} < 0.05$ for 2014). Species with facultative necrophagous habits are scattered but present in very low numbers along the whole gradient.

A similar pattern was found for dung relocation strategies (Figure 4.5). While paracoprids dominate the communities in the semiarid end of the gradient during the wet season, their presence progressively declines with increasing aridity and disappears in site 2 (nearly the driest site). Complementarily, the abundance of endocoprids increases with aridity (Pearson correlation $r = 0.72$ and 0.63 for the wet season of 2013 and 2014 respectively although only significant for 2014), reaching an undoubtable dominance (near 100%) during the whole dry season. Telecoprid relocation strategy only had a anecdotic but large presence only in the semiarid site 9 during both wet seasons.

4.4 Discussion

Aridity proved to be a strong driver of dung beetle community assembly via environmental filtering of the regional pool into local communities in both space and time. While the highly covarying taxonomic and phylogenetic diversities suffered a progressive but mild replacement of the few lineages present in each community with increasing aridity along the gradient, functional diversity remained very low and spatially stable. In contrast, functional space was packed (i.e. trait clustering) during the dry season, varying widely during the wet season and being less packed (i.e. even showing overdispersion). Phylogeny explained nearly two thirds of the dissimilarity among species in the region during each season, leaving in average more than 25% of the dissimilarity to be explained by the functional aspect of diversity. The functional contribution to community change can be exemplified by the directional change in wing loading, coprophagous diet

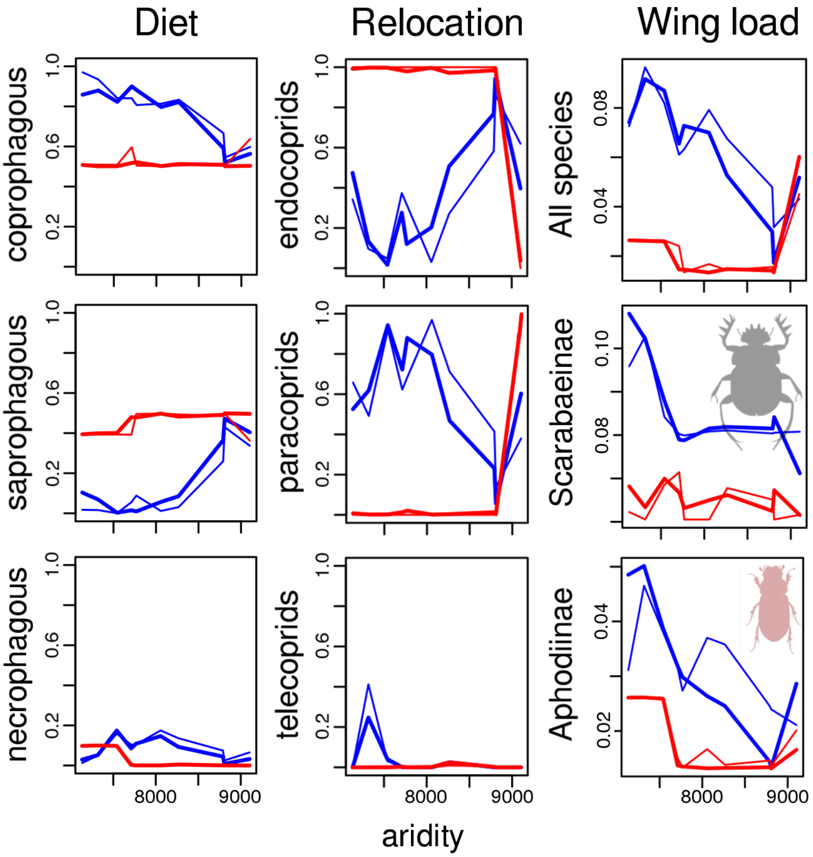

Figure 4.5: Community Weighted Mean of relocation strategy (endocoprid, paracoprid and telecoprid), adult diet preference (coprophagous, saprophagous, necrophagous and, anecdotal and thus not shown, micophagous). In the bottom right corner Community Weighted Mean of wing load (relative to body length) for all species and for each of the two subfamilies (Scarabaeinae and Aphodiinae). For all plots CWM were calculated for dung beetle communities in the wet (blue lines) and dry seasons (red lines) during two consecutive years (2013 in heavy lines and 2014 in thin lines) along a threefold aridity gradient from the Mediterranean sea to the Sahara desert.

and paracoprid habit, which decrease along the aridity gradient during the wet season, and show very low values throughout all of it during the dry season.

Aridity-driven trait selection

Trophic preference (and trophic range) plays a crucial role in arid environments, which are poor in palatable dung, such as the ones present in the studied gradient. Although dung beetles are generally described as coprophagous (Halffter & Edmonds 1982; Hanski & Cambefort 1991), they have a wide range of trophic habits (Scholtz et al. 2009). Indeed, many species in arid regions are basically saprophagous or have a wide trophic plasticity (personal observation), shifting from coprophagy to saprophagy under severe lack of palatable dung (i.e. dung with enough moisture to be processed by each dung beetle species; Holter & Scholtz 2011). This often less considered saprophagy is indeed well represented along our gradient, increasing with aridity. Rather than being anecdotic, its importance is similar to that of coprophagy in the harsher conditions, becoming the main food source for a stable half of the individuals in all communities during the dry season. However, the limited information available on the diet of trophically diverse Aphodiinae beetles, specially in the studied region, requires to take this result with caution. More information on the trophic ecology of dung beetles in the regions, specially for Aphodiinae, are desperately needed to appropriately test this finding.

Dispersal traits are also of primary relevance in dung beetle communities, which are well-known follow a first comes first served lottery dynamics in the comsuption of the highly ephemeral excrements (Hanski & Cambefort 1991; Scholtz et al. 2009). The dominance (and eventual monopolization) of the trophic resource by the first individuals that arrive at a dung dropping is particularly important regarding the small dung droppings (from donkey, dromedar, sheep and goat) that are found in arid areas, as compared to the larger dung pats (from cows or other large herbivores) found in less arid areas, which allow for other competition dynamics. Therefore, body size can give small individuals (typically Aphodiinae species) a competitive advantage in arid environments as they are able to profit from small droppings (Sheridan & Bickford 2011), which do not suffice for larger species. Moreover, dung in arid areas dries out faster (more than 50% water loss in 72h, unpublished data deCastro-Arrazola 2013, and Lumaret 1995; González-Megías & Sánchez-Piñero 2003; Vliet et al. 2009), with the consequent enhancement of its already sparse spatial distribution (Lange 1969). Thus, dispersal is a crucial trait to understand trophic competition among dung beetle species.

Although the drivers of wing loading variation and the effect of flight performance are absolutely unknown for dung beetles (Kojima & Kato 2017; Larsen et al.

2008), wing morphology has been found to respond to environmental conditions in other taxa. Diptera wing shape was found to be driven by altitude (Alves et al. 2016) and temperature (Frazier et al. 2008). Regarding the effects of wing morphology on performance, wing area, length, aspect ratio and wing centroid was found to be positively correlated with a higher acceleration capacity and overall flight capacity (Berwaerts et al. 2002). Finally, wing loading was found to negatively affect flight endurance in Odonata (Gyulavári et al. 2014). That is, smaller wing loadings (i.e. larger wings relative to body mass) have lower flying costs and a longer endurance. This was also suggested for Nitidulidae beetles (Gibb et al. 2006). If this can be extrapolated to dung beetles in search for dung, finding sparser and more ephemeral palatable dung would favor low wing loadings, as found during the dry season and the most arid sites of our transect. In fact, abdominal air sacks in large *Scarabaeus sacer* roller beetles could be understood not only as a mechanism for thermal regulation but also a trait reducing body density and affecting wing loading (Verdú et al. 2012), likely related to flight ability in this species. In other diametrically different ecosystems, such as semideciduous tropical forests, Larsen et al. 2008 anecdotally observed that larger dung beetle species with larger wing loading *tended to fly rapidly and continuously through the forest* while small-bodied species *perched on leaves and occasionally flew short distances*. Indeed, wing loading is consistently selected between open and forest areas in localities from the Brazilian Cerrado and Atlantic Forest (M. Pessoa, P. De Marco Jr, F. Vaz-de-Mello & J. Hortal, unpublished). This might seem to contradict our reasoning, but the radically different habitat structure (tropical forest vs vegetation-less arid system) and spatio-temporal distribution of dung (relatively frequent dung in a humid environment vs extremely-ephemeral and scattered resource) makes difficult to compare the selection processes affecting wing loading in both systems.

The rest of the traits we used to describe functional diversity may not be as suitable as these three to reveal which community assembly rules (i.e. whether environmental filtering and/or limiting similarity) may be driving community structure along the gradient. Traits can be classified into two main classes according to their adequacy for detecting one or the other community assembly mechanisms (Ackerly et al. 2006; Silvertown et al. 2006; Pavoine & Bonsall 2011). Alpha traits, which affect local coexistence, such as biotic interactions involved in direct competition (biotic interactions) for trophic resource, space, etc., will help reveal the importance of limiting similarity. Whereas beta traits that vary as responses to environmental gradients affecting survival as individuals cope with abiotic stress, may reveal the importance of environmental filtering. We carefully selected traits regarding both types of traits. It could be argued that the use of inappropriate traits could have led to the impossibility of revealing true functional turnover between communities (see Villéger et al. 2013). In detail, two species might have very similar values in the measured traits (thus being functionally redundant according to these traits) but be dissimilar regarding other unmeasured traits. For example, information regarding diel activity and inclusion of nesting behavior and poorly known interactions among dung beetles especially relevant in arid systems, such as brood parasitism (González-Megías & Sánchez-Piñero 2003), maybe necessary to enhance our knowledge on the assembly of dung beetle communities. In addition, larval ecology, an usually neglected aspect in most dung beetle community studies, should also be considered. This situation would lead to an apparently low functional distance between species and the misleading attribution of high importance to environmental filtering. However, if another set of traits with higher variability is measured, a significant functional distance between the species could be detected, thus allowing to detect an eventual importance of the opposite assembly rule, limiting similarity. Nonetheless, we do not think this limitation may affect our results, as we carefully selected both types of traits. Firstly, we included traits affecting survival (thus ensuring detection of environmental filtering) such as morphological traits that have been suggested as proxies for reproductive strategy and efficiency (Halffter & Edmonds 1982). Secondly, we included traits affecting coexistence and direct competition (thus ensuring detection of limiting similarity) such as feeding and dispersal traits. In both cases we found that traits analyzed independently had a clear pattern responding to aridity (contrary to Dwyer & Laughlin 2017). Therefore, we are confident that the traits identified allow detecting the main processes determining the assembly of dung beetle communities along the studied gradient.

Effects of aridity on dung beetle community assembly

Here we propose that aridity may constitute such a strong abiotic stress that environmental filtering shapes community structure at two scales: a) at the fine level within subfamilies, selecting optimal trait values with increasing aridity; and b) at the broad scale of subfamilies, favouring the Aphodiinae morphological body-plan and trophic strategies. At the fine scale, wing loading for example, had a clear response to aridity, exhibiting temporal and spatial filtering within Scarabaeinae and Aphodiinae sections of the communities. At the broad scale, the relative abundance of these two subfamilies shows strong variations in their proportions both along space and time. Actually, abundance-based indices were key to understand taxonomic diversity variations along the aridity gradient and between seasons (Chapter 3). Although both subfamilies were present in both seasons and throughout the whole stress gradient, Aphodiinae species dominate in the driest season and sites (see Chapter 3). Indeed, our results highlight the importance of Aphodiinae in the communities subject to arid conditions. Four traits may be important for the adaptation of many species in this subfamily to dry environments: 1) an efficient flight based on low wing loading, which probably allows them to reach sparse trophic source relatively quickly; 2) small size, which allows them to thrive on typically small droppings; and finally 3) facultative saprophagy, which ensures feeding if palatable dung is totally absent.

Abundance-based indices were key to understand taxonomic diversity variations along the aridity gradient and between seasons (Chapter 3). Unfortunately, the phylogenetic and functional abundance-based beta diversities (i.e. Bray-Curtis dissimilarity). The complicated algebra behind hypervolume overlap has not yet allowed to consider abundance in phylogenetic and functional beta diversity indices, preventing us from gaining a deeper understanding of gradual abundance replacement of functional strategies and lineages.

Sticking to the available indices, although functional beta diversity was very low between consecutive sites during both the dry and the wet seasons, the overall volume of functional space (measured by MPD) was much smaller during the dry season. This evidences the , implying a strong constraint difficulty to develop successful functional strategies capable of thriving during the harsh season. This is probably due to both climate and trophic resource availability. That is, the spatially sparse and temporally brief availability of briefly-moist dung may be imposing difficult conditions and a strong filtering process that progressively selects different species (i.e. taxonomic turnover) from a few lineages (small phylogenetic volume) and with specific trait values (i.e. wing loading).

In all, results show coherent patterns between the three facets of diversity and with few other studies in which the three were used simultaneously. A combination of mild taxonomic turnover of species and phylogenetic replacement of lineages with extremely high functional similarity of communities was also found by Villéger et al. (2013) (but see Bishop et al. 2015 for a functional turnover along an altitudinal gradient). Villéger et al. (2013) attributed this pattern to either allopatric speciation (via dispersal limitation) or functional convergence of communities. Functional convergence agrees with the strong environmental filtering reported by our results, especially during the dry season. On the contrary, functional divergence better explains results found during the wet season and is probably due to the more relaxed environment (along with a more abundant and diverse trophic resource) which allows for greater species packing inside the trait space (i.e. higher MNTD). Using a space-for-time equivalence (as in Sundqvist et al. 2013), the seasonal diversity patterns resemble the two extremes of the spatial pattern along the aridity gradient during one of the seasons, in this case, the wet season. We therefore suggest that the during the most unfavorable season there is an homogenization of the conditions along the aridity gradient, and the whole gradient exhibits a desert-like community (similar to Bishop et al. 2015).

4.5 Concluding remarks

To summarize, communities in the most arid sites during the wet season and all sites in the dry season suffer a strong environmental filter that selects a small number of species from a few lineages, especially from the Aphodiinae subfamily (but see Delsinne et al. 2010). Rather than being a subset of the richer communities from the wet season, they constitute a distinct pool of species especially adapted to the harsh desert conditions. Accordingly, rather than losing species, the localities subject to the harsher conditions hold some unique lineages, which appear to be adapted to aridity and low availability of trophic resources.

We believe that in order to relate environmental conditions with ecosystem services (Braga et al. 2013) it is essential to have a solid knowledge of how environment filters species via trait value selection, not only spatially but also temporally. This study covers the first step, increasing our understanding on how environment shapes communities, and uncovering some true dung beetle response traits. Future studies should focus on improving the selection of response traits, which may allow detecting both filtering and limiting similarity processes, and investigating the contribution of these communities to ecosystem functioning along space and time via effect traits.

