Trophic interactions in an arid ecosystem: From decomposers to top-predators

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ABSTRACT

In this review we compile results on interactions above and below ground and food web functioning in an arid environment at the Baza Basin, in the Iberian southeast. Our data reveal that herbivory is difficult to estimate in our system. Some herbivores (rabbits) and granivores (*Messor* ants) create nutrient and detritus-rich patches, with important effects on the diversity and abundance of species both above and below ground. Fluctuations of prey availability, especially those caused by changes in their circadian rhythms, provoke seasonal migrations and omnivory in predators. We also present experimental evidence of the effects of interactions between aboveground and belowground macroarthropods on litter degradation; belowground detritivores are responsible for a high percentage of ground surface litter decomposition. We demonstrate that belowground herbivores and decomposers can dramatically change aboveground multitrophic interactions. Finally, we identify the biotic and abiotic factors controlling aboveground and belowground macrofaunal distribution at a broad scale. We conclude that trophic interactions in this semi-arid area are numerous and complex with many of the interactions involving more than two or three organisms. The interactions between above- and belowground organisms added complexity to this system. These habitats in which organisms deal with extreme abiotic conditions promote odd interactions resulting in an increase of biodiversity. Finally, despite the large research effort devoted to understanding food web structure and dynamics in this area recently, our state of knowledge is still far from providing a complete picture of interactions and their implications in the regulation and functioning of the system.

1. Introduction

The classical paradigm for functioning in arid ecosystems states that extreme abiotic conditions and water limitation are the most important factors structuring desert communities. Responses of individual species to temperature fluctuations or water availability determine their distribution and abundance. The "autoecological hypothesis" (Noy-Meir, 1980) was founded on the view of deserts as simple systems inhabited by a low diversity of organisms driven by "pulse/reserve" dynamics in which producers and consumers take advantage of unpredictable pulses of productivity, retaining reserves to withstand unfavorable periods (Noy-Meir, 1973, 1974). Since productivity pulses are unpredictable, interactions would only occur sporadically.

The view of deserts as simple, diversity-poor systems was challenged by Polis (1991). Available data for the Coachella Valley (California, USA) revealed that deserts were very diverse systems where resource limitation forced animals to interact. Omnivory, intraguild predation, cannibalism, and indirect effects increased the complexity of desert food webs. Further, although deserts are generally conceived as detritivore-driven, donor-controlled systems, where detritivores do not directly affect the renewal rates of resources, a growing consideration of indirect effects structuring community and food webs (e.g., Jones et al., 1994; Polis and Strong, 1996) reinforces the importance of interactions in desert ecosystems. This view of the importance of interactions in arid and semi-arid environments subject to pulsed dynamics is supported by both empirical and theoretical approaches (Chesson et al., 2004; Ayal, 2007).

Extreme variations of temperature and low water availability force many animals to use the soil as a refuge or as the environment where larvae or juvenile stages of many animals develop (Wallwork, 1982). Thus, a further step in understanding the complexity of desert food webs requires connecting the above- and below-ground compartments of the system. Belowground animals can determine the distribution and abundance of plants, with enormous effects on ecosystem structure and functioning (Strong,

1999; Partsch et al., 2006). Interactions (largely indirect, plant-mediated effects) between aboveground and belowground animals have been shown to have a large impact on plant herbivory (Brown and Gange, 1990). In the last decade, the need to study above-belowground connections to understand food web dynamics has been emphasized (Wardle, 2002; Bargett and Wardle, 2003) in order to integrate the herbivore and detritivore food chains into a food web (Moore et al., 2004). Due to the special relevance of detritivory in desert food webs, learning about the structure of above- and below-ground food webs and the interactions between organisms in both levels constitutes an even more pivotal question for the understanding of the ecological dynamics of arid systems.

In this review, we summarize the work that our team is conducting at the Guadix-Baza Basin (Baza Basin hereafter) on food web structure and dynamics, focusing on the interactions between above and belowground organisms. The Baza Basin is located in Granada (southeastern Spain). In this area, potential evapo-transpiration exceeds three times the amount of annual rainfall (250–300 mm). The climate is Mediterranean continental, with strong temperature fluctuations (mean temperature 14.4 °C, ranging from 40 to −14 °C) and highly seasonal. The soil is Gypsiric Regosol, characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. As generally true of desert soils, most ground surface is devoid of litter (58%), which only occurs under shrubs (usually forming a thin, distinct layer at the soil surface) and in ant mounds. The vegetation is an arid open shrubsteppe dominated by *Artemisia herba-alba* Asso and *A. barrelieri* Bess and *Salsola oppositifolia* Desf. shrubs, tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.) and *Retama sphaerocarpa* L. bushes.

In this review, the term aboveground fauna included not only organisms associated with plants, but also the epigeal fauna (some of them usually associated with litter). In contrast, belowground fauna are those organisms associated with the mineral soil. Many organisms in diverse ecosystems use both compartments (above ground and below ground) along their life-cycles, such as for example tenebrionid beetles in the Baza Basin, spending most of their lifespan as immature stages below ground, and as adults in the above ground.

