

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

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Received 9 October 2006; received in revised form 12 February 2007; accepted 16 February 2007

Available online 22 March 2007

Abstract

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

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

1. Introduction

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

dynamics, especially in highly variable systems (Bengtsson and Berg, 2005).

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

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

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

2. Materials and methods

2.1. Study site

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

The soil is a Gypsic Regosol (WRBSR, FAO, 1998), characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (<5% CaCO₃ content). Soil structure ranges from weak fine granular (in the upper centimetres of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually <15–20 cm depth, being the first 1–2 cm where the organic matter concentrates, with values <2% in all cases) and C (Sierra et al., 1990). As a general trait of desert soils, most ground surface is devoid of litter (58%), which only occurs under shrubs (usually forming a thin, distinct layer in the soil surface) and in ant-nest mounds.

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

2.2. Sampling design

To analyse the composition and distribution of the soil macroinvertebrates, we considered two levels in the soil: litter (which appears as a distinct layer of accumulated detritus on the soil surface) and belowground. To sample the litter level, we collected the litter (leaf litter under the shrubs or detritus accumulated around the ant-nest mouth) contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel. Belowground samples were collected in the same spot by

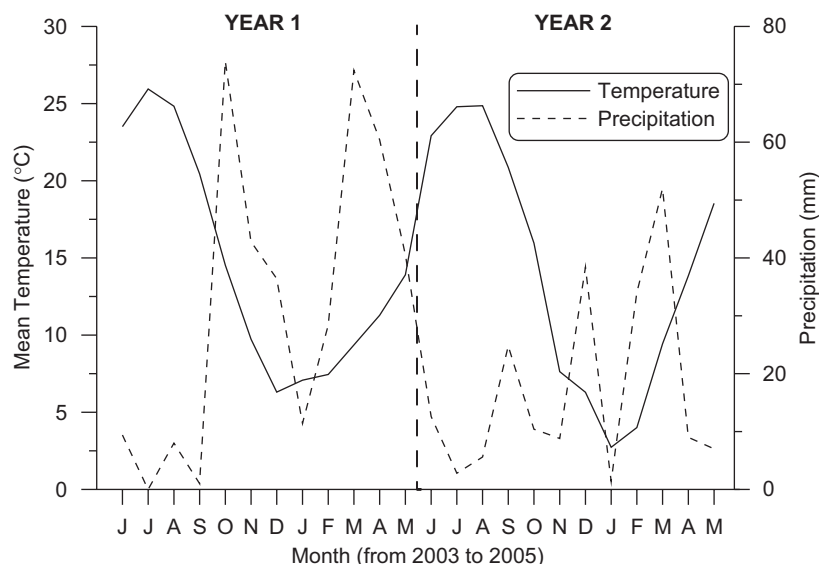


Fig. 1. Monthly mean temperature (°C) and total amount of precipitation (mm) at the study area, during April 2003–May 2005.

using a 10 cm diameter auger. Soil cores were extracted up to 50 cm depth (maximum depth was selected based on preliminary data collected at the study site showing that all taxa and >90% abundance occurred from 0–50 cm depth; Sánchez-Piñero et al., unpublished data). Both litter and core samples were collected in six different microhabitats: under the four dominant types of shrubs in the study site (*Artemisia*, *Salsola*, *Retama* and tussock grasses), in bare soil areas and in *Messor* ant-nests. We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the two years of study. To analyse seasonal variations, we distinguished six sampling periods comprising the three different seasons over the two years of study (thereafter, Summer-1, Winter-1, Spring-1, Summer-2, Winter-2 and Spring-2).

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

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

2.3. Statistical analysis

Beta diversity was calculated using two similarity indexes: the Sorensen index (qualitative, measuring whether assemblages differ in the species present) and the Morisita–Horn index (quantitative, which considers also the abundance of each species in the analysis; Magurran, 2004). Because of the high number of ants in some

samples, Formicidae were excluded for the calculation of the Morisita–Horn index. To compare differences in richness (mean number of taxa per sample), abundance (mean number of individuals per sample) and biomass (mean dry weight per sample) among sampling periods or between years, non-parametric Kruskal–Wallis and Mann–Whitney U tests were used because data were not normally distributed. To test whether the relative frequency of trophic groups differed among sampling periods, we used a Chi-square test. Sorensen and Morisita–Horn indexes were calculated using EstimateS 7.5.0 (Colwell, 2005), while the remaining statistical analyses were conducted using the Statistica software package (StatSoft Inc., Tulsa, USA).