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General discussion

The first observations of the life cycle of the dung beetles date back to the Ancient Egypt (Cambefort 1994; Ratcliffe 2006), and detailed descriptions of many of the ecological functions they perform were already provided by Fabre (1879). However, dung beetle functional ecology is still in its initial phases of development. The thorough literature review of Chapter 1 led to identifying weaknesses in the foundations of the functional ecology for this group. We conclude that it is such a young discipline that, rather than having identifiable gaps, it requires not only to build up knowledge, but its methodology also needs to be revisited. This thesis covers some of these knowledge gaps by evaluating a set of dung beetle functional traits, and explicitly describing the relationships between: 1) effect traits and ecosystem function delivery and 2) environmental gradients and response traits. On the other hand, from the methodological point of view, this thesis highlights the lack of standardized methodology, and contributes to its development by providing examples that may improve the future study of dung beetle effect and response traits.

Identifying and testing effect traits

To identify traits that are responsible for ecosystem functions it would be necessary to: 1) clearly identify an ecosystem function that is delivered by the taxon of interest; 2) hypothesize which traits are involved in the quality and quantity of the delivery of such function (Chapter 1); and finally 3) design an experiment that ensures that the variability in the function delivery is only due to the variability of certain traits (see Chapter 2). Moreover, several traits can explain the variability in the amount of single or multiple ecosystem functions measured in the same experiment.

We selected three ecosystem functions delivered by dung beetles for which no clear effect traits had been already identified (Chapter 1): the widely acknowledged dung removal, dung burial and secondary seed dispersion, a function that has been often studied in the literature. We then suggested some traits that allow evaluating the determinants of the quality and quantity of these three functions that are delivered by different species. Finally, we designed an experiment that provides reliable tests of the role of these traits as responsible for the variability in function delivery. In contrast to the results of Nervo et al. (2014), the results in Chapter 2 indicate that simple traits related to the size of the prothorax (especially prothorax volume), area of protibia and total body length are better predictors of dung burial than body mass. Moreover, dung relocation strategy (the only behavioral trait we used), which has been traditionally related to these three ecosystem functions (e.g. Doube 1990) was not relevant for the delivery of any of them.

This experiment has a number of limitations regarding the extrapolation of its conclusions. Dung removal and dung burial could potentially differ among species because of differences in the time in which species are able to exploit dung. On the other hand, regarding design, the number of mentioned replicates and species could limit the accuracy of the resulting models. The number of species within each behavioral group was clearly not enough to reliably model differences in function delivery in each group. In general, more species would allow more reliable extrapolation of function delivery throughout the diversity of dung beetles.

Despite the above mentioned caveats, the experiment we present is of great value as it is the first that we know of that truly identifies traits responsible for function delivery. We do this by measuring traits and functions for couples, the minimal functional unit for any dung beetle species. The most similar experiments were undertaken by Nervo et al. (2014) and Macagno et al. (2016). The former (Nervo et al. 2014) sets laboratory experiments which are very similar to the monospecific sexual pair mesocosms presented in Chapter 2, but focuses on only one trait (body mass) and one function (dung removal). This does not allow them to identify which traits are more efficient in delivering the measured function. The latter study (Macagno et al. 2016) measures a number of traits with great detail through a geometric morphometry approach, but focuses on rapid behavioral plasticity in the delivery of two functions (nesting depth and brood ball size) by using two morphologically nearly identical, sympatric and syntopic sister species in a burial experiment. This experiment includes species interactions, thus, not allowing to estimate contribution of isolated species to function delivery. Further, two estimates of ecosystem functions are measured, providing great value to understand species competitive divergence, but with, arguably, little relevance for estimating ecosystem function delivery.

Future directions

Knowledge of how dung beetle effect traits deliver ecosystem functions is far from complete. More research is needed to identify the traits that make dung beetles key organisms in the functioning of many ecosystems around the world. In fact, a large variety of experiments are still needed to fully understand ecosystem function delivery by dung beetles.

Efforts should be directed at designing and performing experiments to test the effect of traits on dung removal, dung burial and secondary seed dispersal using other species and perhaps controlling for other conditions in the laboratory, including: atmospheric (temperature, humidity, etc.; Slade & Roslin 2016), dung (humidity, nutrient content; Yoshihara & Sato 2015) and soil (hardness; Osberg et al. 1993). Similarly, studies that evaluate the relationship between dung beetle effect traits and function delivery at various monospecific abundance levels should be designed and performed in the future; here note that there are no documented experiments that control for different levels of abundance. The additive or canceling properties of emerging density-dependent-effects on function delivery should also be experimentally tested. This is an evident follow-up of the experiment presented in Chapter 2, as a path to understand function delivery (quality and quantity) in more realistic situations in nature (Barnes et al. 2014).

Moreover, other functions delivered by dung beetles remain poorly explored or with no associated effect traits, such as bioturbation, control of dung-based organisms, parasite hosts and vectors, etc. Thus, the origin of variations in their delivery is still unknown, and a matter of hypotheses and speculation (Chapter 1). Regarding the function under study, it is important to notice that experimental design has a crucial influence in the conclusions we infer from experiments. Indeed, conclusions depend on how we measure the quantity and quality of functions (Nervo et al. 2017) and, evidently, which species and traits are used in experiments. For example, nutrient cycling can be estimated by measuring multiple variables of varying relevance. It can be easily but very coarsely estimated by measuring the removed dung from the original dung pat (Wu & Sun 2010; Nervo et al. 2014; Tixier et al. 2015b,a; Nervo et al. 2017), Chapter 2), which takes into account the activity of endocoprids but fails to evaluate the final destination of the removed dung. To account for the direction of the removal, dung burial can be measured (Chapter 2, Osberg et al. 1993; Horgan 2001; Ryan et al. 2011), which dismisses the activity of strict endocoprids but is more relevant to describe the pass of nutrients from soil surface to the underground compartment. It can also be estimated by directly measuring nitrogen increase in the soil (Gillard 1967), but this may not be enough if we consider nutrient cycling complete when plants uptake those nutrients. The ultimate way of measuring nutrient cycling delivered by dung beetles would be to measure how much of the desired nutrient (i.e. nitrogen, etc.) present in the dung is later present in plant tissues (Yoshihara & Sato 2015; Nervo et al. 2017). Some studies have indirectly accounted for this by measuring the next step of nutrient cycling, plant growth (Slade & Roslin 2016; Nervo et al. 2017) and plant community composition (Nervo et al. 2017).

Understanding how individuals and species with a limited number of traits deliver several different ecosystem functions is still poorly studied (Chapter 2) and it is usually done using a limited number of traits. The closest research up to date focuses on multifunctional delivery related to multispecies community diversity (skipping monospecific treatments). Thus, they focus on interspecific competition/facilitation effects on function delivery using natural or artificially-built controlled communities (O'Hea et al. 2010; Yoshihara & Sato 2015; Manning et al. 2016; Milotić et al. 2016; Nervo et al. 2017). However, none of them measures any traits and, thus, functional diversity either. Dias et al. (2013) presents an interesting pitfall when performing such experiments, as Community Weighted Mean and Functional Diversity of the community might affect the overall delivery of the ecosystem function (see Barnes et al. 2014 for an integrative approach in the field).

All these experiments produce a large volume of function and trait data. Function data is dependent on environmental conditions (see discussion above) but trait data is *a priori* independent of experimental conditions. Rather, it depends on field conditions at which dung beetles were collected, unless individuals are bred in laboratory conditions. This intraspecific trait variability (see Griffiths et al. 2016) requires detailed tracking of the way traits are measured (Buse et al. 2018). In fact, a handbook of standardized trait measurement methodologies (such as, e.g. Pérez-Harguindeguy et al. 2013 or Moretti et al. 2017) is needed to ensure the reliability and comparability of dung beetle trait measurements. Once measurement standardization is attained, the produced trait data could be of great value and should be gathered in a worldwide database of dung beetle traits, following the example of TRY (Kattge et al. 2011). We encourage that similar databases are developed for other taxa (but see Jones et al. 2009; Parr et al. 2016).

Identifying and testing response traits

A priori, experiments such as those designed to test the relationship between effect traits and ecosystem functions may seem a suitable way to test the response of traits to environmental variability. Indeed, they are very useful to measure traits, specially those that are difficult (or simply impossible) to measure in the field. Some traits such as dispersal capacity, trophic range (Stavert et al. 2014; but see Gómez & Kolokotronis 2016 for a tool that allows *a posteriori* measurement in collected dung beetles), diel activity and some physiological traits related to regulation of body temperature (Gallego et al. 2016) have been measured in laboratory experiments. However, while these laboratory experiments are adequate to measure trait plasticity, they are not useful to understand the response of traits to environmental conditions at broader time scales. Probably, a response is detectable at the ecological (environmental filtering) and evolutionary (adaptation) time scales. Thus, natural experiments such as environmental gradients, where these broad scale temporal processes have already taken place, seem a more suitable option to assess trait-mediated responses to the environment.

In a sense, the filtering of species from the regional pools to assemble local communities can be regarded as a process in the short temporal scale that selects optimal trait values. These optimal trait values may be reflected by Community Weighted Mean (i.e., the average trait value of all individuals in a community). In a larger temporal scale, environmental filtering could have enough effect on populations so that individuals with the best trait values have a differential fitness and, thus, provoke a directional change in the species trait mean value, resulting in local adaptation that would allow the species to pass through the environmental filter that had previously discarded them from the local community. In addition to short-term species' plasticity and environmental filtering, species could evolutionarily respond by changing their response traits through adaptive processes.

In order to study the response of dung beetles to environmental variations we designed a geographically-explicit transect along an aridity gradient, while Chapter 4 tries to identify the mechanisms determining community assembly through the study of trait responses. The success in identifying certain traits that respond to aridity proves their validity as functional traits. Among the traits measured as continuous variables, our results show that wing loading, a trait likely related to dispersal, has a clear response to aridity. Further, some categorical traits have provided interesting patterns that can be discussed in a wider context than the mere patterns in the range of the aridity gradient towards the Sahara desert. This is the case of the combined behavioral trait of dung relocation strategy and the feeding trait of trophic preference. Although these traits are clearely related to each other (because of the diverse and poorly known diet of many Aphodiinae adults and larvae), they have clear replacement patterns with increasing aridity, both in space and time (i.e. along the gradient and between wet and dry seasons, respectively).

This field study seeking to identify traits that respond to aridity variations and explain the taxonomic diversity patterns (Chapter 3 and Chapter 4), had a number of limitations that cannot be overlooked. The design of the transect is to some extent constrained to finding the *ideal natural experiment*. Thus, we reckon that avoiding or, at least, minimizing the covariation of environmental variables is nearly unavoidable.

The transect was designed to capture a threefold variation in aridity, but it also varied in altitude, which increases from the semiarid site up to a third of the transect, to then remain stable through the middle part and gently decrease in the most arid sites approaching the Sahara. The maximum altitude at the first third of the gradient may have made a difference in environmental conditions or limited the dispersal of some species between the coastal region and the rest of the gradient. Additionally, two out of the ten sites have fairly different soil conditions that can severely influence the composition (and, thus, functional structure) of dung beetle communities (Davis et al. 2016). At the arid side of the gradient, sampling site *mor4* clearly introduces a soil type disruption with deeper sands that enable the presence of stable populations of telecoprids (several *Scarabaeus* species, which were found in all four survey campaigns), which incorporate a distinct combination of traits. Indeed, these novel traits have an effect in all studied functional patterns. A better selection of this site without deep sands might have improved the direct association of functional patterns with variations in aridity and, thus, the identification of some other traits with a clear response to this environmental gradient. The other site that limits the interpretation of both taxonomic and functional patterns is the least arid site *mor10*. The drop in abundance, richness and complete shift in functional structure is most probably due to the anthropogenic influence (dominance of croplands, Vessby 2001; Buse et al. 2015; potential use of antihelmintics, Kryger et al. 2005; Römbke et al. 2010; and greater urbanization Davis et al. 2012; Nichols et al. 2013), perhaps in combination with some coastal influence (through soil salinity). A more homogeneous gradient, in terms of habitat, would have probably resulted in more clear patterns at all diversity levels (taxonomic, phylogenetic and functional).

Apart from the field design, the selection of traits depends on the possibility of measuring them from preserved specimens, time and technology investment, and the availability of data in the literature. In our case, the traits that were finally used were mainly morphological, whereas it was not possible to measure potentially key temporal and physiological traits. Indeed, physiological traits related to temperature (Gallego et al. 2016) and water economy (Chown et al. 2011; Duncan 2002) would have been of special interest. However, measuring these traits requires laboratory experiments that constitutes a research project by itself. A caveat related to the selection of traits in the study of functional response of dung beetles to aridity is the lack of *a priori* hypotheses for several of the morphological traits. This reinforces the evident need to develop dung beetle trait ecology.

Despite these limitations, our study of the taxonomic patterns and the mechanisms behind them (Chapter 3 and Chapter 4) is unique in many aspects. It is of great value to understand dung beetle diversity and assemblage structure, biogeographical patterns and dung beetles response traits along aridity. In the more broad ecological sense, this study contributes to the insufficient corpus of studies that raise the importance of understanding arid systems and their seldom studied temporal dynamics. On the spatial dimension, the use of the partitions of beta diversity to better understand the compositional and abundance changes along such an explicit gradient will prove more and more useful in the future. A noteworthy contribution of Chapter 4 is the analysis of true replacement and nestedness (Baselga et al. 2017) of not only taxonomic diversity but also phylogenetic and functional diversity. This framework provides a whole new dimension of the way to understand the progressive change of communities following environmental variation. Results show a reasonably high taxonomic turnover (Chapter 3), but a very low total functional beta diversity (Chapter 4). This might indicate an inappropriate selection of traits that leads to the impossibility of revealing true functional turnover between communities (Villéger et al. 2013). Villéger et al. (2013) attributed this pattern to either allopatric speciation (via dispersal limitation) or functional convergence of communities (or even to a certain degree of functional redundancy between species in different communities). Such functional convergence is in agreement with the strong environmental filtering, especially during the dry season, identified in Chapter 4.

The higher relative abundance of endocoprids (as all are Aphodiinae species these terms are used interchangeably in this text) in the desert communities in the wet season (Chapter 3; Abdel-Dayem et al. 2016; but see Labidi et al. 2012) may indicate a spatial shift in dung use strategies from para- and telecoprid beetles (as all are Scarabaeinae species these terms are used interchangeably in this text) to endocoprids and more generalist saprophagous species. Such shift would also occur in time, for endocoprid species dominate in abundance during the dry season throughout the whole gradient, totaling > 95% of individuals in all local communities. The existence of such shift in dung use strategy relies on the assumption that all Aphodiinae species are coprophagous, as is the case for the great dominance of endocoprid Aphodiinae species towards wet and cold environments in northern latitudes (Hanski & Cambefort 1991). However, it is likely that this shift in dominance gives them a competitive advantage against the usually more competitive Scarabaeinae, which are nearly absent in the less favorable season (Sullivan et al. 2016). This does not mean that Aphodiinae species fill the temporal and/or environmental gap left by Scarabaeinae. On the contrary, it might indicate that in extreme environments copro-saprophagous Aphodiinae species, especially those occurring in large numbers such as *Anomius baeticus* and *Bodilus beduinus*, could negatively affect, and end up displacing, Scarabaeinae species.