2. Aboveground interactions

As in any terrestrial ecosystem, desert food webs can be conceived as structured on the basis of three main trophic levels (Ayal, 2007): producers, which provide living plant tissue, seeds and litter; primary consumers, comprising herbivores, granivores and detritivores; and secondary consumers, including predators and parasitoids. However, high levels of omnivory in both primary (some detritivores are cannibalistic or may predate on other species opportunistically; see below) and secondary consumers (predators also feed on fruits or plant material at least in some periods of the year), enhanced by low resource availability, results in a diffuse trophic level structure and a higher complexity of interactions in these systems (Polis, 1991). This complexity of desert food webs is further complicated by unpredictable and extreme conditions, which amplify the effects of spatial and temporal (seasonal and interannual) variability, causing important changes in both the occurrence and strength of interactions (Polis, 1991). In fact, the effect of abiotic factors has been shown to be more influential on aboveground (ground surface litter) assemblages, as temperature and moisture determine the use of litter both as refuges and as food resources (Doblas-Miranda et al., 2009a). Seasonal changes in temperature and water availability affecting plant growth and animal activity are thus essential to understanding interactions in these arid systems (see below).

Aboveground assemblages at the Baza Basin are largely dominated by detritivores (mainly tenebrionid beetles) and omnivores (mainly Formicidae) at ground level, whereas herbivores (especially curculionid and chrysomelid beetles, the lepidopteran *Heterogynis andalusica* Daniel, and homopterans) dominate the shrub canopy level (Sánchez-Piñero, 1994). Other important herbivores are domestic ungulates (sheep) and lagomorphs (rabbits and hares). Predatory arthropods, mostly spiders, comprise 10% (shrub canopy) to 16% (ground level) of total biomass, but birds (shrikes, warblers, larks, wheatears, etc), lizards (ocellated lizard, geckos), and mammals (mainly foxes) are important predaceous animals in the study site. Most of these animals are involved in complex interactions among them, and with plants (Fig. 1).

2.1. Herbivores-plant interactions

Herbivores are among the most abundant species in most terrestrial ecosystems, and their role in shaping food web dynamics and functioning has been well-known for many years (Olff et al., 1999). Ecosystems can contain a variety of vertebrate and invertebrate herbivore species (Olff et al., 1999). Insect herbivores are among the most abundant organisms in earth both in terms of biomass and diversity (Schoohoven et al., 2005). In the Baza Basin, invertebrate and, in particular, insect herbivores are very abundant (Sánchez-Piñero, 1994). In this area, insect herbivores feeding on shrubs are characterized mainly by their specialist character: most beetle (Curculionidae, Chrysomelidae) species with ≥5 individuals are monophagous (26 species, 58% only found on 1 shrub species) or oligophagous (10 species, 22% of species associated with 2 shrub species) herbivores (Sánchez-Piñero, 1994). In fact, the dominant species on shrubs are specialist on just one shrub species (*Sibinia iberica* Hoffmann on *Gypsophyla struthium* L.; *Lepidapion cretaceum* Rosenhauer and *Gonioctena variabilis* Olivier on *Retama sphaerocarpa*; *Pseudoprotapion baeticum* on *Ononis tridentata*; *Galeruca artemisiae* Rosenhauer on *Artemisia barrelieri*; *Temnorhinus* sp. on *Salsola vermiculata*). Similarly, the dominant Lepidoptera in the area, *Heterogynis andalusica* Daniel, is a specialist on *Artemisia* (*A. herba-alba* and *A. barrelieri*) shrubs. Although insect herbivory is difficult to detect and measure (see below), rough estimates at the study site suggest that shrub canopy herbivores may constitute as much biomass as epigeal detritivores (Sánchez-Piñero, 1994).

Among vertebrate herbivores, ungulates are among the main biotic agents that influence habitat heterogeneity in terrestrial systems by altering plant and animal abundance and diversity (Olff et al., 1999). Arid and semi-arid areas in Spain are no an exception, and particularly in the Baza Basin a strong effect of domestic ungulates has been observed on plants. During last years, the study area has zones with different ungulate (sheep almost exclusively) pressure ranging from 7.6 to 28.9 pellets/100 m^2/month (very low
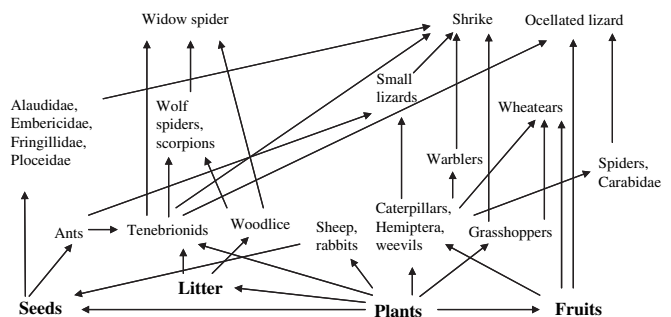

Fig. 1. Schematic diagram of some of the aboveground interactions at the Baza Basin including vertebrate and invertebrate animals.

Table 1
Soil cover (%,mean ± 1 SE) and plant species richness in the Barranco del Espartal (Baza Basin, Spain) during two consecutive years (2007, wet year, and 2008, dry year).