3. Results

3.1. Taxonomic composition of the assemblage

A total of 19 842 individuals belonging to 158 invertebrate taxa were collected (Appendix A). Density of macroinvertebrates was 101 individuals/m² (56 individuals/m² excluding ants) in litter and 1559 individuals/m² (217 individuals/m² excluding ants) belowground. Mean biomass was 0.50 g/m² in litter and 1.61 g/m² belowground.

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

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

3.2. Trophic composition

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

The belowground assemblage was amply dominated by non-in situ-consumers in terms of abundance, but detritivores,

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

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

non-in situ-consumers and herbivores represented a similar proportion of biomass. Predators represented the lowest percentage of both abundance and biomass belowground (Table 1).

3.3. Annual variation

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

3.4. Seasonal variations in assemblage composition

Richness ($H = 95.93$, $P < 0.0001$, d.f. = 5873), abundance ($H = 97.54$, $P < 0.0001$, d.f. = 5873) and biomass ($H = 90.75$, $P < 0.0001$, d.f. = 5873) varied significantly among sampling periods at the litter level (Fig. 2): for the three variables, the lowest values occurred in Summer-1, while Winter-1 and Spring-2 were the periods with the highest means. The pattern of seasonal variations differed between years in the three variables, reaching the highest values in winter during the first year, while the maximum values occurred in spring during the second year.

At belowground level, only Spring-2 showed significantly higher values of richness ($H = 11.68$, $P < 0.05$, d.f. = 5873), abundance ($H = 21.6$, $P < 0.001$, d.f. = 5873) and biomass ($H = 14.92$, $P < 0.05$, d.f. = 5873; Fig. 2) than the rest of the sampling periods.

Similarity in assemblage composition also varied between sampling periods (Table 2). At the litter level, the Sorensen index between sampling periods was about 50%, showing high differences between seasons. The Morisita–Horn index was higher than Sorensen index values in most cases, only Summer-1 showing a lower similarity than the other sampling periods, indicating that the abundance of

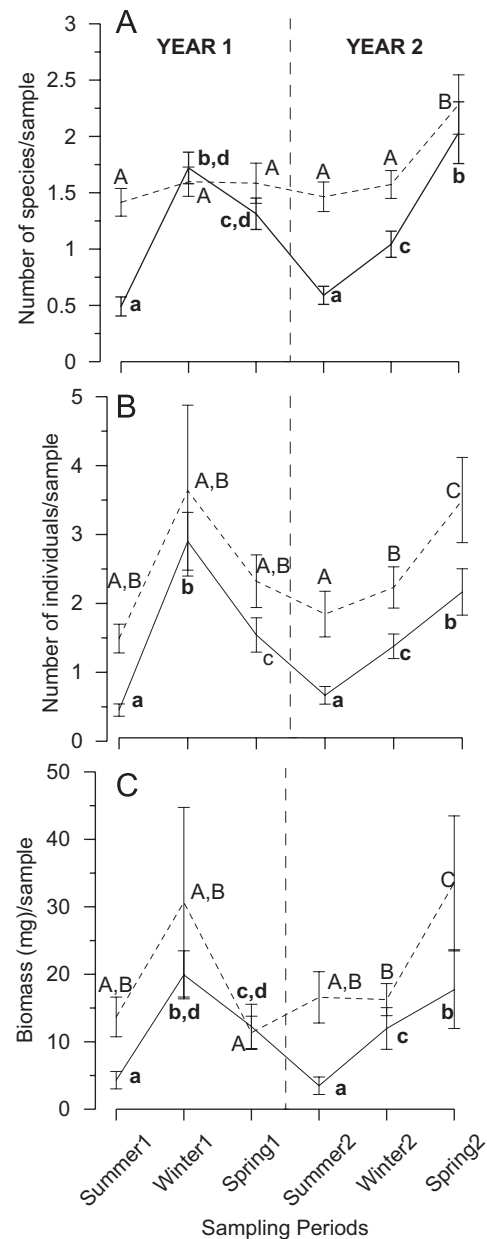


Fig. 2. Species richness (A) mean number of species per sample, (B) abundance (mean number of individuals per sample, excluding Formicidae) and (C) biomass (mean mg of dry weight per sample) of soil macroinvertebrates per sampling period. Solid line: litter level; shaded line: belowground level.