Both the diversity and abundance of these two subfamilies showed a clear replacement through space and time, related to changes in the balance of water availability and temperature (Figure 4.1). At the sight of such pattern a hypothesis covering a larger proportion of the Palearctic geography arises. We suggest that the basic principles of the water-energy hypothesis (as adapted to other insect groups, see e.g. Hawkins & Porter 2003; Keil et al. 2008) seem to operate in a slightly different way, with Aphodiinae being dominant at both edges of the precipitation-temperature gradient. The relative abundance of Scarabaeinae burrowers (i.e. paracoprids and telecoprids, which nest in the ground) shows a unimodal curve with a maximum around the milder Mediterranean climatic conditions. In contrast, the endocoprid (and saprophagous) Aphodiinae species, which nest in the dung pat or next to the soil surface, are proportionally more abundant at the two harsher extremes of the gradient in the Palaearctic, both at the cold temperatures of the European winter of northern regions and in the extreme dry season of pre-Saharian arid environments (Figure 4.1). This may be an effect of large-scale intraguild competitive displacement at the subfamily level (Hanski & Cambefort 1991; Lumaret 1995). Here we hypothesize that the ability of many Aphodiinae species to use different resources for feeding and nesting may allow them to maintain populations in more limiting conditions, and their relative abundance will diminish when and where milder conditions allow Scarabaeinae to thrive and hold large populations and species-rich communities.

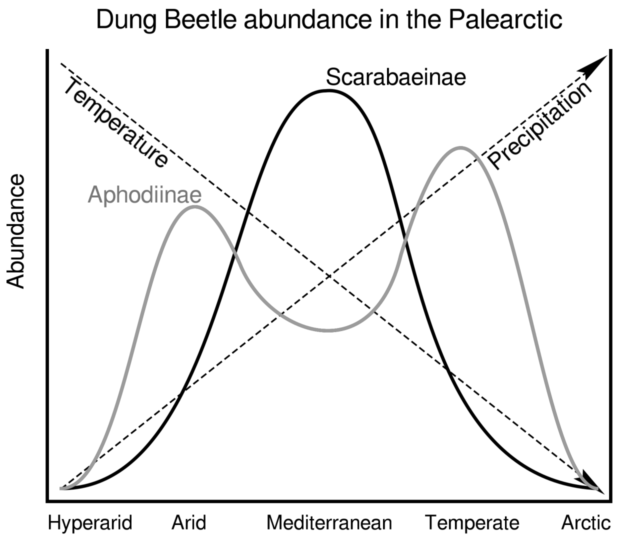

Figure 4.1: Theoretical diagram illustrating a suggested latitudinal replacement of the two most diverse and abundant subfamilies of dung beetles in the Palaearctic region: Aphodiinae and Scarabaeinae. Aphodiinae dominate in cooler north temperate regions (Hanski & Cambefort 1991 and references therein), which are greatly replaced by Scarabaeinae in the milder Mediterranean regions (Lobo et al. 2002; Scholtz et al. 2009) declining as water availability becomes a limiting factor (resulting in a cascade effect through net primary productivity, herbivores and finally dung availability), enabling facultative saprophagous Aphodiinae species to dominate in arid regions (this study; Abdel-Dayem et al. 2016; but see Labidi et al. 2012).

This suggested hypothesis needs future testing by analyzing data across the whole Palearctic latitudinal range.

Future directions

Regarding patterns of continuous traits, dung beetle dispersal has received little attention (Roslin 2000; Arellano et al. 2008; Silva & Hernández 2015) and there is no study on wing loading specifically. Thus, this is one of the few studies using wing loading in dung beetles (the only other studies focusing on habitat fragmentation; Larsen et al. 2008; Barnes et al. 2014). For this reason, the conclusions driven from Chapter 4 are rather speculative, but the clear patterns of the Community Weighted Mean of this trait for both Scarabaeidae subfamilies seem convincing enough to promote future work on the importance of dispersal traits in open habitats, such as arid environments.

Whether the relationship found between aridity and dispersal capacity of dung beetles occurs only in the Saharan fauna or it replicates in other regions in the world remains to be tested. Other warm deserts in the world should be studied (I. deCastro-Arrazola et al., in preparation) using identical sampling designs that cover a long aridity gradient in a spatially explicit transect and as homogeneous as possible vegetation and soil conditions. It is important, however, to bear in mind that other regions have had different evolutionary histories shaping the taxonomic composition and functional structure of their regional pools of dung beetles. If aridity imposes a strong environmental filtering related to dispersal ability, the communities along an aridity gradient will exhibit an average wing loading near the optimum at each level of aridity stress. However, although aridity is the ultimate and most evident factor defining the environmental gradient, trophic resource (i.e. dung) preferences play a key role as the biologically meaningful and direct driver of dispersal capacity of dung beetles in arid systems. That is, wing loading patterns may not be only determined by the evolution of the regional pool, but also by the present and past availability of trophic resources.

As mentioned previously, laboratory experiments are very often the only way to measure response traits, such as flight-efficiency. Other response traits (e.g. trophic range, diel activity, etc.) are easier to measure in the field, where environmental conditions are kept unaltered providing more realistic results. On the other hand, no experiments of function delivery have been performed in semi-arid nor arid areas, where soils are especially nutrient-poor and very often suffer from severe compaction. In these systems, dung beetles may be keystone species for vegetation maintenance. They not only contribute to seed dispersal and seedling emergence (Chapter 2), but also incorporate nutrients into the soil that would otherwise be sequestrated in plant-inaccessible dry dung piles and pellets on the surface (Lumaret 1995; Vliet et al. 2009).

As progressively more and more response traits, effect traits and their associated functions, are being identified and evaluated in different environmental conditions and anthropogenic perturbation levels, writing a handbook of standardized measurement methodologies is urgent. Likewise, a worldwide database of dung beetle traits could already be assembled gathering the efforts of dung beetle trait ecologists up to date.

Response and effect traits

In a macroecological sense, the environment can be simplified to the balance between energy (basically from the sun) and water (Capra 1996). In this hyper simplified frame, ecosystems are open systems in which a continuous flux of energy and water is needed to keep a dynamic equilibrium. This balance is sustained on the basis of a constant management of incoming energy, water and matter by the species. This management is no other than ecosystem functions. With the loss of ecosystem functions, the equilibrium moves to a new equilibrium point (thus, a dynamic property; Maturana & Varela 1996).

These readjustments between dynamic equilibriums are easily seen after natural or anthropogenic perturbations. As far as we know, no documented studies focus on the influence of either naturally occurring environmental gradients or natural perturbations (such as floods, droughts, fires, etc.) on dung beetle ecosystem function delivery. This contrasts with the many studies focusing on the effects of anthropogenic disturbance on ecosystem function delivery (Nichols et al. 2007): fragmentation (Andresen 2003; Rosenlew & Roslin 2008; Barnes et al. 2014), habitat/vegetation degradation (Horgan 2005; Braga et al. 2013) and global change (Penttilä et al. 2013; Slade & Roslin 2016). The thorough work of Barnes et al. (2014) and the outstanding effort of Derhé et al. (2016) require special attention for being among the few to carefully measure and analyze the interactions between environment, traits and ecosystem function. However, their results are not as clear as expected mainly due to the selection of behavioral and trophic response traits that have little effect on function delivery. It is evident that further studies of how species respond to environment (exemplified in Chapter 4) and affect the contribution of dung beetles to ecosystem functioning (as exemplified in Chapter 2) is needed to understand how environmental variations affects the functioning of ecosystems. In this sense, Chapter 4 only provides a preliminary step that allows speculating about the functional effects of aridification, one of the consequences of global change in drylands (Cherlet et al. 2018). A purely temporal and a space-for-time interpretation (França et al. 2016) of the results is a useful contribution to predicting the evolution of the ecosystem under this present anthropogenic perturbation.

The wet season and the semi-arid sites of the gradient show fairly abundant, taxonomically rich dung beetle communities and high trait diversity, most probably indicating a larger delivery of ecosystem functions (Manning et al. 2016). On the contrary, it is clear that the dry season and the driest sites in the gradient exhibit an equilibrium based on a few species that are able to use the high energy that enters the ecosystem to cycle the little available amount of water and matter. In these low-productive systems, detritivores are specially important (Polis 1991). The detritivore groups recycle the dead matter and make it available for the rest of the actors of the ecosystem. In deserts, termites and darkling beetles process dead plant matter (Sánchez-Piñero & Gómez 1995), dermestids and trogids mainly thrieve on carrion (Sánchez-Piñero 1997; Scholtz & Caveney 1988) and the focal taxon in this thesis, dung beetles, mainly process dung (Holter & Scholtz 2007). These relocate it to the underground compartment and make it available for microbiota to process complex tissues into simplified nutrients that can be incorporated by the vegetation. This simplified structure is present during the dry season not only in the driest sites, but all along the gradient in a very homogeneous way. Therefore, it can be reliably predicted that increasing aridity, will lead to a loss of ecosystem functions and a displacement of the equilibrium of the ecosystems in the whole gradient during the wet season to a new simplified structure. This implies that human-driven aridification may lead to a reduction in the ecosystem services (i.e. human-profitable ecosystem functions) that make human survival impossible (Cherlet et al. 2018). This is not bad *per se*, as desert ecosystems have the same right to exist as humans do.

Final considerations

The double effort of Chapter 3 and 4 leads to an intriguing question: *Are taxonomy and functional analysis complementary? Or is functional ecology developed enough to skip taxonomic efforts?* It is clear that taxonomy describes diversity patterns and, although ecology can also describe functional patterns, traits are used to shed light on the mechanisms that produce those taxonomic patterns. A couple of immediate questions come to mind: *Are taxonomic patterns useful? What do we seek to understand when analyzing taxonomic patterns?* If the aim is to understand how nature works, then functional ecology should be enough. *Why do we need to classify individuals in a community in discrete categories, called* species, *if we can measure traits and describe the community in detail as the combined continuous distributions of traits?* Taking this reasoning to the limit, measuring all possible traits would lead to distinguishing any two individuals in the world (perhaps except for clones). But gathering and handling all that amount of information is probably useless and inefficient.

This leads to the question: *What is the minimum amount of traits to measure and reach the same taxonomic conclusions with functional methods?* Probably, it would require measurement of many more individuals to achieve a representative portion of the community. However, this would lead to two new methodological issues: quantity and quality. That is, which percentage of the individuals in a community should be measured and which selection criteria should be used. In fact, independently of the criteria to use, it would lead to an additive bias: 1) bias at field sampling and 2) bias at the selection of individuals to measure. Perhaps, this would require the birth of a *quantitative trait ecology* resembling methods used in *quantitative genetics*. It is clear that, as of today, functional ecology is still far from moving on independently of taxonomy.

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Conclusions

Chapter 1:

(1) Functional ecology of dung beetles is still not well developed. In particular, traits are not often measured and, when they are, there is a lack of standard methodology, making impossible to combine and/or compare them with traits measured in other studies. Moreover, the used traits usually lack proven functionality, that is, relation with an environmental factor or an ecosystem function.

(2) Most of the studies using functional diversity as the response to environmental variability use traits with no proven nor hypothesized functionality. Thus, they actually analyze patterns of trait diversity, without a functional interpretation. These studies do not try to identify individual response traits, but just analyze the patterns of overall trait diversity. Moreover, most of these studies analyze responses to anthropogenic disturbance (a complex combination of many altered factors). Thus, patterns of trait diversity are difficult to interpret as the response to any single environmental factor.

(3) Most of the studies focusing on the variation of ecosystem function delivery do not identify individual effect traits nor the mass effect in a single species, but are rather understood in the scope of Biodiversity~Ecosystem Functioning (BEF). These compare the different function delivery of several natural communities under varying environmental disturbances (mostly anthropogenic) or artificial communities in the laboratory.

(4) The most frequently measured traits are related to morphology, feeding traits and diel activity, while physiology, reproduction and dispersal traits remain largely unexplored. Similarly, functions such as dung removal and secondary seed dispersal have been fairly studied, whereas most of the rest lack formal evaluation to find associated effect traits. Finally, environmental variables such as vegetation structure (land use change, fragmentation, etc.) have received most attention, but the response of traits to most of the rest (dung availability, soil, humidity and temperature) is totally unknown.

Chapter 2:

(5) There is a relationship between the morphological traits body size, prothorax size and protibia area and two important functions provided by dung beetles, dung removal and dung burial. There is also a negative effect of the elongation of certain structures (as length of fore and hind tibiae) and relatively longer body shapes (as in endocoprid aphodine beetles) on burrowing efficiency.

(6) Behavior (i.e. dung relocation strategy) did not show a significant effect on performance in neither dung removal nor burial, mainly because: 1) the wide array of morphological traits included in the analysis already account for the differences in morphological design of the major behavioral strategies; 2) the small number of species included in the experiment (three endocoprids, four paracoprids and two telecoprids) and large intraspecific variability in function delivery; and 3) the interspecific size overlap.

(7) There is a differential effect of species regarding seedling emergence. This result strongly suggests that behavioral differences among species are also involved in the final outcome of dung beetle activity on seedling emergence. Differences in species' activity in the soil-dung interface, influencing soil surface properties, may explain the positive effect of endocoprids and shallow nesting species in seedling emergence.

Chapter 3 and Chapter 4:

(8) The structure of dung beetle communities along the aridity gradient in the north of the Sahara shows a clear taxonomic replacement. Desert communities are not impoverished subsets of species from species-rich communities from milder climatic conditions, but rather unique combinations of species adapted to such conditions. Whether this pattern of pre-eminence of species replacement with increasing aridity is common in other warm desert communities needs further investigation since no other studies partitioned beta diversity along aridity gradients before.

(9) Species replacement is probably the result of a climate-driven environmental filtering as well as a response to dung availability for feeding and nesting. Such a filtering results in an ordered replacement of functionally-different species in space and time, as generalist and saprophagous dung beetles become dominant in desert conditions and dryer seasons.

(10) During the driest season, environmental conditions become harsher leading to a spatial homogeneity of dung beetle communities. In the driest sites, environmental conditions present very low seasonal variations, leading to a temporal homogeneity of the composition of communities. Loss of the spatial and temporal replacement leads to easily predicting a reduction of richness and a generalized loss of diversity with climate change.

(11) Aridity is a strong driver of community assembly via environmental filtering of the regional pool of dung beetles into local communities at the temporal and spatial dimensions. Spatially, while the highly covariating taxonomic and phylogenetic diversities suffered a progressive but mild replacement (phylogenetic turnover) of the few lineages present in each community with increasing aridity, functional diversity remained very low and spatially stable. On the other hand, functional space was packed (trait clustering) during the dry season but remained widely variable and much less packed (i.e. overdispersion) during the wet season.

(12) Functional traits provide key information on the mechanisms behind the patterns of taxonomic replacement. The strong spatial and temporal environmental filter imposed by aridity on dung beetle communities selected species with adequate trait values to cope with such restrictive conditions. We found a directional change in the abundance weighted average of wing loading, coprophagous diet and paracoprid habit with decreasing values along the aridity gradient during the wet season and very low values along the whole gradient during the dry season.

(13) In order to relate environmental conditions with ecosystem services, future studies should focus on better selecting response traits (appropriate for detecting both assembly rules) and investigating the contribution of these communities (via effect traits) in ecosystem functioning along space and time.