Year	Ungulates	Bare soil	Annuals	Perennials	Woody	Total sp.
2007	Present	32.7 ± 2.7	14.2 ± 4.2	16.5 ± 2.6	36.7 ± 5.8	38
	Absent	12.5 ± 4.8	48.7 ± 10.5	15.2 ± 6.1	23.7 ± 1.2	38
2008	Present	56.5 ± 5.3	1.5 ± 0.6	14.5 ± 3.7	27.5 ± 4.7	29
	Absent	64.8 ± 3.2	2.8 ± 1.1	9.2 ± 3.7	23.2 ± 1.8	27

to medium pressure); with periods of >100 pellets/100 m^2/month followed by several months without grazing. The ungulate effect on plants was more evident during wet years than during dry years (Table 1). Grazed areas show a greater cover of bare soil, shrubs, and tussock grasses, and a lower cover of annuals in a wet year (Table 1). Interestingly, the total plant diversity is almost exactly the same in both areas. Although shrub cover does not vary between years in the ungrazed area, it shows a strong reduction in the grazed one, which again suggests an effect more important than usually suggested for ungulates upon shrubs.

The poor perception of the effect of ungulate herbivores on plant biomass in deserts is probably a direct consequence of the difficulty in quantifying it. Many plants are certainly almost not consumed by ungulates (*Ononis tridentata*, *Gypsophila struthium*), whereas in some others that are browsed (sometimes heavily) quantification is difficult. For example, browsed *Salsola vermiculata* with scale-like leaves are difficult to differentiate from those lost for other causes; however, *Salsola* shrubs in the ungrazed area are larger than in the grazed one, which suggests effects of ungulates (Abril and Hódar, in preparation). On the other hand, *Retama* is highly consumed at two specific times: during flowering, when browsing is difficult to quantify because a high number of fallen flowers, and during autumn when legumes and cladodes are abscised to soil and grazed once they fall. In these conditions, any assessment of the importance of ungulate herbivory as a process removing plant biomass is problematic. Assuming that differences in biomass between grazed and ungrazed areas in the Baza Basin are due exclusively to ungulate removal, domestic animals may remove around 50% of herbaceous biomass (Abril and Hódar, unpublished data), which agrees with the 50−75% of biomass consumed by livestock grazing in desert areas of Israel (Ose et al., 2002). For woody vegetation, our focal area had very low biomass removal due to ungulates, but previous studies in the area have shown that ungulates and herbivores have important effect on the performance and reproduction of some plants. Ungulates influence reproduction and growth pattern in the plants *Anthyllis cytisoides* L. (Escos et al., 1996; Alados et al., 1997) and *Periploca laevigata* Ait. (Alados et al., 2002; Barroso et al., 2003), and consume a high proportion of seeds produced by the Brassicacea *Moricandia moricandioides* Boiss. (Gómez, 1996). In this case, ungulates not only affected seed production but also had a significant effect on plant distribution patterns.

Many herbivores also interact with plants by feeding on seeds (Fig. 1). Apart from the importance of this way of obtaining energy and nutrients, granivores have other effects since they determine the fate of plant reproduction. The main seed predators in the Baza Basin are birds and ants, since rodents are very scarce. Many of the resident birds in the Baza Basin feed exclusively on seeds (Fringillidae, Emberizidae) or combined with insects and plant material (*Alectoris rufa* L., Alaudidae, Ploceidae; Jiménez et al., 1991; Hódar, 1995). Among ants, *Messor barbara* L. is the most abundant species, representing on average 50−60% of insect captures in pitfalls during summer (Sánchez-Piñero, 1994). *Messor* carries the seeds to the ant nests, producing mounds at their entrance, with similar effects of concentrating seeds and nutrients as rabbit

latrines (Sánchez-Piñero and Gómez, 1995). Some plant species, i.e. *Nonea micrantha* Boiss. and Reiter (Boraginaceae), are significantly linked to these ant mounds (Abril and Hódar, unpublished data; see also Granivores-soil fauna).

2.2. Non-trophic effects of herbivores: rabbit latrines and ant mounds

The effects in soil nutrient availability and litter decomposition that large herbivores promote in dry areas via ANPP removal, trampling, and dung deposition, are poorly understood (see Sankaran and Augustine, 2004). In general dry areas have poor soils, and ungulate feces represent a considerable input of nutrients that probably overcomes the amount of nutrients removed by grazing. An especially interesting case is the latrines of rabbits (*Oryctolagus cuniculus* L.). Rabbit is, together with hare (*Lepus granatensis* Rosenhauer) the main wild herbivore in the area. Rabbit latrines are accumulations of rabbit pellets used by these animals as territorial landmarks and social arenas, and represent strong concentrations of nutrients and organic matter relative to the surrounding. The abundance and biomass of annual plant species in rabbit latrines is much higher than in control areas during wet years (Abril and Hódar, unpublished data) despite their continuous digging activities. In contrast, the opposite pattern occurs in dry years, the abundance and biomass of annual plant species in control areas is much higher than in rabbit latrines probably due to lack of water. These results suggest that latrines act as fertile islands in areas of poor soils (Willott et al., 2000), providing opportunities for different plant species that require nutrient-rich patches. Pellets not only add nutrients, but also seeds (Malo et al., 1995; Dellafiore et al., 2008, 2010). More interestingly, rabbits (and hares) are also very efficient seed dispersers of the broom *Retama sphaerocarpa* (Izhaki and Neeman, 1997; Dellafiore et al., 2008), a frequent component of vegetation in the southeastern arid and semi-arid zones of Spain (Moro et al., 1997; Lopez-Pintor et al., 2003; Padilla and Pugnaire, 2009).