dominant taxa remained similar between seasons. The Sorensen index between sampling periods was higher at belowground level than at the litter level, and the Morisita–Horn index showed higher variations belowground than at the litter level. Differences in similarity between seasons did not show a consistent pattern in both years, showing very different Morisita–Horn indexes between winter and summer at litter, and winter and spring belowground. Also, assemblage composition showed marked variations for the same season between the two years (Table 2).

Table 2
Similarity in species composition between sampling periods in (A) litter and (B) belowground levels

	Summer-1	Winter-1	Spring-1	Summer-2	Winter-2	Spring-2
<i>(A) Litter</i>						
Summer1	*	0.35	0.27	0.49	0.49	0.60
Winter1	0.47	*	0.92	0.87	0.88	0.79
Spring1	0.27	0.52	*	0.77	0.78	0.71
Summer2	0.51	0.56	0.51	*	0.91	0.84
Winter2	0.39	0.57	0.43	0.55	*	0.85
Spring2	0.44	0.58	0.51	0.52	0.54	*
<i>(B) Belowground</i>						
Summer1	*	0.75	0.66	0.82	0.77	0.85
Winter1	0.69	*	0.34	0.99	0.64	0.96
Spring1	0.52	0.57	*	0.40	0.82	0.43
Summer2	0.62	0.65	0.54	*	0.69	0.98
Winter2	0.63	0.70	0.53	0.66	*	0.73
Spring2	0.52	0.59	0.42	0.54	0.63	*

In each case, Sorensen index values are shown in lower diagonal and Morisita–Horn index values in upper diagonal. Bold numbers indicate similarities between consecutive seasons and italics indicate similarities between the same season in different years.

Table 3
Mean biomass (\pm S.E.) of the different trophic groups in each sampling period in litter and belowground

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

Letters behind the numbers indicate statistically different means.

3.5. Temporal variations in trophic structure

At the litter level, biomass of all trophic groups differed among seasons ($H > 11.33$, $P < 0.05$, d.f. = 5873 in all cases; Table 3), most trophic groups showing a common pattern of increase in Winter-1 and Spring-2 (except non-in situ-consumers, that only showed a small increase of biomass during the first spring). The relative frequency of trophic groups in the litter assemblage also varied among sampling periods ($\chi^2 > 10.18$, $P < 0.05$, d.f. = 4 in all cases).

At belowground level, the biomass of detritivores ($H > 13.09$, $P < 0.05$, d.f. = 5873) and predators ($H = 18.05$, $P < 0.01$, d.f. = 5873) differed significantly among seasons (Table 3), with higher biomass in Spring-2. There were also significant differences in the trophic structure

among sampling periods belowground ($\chi^2 > 9.36$, $P < 0.05$, d.f. = 3 in all cases).

4. Discussion

4.1. Community composition

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

The macrofaunal assemblage at the study site was dominated by arthropods both in terms of abundance and biomass. The assemblage differed to those reported in more humid temperate and tropical habitats, where

Lumbricidae is generally the dominant group together with other taxa such as termites (in tropical regions), ants and beetles (e.g., Decaëns et al., 1998; Barros et al., 2002). The dominance of Formicidae and Coleoptera has been indicated as a general trait of ground dwelling assemblages in the Mediterranean and desert systems (Ghabbour and Shakir, 1980; Legakis, 1994; Sánchez-Piñero, 1994, Ph.D. Thesis).

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

4.2. Temporal variability

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

The results highlight two interesting traits in the seasonal variations of the assemblage: the differences in seasonal

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

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

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

Acknowledgements

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

Appendix A

List of taxa, total number of individuals (No. Indiv.) in litter and belowground, and trophic group of the macroarthropods collected at the study site during the two years of the study. In taxa with different trophic roles in litter and belowground, trophic group in each level (litter/belowground) is also indicated (see Table A1).