Conclusiones

Capítulo 1:

(1) La ecología funcional de escarabeidos coprófagos aún no está bien desarrollada. En particular, habitualmente no se miden rasgos y, cuando se miden, hay una falta de metodología estandarizada, impidiendo que se combinen y/o se comparen con los rasgos medidos en otros estudios. Además, el uso de rasgos está falto de una funcionalidad demostrada, es decir, la relación con un factor ambiental o una función ecosistémica.

(2) La mayoría de estudios que usa ecología funcional como la respuesta a la variabilidad ambiental usa rasgos sin una funcionalidad ni demostrada ni hipotetizada. Por lo tanto, en realidad analizan patrones de diversidad de rasgos, sin una interpretación funcional. Estos estudios no intentan identificar rasgos de respuesta individuales, sino que analizan los patrones de diversidad total de los rasgos disponibles. Además, la mayoría de los estudios analizan las respuestas a perturbaciones antrópicas (una combinación compleja de varios factores alterados). Por ello, los patrones de diversidad son dificiles de interpretar como respuestas a un único factor ambiental.

(3) La mayoría de los estudios que se centran en la variación del desarrollo de las funciones ecosistémicas no identifican rasgos de effecto individuales ni el efecto de la abundancia en una especie por sí sola, sino que se engloban en el ámbito de la relación Biodiversidad~Funcionamiento Ecosistémico (BEF, por sus siglas en inglés). Estos comparan el desarrollo de las funciones por parte de comunidades naturales bajo diferentes perturbaciones ambientales (en su mayoría antrópicas) o comunidades artificiales en el laboratorio.

(4) Los rasgos má frecuentemente medidos están relacionados con morfología, alimentación y actividad diaria, mientras la fisiología, reproducción y rasgos de dispersión siguen inexplorados. De manera similar, funciones como la retirada de excremento y la dispersión secundaria de semillas se han estudiado bastante, mientras la mayoría del resto siguen sin tener una evaluación formal de su relación con rasgos de efecto. Finalmente, variables ambientales

como la estructura de la vegetación (cambio en el uso del suelo, fragmentación, etc.) han recibido la mayor parte de la atención, pero la respuesta de rasgos a la mayoría del resto (disponibilidad de excremento, suelo, humedad y temperatura) es totalmente desconocida.

Capítulo 2:

(5) Existe una relación entre los rasgos morfológicos de tamaño corporal, tamaño del protórax y área de la protibia y dos funciones importante desarrolladas por escarabeidos coprófagos, retirada y enterramiento de excremento. También encontramos un efecto negativo de algunos rasgos en la eficiencia cavadora: el alargamiento de las tibias anterior y posterior (relacionado con una morfología de telecóprido) y una forma del cuerpo relativamente más alargada (característica de los endocópridos).

(6) El comportamiento (i.e. estrategia de relocalización de excremento) no mostró un efecto significativo en la eficiencia ni en la retirada ni en el enterramiento del excremento, principalmente por: 1) el amplio abanico de rasgos morfológicos incluidos en el análisis ya recogen las diferencias en el diseño morfológico de las principales estrategias comportamentales; 2) el pequeño número de especies incluidos en el experimento (tres endocópridos, cuatro paracópridos y dos telecópridos) y la gran variabilidad intraespecífica en el desarrollo de las funciones; y 3) el solapamiento interespecífico de tamaños corporales.

(7) Existe un efecto diferencial entre especies en la emergencia de plántulas. Este resultado sugiere firmemente que las diferencias comportamentales entre las especies también están incluidas en el resultado final de la actividad de los escarabeidos coprófagos en la emergencia de plántulas. Las diferencias en la actividad de las especies en la interfase excremento-suelo, que influye en las propiedades del suelo, pueden explicar el efecto positivo de los endocópridos y las especies con nidificación superficial en la emergencia de plántulas.

Capítulo 3 y Capítulo 4:

(8) La estructura de las comunidades de escarabeidos coprófagos a lo largo del gradiente de aridez en el norte del Sahara muestra un claro reemplazo taxonómico. Las comunidades de desierto no son un subconjunto de las presentes en condiciones más suaves sino un conjunto único de especies adaptadas a dichas condiciones. Si este patrón de reemplazo de especies con aridez creciente es común en comunidades de otros desiertos cálidos necesita ser más

investigado, dado que no se conocen otros estudios que hayan realizado la partición de la varianza de beta diversidad a lo largo de gradientes de aridez.

(9) El reemplazo de especies es probablemente el resultado del filtrado ambiental promovido por el clima además de una respuesta a la disponibilidad de excremento para la alimentación y la nidificación. Este filtrado provoca un reemplazo ordenado de especies funcionalmente diferentes en el espacio y el tiempo, a medida que especies de escarabeidos generalistas y saprófagos se van haciendo cada vez más dominantes en condiciones desérticas y en la época más seca.

(10) Durante la época más seca, las condiciones ambientales se hacen cada vez más duras provocando una homogeneización espacial de las comunidades de escarabeidos coprófagos. En los puntos más secos, las condiciones ambientales muestran muy poca variación estacional, lo que homogeneiza temporalmente la composición de las comunidades. La pérdida del reemplazo espacial y temporal innevitablemente hace pensar en una reducción de la riqueza y a una pérdida generalizada de la diversidad con el cambio climático.

(11) La aridez es un fuerte factor que determina el ensamblaje de comunidades via filtrado ambiental del *pool* regional de escarabeidos coprófagos a las comunidades locales en la dimensión espacial y en la temporal. Espacialmente, mientras las fuertemente correlacionadas diversidades taxonómica y filogenética sufren un progresivo pero suave reemplazo (reemplazo filogenético) de los escasos linajes presentes en cada comunidad con la creciente aridez, la diversidad funcional se mantuvo muy baja y espacialmente estable. Por otro lado, el espacio funcional se mostró empaquetado (agrupamiento de rasgos) durante la época seca pero se mantuvo ampliamente variable y mucho menos empaquetado (i.e. sobredispersión) durante la época húmeda.

(12) Los rasgos funcionales ofrecen información clave para entender los mecanismos responsables de los patrones taxonómicos de reemplazo. El fuerte filtrado ambiental temporal y espacial impuesto por la aridez en las comunidades de escarabeidos coprófagos seleccionó especies con los valores de rasgos para hacer frente a las restrictivas condiciones ambientales del desierto. Encontramos un cambio direccional decreciente en la media ponderada por la abundancia de los valores de carga alar, dieta coprófaga y comprotamiento paracóprido a lo largo del gradiente de aridez en la época húmeda y valores muy bajos a lo largo del gradiente en la época seca.

(13) Para poder relacionar condiciones ambientales con funciones ecosistémicas, estudios futuros deberían centrarse en seleccionar mejor los rasgos de respuesta (apropiados para detectar ambas reglas de ensamblaje de comunidades) e investigar la contribución de las comunidades (via rasgos efecto) en el funcionamiento ecosistémico a lo largo del espacio y el tiempo.

A Appendices to Chapter 1

	Categ.	Trait	How is the trait responding to each environamental variable?
Precipitation (relative humidity)	Feed.	Dung burial rate	Low humidity dries dung fast, thus increasing competiton
	Feed.	Dung relocation strategy	Telecoprids may not be able to access dung through the crust of very dry dung pads
	Feed.	Feeding mechanism	Dry dung has no liquid fraction, thus grindding may be advantegeous in dry environments
	Feed.	Soil relocation	Soil at the entrance of the burrow may prevent high dessication rates in the nest
	Morph.	Body size	Fresh body mass is mostly due to water content, beetles living in humid habitats may be heavier
	Move.	Flight distance, time	Flightless beetles have been found in deserts
	Physio.	Dessication resistance	Obvious
	Physio.	Inundation resistance	Obvious
	Physio.	Respiratory pattern	Some special breathing system have been found in deserts
	Physio.	Salinity tolerance	Salinity normally affects organisms through water in soil
	Physio.	Soil acidity tolerance	Dependent on water balance in soil
	Repro.	Antimicrob. in brood masses	Anticrobials might limit fungi growth (enhanced by humidity) on brood masses
	Repro.	Burrow depth	Deep nests are protected from dessication by the buffering effect of soil
	Repro.	Cover burrow walls with dung	Low humidity may induce some species to cover burrow walls with dung to prevent evaporation
	Repro.	Dung burial rate	Low humidity dries dung fast, thus increasing competiton
	Repro.	Dung relocation strategy	Kleptocoprids have been specially described in dry habitats
	Repro.	Egg length, volume, weight	Dry environments may require bigger eggs with bigger water reserves to survive until hatching
	Repro.	Burrow ramification	Dryer soils make ramifications shorter (sowig1996)
	Repro.	Soil relocation	Soil at the entrance of the burrow may prevent high dessication rates in the nest
	Time	Colonization moment	Dung dries fast in dry enviroments, early colonization is key in this environments
Predation risk	Feed.	Dung burial rate	Faster beetles spend less time visible to predators
	Morph.	Body color	Beetles with color more similar to their environment have lower chances of being predated
	Morph.	Glossiness, iridiscence	Mat beetles are less visible to predators
	Repro.	Dung burial rate	Faster beetles spend less time visible to predators
	Move.	Escaping strategy	Beetles with the right escaping strategy escape from predators
Temperature	Feed.	Dung burial rate	Activity is higher/faster at higher temperatures
	Morph.	Body hairiness	Hairiness may help temperature regulation (see other taxa)
	Morph.	Body size	Temperature gain/loss is related to volume/surface rates
	Physio.	Air sacs, subelytral cavity	It is been suggested that aerial sacs are aimed at heat dissipation during flight
	Physio.	Dessication resistance	Temperature interacts with humidity and thus, dessication processes
	Physio.	Respiratory pattern	Special breathing patterns have been observed in desert beetles (very related to avoiding dessication)
	Physio.	Resting metabolic rate	Temperature influences metabolism (based on faster thermodynamic/enzymatic processes)
	Physio.	Thermal resistance	Obvious
	Physio.	Volatile detection ability	Beetle volatile detection-ability may be improved by temperature (makes substances more volatile)

Temperature	Repro.	Antimicrob. in brood masses	Anticrobials might limit fungi growth (enhanced by temperature) on brood masses
	Repro.	Burrow depth	Deep nests provide a buffered temperature-stability for dehydration-sensitive larva-pupae
	Repro.	Dung burial distance	Periodic stops to cool down temperature may affect rolling distance in telecoprids
	Repro.	Dung burial rate	Activity is higher/faster at higher temperatures
	Time	Colonization moment	Temperature also dries out dung, early colonizers have fresher dung
	Time	Daily activity time	High temperatures during the day may force some species to be night-active
	Time	Parity	Appropriate temperature lengthens beetle longevity in laboratory experiments
	Time	Yearly activity time	Temperature and dung availability are probably the drivers of phenology
	Time	Voltinism	Wider range of appropriate temperature along the year allow multiple generations
Competition for dung	Feed.	Dung burial amount	Beetles with lower competitive ability can end up with less dung to eat
	Feed.	Dung burial distance	The dung pad is the attractant of dung beetles and thus of competitors
	Feed.	Dung burial rate	Faster beetles acquire more dung in less time
	Feed.	Dung relocation strategy	Endocoprids do not relocate dung, thus they under constant competitive stress
	Morph.	Body size	Bigger beetles are better competitors
	Morph.	Metatibia length	Longer metatibias allow rolling away a bigger brood mass in a single *trip*
	Morph.	Metatibia width	Wider metatibias (paracoprids) are more efficient at digging
	Morph.	Volume of prothorax	Competition may select for bigger prothorax volume
	Move.	Flight distance, time	Competition forces beetles to arrive earlier (flying) rather than later (flightless)
	Repro.	Antimicrob. in brood masses	Not only among beetles (kleptocoprids included) but also with fungi, bacteria etc.
	Repro.	Burrow depth	Deep nests are a way to avoid competition for space under the pad (paracoprids)
	Repro.	Clutch size	Clutch size may be determined by the speed of nest provisioning
	Repro.	Dung burial amount	Beetles with lower cometitive ability can end up with less dung to eat
	Repro.	Dung burial distance	The dung pad is the attractant of dung beetles and thus of competitors
	Repro.	Dung burial rate	Faster beetles acquire more dung in less time
	Repro.	Dung relocation strategy	Endocoprids dont relocate dung, thus they under constant competitive stress
	Time	Colonization moment	The drying out of dung imposes a strong competition even before arriving to the dung source
	Time	Daily activity time	Competition during the day may force beetles to be active at night, thus requiring bigger omatidia
	Time	Yearly activity time	Competition is stronger in relation to dung availability through the year
Vegetation structure	Feed.	Dung burial distance	Vegetation structure might require iridiscence for intraspecific location
	Morph.	Glossiness, iridiscence	Vegetation structure might require glossiness for intraspecific location
	Move.	Escaping strategy	Complex vegetation strucure (thus hidding places) might favour flying escaping strategies
	Move.	Flight distance, time	Different wing loading is needed for open and closed (forestal) habitats (see in birds)
	Physio.	Volatile detection ability	Complex vegetation structure makes detection of dung odours more difficult than in open areas
	Repro.	Dung burial distance	Complex veg.struc makes difficult for telecoprids to roll their ball very far away

	Categ.	**Trait**	**How is the trait responding to each environamental variable?**
Dung distribution	Feed.	Adult diet	Saprofagous dont care about dung distribution, neither necrophagous
	Feed.	Adult diet range	Having a broad diet range allows beetles to live in plaecs with sparser dung
	Feed.	Dung relocation strategy	Telecoprids need more dung per feeding/reproducing event than endocoprids
	Morph.	Body size	Spatial dung clustering allows for greater community biomass and perhaps individual biomass
	Morph.	Volume of prothorax	Sparser dung requires greater flying muscles to move from pad to pad
	Move.	Escaping strategy	If dung is very sparse, flying away is very risky as the beetle may not find any other dung nearby
	Move.	Flight distance, time	Sparser dung requires greater flying capacity (wing load). Thus, flightless beetles are often detritivores
	Physio.	Volatile detection ability	Better volatile detecting abilities are needed to find sparse dung
	Repro.	Dung burial amount	Clustered dung allows for bigger species that need to bury more dung per event
	Repro.	Dung relocation strategy	Telecoprids need more dung per feeding/reproducing event than endocoprids
	Time	Colonization moment	Dung distribution determines the arrival moment of species
	Time	Yearly activity time	Species with frequent/great dung requirements may shift their yearly phenology
Soil	Morph.	Metatibia width	Wider metatibias (paracoprids) are more efficient at digging
	Morph.	Protibia length, width, area	Wider protibias are more efficient at digging
	Move.	Escaping strategy	The softer the soil the easier to escape by burial, the harder the more difficult
	Physio.	Inundation resistance	Different soils keep more water, on the other extreme, sand drains very easily
	Physio.	Salinity tolerance	Soils can be very saline, inducing beetles to be resistant to thrieve
	Physio.	Soil acidity tolerance	Soils can be very acid, inducing beetles to be resistant to thrieve
	Repro.	Burrow depth	Soil hardness probably determines burow ease and, thus, depth
	Repro.	Burrow ramification	Deep and hard layers of soil may force beetles to ramificate their burrows instead of going deeper
	Repro.	Cover burrow walls with dung	Very sandy/crumbly soils may require stronger burrow walls (by covering with dung)
	Repro.	Dung burial distance	Telecoprids may be forced to roll al longer distance in search for softer soils
	Repro.	Soil relocation	Burrows may be made by soil relocation (to surface) and compaction depending on soil structure
Light / radiation	Morph.	Body color	Darker colors may protect from radiation in open areas
	Morph.	Body hairiness	Hairiness may protect from radiation (see mammals etc.)
	Morph.	Cuticule structure	High radiation may induce thicker or reticulated elytra
	Morph.	Glossiness, iridiscence	Matt beetles may be protected from radiation, certain light conditions allow iridiscence (signalling)
	Time	Daily activity time	Low light intensity requires bigger omatidia

Table A.1: Dung beetle traits responding to environmental filters or evolutionary forces (left-most column in vertical). Traits are categorized in the main aspects of dung beetle life-history. The mechanism behind the response of each trait is succinctly explained, often providing an example.