Ants, especially granivorous *Messor* species, and detritivorous arthropods (mostly Tenebrionidae) are the dominant groups at ground level in the Baza Basin (Sánchez-Piñero, 1994), as in other desert ecosystems (Louw and Seely, 1982). Granivorous ants (*Messor* spp.) accumulate large quantities of debris (mostly seed husks, but also insect remains and dead ants) around the ant nest entrances, creating resource islands for detritivores (Sánchez-Piñero and Gómez, 1995). This interaction, however, has an enormous impact on detritivores: beetle density was found to be 450 times higher on ant nests (15.75 individuals/m^2) than in random areas without ant nests (0.035 individuals/m^2) (Sánchez-Piñero and Gómez, 1995); 0.35% of area covered by ant nests supported 60% of epigeal detritivores. Similarly, preliminary data on ground surface dwelling microarthropods (dominated by detritivorous Oribatid mites) show that ant-nests support 8 times higher densities than shrub-canopy patches (whereas they are almost absent in bare soil areas; Gómez-Ros et al., 2006).

The interactions between detritivores and ants were, however, not always positive; occasionally occurred predation on beetles by ants (mostly small scarabs, but also large tenebrionids) and vice versa (some tenebrionids were observed capturing active ants). The concentration of food and the interaction with ants has promoted the specialization of some species (such as the beetle *Morica hybrida* Charpentier) to use this resource (Sánchez-Piñero and Gómez, 1995).

The impact of ant nests goes beyond detritivores, that is, predators use ant nest mounds as patches to look for prey. Thus, ant nest debris accumulations appear frequently disturbed by birds and foxes, and Hódar et al. (1996) suggest that the ocellated lizard may use ant nests to find tenebrionids during the summer, when the beetles are strictly

nocturnal. However, interactions with ants likely prevent *Eresus* burrowing spiders from placing their burrows in or near ant-nest mounds, despite high prey availability (Pérez-Zarcos and Sánchez-Piñero, in preparation). This indicates that the use of ant nest mounds may also influence predator–prey interactions in the system.

2.3. Predator-herbivore-detritivore interactions

Extreme conditions in the arid Baza Basin have important consequences for predator–prey interactions inducing strategies including short distance migrations and diet shifts (Fig. 1). At the soil surface, three main arthropod groups, namely Orthoptera and Tenebrionidae (in term of biomass) and Formicidae (in number of individuals, Sánchez-Piñero, 1994), represent the staple food for the first level of predators (arachnids, reptiles, and insectivorous birds). Although ground-dwelling arthropods are abundant, they not always are available for predators. During summer, both Tenebrionidae and Formicidae shift to nocturnal activity, which makes difficult their detection by predators. Ayal (2007) stresses the importance of prey visual detection by predators, but overlooks the effects of circadian changes in activity. Thus, tenebrionid beetles are abundant during summer in the Baza Basin, but only nocturnal animals (such as the blackwidow spider *Latrodectus lilianae*, Hódar and Sánchez-Piñero, 2002) can prey on them. Even for relatively large ectotherms such as the ocellated lizard *Lacerta lepida* Daudin, a crepuscular activity is suggested, since tenebrionid beetles represent 40–80% of its captured biomass in summer when the beetles are almost strictly nocturnal (Hódar et al., 1996). When predators are unable to change their circadian activity rhythms in response to their prey, they have to migrate, as in the case of the southern grey shrike *Lanius meridionalis* Temminck (Hódar, 2006) which maintains 0.2 individuals/10 ha year round on average, but is almost absent during July and August (Hódar, 1996). During summer, birds such as Alaudidae change from being insectivorous to granivorous (Hódar, 1996). Some species are also partially frugivorous during summer, eating fruits of caper (*Capparis spinosa* L.) and ephedra (*Ephedra fragilis* Desf.) available during the hottest months of the year. The black wheatear (Hódar, 1995) and the ocellated lizard (Hódar et al., 1996) are two further cases of this strategy. Diet change is a well-known strategy for Mediterranean birds during autumn–winter (Senar and Borrás, 2004), but is less common during summer. Therefore, changes in circadian activity rhythms of prey is an important factor determining predator occurrence and omnivory in our system.

3. Belowground interactions

Interactions below ground are complex due to the diversity or organisms involved, including bacteria, fungi, protists, microfauna (e.g., most nematodes, tardigrades), mesofauna (e.g., micro-arthropods such as Collembola and Acarina) and macrofauna (macroarthropods, Oligochaetes, vertebrates such as Scincidae and Blanidae), spanning over several orders of magnitude in size and with astounding functional diversity (Coleman and Crossley, 1996; Bardgett, 2005). Belowground organisms in deserts are both taxonomically and functionally as diverse as in any other ecosystem (Wallwork, 1982; Fierer and Jackson, 2006), although drought conditions favor the dominance of decomposition by fungi over bacteria in these systems (McLain and Martens, 2006).

Our studies at the Baza Basin have focused on macroarthropods (Doblas-Miranda et al., 2007, 2009a,b,c), since Oligochaetes are scarce in the study area (Doblas-Miranda et al., 2007), and microarthropods appear in low abundance below the ground surface, where they are actually composed mainly of first instar larvae of macroarthropods and small ant species (Gómez-Ros et al., 2006). Due to the opacity of

the soil environment, the study of interactions becomes a very difficult task, and experimental approaches to address the questions below are an important future goal in our research program. Nonetheless, our current data highlight some important features of interactions among belowground organisms and soil food webs. First, our data show that, as in the above ground level, the spatio-temporal mosaic generated by microhabitat and seasonal variations belowground results in a dynamic community and trophic structure (Doblas-Miranda et al., 2007, 2009b). The effect of seasonal variations on abiotic conditions and resource availability (and palatability) provokes changes in the vertical distribution of detritivores with relevant consequences on the connection between above- and belowground food webs (Doblas-Miranda et al., 2009b).