Table A1

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

Table A1 (continued)

Class	Order	Family	Genus/species	No. Individ.		Trophic group
				Litter	Belowg.	
			<i>Notochilus crassicornis</i>	2	0	Herbivore
		Miridae	<i>Laurinia</i> sp.	4	0	Herbivore
			<i>Halticus</i> sp.	1	0	Herbivore
		Stenocephalidae	<i>Dicranocephalus</i>	1	0	Predator
		Aphidae		1	0	Herbivore
		Cercopidae	<i>Cercopis</i> sp.	1	1	Herbivore
		Cicadellidae		2	0	Herbivore
		Cicadidae		0	1	Herbivore
		Cydnidae		8	1	Herbivore
		Nabidae		1	0	Predator
		Unidentified Hemiptera		13	9	
	Neuroptera	Myrmeleontidae larva		1	0	Predator
	Coleoptera	Carabidae	<i>Harpalus tenebrosus</i>	1	0	Omnivore
			<i>Cymindis lineola</i>	1	0	Omnivore
			<i>Ditomus capito</i>	1	10	Herbivore/non-in situ-consumer
			<i>Demetrias atricapillus</i>	1	0	Predator
			<i>Carabus lusitanicus</i>	1	0	Predator
			<i>Microlestes</i> spp.	44	5	Predator/non-in situ-consumer
			<i>Orthomus expansus</i>	7	2	Predator/non-in situ-consumer
			<i>Singilis alternans</i>	0	1	Non-in situ-consumer
			<i>Synthomus fuscomaculatus</i>	2	1	Predator/non-in situ-consumer
			Unidentified larvae	23	10	Predator
		Staphylinidae	<i>Ocypus ophthalmicus</i>	1	0	Predator
			Unidentified adults	31	3	
		Histeridae	<i>Hister grandicollis</i>	1	0	Predator
		Thorictidae	<i>Thorictus</i> sp.	2	3	Detritivore/non-in situ-consumer
		Melyridae	<i>Axynotarsus</i> sp.	1	0	Herbivore
			Unidentified species 1	0	1	Soil Dweller
			Unidentified larva 1	2	5	Detritivore
			Unidentified larva 2	0	1	Detritivore
			Unidentified larva 3	0	6	Detritivore
		Eucnemidae	Unidentified larvae	0	2	Detritivore
		Elateridae	<i>Cardiophorus</i> sp.	2	0	Herbivore
			<i>Cardiophorus</i> sp. larva	1	19	Herbivore
		Cebrionidae	<i>Cebrion</i> <i>granatensis</i> larvae	1	175	Herbivore
		Buprestidae	<i>Julodis onopordi</i>	0	1	Herbivore
			<i>Julodis onopordi</i> larvae	0	10	Herbivore
		Lathrydidae	Unidentified larvae	2	0	Fungivore
		Anobiidae		2	0	Detritivore
		Anthicidae		16	1	Detritivore
			Unidentified larva	1	0	Detritivore
		Meloidae	<i>Berberomeloe majalis</i> hypnotheca	0	1	Non-in situ-consumer
			Mylabrin hypnotheca	0	1	Non-in situ-consumer
		Melandrydae	Unidentified larvae	1	13	Detritivore
		Tenebrionidae	<i>Pimelia integra</i>	10	2	Detritivore
			<i>Pimelia monticola</i>	6	0	Detritivore
			<i>Pimelia</i> spp. larvae	7	19	Detritivore
			<i>Morica hybrida</i>	2	0	Detritivore
			<i>Morica hybrida</i> larvae	2	14	Detritivore
			<i>Tentyria incerta</i>	6	1	Detritivore
			<i>Tentyria incerta</i> larvae	10	6	Detritivore
			<i>Scaurus</i> spp. larvae	4	14	Detritivore
			<i>Alphasida clementei</i>	1	0	Detritivore
			<i>Alphasida clementei</i> larvae	0	17	Detritivore
			<i>Heliotaurus ruficollis</i> larvae	14	26	Detritivore
			<i>Asida cincta</i>	4	0	Detritivore
			<i>Asida rectipennis</i>	1	0	Detritivore
			<i>Asida</i> spp. larvae	1	11	Detritivore
			<i>Phylan gibbulus</i>	1	1	Detritivore
			Unidentified larvae	4	9	Detritivore
		Cetoniidae	Unidentified larva	0	1	Herbivore
		Dinastydae	Unidentified larva	0	1	Detritivore