	Categ.	Trait	How is the trait providing the function?
Pollination	Morph.	Body color	Beetles with *flowery colors* may be attracted to flowers that look like females
	Morph.	Body hairiness	More hair enables pollen attachment
	Morph.	Body size	Bigger adults have more pollen attachment surface
	Morph.	Cuticule structure	Rougher surface may enable polen attachment
	Move.	Flight distance, time	Longer flight distance helps encounter more flowers of same species
	Physio.	Volatile detection ability	Dung smelling flowers may trick dung beetles capable of detecting such volatiles to pollinate them
	Time	Daily activity time	Night-active individuals wont pollinate day-open flowers
	Time	Yearly activity time	Individuals that are active in winter wont polliate summer flowers, and opposite
Bioturbation (+veg. Enhance.)	Feed.	Adult diet	Beetles that are not based on dung, wont bury, thus, wont bioturbate
	Move.	Escaping strategy	Escaping by burying means greater bioturbation, flight doesnt
	Physio.	Thermal resistance	Probably beetles that dont thermoregulate need to bury more often, thus bioturbating more than those who do thermoregulate
	Repro.	Burrow depth	Deeper burrows contribute more to drainage and aeration
	Repro.	Burrow length	Tunnel length means better drainage and aeration
	Repro.	Burrow ramification	Ramification leads to longer tunnels, thus contribute more to drainage and aeration
	Repro.	Cover burrow walls with dung	Tunnels with a layer of dung on walls may be more water or air proof than tunnels without
	Repro.	Dung burial distance	Bioturbating spread around an area might be more benefitial than only below the original dung pat
	Repro.	Dung relocation strategy	Endocoprids dont make tunnels, thus dont help bioturbation
	Repro.	Soil relocation	Soil relocation is basic to soil aeration
	Time	Parity	Even with same amount of dung, more burrows mean more bioturbation
Nutrient cycling (burial amount)	Feed.	Adult diet	I.e. necrophagous won't eat any dung, thus not burying any nutrients
	Feed.	Larval diet	If larvae feed on smth different from dung, adults wont bury any dung
	Morph.	Body size	Bigger adults bury more dung for eating themselves and their larvae
	Morph.	Clypeus width, shape	Probably there is a optimum of length, width, shape in clypeus which means better digging ability
	Morph.	Larval body dry mass	Bigger pupas need more dung to be buried by the adult
	Morph.	Metatibia length	Longer metatibias make bigger balls that are finally buried
	Morph.	Metatibia width	Wider/robust metatibias mean greater ability to dig
	Morph.	Protibia length, width, area	Wider protibias handle more dung
	Morph.	Volume of prothorax	Bigger pronotum means bigger digging muscles,thus better digging ability
	Physio.	Resting metabolic rate	More active individuals need more dung intake, thus burial (except beetles that eat at dung pat)
	Repro.	Cover burrow walls with dung	This strategy needs burying more dung than not doing it
	Repro.	Dung burial amount	This trait may constitute a trait-function continuum
	Repro.	Dung relocation strategy	Endocoprids dont bury at all, so this nesting behavior is negatively correlated with burial quantity
	Time	Colonization moment	Early colonizers get the chance to bury more dung because there is more available, and softer to handle
	Time	Parity	At identical burial amount per event, more events will contribute more to nutrient cycling

	Categ.	Trait	How is the trait providing the function?
Parasite (host or vector)	Feed.	Feeding mechanism	Destruction of nematode eggs etc. reduces parasite populations and the chance that the beetle itself acts like a vector
	Feed.	Ingested particle size	Bigger particles allow ingesting more parasites
	Morph.	Body hairiness	Hairyness also helps attachment of parasites
	Morph.	Body size	Bigger volume enables more parasites to attach to the host
	Morph.	Cuticule structure	Rough structures/textures help parasite attacment
	Move.	Flight distance, time	Flighing longer distances makes the individual a better vector
	Repro.	Antimicrob. in brood masses	If there are really antimicrobial substances, parasites should be affected by them
	Repro.	Burrow depth	Probably there is an optimum depth at which parasites thrieve, and avoid parasite predators
	Time	Colonization moment	Earlier colonization means fresher dung and probably parasite survival
Nutrient cycling (quality)	Feed.	Ingested particle size	Bigger particle sizes ingested mean m greater variety ofoare nutrients processed
	Repro.	Antimicrob. in brood masses	If antimicrobial substances are present microbe/fungi-decomposition may be inhibited
	Repro.	Burrow depth	Probably there is an optimum depth at which microbes/fungi decompose dung
	Repro.	Burrow length	Longer tunnels improve bioturbation and thus microbial decomposition
	Repro.	Burrow ramification	Wider ramification spreads nutrients more
	Repro.	Clutch size	If same amount of dung is buried in separate brood masses, more dung-surface is available for decomposition processes
	Repro.	Dung burial distance	Probably there is an optimum spread of dung in soil so that competition among decomposers is lower
	Repro.	Dung relocation strategy	Endocoprids dont bury at all, so this nesting behavior is negatively correlated with below surface microbial decompostion
	Repro.	Soil relocation	Probably there is an optimum relocation of soil when burying that improves bioturbation and thus microbial decomposition
	Time	Colonization moment	Higher humidity of buried dung makes easier dung decomposition by microbes, etc.
	Time	Yearly activity time	Probably there is an optimum season when microbial decomposition is best
Nutrient cycling (removal amount)	Feed.	Adult diet	I.e. necrophagous won’t eat any dung, thus not cycling any nutrients
	Feed.	Larval diet	If larvae feed on smth different from dung, adults wont remove any dung
	Morph.	Body size	Bigger adults remove more dung for eating themselves and their larvae
	Morph.	Metatibia length	Longer metatibias make bigger balls
	Morph.	Protibia length, width, area	Wider protibias handle more dung
	Move.	Flight distance, time	Early arrival to dung pat, may avoid competition and thus removes more dung
	Physio.	Resting metabolic rate	More active individuals need more dung intake
	Physio.	Volatile detection ability	If early detection is paired with early arrival to dung pat, it avoids competition and thus removes more dung
	Repro.	Cover burrow walls with dung	This strategy needs removing more dung than not doing it
	Repro.	Dung burial amount	More burial amount means more removal
	Repro.	Dung relocation strategy	Kleptoparasites don’t bury, thus, they dont remove nutrients at all
	Time	Colonization moment	Early colonizers get the chance to remove more dung because there is more available, and softer to handle
	Time	Parity	At identical burial amount per event, more events will contribute more to removal

Second seed dispersal	Feed.	Active seed removal from dung	The more seeds the beetle removes and abandons on the surface, the greater chances to germinate
	Feed.	Adult diet	Necrophagous wont disperse any seeds
	Feed.	Ingested particle size	Smaller ingested particle size avoids ingesting seeds, by chance
	Morph.	Body size	Greater dung amount contains more seeds to disperse
	Morph.	Metatibia length	Longer metatibias make bigger balls that contain more seeds, and these are buried with more nutrients for future seedlings
	Morph.	Protibia length, width, area	Greater dung amount contains more seeds to disperse
	Move.	Flight distance, time	Flight allows reaching inaccessible dung or arriving earlier and relocating seeds before seed predation in surface (rodents, ants)
	Repro.	Active seed removal from dung	The more seeds the beetle removes and abandons on the surface, the greater chances to germinate
	Repro.	Antimicrob. in brood masses	Antimicrobial substances may kill or inhibit seed germination
	Repro.	Burrow depth	Probably there is a optimum depth at which seeds germinate and emerge
	Repro.	Burrow ramification	Ramification leads to shallower and greater horizontal spread of seeds; enabling emergence and reducing seedling competition
	Repro.	Clutch size	Probably there is an optimum size of brood mass to enhance emergence probability
	Repro.	Dung burial amount	Greater dung amount contains more seeds to disperse
	Repro.	Dung burial distance	Probably there is an optimum of seedling density, thus xy relocation of seeds out of the original dung lowers seedling competition
	Repro.	Dung burial rate	Earlier or immediate relocation of seeds avoids seed predation in surface (rodents, ants)
	Repro.	Dung relocation strategy	Endocoprids dont bury but their activity (specially in big abundances) may improve germination and emergence
	Repro.	Soil relocation	Relocation of soil puts into circulation the seed bank that might be buried deep and with low or null emergence probabilities
	Time	Colonization moment	Earlier colonization and relocation of the seed may lead to better germination
Predation	Feed.	Adult diet	Dung feeders dont predate. It may be fuzzy coded
	Morph.	Body size	Among insects, predators are usually smaller than their prey
	Morph.	Clypeus width, shape	Apparently there may be special clypeus morphologies to predate over millipedes
	Physio.	Volatile detection ability	Beetles capable of detecting volatiles may detect they prey (as milipedes)
Reg. Dung Orgs.	Feed.	Feeding mechanism	Grinding may destroy eggs and cists present in the dung
	Morph.	Body hairiness	Mites may predate over fly eggs etc.
	Morph.	Body size	Bigger beetles remove more dung, competing with other orgs. Also they destroy more eggs and cists in the original dung pat
	Repro.	Dung burial amount	Removing great amount of dung is a great competition force versus other dung dependent organisms
	Repro.	Dung burial rate	It may be possible to measure *greedyness*; i.e. competitive ability to fight for dung
	Repro.	Dung relocation strategy	Endocoprids may destroy more eggs in dung pat
	Time	Colonization moment	Earlier colonization competes more with very fast reproducin flies etc.

Table A.2: Traits affecting the ecosystem functions (left-most column in vertical) delivered by dung beetles. Traits are categorized in the main aspects of dung beetle life-history. The mechanism behind the effect of each trait is succinctly explained, often providing an example.

B Appendices to Chapter 2

Variable descriptions

Measurement	Method (unit)	Description
Dung removal	scale (± 0.1 g)	Difference between the dry weight of 100 g control dung samples and the dry weight of dung remains
Dung burial		
Dry weight of buried dung	scale (± 0.1 mg)	Dry weight of buried dung masses
Burial depth	ruler (± 1 mm)	Depth of buried dung masses
Length of buried dung masses	calliper (± 0.1 mm)	Maximum diameter of buried dung masses
Width of buried dung masses	calliper (± 0.1 mm)	Minimum diameter of buried dung masses
Volume of buried dung masses	calculated (mm^3)	Ellipsoid volume of buried dung masses
Seedling emergence		
Hordeum vulgare	visual count	Number of *Hordeum vulgare* emerged seedlings
Anthyllis cytisoides	visual count	Number of *Anthyllis cytisoides* emerged seedlings
Cistus albidus	visual count	Number of *Cistus albidus* emerged seedlings
other	visual count	Number of emerged seedlings of other species

Table B.1: Measurements used to quantify functional performance of 10 dung beetle species and 3 ecosystem functions in a mesocosm experiment.

Measurement	Method	Description
Dung relocation strategy	observation	Endocoprid, Paracoprid or Telecoprid
Body		
Body dry mass	scale (± 0.1 mg)	Dry weight after drying for 72h in an oven at 70°C
Body length	calculated	Sum of head length, pronotum length and elytra length
Body volume	calculated	Volume of ellipsoid with radiae body length, pronotum width and pronotum height
Body density	calculated	Dry mass divided by body volume
Head		
Head length	image analysis	Distance from clypeus to vertex (horns not included) along symmetry axis
Head width	image analysis	Maximum width of head (normally at genas)
Head area	calculated	Area of ellipse with radiae head length and head width
Pronotum		
Pronotum length	image analysis	Distance from front to back of pronotum along symmetry axis
Pronotum width	image analysis	Maximum width of pronotum
Pronotum height	image analysis	Distance from between procoxas to highest point of pronotum
Pronotum volume	calculated	Half of the volume of ellipsoid with radiae pronotum length, pronotum width and pronotum height
Abdomen		
Elytra length	image analysis	Distance from base of elytra (coinciding with scutellum base) to elytra apex
Elytra width	image analysis	Maximum width of elytra
Elytrum area	image analysis	Area within the outline of an elytrum
Protibia		
Protibia length	image analysis	Distance from joint with profemur to the base of claw
Protibia area	image analysis	Area within the outline of the protibia
Protibia tooth length	image analysis	Distance from inner side of protibia to the apex of distal tooth of protibia
Metatibia		
Metatibia length straight	image analysis	Distance from joint with metafemur to insertion point of metatarsii
Metatibia length curved	image analysis	Distance from same landmarks but along the axis of the metatibia
Metatibia area	image analysis	Area within the outline of the metatibia

Table B.2: Description of dung beetle traits measured after a mesocosm experiment quantifying functional performance of 10 dung beetle species and 3 ecosystem functions. All traits measured with image analysis tools have an accuracy of ±0.001 mm for distances and ±0.001 mm^2 for areas. All measurements were done on images taken perpendicularly to the distance of interest, that is, maximizing the distance or area to measure.

Model selection

Response variables: A) Dung removal (squared root transformed), B) dung burial (log transformed), C) seedling emergence (count). Explanatory variables: Comp1 = PLS component 1; Comp2 = PLS component 2; Comp 3 = PLS component 3; FG = Functional group based on dung exploitation behavior (Endocoprid, Paracoprid, Telecoprid); sp = species (*Acrossus luridus, Aphodius foetidus, Bubas bubalus, Euorodalus tersus, Onthophagus opacicollis, O. ruficapillus, O. vacca, Scarabaeus puncticollis, S. sacer*).