Second, the community inhabiting the soil beneath the ground surface is mainly dominated by detritivores and herbivores, with predators constituting a small proportion of the abundance and biomass in this subsystem. Thus, natural enemies in the soil appear to be mostly pathogens and parasites, as indicated by others (Brown and Gange, 1990), showing that greater effort to understand the role of microorganisms and microinvertebrates in soil food web interactions is required.

Third, although detritivores have usually been considered as the main players in belowground food webs, our results reveal that herbivores are almost as important as detritivores in terms of abundance and biomass (Doblas-Miranda et al., 2007). The dominant belowground herbivores (larvae of Cebrionidae and Melolonthidae beetles, and Margarodidae homopterans) are generalist species which feed on roots of different shrubs and annual plants. Strategies to cope with unfavorable abiotic conditions and resource limitations differ between beetles and margarodids:cebrionids perform vertical seasonal migrations to feed on deeper shrub resources in summer, when roots of annual plants are unavailable, whereas margarodids remain inactive as "ground pearls" in the soil. The generalist diet of the dominant root herbivores contrast with the specialization of aboveground shrub herbivores (Sánchez-Piñero, 1994). Generalism has been pointed out as a trait of root herbivores (Scheu and Setälä, 2002).

3.1. Detritivore–detritivore interactions

Detritivores constitute a dominant trophic group belowground, representing more than 30% of total biomass of invertebrates in soil (Doblas-Miranda et al., 2007). Although detritus dominate their diet, most detritivores are largely omnivorous, rendering interactions among detritivores complex due to a combination of competitive and predatory relationships. Thus, exclusion experiments measuring the relative contribution of belowground and aboveground macroarthropods on ground surface litter decomposition revealed that the effects of both groups (enhancing decomposition by 1.23 times) were not additive, suggesting that interactions between detritivores decreased the net effect of both types (or stages of the same species, see below) of detritivores on decomposition (Doblas-Miranda et al., 2007; González-Megías et al., in preparation). In fact, our observations in the study site indicate that tenebrionid beetle larvae interact through a combination of exploitative and interference competition, but also, at least for some tenebrionids such as *Pimelia* spp., predation on other larvae has been detected; the extent and importance of predation and cannibalism among tenebrionid larvae remains largely unknown however. In addition, predation of belowground larvae by epigeal adults when they are close to the surface or in litter has been observed in many species (i.e. *Pimelia* spp., *Tentyria incerta*, *Morica hybrida*). Nonetheless, the extent and relevance of these interactions remains as a question requiring further study. In general, our data also indicate that tenebrionid larvae do not show significant niche partitioning

since most larvae are active during all seasons (as they usually require more than one year to complete development), and use the different microhabitats studied with a similar pattern of vertical distribution (Sánchez-Piñero et al., in preparation). However, larvae of different species show different degrees of aggregation and interspecific association (Sánchez-Piñero et al., in preparation), indicating that interactions between species at finer niche scales may be more thoroughly analyzed. Mechanisms and interactions regulating density of larvae remains an open question.

Complex interactions among detritivores have been studied in another group of strict detritivores, the dung beetles (Fig. 2). In grazed Mediterranean arid areas, dung beetles are an abundant and important component of communities. In our study sites, these communities are diverse, including 47 species of scarab beetles (Sánchez-Piñero and Ávila, 2004). Whereas Scarabaedae (principally *Scarabaeus, Onitis* and *Onthophagus* species) and a few Aphodiidae (*Acrossus luridus*) dung beetles are telocoprid or paracoprid nest builders, excavating burrows for nesting, other Aphodiidae dung beetles use alternative nesting strategies. Among the dominant Aphodiidae species, *Euorodalus tersus* and *Mecynodes leucopterus* are brood parasites in our study area, because rapid dung desiccation (46.5% water loss in 24 h) prevents endocoprid nesting (i.e., nesting within the dung). Thus, these species are able to actively locate and reach *Scarabaeus* and *Onthophagus* nests (González-Megías and Sánchez-Piñero, 2004). Field and laboratory experiments showed that brood parasitism by Aphodiidae affected 12% (*Scarabaeus puncticollis* nests) to 47% (*Onthophagus merdarius*) nests, causing high mortality (66%) of host larvae (González-Megías and Sánchez-Piñero, 2003). Experimental manipulation of *Onthophagus* brood masses in the laboratory demonstrated that aphodiid larvae actively killed host larvae within the brood mass, although the dung-feeding aphodiid larvae did not consume the host larvae, but only killed them apparently to eliminate competing larvae of the host (González-Megías and Sánchez-PiñGonz ero, 2003). Thus, bizarre interference competition of aphodiid larvae through brood parasitism shows that trophic interactions between belowground detritivores could be very complex (Fig. 2).

