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Different structuring factors but connected dynamics shape litter and belowground soil macrofaunal food webs

Enrique Doblas-Miranda [a,b,*], Francisco Sánchez-Piñero [a], Adela González-Megías [a]

[a] Universidad de Granada, Departamento de Biología Animal, Campus Fuente Nueva s/n, ES-18071 Granada, Spain
[b] Centre d'étude de la forêt. Université de Québec à Montréal. Case postale 8888, succursale Centre-ville, Montréal (Québec) H3C 3P8, Canada

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ABSTRACT

Factors determining the distribution and structure of soil and litter macrofaunal assemblages remain still poorly understood, despite the overriding importance of the spatio-temporal mosaic of biotic and abiotic conditions as main drivers of soil biota and processes. Analysis of the effects of different factors on soil communities have been usually restricted to responses to litter, despite the fact that litter and mineral soil layers are connected. Therefore, whether organisms using the litter layer respond to the same biotic and abiotic factors as organisms using the mineral soil still remains poorly known. We hypothesize that the role of biotic and abiotic factors as determinants of the distribution of faunal components of soil communities differ between litter and mineral soil assemblages in arid systems and that both levels are connected by animals moving across both levels. During two years, macroinvertebrates were sampled in litter and soil at an arid region of SE Spain, and different biotic and abiotic factors were measured. We performed structural equation model analysis to uncover the factors related to macrofaunal distribution. Our results show that abiotic factors, litter production and litter and root quality, as well as relationships among different trophic groups were key factors affecting faunal densities in our system. While abundance variations in litter assemblages were principally related to temperature and moisture, belowground faunal densities responded to resource factors. Despite differences in structuring factors at both levels, faunal interactions link both assemblages across the litter–belowground interface. The results highlight three important issues to understand soil communities and food web structure. First, abiotic factors structure soil macrofaunal food webs directly and indirectly, because of the effect of litter as habitat, and not only as food. Second, overlooking the differences found between above and belowground regulation may cause problems in the interpretation of food web structure and dynamics. Third, our models also suggest that both litter and belowground assemblages are dynamically connected.

1. Introduction

The factors explaining the patterns of distribution and abundance of organisms have long been an objective in ecology (Gaston, 2000). Organisms live in heterogeneous habitats that vary in abiotic conditions (e.g., temperature, moisture) and in the composition and abundance of resources which affect their distribution (Polis et al., 1996). In addition, interactions among organisms constitute important mechanisms structuring communities (Lawton, 1999). However, what factors determine the distribution and structure of litter and soil macrofaunal assemblages remains still poorly understood (Scheu and Schaeffer, 1998; Ettema and Wardle, 2002), despite the overriding importance of the spatio-temporal mosaic of biotic and abiotic conditions as main drivers of soil biota and processes (Ettema and Wardle, 2002; Wardle, 2005).

Plant species are able to modify their near environments and potentially influence fundamental properties of soil food webs due to the complex interaction among plants, soil properties and soil organisms (Van der Putten, 2005). Two main factors that are part of the "resources" offered by a plant species have been commonly indicated as structuring forces of soil assemblages: resource availability and quality (Bardgett et al., 1998; Tiunov and Scheu, 2004) and microhabitat characteristics (Moore et al., 2004; Sabo et al., 2005). Due to the interactions among these factors, whether resources or habitat traits are provoking the observed responses is often difficult to distinguish (Scheu and Schaeffer, 1998). Further, interactions among trophic groups may be related to the observed responses of soil organisms. Thus, prey

* Corresponding author. Tel.: +34 958 24 23 09; fax: +34 958 24 32 38.
E-mail address: edoblasm@ugr.es (E. Doblas-Miranda).

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availability (in a bottom-up context) or predator free microhabitats (in a top-down scenario) may be also responsible for the observed responses (Wardle et al., 1999; Scheu et al., 2003).

Analysis of the effects of different factors on soil communities have been usually restricted to responses to litter (see reviews by Wardle, 2002; Bardgett et al., 2005), despite the fact that roots have been recently shown to represent an important source of carbon for soil invertebrates (Pollierer et al., 2007) and that litter and mineral soil layers are connected. Thus, although the community of invertebrates that lives on the leaf litter has been found to be relatively (but not completely) isolated from that of the underlying soil layers (Heal and Dighton, 1986; Doblas-Miranda et al., 2009a), whether the organisms using the litter layer respond to the same factors than organisms using the belowground layer and the effects of litter traits and its fauna on the belowground system have not been addressed. Although in systems where the litter layer is thick and gradually mixes with roots and the mineral soil (as in mull soils) this may not be evident, in habitats where a discrete boundary between the litter layer and the mineral soil exists, as in arid and semiarid regions (comprising ca 30% of emerged lands), faunal elements may show responses to different factors in each layer. In these extreme environments, temperature and moisture suffer higher fluctuations in the ground surface than belowground and their effects maybe more limiting for litter dwellers than for belowground dwellers (Wallwork, 1982), although whether abiotic factors are the main drivers of the distribution and community structure of soil organisms remains unclear (Peterson et al., 2001).