B.0.1 Dung removal

1. Structure of random component

Model-1: Dung removal   Comp1 + Comp2 + FG, random = 1 + Comp1+ Comp2 | sp
Model-2: Dung removal   Comp1 + Comp2 + FG, random = 1 + Comp1 | sp
Model-3: Dung removal   Comp1 + Comp2 + FG, random = 1 + Comp2 | sp
Model-4: Dung removal   Comp1 + Comp2 + FG, random = 1 | sp

Model	df	AIC	BIC	logLik	Deviance	Chi-sq	Chi-df	p
Model-4	7	122.55	138.18	-54.272	108.55	-	-	-
Model-2	9	125.65	145.76	-53.826	107.65	0.893	2	0.6400
Model-3	9	126.54	146.65	-54.272	108.54	0.000	0	1.0000
Model-1	12	131.59	158.40	-53.797	107.59	0.950	3	0.8135

2. Mixed effects model vs. fixed effects model

Model-4: Dung removal   Comp1 + Comp2 + FG, random = 1 | sp
Model-5: Dung removal   Comp1 + Comp2 + FG

Model	df	AIC	BIC	logLik	LR test	p
Model5	6	136.5062	149.4595	-62.25308	-	-
Model6	7	136.0545	151.1667	-61.02723	2.451702	0.1174

3. Selection of fixed effects model

Model-5: Dung removal   Comp1 + Comp2 + FG
Model-6: Dung removal   Comp1 + Comp2

Model	AIC	BIC	logLik
Model-5	136.5062	149.4595	-62.25308
Model-6	131.7882	140.5468	-61.89408

	Resid. df.	Resid.	Dev df	Deviance	p
Model-5	64	19.513			
Model-6	66	20.045	-2	-0.53269	0.4174

4. Final model

Model: Dung removal   Comp1 + Comp2

Coefficients:				
	Estimate	**S.E.**	**t**	**p**
Intercept	2.6078104	0.06634525	39.30666	<0.0001
Comp1	0.1553737	0.01735888	8.95067	<0.0001
Comp2	0.2188326	0.07503043	2.91658	0.0048

B.0.2 Dung burial

1. Structure of random component

Model-1: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp1 + Comp2 + Comp3|sp

Model-2: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp1 + Comp2|sp

Model-3: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp1 + Comp3|sp

Model-4: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp2 + Comp3|sp

Model-5: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp1|sp

Model-6: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp2|sp

Model-7: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 + Comp3|sp

Model-8: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1|sp

	df	AIC	BIC	logLik	Deviance	Chisq	Chi df	p
Model-8	8	45.635	63.508	-14.817	29.635	-	-	-
Model-5	10	49.635	71.976	-14.817	29.635	0	2	1
Model-6	10	49.635	71.976	-14.817	29.635	0	0	<0.0001
Model-7	10	49.635	71.976	-14.817	29.635	0	0	1
Model-2	13	55.635	84.678	-14.817	29.635	0	3	1
Model-3	13	55.635	84.678	-14.817	29.635	0	0	1
Model-4	13	55.635	84.678	-14.817	29.635	0	0	<0.0001
Model-1	17	63.635	101.614	-14.817	29.635	0.0001	4	1

2. Mixed effects model vs fixed effects model

Model-8: Dung burial   Comp1 + Comp2 + Comp3 + FG, random = 1 | sp

Model-9: Dung burial   Comp1 + Comp2 + Comp3 + FG

	df	AIC	BIC	logLik	L Ratio	p
Model-9	7	66.3329	81.33485	-26.16645		
Model-8	8	68.3329	85.47798	-26.16645	1.935027e-08	0.9999

3. Selection of fixed effects model

Model-9: Dung.burial   Comp1 + Comp2 + Comp3 + FG

Model-10: Dung.burial   Comp1 + Comp2 + Comp3

Model	df	AIC	BIC	logLik
Model-9	7	43.63466	59.27341	-14.81733
Model-10	5	42.01809	53.18862	-16.00905

	Resid. df	Resid.	Dev df	Deviance	p
Model-9	63	6.2072			
Model-10	65	6.4254	-2	-0.21816	0.3305

4. Final model

Model : Dung burial   Comp1 + Comp2 + Comp3

Coefficient:

	Estimate	S.E.	t	p
Intercept	0.504493	0.037851	13.328	<0.0001
Comp1	0.101256	0.009885	10.244	<0.0001
Comp2	0.109439	0.047833	2.288	0.02540
Comp3	0.302147	0.109822	2.751	0.00768

B.0.3 Seedling emergence

1. Structure of random component

Model-1: Emergence   Comp1 + FG, random = 1 | sp

Model-2: Emergence   Comp1 + FG, random = 1 + Comp1 | sp

	df	AIC	BIC	logLik	Deviance	Chisq	Chi df	p
Model-1	5	591.09	601.72	-290.54	581.09	-	-	-
Model-2	7	595.06	609.95	-290.53	581.06	0.0245	2	0.9878

2. Mixed effects model vs fixed effects model

Model-1: Emergence   Comp1 + FG, random = 1 | sp

Model-3: Emergence   Comp1 + FG

	df	AIC	BIC	logLik	Deviance	Chisq	Chi df	p
Model-3	4	638.40	646.91	-315.20	630.40	-	-	-
Model-1	5	591.09	601.72	-290.54	581.09	49.31	1	<0.0001

3. Structure of fixed effects model

Model-1: Emergence Comp1 + FG, random = 1 | sp

AIC	BIC	logLik	deviance	df residuals
591.1	601.7	-290.5	581.1	57

Random effects:

Variable	Name	Variance	S.D.
sp	Intercept	0.1841	0.429

Fixed effects:

	Estimate	S.E.	z	p
Intercept	1.94390	0.26957	7.211	< 0.0001
Comp1	0.19722	0.05515	3.576	0.00035
FG (paracoprid)	0.46800	0.35100	1.333	0.18243
FG (telecoprid)	-0.03817	0.45593	-0.084	0.93327

3. Final model

Model-4: Emergence Comp1, random = 1 | sp

AIC	BIC	logLik	deviance	df residuals
589.3	595.6	-291.6	583.3	59

Random effects:

Variable	Name	Variance	S.D.
sp	Intercept	0.2445	0.4945

Fixed effects:

	Estimate	S.E.	z	p
Intercept	2.14856	0.17413	12.339	< 0.0001
Comp1	0.18982	0.05355	3.545	0.00039

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Site	**Municipality**		**Latitude**		**Longitude**		**Aridity**	**Altitude**	**Cow dung ($gr/100m^2$)**	**Other dung ($gr/100m^2$)**
mor10	Saïdia	a	35.08605	N	2.28714	W	2864	1	1291.61	1385.54
		b	35.08260	N	2.27282	W	2871	5	709.71	1195.24
mor9	Bni-Drar	a	34.89106	N	2.01928	W	2694	467	737.75	1299.58
		b	34.88659	N	2.00943	W	2671	453	590.67	1238.22
mor8	Guenfouda	a	34.45488	N	2.03989	W	2476	842	0	1106.00
		b	34.44317	N	2.03771	W	2443	852	16.25	1103.75
mor7	North of	a	34.14451	N	2.05680	W	2278	907	0	1061.67
	Aïn-Beni Mathar	b	34.13533	N	2.05412	W	2278	906	0	1061.33
mor6	South of	a	33.78164	N	1.99615	W	2228	1078	0	1102.00
	Aïn-Beni Mathar	b	33.79516	N	1.99353	W	2236	1076	0	1104.00
mor5	North of Tendrara	a	33.26954	N	1.98332	W	1934	1223	35.00	1064.00
		b	33.28416	N	1.97771	W	1952	1213	0	1055.00
mor4	Between Tendrara	a	32.83676	N	2.06539	W	1714	1329	17.75	1020.25
	and Bouarfa	b	32.85788	N	2.06149	W	1755	1347	2.50	1034.83
mor3	East of Bouarfa	a	32.50570	N	1.89055	W	1206	1127	0	777.67
		b	32.21061	N	1.68693	W	1213	1319	0	844.00
mor2	Between Bouarfa	a	32.20064	N	1.66292	W	1170	1283	0	817.67
	and Figuig	b	32.49803	N	1.87541	W	1214	1126	15.00	785.00
mor1	West of Figuig	a	32.14916	N	1.26801	W	894	905	0	599.67
		b	32.15368	N	1.30344	W	900	897	0	599.00

Table C.1: Localization (municipality and coordinates), altitude and amount of dung of each replicate and site sampled. Dung availability variables (cow dung and other dung) are presented as an average of the amount found in the four sampling campaigns. Aridity is here presented as the raw original variable, but note that for analysis the inverse of aridity was used in order to have directly interpretable results with increasing aridity.

Table C.2: Summary of the GLRs evaluating the effects of the extracted PLS components on species richness and log abundance for the wet and dry seasons. Values in bold indicate regression coefficients of components that differ significantly from zero after Bonferroni correction ($p < 0.0125$).

	Estimate ± SE	t	p
Richness			
Wet season			
Intercept	**18.000±0.316**	**56.873**	**<0.0001**
Component 1	**1.070±0.087**	**12.280**	**<0.0001**
Component 2	**1.105±0.213**	**5.186**	**0.0020**
Component 3	**0.850±0.213**	**3.995**	**0.0072**
Dry season			
Intercept	**8.600±0.523**	**16.452**	**<0.0001**
Component 1	0.259±0.168	1.547	0.1600
Abundance			
Wet season			
Intercept	**1.742±0.116**	**14.964**	**<0.0001**
Component 1	0.143±0.053	2.707	0.0268
Dry season			
Intercept	**2.065±0.125**	**16.495**	**<0.0001**
Component 1	**0.135±0.037**	**3.692**	**0.0061**

Wet Season							
2013				2014			
Semiarid	stat	p.value	signif	*Semiarid*	stat	p.value	signif
Amidorus cribricollis	1	0,010	**	*Aphodius foetidus*	1	0,025	*
Euonthophagus crocatus	1	0,010	**	*Euonthophagus crocatus*	1	0,025	*
Onitis numida	1	0,010	**	*Onitis numida*	1	0,025	*
Onthophagus maki	1	0,010	**	*Onthophagus maki*	1	0,025	*
Onthophagus andalusicus	1	0,010	**	*Onthophagus andalusicus*	1	0,025	*
Onthophagus taurus	1	0,010	**	*Onthophagus opacicollis*	1	0,025	*
				Onthophagus taurus	0,972	0,02	*
				Calamosternus mayeri	0,863	0,035	*
Intermediate section				*Intermediate section*			
Mecynodes leucopterus	0,853	0,030	*	*Alocoderus hydrochaeris*	1	0,005	**
Onthophagus nebulosus	0,698	0,025	*	*Mecynodes leucopterus*	0,859	0,005	**
				Onthophagus nebulosus	0,733	0,01	**
Desert				*Desert*			
Bodilus beduinus	0,918	0,005	**	*Bodilus beduinus*	0,887	0,025	*
Chilothorax hieroglyphicus	0,897	0,005	**	*Chilothorax hieroglyphicus*	0,835	0,045	*

Dry Season							
2013				2014			
Semiarid	stat	p.value	signif	*Semiarid*	stat	p.value	signif
Anomius baeticus	0,983	0,015	*	*Anomius baeticus*	0,99	0,025	*
Rest of gradient				*Rest of gradient*			
Chilothorax hieroglyphicus	1	0,015	*	*Bodilus beduinus*	0,956	0,025	*
Bodilus beduinus	0,98	0,015	*				

Table C.3: Species with significant Indicator Values (IndVal, DeCaceres & Legendre, 2009) per year (2013 and 2014) and season (wet and dry) at 10 sampling sites (spaced ca. 40 Km) along a ca. 400 Km transect from the Sahara desert to the semiarid Mediterranean coast (see map in Figure 3.1). Species were selected for three sections of the gradient in the wet season and only for two sections for the dry season following the groupings of a cluster analysis based on Bray-Curtis dissimilarity index.

	2013																			
	Wet Season										Dry Season									
	Desert								Semiarid		Desert								Semiarid	
Scarabaeinae	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**
Bubas bison																				
Bubas bubaloides				2		3														
Cheironitis ungaricus											22	5	3	1	1	1	28	7	39	97
Copris hispanus																				
Euoniticellus fulvus									1								2			
Euoniticellus pallens	1					1				1	1						1			4
Euonthophagus bedeli		3	10	5	40	188	25	60					1							
Euonthophagus crocatus								81	121	3							7			
Gymnopleurus flagellatus								15	69											
Gymnopleurus sturmi									264											
Onitis alexis																				
Onitis belial																				
Onitis ion									15	1										
Onitis numida								3	25	10										
Onthophagus aerarius		1	3	2	2	5	2	1												
Onthophagus andalusicus								7	169	11										
Onthophagus maki								5	19	12										
Onthophagus nebulosus	15	55	105	269	416	658	164	290	10	1										
Onthophagus nigellus									10											
Onthophagus opacicollis									1	3										
Onthophagus taurus								2	3	4							2	1		1
Onthophagus transcaspicus	1	1									36									
Onthophagus triggiber									11											
Onthophagus vacca																				
Scarabaeus aegyptiacus																				
Scarabaeus puncticollis				3			1							1						
Scarabaeus sacer			1	4		1							1	11						
Scarabaeus semipunctatus														1						
Scarabaeus variolosus																				
Total	**17**	**90**	**119**	**285**	**458**	**856**	**192**	**464**	**718**	**46**	**59**	**5**	**5**	**14**	**1**	**1**	**40**	**8**	**39**	**102**

	Desert								Semiarid		Desert								Semiarid	
Aphodinae	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**
Alocoderus hydrochaeris			1			8	1			2										
Amidorus cribricollis								11	50	1										
Ammoecius numidicus																				
Anomius baeticus																	15	1137	2899	6422
Aphodius fimetarius																				
Aphodius foetidus								2	13											
Bodilus beduinus	10	24	6		1	2	5				15	703	222	1320	404	348	176	4	1	5
Bodilus ictericus										27	4		3	5	2	2	11	13	15	19
Calamosternus granarius								1												
Calamosternus lucidus		1	2	1		5														
Calamosternus mayeri		1		22	4	5	13		26	4										
Chilothorax hieroglyphicus	18	353	142	3		215	16				20	34	30	80	178	3	8			
Chilothorax lineolatus									2	4										
Chilothorax melanostictus							1													
Colobopterus erraticus										27										
Eremazus unistriatus	1																			
Erytus cognatus			5	2	1	6														
Esymus finitimus		1	2	41	4	3														
Euorodalus tersus				2						3										
Labarrus lividus															1					
Mecynodes leucopterus		1	8	50	1	156	89	10												
Mendidaphodius sitiphoides																				
Mendidius palmenticola					4															
Otophorus haemorrhoidalis																				
Plagiogonus nanus																				
Pleurophorus mediterranicus					3															
Pleurophorus pannonicus																				
Rhyssemus bedeli																				
Rhyssemus nsp																				
Rhyssemus vaulogeri																				
Subrinus sturmi																				2
Subrinus vitellinus																				2
Total	**29**	**381**	**166**	**121**	**18**	**400**	**125**	**24**	**91**	**68**	**39**	**737**	**255**	**1405**	**585**	**353**	**210**	**1154**	**2915**	**6450**

Table C.4: Dung beetle abundance in 2013 per season (wet and dry) along a transect from the Sahara desert to the semiarid Mediterranean coast (see map in Figure 3.1). Names of species are grouped by subfamily. Totals per site (i.e. community) are given for each subfamily.