3.2. Granivore-soil fauna interactions

As in the aboveground level, resource patches originated by the accumulation of large quantities of debris around ant nests of granivorous *Messor* ants provoke important effects on the distribution of belowground macroarthropods (Doblas-Miranda et al., 2007, 2009b,c).

Belowground detritivore biomass was 1.5–3 times higher in ant nest mounds than in the soil below the canopy of the dominant shrubs in the study area, and more than 37 times the biomass of detritivores in the soil in bare soil areas (Doblas-Miranda et al., 2009c). The effects of granivores on soil fauna are largely indirect, due to the accumulation of plant debris (similar to litter accumulated under the canopy of the most productive shrubs in the area; see Doblas-Miranda et al., 2009b) and ant remains around nest entrances. Nonetheless, the effect of ant nest debris accumulations was temporally variable: ant nests support a higher belowground fauna during winter and spring periods, when detritus is moistened and palatable for belowground animals (Doblas-Miranda et al., 2009b). Interestingly, larvae of most tenebrionid beetles in our study site appear to require more than one year to complete development, suggesting that larvae use ant nest debris, as well as feed on surface litter during winter and spring, and use alternative food resources (roots) in summer.

The fact that belowground tenebrionid larvae use litter in ant nest mounds induces predatory interactions by ants. Thus, in a few instances we have observed ants carrying captured larvae alive into the nest. However, the low frequency of these observations suggests that predation on larvae by ants is anecdotal, and that the interaction is largely a commensalism favoring mostly larvae.

4. Linking above- and below-ground compartments

Above- and below-ground biota have been traditionally considered isolated and hermetic food-web compartments (Bargett and Wardle, 2003; Wardle et al., 2004; Moore et al., 2004), despite being ecologically and functionally linked in many different ways
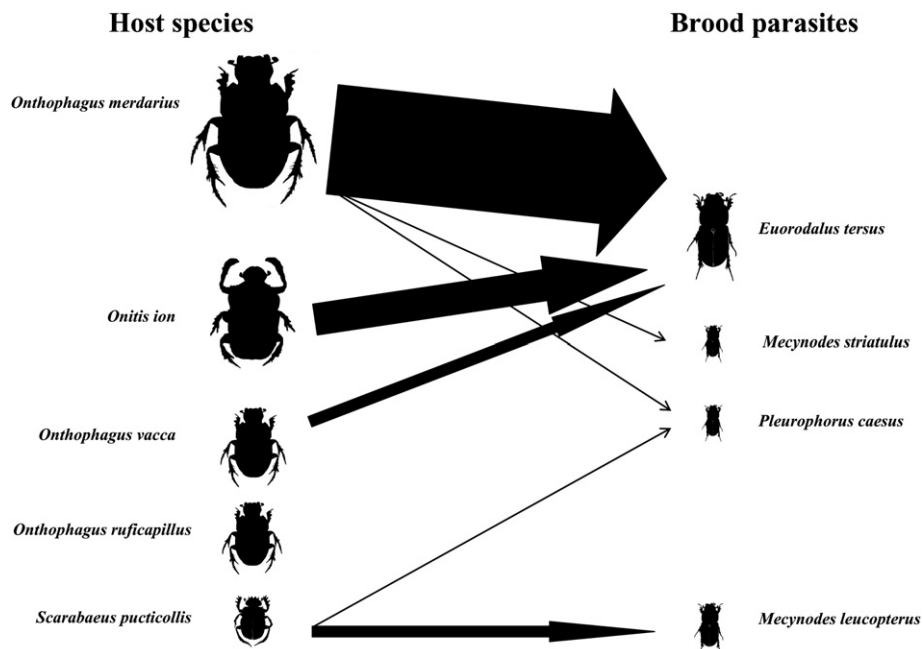

Fig. 2. The host-brood parasite interactions of dung beetles at the Baza Basin. Beetle size indicates the relative abundance of the species in the focal area. The intensity of the interactions is related to arrow size.

(Scheu, 2001; Bargett and Wardle, 2003; Wardle et al., 2004; Bezemer et al., 2005). Consequently we still lack an accurate and complete understanding of the functioning of most terrestrial food webs.

In terrestrial food webs, plants are among the most abundant organisms, and their role connecting above- and below-ground compartment has been emphasized in recent years. Aboveground vegetative and reproductive tissues as well as the root system are used as a resource for many species. Vertebrate and invertebrate herbivores play an important role in food web dynamics by consuming plants, but also by affecting other members of the community of the same and different guilds (Agrawal, 1998; Bezemer et al., 2005; Denno and Kaplan, 2007; Gómez and González-Megías, 2007; González-Megías and Müller, 2010). These interactions occurred not only between herbivores of the same compartment (above or below ground) by for example depleting the resource (competition) but also between members of different compartment by for example altering plant quality and palatability for herbivores (Scheu, 2001; Bargett and Wardle, 2003; Porazinska et al., 2003; Schröter et al., 2004; Kaplan et al., 2008; González-Megías and MüGonz ller, 2010). Recent studies also highlight the effect of herbivores on attracting their predators or predators of other food web members by their effect on plants (Scheu, 2001; Bezemer et al., 2005; Soler et al., 2005; Wolfe et al., 2005; Hopkins et al., 2009).