In this paper, we explore the factors that influence the structure of a soil macrofaunal community in a desert area of SE Spain using structural equation models. Our goal in this study was to investigate the effects of temperature and moisture, resource availability and quality, and the presence of different, potentially interacting trophic groups, in the structure of the macrofaunal food web at litter and belowground soil levels. Our hypotheses are: 1) abiotic factors are more important determinants of the structure of soil communities in the more variable litter level; 2) resources are more important factors determining the structure of assemblages at buffered belowground level; 3) macroinvertebrates able to use resources at both levels connect litter and belowground soil macrofaunal food webs.

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). Potential evapo-transpiration exceeds annual rainfall (250–300 mm) three times. Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40 °C 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) spring, from March to May; 2) summer, from June to September; and 3) winter, from October to February.

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

As a general trait of desert soils, most ground surface is devoid of litter (58%), which mainly occurs under shrubs (usually forming a thin, distinct layer on the soil surface). The vegetation is an arid open shrubsteppe dominated by *Artemisia herba-alba* Asso and *A. barrelieri* Bess, *Salsola oppositifolia* Desf. and *Retama sphaerocarpa* L. shrubs and tussock grasses (*Stipa tenacissima* Kunth and *Ligeum spartum* L.), which act as "island microhabitats" aggregating most soil macrofauna (Doblas-Miranda et al., 2009b).

Analysis were carried out focusing on soil macroinvertebrates due to their relevant effect on decomposition processes in our system (Doblas-Miranda, 2007) and to the relatively low abundances of microarthropods in the study area (Gómez-Ros et al., 2006). Also, soil macroarthropods are a diverse and abundant component of the soil biota performing important roles in soil ecological processes (Wolters, 2000), with potentially high implications in nutrient limited desert soils (Whitford, 2000). Soil macrofauna also constitute key organisms in the connection between above- and belowground subsystems (Coleman, 1996; Wardle, 2002). The soil macroinvertebrate assemblage at the study site is dominated by arthropods both in terms of abundance and biomass (Doblas-Miranda et al., 2007). The most important groups are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae and Cebrionidae larvae and Carabidae adults), Hemiptera (*Dimargarodes mediterraneus* Silvestri, 1908), Embioptera (*Haploembia palaui* Stefani, 1955), Araneae, Isopoda (*Porcelio* sp.), Julida (*Julus* sp.), Geophilomorpha (*Pseudohimantarium mediterraneum* Chalaude and Ribaut, 1909) and Thysanura (relative abundances of taxa are provided in Doblas-Miranda et al., 2007), constituting 92.2% of the total abundance and 76.1% of the total biomass.

2.2. Sampling design

To study the effect of abiotic and biotic variables on macroinvertebrate distribution, we: 1) estimated macroinvertebrate abundance, 2) measured temperature and moisture and 3) measured productivity and quality of litter and roots. Samples were collected under the canopy (at aprox. 5 cm from the trunk) of the four dominant types of shrubs in the study site (*Artemisia* spp., *S. oppositifolia*, *R. sphaerocarpa* and *S. tenacissima*) and in bare soil areas, considered as five different microhabitats: (1) *Artemisia*, (2) *Salsola*, (3) *Retama*, (4) *Stipa* and (5) bare soil, respectively. Samples were collected monthly from October 2003 to May 2005, along five sampling periods: (1) Winter-1, (2) Spring-1, (3) Summer-1, (4) Winter-2 and (5) Spring-2.

To analyse the distribution of the soil macroinvertebrates, we considered two levels in the soil: litter and belowground. To sample the litter level, we collected the leaf litter under the shrubs contained in a 10 cm diameter plastic cylinder placed on the ground by cutting the soil surface with a flat shovel. Belowground samples were collected in the same spot by using a 10 cm diameter auger, up to 50 cm depth. We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but even, number of replicates per microhabitat) during the 20 months of study. 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.

Because of the large number of potential species interactions in the study site, it is methodologically better to focus on the interactions between selected functional groups of species (Rae et al., 2006). Macroinvertebrates were thus classified into five different trophic groups (Doblas-Miranda et al., 2007):