	2014																			
	Wet Season										Dry Season									
	Desert								Semiarid		Desert								Semiarid	
Scarabaeinae	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**
Bubas bison									2	4										
Bubas bubaloides		14	4	33	5	2	9	12												
Cheironitis ungaricus											2	2	2	1	1	7	8	8	40	29
Copris hispanus									1											
Euoniticellus fulvus							3	2											1	
Euoniticellus pallens	5						4		1									3		4
Euonthophagus bedeli		15	15	9	11	387	487	40				2			1					
Euonthophagus crocatus								453	75	1								1		
Gymnopleurus flagellatus							1	49	82											
Gymnopleurus sturmi								2	81										1	
Onitis alexis																			2	3
Onitis belial									3	2										
Onitis ion								9	31											
Onitis numida								10	13	5										
Onthophagus aerarius	1	2		1	4															
Onthophagus andalusicus								26	174	4										
Onthophagus maki								23	35	5										
Onthophagus nebulosus	11	72	482	752	285	638	745	603	10			2				1				
Onthophagus nigellus									11											
Onthophagus opacicollis								1	1	1										2
Onthophagus taurus							1	12	4	1							1			1
Onthophagus transcaspicus	20		1								128	5	4							
Onthophagus triggiber									6											
Onthophagus vacca								2												
Scarabaeus aegyptiacus				3																
Scarabaeus puncticollis				4			1							1	1		1			
Scarabaeus sacer			1	33									1	5	1		1	1		
Scarabaeus semipunctatus				3										1						
Scarabaeus variolosus									2											
Total	**37**	**103**	**503**	**838**	**305**	**1027**	**1251**	**1244**	**532**	**23**	**130**	**11**	**7**	**8**	**4**	**8**	**11**	**13**	**44**	**39**

	Desert								Semiarid		Desert								Semiarid	
Aphodinae	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**	**mor1**	**mor2**	**mor3**	**mor4**	**mor5**	**mor6**	**mor7**	**mor8**	**mor9**	**mor10**
Alocoderus hydrochaeris				4	3	8	12													
Amidorus cribricollis								2	26											
Ammoecius numidicus									3											
Anomius baeticus																	15	5529	22722	5129
Aphodius fimetarius										5										
Aphodius foetidus								2	11	1										
Bodilus beduinus	4	1695	1547	267	17	11		1			3	3059	445	274	1468	369	645	109	17	34
Bodilus ictericus	2					6	1					3	1	2	4	9	14	6	16	25
Calamosternus granarius																				
Calamosternus lucidus	2	1	19	16	19	6	1				1									
Calamosternus mayeri			2	8	3	6	32	7	92	11										
Chilothorax hieroglyphicus	11	25	39	16	10	1	15					9		1	4	4	3			
Chilothorax lineolatus										8										
Chilothorax melanostictus							5													
Colobopterus erraticus							1			2										
Eremazus unistriatus	8	1																		
Erytus cognatus			7	129	2		2													
Esymus finitimus			2	40	1		2													
Euorodalus tersus			3	1					2	7										
Labarrus lividus	4		2																	2
Mecynodes leucopterus			56	387	17	102	430	13		1			1							
Mendidaphodius sitiphoides				1																
Mendidius palmenticola					5															
Otophorus haemorrhoidalis									1											
Plagiogonus nanus						4														
Pleurophorus mediterranicus					4															
Pleurophorus pannonicus					1															
Rhyssemus bedeli					1															
Rhyssemus nsp											2									
Rhyssemus vaulogeri					1															
Subrinus sturmi																				
Subrinus vitellinus													3					1	1	20
Total	**31**	**1722**	**1677**	**869**	**84**	**144**	**501**	**25**	**135**	**35**	**6**	**3071**	**450**	**277**	**1476**	**382**	**677**	**5645**	**22756**	**5210**

Table C.5: Dung beetle abundance in 2014 per season (wet and dry) along a transect from the Sahara desert to the semiarid Mediterranean coast (see map in Figure 3.1). Names of species are grouped by subfamily. Totals per site (i.e. community) are given for each subfamily.

Variable-name	Used	Unit	Scale	Description	Source
Vegetation					
Vegetation height		cm	Replicate (averaged to site/campaign)	Visually estimated vegetation height over an area of ca. 1000 m^2	Present sampling
Vegetation cover		%	Replicate (averaged to site/campaign)	Visually estimated vegetation cover over an area of ca. 1000 m^2	Present sampling
Dung					
Total dung	✓	g/100 m^2	Replicate (averaged to site/campaign)	Estimated available total dung in 1000 m^2 (=2 transects 250 m by 2 m wide)	Present sampling
Cow dung	✓	g/100 m^2	Replicate (averaged to site/campaign)	Estimated available cow dung in 1000 m^2 (=2 transects 250 m by 2 m wide)	Present sampling
Other dung	✓	g/100 m^2	Replicate (averaged to site/campaign)	Estimated available dung not from cow in 1000 m^2 (=2 transects 250 m by 2 m wide)	Present sampling
Dung richness		g/100 m^2	Replicate (averaged to site/campaign)	Number of dung types (i.e. cow, sheep/goat, donkey/horse, dromedar, carnivore, other)	Present sampling
Cow presence		count	Replicate (averaged to site/campaign)	Binary variable accounting for presence/absence of cows	Present sampling
Space					
Altitude over sea level	✓	m	Replicate (averaged to site)	Elevation over sea level	Hijmans et al. (2005)
Moran eigenvector maps	✓	no units	Transect design	Several vectors of eigenvalues that describe spatial relations between sampling sites	Present sampling, Borcard et al. (2004)
Climate					
Mean annual aridity	✓	no units	Replicate (averaged to site)	MAP / MAE (=Mean Annual Precipitation / Mean Annual potential Evapo-transpiration)	Trabucco & Zomer (2009)
Mean monthly extraterrestrial radiation	✓	W/m^2	Replicate (averaged to site/season)	Mean monthly potential evapotranspiration (1950-2000) for each campaign (april-sept)	Trabucco & Zomer (2009)
Mean monthly precipitation	✓	mm	Replicate (averaged to site/season)	Mean monthly precipitation (1950-2000) for each campaign (april-sept)	Hijmans et al. (2005)
Mean annual precipitation	✓	mm	Replicate (averaged to site/year)	Mean annual precipitation (1950-2000) for each year (2013-2014)	Hijmans et al. (2005)
Mean monthly temperature	✓	ºC	Replicate (averaged to site/season)	Mean monthly temperature (1950-2000) for each campaign (april-sept)	Hijmans et al. (2005)
Mean site temperature	✓	ºC	Site/campaign	Mean temperature (averaged from values every 20min during 72h trap activity)	Present sampling
Standard deviation site temperature	✓	ºC	Site/campaign	Standard deviation of temperatures measured every 20min during 72h trap activity	Present sampling
Max site temperature		ºC	Site/campaign	Maximum temperature measured every 20min during 72h trap activity	Present sampling
Min site temperature		ºC	Site/campaign	Minimum temperature measured every 20min during 72h trap activity	Present sampling
Mode site temperature		ºC	Site/campaign	Mode of temperatures measured every 20min during 72h trap activity	Present sampling
Max (percentile 80) site temperature		ºC	Site/campaign	Maximum (percentile 80) of temperatures measured every 20min during 72h trap activity	Present sampling
Min (percentile 20) site temperature		ºC	Site/campaign	Minimum (percentile 20) of temperatures measured every 20min during 72h trap activity	Present sampling
20-80% range site temperature		ºC	Site/campaign	Range (percentile 20 to percentile 80) of temperatures measured every 20min during 72h trap activity	Present sampling
Percentage of 24h with temperature >10ºC		% day	Site/campaign	Percentage of day (24h) in which temperature >10ºC measured every 20min during 27h trap activity	Present sampling
Percentage of 24h with temperature >15ºC		% day	Site/campaign	Percentage of day (24h) in which temperature >15ºC measured every 20min during 27h trap activity	Present sampling
Percentage of 24h with temperature >20ºC		% day	Site/campaign	Percentage of day (24h) in which temperature >20ºC measured every 20min during 27h trap activity	Present sampling
Percentage of 24h with temperature >25ºC		% day	Site/campaign	Percentage of day (24h) in which temperature >25ºC measured every 20min during 27h trap activity	Present sampling
Mean monthly potential evapo-transpiration		mm	Replicate (averaged to site/season)	Mean monthly potential evapotranspiration (1950-2000) for each campaign (april-sept)	Trabucco & Zomer (2009)

Variable-name	Used	Unit	Scale	Description	Source
Soil					
Bare soil cover	✓	%	Replicate (averaged to site/campaign)	Visually estimated bare soil cover (no vegetation) over an area of ca. 1000 m^2	Present sampling, Tovar (2015)
Soil structure 0-10 cm	✓	0,1,2	Replicate (averaged to site)	Visually estimated soil clustering (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Soil hardness 0-10 cm	✓	0,1,2	Replicate (averaged to site)	Manual estimation of soil resistance to compression (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Gravel content 0-10 cm	✓	%	Replicate (averaged to site)	Soil fraction of over 2mm (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Sand content 0-10 cm	✓	%	Replicate (averaged to site)	Soil fraction suspended in water after 3 min (Boyoucos method) (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Silt content 0-10 cm	✓	%	Replicate (averaged to site)	Soil fraction left after calculating sand and clay contents (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Clay content 0-10 cm	✓	%	Replicate (averaged to site)	Soil fraction suspended in water after 90 min (Boyoucos method) (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Bulk density 0-10 cm	✓	g/cm^2	Replicate (averaged to site)	Dry mass / volume (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Water field capacity 0-10 cm	✓	m^3 / m^3	Replicate (averaged to site)	Water content extracted from soil at 33 kPa (Richards Membrane Method) (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Permanent wilting point 0-10 cm		m^3 / m^3	Replicate (averaged to site)	Water content extracted from soil at 1500 kPa (Richards Membrane Method) (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Available water 0-10 cm		m^3 / m^3	Replicate (averaged to site)	Water content retained by soil (mass difference after 24h at 105°C) (upper 0-10cm of 3cores, ø4cm)	Present sampling, Tovar (2015)
Soil structure 10-20 cm		0,1,2	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Soil hardness 10-20 cm		0,1,2	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Gravel content 10-20 cm		%	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Sand content 10-20 cm		%	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Silt content 10-20 cm		%	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Clay content 10-20 cm		%	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Bulk density 10-20 cm		g/cm^3	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Water field capacity 10-20 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Permanent wilting point 10-20 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Available water 10-20 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, middle 10-20cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Soil structure 20-30 cm		0,1,2	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Soil hardness 20-30 cm		0,1,2	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Gravel content 20-30 cm		%	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Sand content 20-30 cm		%	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Silt content 20-30 cm		%	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Clay content 20-30 cm		%	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Bulk density 20-30 cm		g/cm^3	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Water field capacity 20-30 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Permanent wilting point 20-30 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)
Available water 20-30 cm		m^3 / m^3	Replicate (averaged to site)	Same as above, lower 20-30cm segment of 3 soil cores (ø4cm, 30cm deep)	Present sampling, Tovar (2015)

Table C.6: Summary of grouped variables used (variables used in the final analyses have been marked with a tick mark ✓).

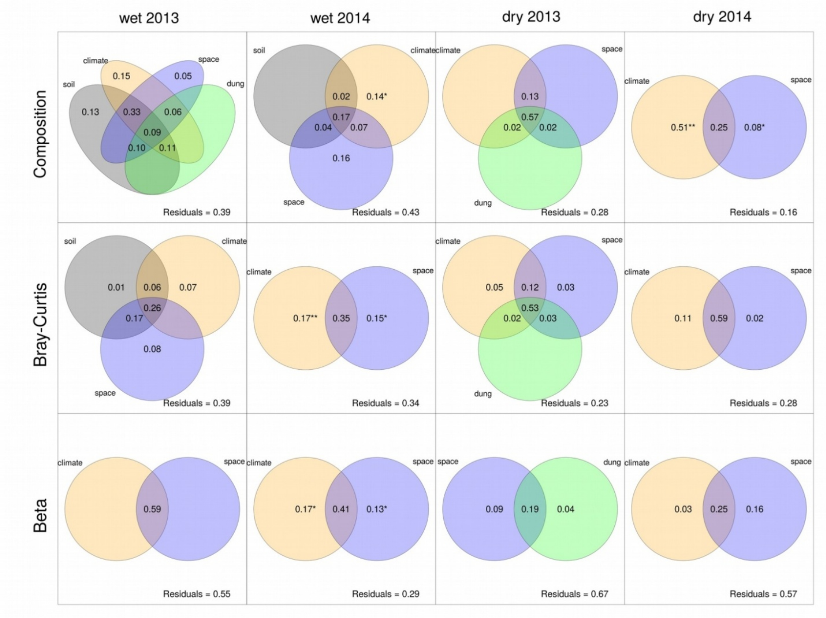
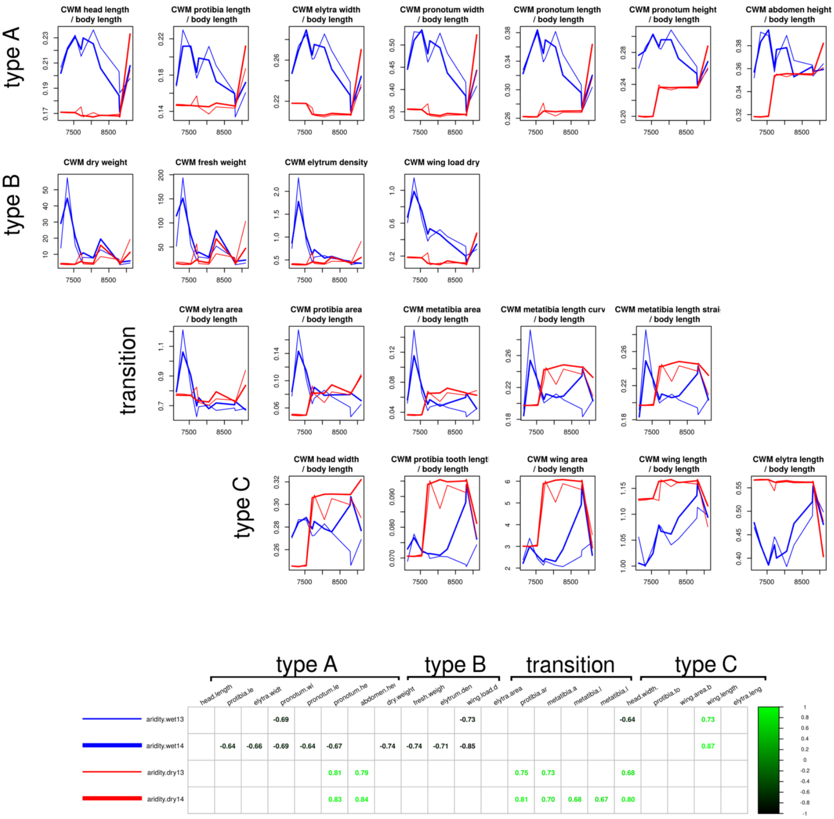


Figure C.1: Variation partitioning of Dung Beetle community variance in raw species composition (based on RDA), beta diversity and Bray-Curtis dissimilarities (based on dbRDA) along the studied aridity gradient. Community variations in four sampling campaigns: two consecutive years in the wet season (after the rainy season) and two consecutive years in the dry season (before the rainy season) are explained by up to four groups of variables (climate, space, soil and dung availability). Numbers in each fraction are adjusted R^2 values. Statistical significance of testable pure fractions (based on partial RDA or dbRDA) are shown with * ($p < 0.05$) and ** ($p < 0.01$).