However, food webs include not only producers, herbivores, and predators, but also decomposers (Scheu, 2001; Bargett and Wardle, 2003; Porazinska et al., 2003; Schröter et al., 2004; González-Megías and MüGonz ller, 2010). The role of decomposers range from enhancing nutrient cycling and the breakdown of the organic matter (Bargett and Wardle, 2003; Bardgett et al., 2005) to affecting other above- and below-ground members of the community through their effect on plant performance, phenotype, and chemical defense (Wurst et al., 2004; Blouin et al., 2005; Poveda et al., 2005; Lohmann et al., 2009; González-Megías and MüGonz ller, 2010). In the Baza Basin we have some examples of above- and below-ground interactions between species belonging to different components of a food web. We also have obtained a general picture of the importance of biotic and abiotic factors as regulation forces of above- and below-ground communities at the community level.

4.1. Multitrophic interaction on a plant-based food web

In the Baza Basin, many species (see Belowground interaction above) spend most of their lives below ground, interacting with other animals and also with plants, and emerging to above ground as adults. Moreover, the effects of above- and below-ground organisms on plants can be direct (by consuming tissue) or indirect (by for example altering plant quality), and therefore, sometimes there are numerous mechanisms by which two species affect each other (Fig. 3). Using a Brassicaceae species, *Moricandia moricandioides,* as a model system, we have investigated the effect of above- and below-ground insect herbivores, detritivores, and predators on other members of the community, and on the performance and reproduction of the host plant (González-Megías and Müller, 2010; González-Megías in prep., González-Megías and Gómez in prep.). *Moricandia moricandioides* is a short-lived endemic plant of arid and semi-arid areas of the Iberian Peninsula. This plant is used by different guilds of above- and below-ground herbivores, butterfly species dominating as floral and leaf herbivores, and beetles as root herbivores.

Floral herbivores in *M. moricandioides* had an important effect on different species of sap-suckers and on seed predators, but curiously some of the effects were evident only in the presence or absence of root herbivores. Additionally, root herbivores negatively affected
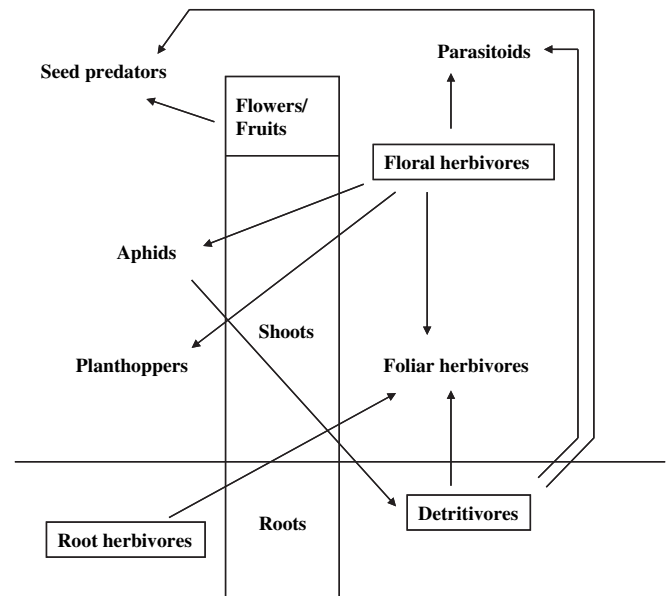

Fig. 3. Effects of floral herbivores, root herbivores and decomposers on other organisms associated with *M. moricandioides*.

insects feeding on leaves in the above ground (Fig. 3). These results reinforce the idea proposed by other authors that organisms feeding on different parts of the plant can affect each other. Detritivores also played an important role in regulating the food web by negatively affecting seed predators. Moreover, detritivores affected also the fourth trophic level by somehow positively increasing parasitism rate in floral herbivores (Fig. 3). Parasitoids were more abundant on plants with detritivores in the soil than those without detritivores. Even more interesting, detritivores also have an indirect positive effect on plants by positively altering pollinator abundance and visitation rate, whereas floral herbivores negatively affected pollination rate. These interactions can be very important for short-lived plants that only reproduce once or a few times in their lives, and especially in stochastic environments, such as arid systems, where plants have short periods of ideal conditions for flowering and pollination (Ashman et al., 2004; Horvitz et al., 2010).

Many of these interactions are probably mediated by the plant through the effect of above- and below-ground organisms on plant quality. Indeed, above and belowground herbivores were involved in the induction or suppression of glucosinolates (defensive chemical inducible compounds of Brassicaceae species; González-Megías and MüGonz ller, 2010). However, the effect of floral herbivores on glucosinolate induction was mediated by the presence of detritivores. This effect was not only related to the intensity of the interaction between floral herbivores on some specific glucosinolate compounds, but also in the identity of the glucosinolates affected by floral herbivores. Because glucosinolates are produced by the plants to inhibit herbivores, detritivores are indirectly affecting other organisms feeding on the host plant by altering the floral herbivores-glucosinolate induction interaction. This indirect effect can have important consequences for the population dynamics of the insect species affected. Not only plant quantity but also plant quality is vital for the development and reproduction of herbivore species.

The effects of above- and below-ground herbivores and detritivores on other members of the community suggested that these guilds would have an important effect on plant performance and reproduction. In *M. moricandioides*, floral herbivores reduced the number of seeds produced by half and the number of seedlings by two-thirds (González-Megías in prep.). Root herbivores and

detritivores only had a significant effect on above- and below-ground plant quality, but no net effect on plant reproduction.