Table A1 (continued)

Class	Order	Family	Genus/species	No. Individ.		Trophic group
				Litter	Belowg.	
		Geotrupidae	<i>Bolbelasmus bocchus</i>	0	2	Fungivore
		Aphodiidae	<i>Aphodius baeticus</i>	0	6	Detritivore
			<i>Aphodius baeticus</i> larvae	11	9	Detritivore
		Melolonthidae	<i>Elaphocera segurensis</i>	0	1	Herbivore
			<i>Rhizotrogus toletanus</i>	1	5	Herbivore/non-in situ-consumer
			<i>Rhizotrogus toletanus</i> larvae	0	6	Herbivore
			Unidentified larvae	6	47	Herbivore
		Cerambycidae	<i>Iberodorcadion mucidum</i> larva	0	1	Herbivore
		Chrysomelidae	<i>Chrytocephalus</i> sp. larva	1	0	Herbivore
			<i>Galeruca augusta</i>	2	0	Herbivore
			Unidentified larvae	4	1	Herbivore
		Curculionidae	<i>Coniocleonus obliquus</i>	1	0	Herbivore
			<i>Cycloderes submetallicus</i>	0	1	Non-in situ-consumer
			Unidentified larvae	65	8	Herbivore
		Unidentified larvae		5	13	
	Diptera	Asilidae larvae		3	12	Predator
		Tipulidae larvae		4	2	Herbivore
		Unidentified Diptera		13	53	
	Lepidoptera	Noctuidae	<i>Agrotis</i> spp.	1	0	Herbivore
			<i>Agrotis</i> spp. larvae	5	1	Herbivore
		Geometridae larvae		1	0	Herbivore
		Pterophoridae pupae		13	48	Herbivore
		Pyrilidae larvae		2	1	Herbivore
		Unidentified larvae		17	5	Herbivore
	Hymenoptera	Formicidae	<i>Crematogaster lestrigum</i>	123	24	Omnivore/non-in situ-consumer
			<i>Aphaenogaster</i> sp.	1	1	Omnivore/non-in situ-consumer
			<i>Botryomirmex</i> sp.	2	0	Omnivore
			<i>Messor barbarus</i>	286	1057	Omnivore/non-in situ-consumer
			<i>Messor bowieri</i>	58	493	Omnivore/non-in situ-consumer
			<i>Messor</i> spp. pupae	0	14	Non-in situ-consumer
			<i>Monomorium</i> sp.	3	0	Omnivore
			<i>Tapinoma nigerrimum</i>	103	38	Omnivore/non-in situ-consumer
			<i>Diplorhoptrum</i> sp.	28	1037	Omnivore/non-in situ-consumer
			<i>Pheidole palidula</i>	40	158	Omnivore/non-in situ-consumer
			<i>Tetramorium semilaeve</i>	92	10377	Omnivore/non-in situ-consumer
			<i>Plagiolepis pigmea</i>	247	324	Omnivore/non-in situ-consumer
			<i>Plagiolepis schmitzi</i>	136	475	Omnivore/non-in situ-consumer
			<i>Leptothorax specularis</i>	95	319	Omnivore/non-in situ-consumer
			<i>Lasius niger</i>	4	59	Omnivore/non-in situ-consumer
			<i>Camponotus</i> sp.	4	0	Omnivore
			<i>Oxyopomyrmex</i> sp.	24	80	Omnivore/non-in situ-consumer
			Unidentified Formicidae	64	128	Omnivore/non-in situ-consumer
		Bethylidae		5	2	Predator
		Mutillidae		0	1	Predator
		Platygastridae		1	0	Predator
		Cynipidae		0	1	Non-in situ-consumer
		Chalcidoidea		1	0	Predator
		Sphecidae		0	1	Predator
		Unidentified pupae		2	6	Non-in situ-consumer

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