D Appendices to Chapter 4

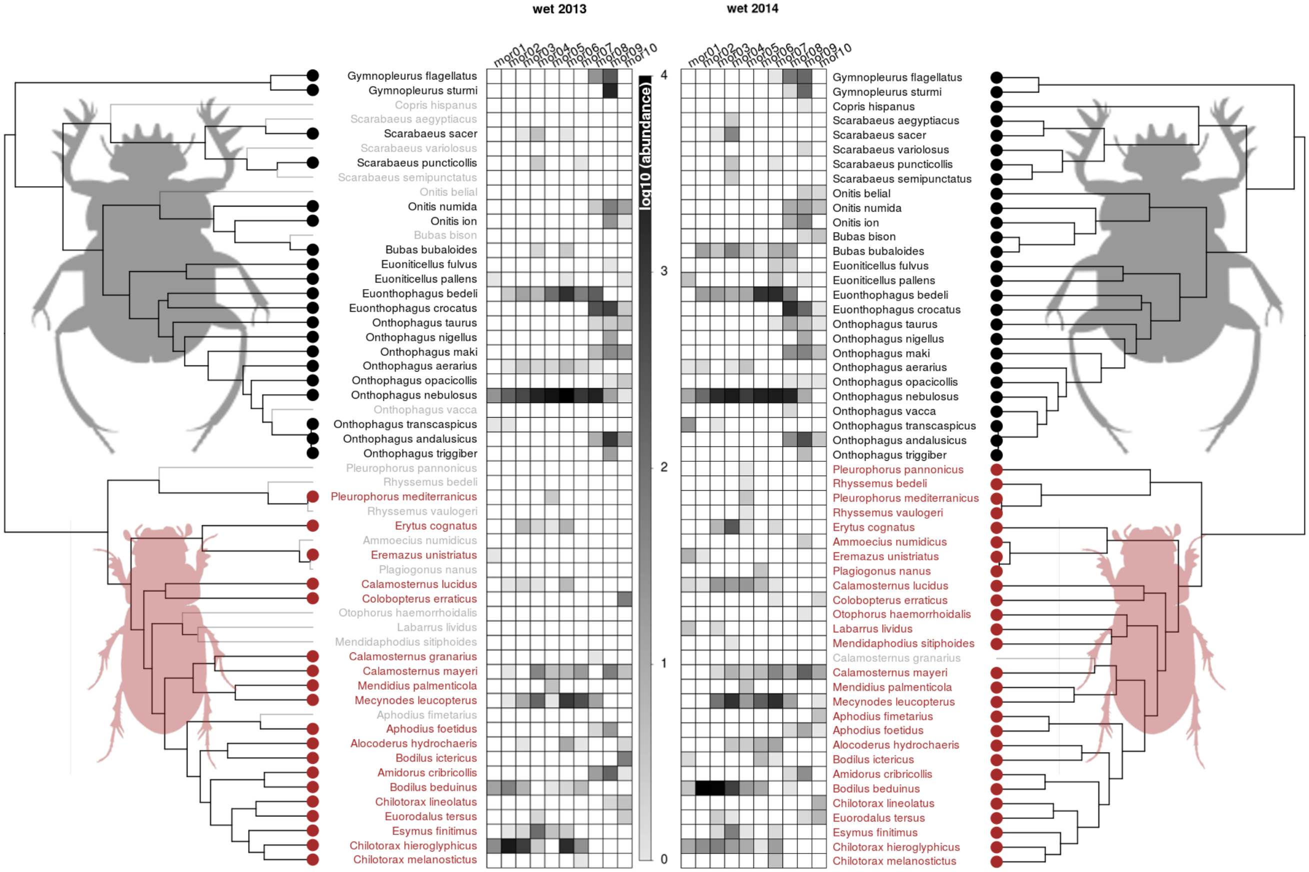
		Scarabaeinae					Aphodiinae				
Trait	**units**	**n**	**min**	**mean**	**sd**	**max**	**n**	**min**	**mean**	**sd**	**max**
Feeding relocation strategy											
endocoprid	%	29	0.00	0.00	0.00	0.00	32	0.00	0.84	0.27	1.00
paracoprid	%	29	0.00	0.76	0.44	1.00	32	0.00	0.16	0.27	1.00
telecoprid	%	29	0.00	0.24	0.44	1.00	32	0.00	0.00	0.00	0.00
Adult trophic habit											
saprophagous	%	29	0.00	0.02	0.09	0.50	32	0.00	0.30	0.39	1.00
coprophagous	%	29	0.50	0.92	0.12	1.00	32	0.00	0.68	0.39	1.00
micophagous	%	29	0.00	0.00	0.00	0.00	32	0.00	0.00	0.02	0.10
necrophagous	%	29	0.00	0.06	0.09	0.20	32	0.00	0.02	0.05	0.20
Dry biomass	mg	29	3.620	111.036	144.954	579.860	29	0.500	2.549	2.188	8.880
Fresh weight	mg	29	13.980	478.854	657.297	2597.300	29	1.000	8.505	7.893	30.000
Body length	mm	29	5.213	14.127	7.711	31.306	29	3.205	5.222	1.560	8.447
Head length	mm	29	1.203	3.154	1.638	6.904	29	0.557	0.943	0.281	1.525
Head width	mm	29	1.638	4.191	2.501	10.466	29	0.838	1.356	0.466	2.258
Pronotum height	mm	29	1.513	3.876	1.920	7.999	29	0.698	1.236	0.334	1.869
Pronotum length	mm	29	1.969	4.892	2.317	9.425	29	0.844	1.412	0.452	2.445
Pronotum width	mm	29	2.762	7.437	4.034	16.685	29	1.130	1.923	0.635	3.392
Abdomen height	mm	29	2.121	5.309	2.741	11.389	29	0.958	1.689	0.562	2.607
Elytrum area	mm^2	29	3.092	27.983	31.964	126.458	29	1.062	3.164	1.820	6.495
Elytra length	mm	29	2.040	6.081	3.755	14.977	29	1.804	2.867	0.827	4.476
Elytra width	mm	29	1.565	3.744	2.041	8.980	29	0.605	1.152	0.364	1.910
Elytrum weight	mg	29	0.280	5.287	7.108	28.540	29	0.000	0.216	0.196	0.660
Protibia area	mm^2	29	0.357	4.257	5.256	20.708	29	0.067	0.212	0.152	0.568
Protibia length	mm	29	1.080	3.666	2.573	10.144	29	0.367	0.663	0.239	1.110
Protibia tooth length	mm	29	0.356	0.995	0.561	2.391	29	0.216	0.378	0.145	0.723
Metatibia area	mm^2	29	0.240	2.669	2.970	11.398	28	0.041	0.166	0.125	0.529
Metatibia length straight	mm	29	1.140	3.752	2.971	11.764	28	0.470	0.952	0.353	1.726
Metatibia length curved	mm	29	1.150	3.811	3.040	11.983	28	0.472	0.955	0.355	1.725
Wing area	mm^2	29	8.597	70.052	74.817	264.918	27	3.363	13.046	8.676	42.505
Wing length	mm	29	5.287	13.787	7.448	27.757	27	3.230	5.880	1.823	10.064
Wing load	mg/mm^2	29	0.346	1.199	0.559	2.189	27	0.092	0.200	0.105	0.566

Table D.1: Summary of trait values for Aphodiinae and Scarabaeinae dung beetle species in the wet and dry seasons during two consecutive years along a threefold aridity gradient from the Mediterranean sea to the Sahara desert. Traits were gathered from literature and field observations (Feeding relocation strategy and Adult trophic habits) and measured values (quantitative traits: all other traits) (see Table 4.1 for description of each trait). Column *n* refers to number of species for which the trait could be measured, *min* to minimum value in any measured species, *mean* is the average value for *n* species (non weighted), *sd* is standard deviation and *max* is maximum value for any measured species.



	head.length	protibia.le	elytra.widt	pronotum.wi	pronotum.le	pronotum.he	abdomen.hei	dry.weight	fresh.weigh	elytrum.den	wing.load.d	elytra.area	protibia.ar	metatibia.a	metatibia.l	metatibia.l	head.width.	protibia.to	wing.area.b	wing.length	elytra.leng
aridity.wet13				-0.69							-0.73						-0.64			0.73	
aridity.wet14		-0.64	-0.66	-0.69	-0.64	-0.67		-0.74	-0.74	-0.71	-0.85									0.87	
aridity.dry13						0.81	0.79						0.75	0.73			0.68				
aridity.dry14						0.83	0.84						0.81	0.70	0.68	0.67	0.80				

Figure D.1: Patterns and correlations of Community Weighted Mean of all cuantitative traits measured in dung beetle communities in the wet and dry seasons during two consecutive years along a threefold aridity gradient from the Mediterranean sea to the Sahara desert. Three types of traits are proposed according to their pattern along the aridity gradient.


wet 2013
wet 2014
mor01
mor02
mor03
mor04
mor05
mor06
mor07
mor08
mor09
mor10
log10 (abundance)
4
3
2
1
0
Gymnopleurus flagellatus
Gymnopleurus sturmi
Copris hispanus
Scarabaeus aegyptiacus
Scarabaeus sacer
Scarabaeus variolosus
Scarabaeus puncticollis
Scarabaeus semipunctatus
Onitis belial
Onitis numida
Onitis ion
Bubas bison
Bubas bubaloides
Euoniticellus fulvus
Euoniticellus pallens
Euonthophagus bedeli
Euonthophagus crocatus
Onthophagus taurus
Onthophagus nigellus
Onthophagus maki
Onthophagus aerarius
Onthophagus opacicollis
Onthophagus nebulosus
Onthophagus vacca
Onthophagus transcaspicus
Onthophagus andalusicus
Onthophagus triggiber
Pleurophorus pannonicus
Rhyssemus bedeli
Pleurophorus mediterranicus
Rhyssemus vaulogeri
Erytus cognatus
Ammoecius numidicus
Eremazus unistriatus
Plagiogonus nanus
Calamosternus lucidus
Colobopterus erraticus
Otophorus haemorrhoidalis
Labarrus lividus
Mendidaphodius sitiphoides
Calamosternus granarius
Calamosternus mayeri
Mendidius palmenticola
Mecynodes leucopterus
Aphodius fimetarius
Aphodius foetidus
Alocoderus hydrochaeris
Bodilus ictericus
Amidorus cribricollis
Bodilus beduinus
Chilotorax lineolatus
Euorodalus tersus
Esymus finitimus
Chilotorax hieroglyphicus
Chilotorax melanostictus

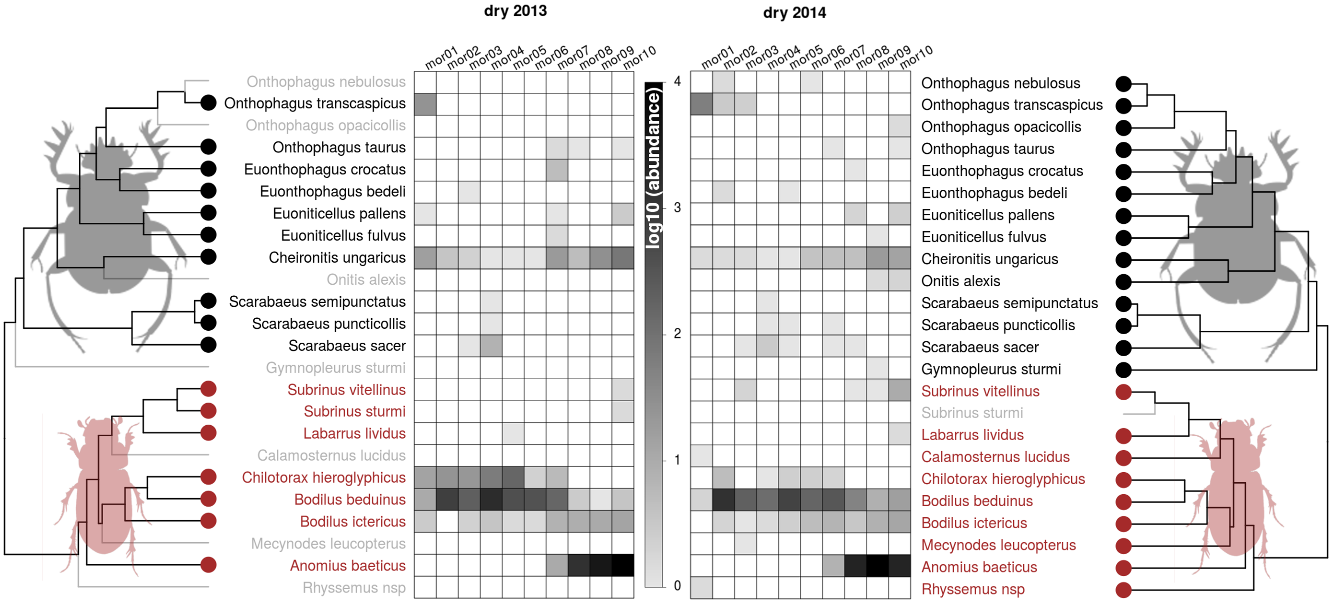


Figure D.2: Summary of abundances of species in each of the four sampling campaigns and their phylogenetic relations. For each campaign the phylogenetic relations use codes for a) Scarabaeinae species: black circles and names, b) Aphodiinae species: brown circles and names and c) absent species: grey branches, no circles and grey names. Indeed, note that in the matrices absent species have all white squares (representing no abundance at sampling sites) in contrast with present species which have grey shading in one site at least. Grey intensity refers to $log10$ (abundance) for each species and site.

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Gracias a los que me han dado el dinero y, como son incompatibles, me han quitado el tiempo. Ahora que esta tesis se termina me quedo sin dinero, pero gano todo el tiempo del mundo!

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About the author

Indradatta deCastro-Arrazola was born in Halifax, Canada, in 1986. He completed a degree in Biology starting at the Euskal Herriko Unibertsitatea (Basque Country, 2004-2007), continuing at the Aristoteleo Panepistimio Thessalonikis (Greece, 2007-2008) and finisihing at the Universidad de León (Spain, 2008-2009). In 2010 he completed Master studies in Biodiversity and Conservation Biology at Universidad Pablo de Olavide (Spain), including the Master Thesis *Spatial distribution of Opiliones in four shrublands of the Cantabrian mountain range, NW Iberian Peninsula. The importance of vegetation structure.* He then decided to plunge into numeric ecology by attending the Module in Quantitative Ecology at the University of South Bohemia (Czech Republic). He was there employed by Francesco de Bello as a bioinformatics technician to develop an R package for the implementation of two null model paradigms related to the selection of species pools in functional diversity research.

From 2013 to 2016 he has been employed by the National Museum of Natural Sciences (Spain) in order to perform doctoral research within the project *Disentangling the geographic and evolutionary determinants of the diversity of Western Palaeartic dung beetles*, on dung beetle diversity patterns in the arid areas of the Palearctic, as well as, the importance of the development of dung beetle effect and response trait-based ecology. This work has been conducted initially at the University of Granada (Spain) and then at the National Museum of Natural Sciences (Spain), under the supervision of Joaquín Hortal and Francisco Sánchez-Piñero. This work could not have been completed without the visiting periods at University of Pretoria (South Africa) under the supervision of Clarke Scholtz and Adrian Davis, at Universidad Autónoma del Estado de Hidalgo (Mexico) under the supervision of Claudia Moreno and finally at the Swiss Federal Research Institute WSL (Switzerland) under the supervision of Marco Moretti. While working on his thesis, he taught several R courses on ecological data management, exploration and analysis optimization.


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