This example indicates that in arid systems short-lived plants such as *M. moricandioides,* interact directly and indirectly with a high number of species. The effect of one member of the community on another one will depend on the presence of other members of the community. These studies also reinforce the idea that in arid systems above- and below-ground interactions are as important as in other temperate or agricultural systems where most studies have been conducted.

4.2. Belowground effect on aboveground decomposition process: interaction between detritivores

The importance of decomposition processes in the functioning and dynamic of ecosystems is well-known (Wardle, 2002; Bardgett, 2005; Hättenschwiler et al., 2005). Many studies show the role of different groups of soil decomposers on root and litter decomposition (Santos et al., 1981; Herlitzius, 1983; Maraun and Scheu, 1996; Bardgett, 2005). One the most important guilds affecting root decomposition includes macro-invertebrates (Lavelle et al., 1997; Whitford, 2000; Wolters, 2000). Indeed, some authors highlight the main role of macroarthropods in root decomposition in arid and semi-arid systems (Santos and Whitford, 1981; Whitford et al., 1982; Schaefer et al., 1985; Ouédrago et al., 2003). However, whether epigeal and belowground decomposers interact, and the intensity of this interaction, is a question that remains unknown in most systems (Hairston, 1989; Scheu et al., 1999b; Tscharntke and Hawkins, 2002). Arid and semi-arid systems are ideal to study interactions between epigeal and belowground decomposers because aboveground litter is patchily distributed and forms a thin, discrete layer at the soil surface. This is the case in the Baza Basin where in addition detritivore assemblages above and below ground are remarkably different (Doblas-Miranda et al., 2009b). In this area, macro-invertebrates are very abundant both above the surface (70% in terms of biomass) and below ground (more than 30%; Doblas-Miranda et al., 2007). Interestingly, belowground fauna plays an important role not only in root but also in litter decomposition, as shown by litter-bag experiments (González-Megías et al., in prep.). Migration of belowground fauna to the surface results in both above- and below-ground detritivores interacting by sharing the same resources. Curiously, litter decomposed faster when only belowground fauna had access into litter-bags than when both types of fauna or only aboveground fauna were allowed to feed in the litter-bags (González-Megías et al., under prep.). The mechanism by which the effect of both types of fauna on litter decomposition is not additive is still unknown. One of the mechanisms could be the exclusion of potential predators at the same time that we excluded aboveground detritivores from the surface, but also may be a result of interference competition among detritivores.

4.3. Factors structuring above- and below-ground detrital-based food web

Trophic interactions partially shape the structure, and therefore the functioning, of terrestrial food webs (Lawton, 1999). However, in addition to biotic factors, abiotic ones are involved on the structuring of the communities (Polis et al., 1996; Gaston, 2000). In particular, how litter and belowground assemblages are structured, and the factors determining this structure are still poorly understood (Scheu and Schaefer, 1998; Ettema and Wardle, 2002). This is mainly important in arid and semi-arid ecosystems, where the differences between above and below ground environmental conditions are large in terms of temperature and moisture fluctuation for example. The differences in abiotic conditions between above (i.e., litter layer) and below ground (soil) suggest that the relative importance of

biotic and abiotic factors at each level could vary. Traditionally it has been assumed that the role of abiotic factors were the key factors structuring desert environments and soil food web dynamics (Noy-Meir, 1985; Whitford, 1989). By obtaining information about above- and below-ground assemblage composition, and resource quality and quantity as well as abiotic factors such as moisture and temperature we explored this question in the Baza Basin (Doblas-Miranda et al., 2009a). As expected, a combination of biotic and abiotic factors appeared to be key factors shaping the litter and soil detrital-based food web. However, abiotic factors dominated as regulatory factors on the aboveground level whereas biotic factors (i.e., resource quality) appeared as the main factors controlling the belowground level. An important result is that the interactions between the above- and below-ground fauna occur as a connection between the two levels. In this case, detritivores and predators appear to be the interacting groups. Detritivores are also a connection between both levels by migrating from the soil to the litter layer not only to feed, but also by emerging as adults. The connections between the two levels highlight the importance of integrative studies when looking for the factors structuring food webs and also indicate that the connection between the two levels is dynamic.

5. Final remarks

The study of the interactions among organisms inhabiting the Baza Basin is far from a complete view of our system, and more studies are necessary to accurately predict the number and intensity of the interactions, as well as their role in the functioning of the ecosystem. This review has highlighted some of the factors contributing to the complexity in our system: 1) Trophic interactions in this semi-arid area are numerous and complex, with many of the interactions involving more than two or three organisms. The interactions between above- and below-ground levels frequently involving different life stages of the same organisms, add complexity to this system. In addition, these types of habitats where organisms have to deal with extreme abiotic conditions promoted the occurrence of odd interactions between organisms, producing an increase of both species and interaction diversity; 2) Due to the particular characteristics of the plants (i.e., small scale-like leaves) and animals (i.e., pulsed phenologies) living in this system, it is very difficult to quantify some of the effects of the organisms on each other. Indeed the quantification of actual consumption of plant biomass by invertebrates and vertebrates is at the moment far from complete; and finally 3) The study area, as most semi-arid habitats, showed high temporal and spatial variability in abiotic conditions and distribution of resources, conforming to a dynamic ecological scenario where interactions greatly fluctuate over time and space. Long-term studies are therefore necessary to understand the dynamics and the interactions in these systems.

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