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Different microhabitats affect soil macroinvertebrate assemblages in a Mediterranean arid ecosystem

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ABSTRACT

Spatio-temporal variability is a key factor in conservation, management and restoration of ecosystems. Spatial heterogeneity is caused in many cases by organisms that are able to modify their environments. This is especially relevant in arid systems, where organisms such as shrubs and ants create patches of high nutrient availability (fertile islands) surrounded by a low-nutrient matrix. Although variations in structure and physiology among shrubs provoke differences in their effects as fertile islands, whether different microhabitats vary in their influence on animal communities is poorly known. The principal aim of our study is to analyse the effects of different shrub species and *Messor* harvester ant-nest mounds on the structure of soil macroarthropod assemblages in a strongly seasonal desert location of SE Spain. Shrub microhabitats and ant-nest mounds maintained higher species density, abundance and biomass of soil macroinvertebrates than the surrounding soil matrix. The different microhabitats differed in taxonomic and trophic composition, abundance, and biomass of soil macroinvertebrates, at both litter and belowground levels. Also, variations of invertebrate abundance among microhabitats changed throughout sampling periods. Thus the spatio-temporal heterogeneity of the study site affected the distribution and dynamics of the macroinvertebrate community. The above results indicate that the spatio-temporal mosaic created by microhabitat and seasonal variations on macroinvertebrate assemblages is a relevant issue to be considered in conservation, sustainable management and environmental restoration in heterogeneous arid systems to preserve their biodiversity and ecosystem functioning.

1. Introduction

Spatial heterogeneity is a key factor to understand the structure and dynamics of populations, communities and ecosystems (Stewart et al., 2000), which constitutes a fundamental issue in conservation, sustainable management and environmental restoration (Pickett et al., 1997; Fischer et al., 2008). The spatial heterogeneity is in many cases created and maintained by organisms that are able to profoundly modify their environments, exerting an important influence on community structure and ecosystem level processes via their effects on nutrient dynamics and the creation of microsites (Jones et al., 1994). Plants are clear examples of ecosystem engineers, affecting the distribution of soil fauna in many different environments (e.g., Coulson et al., 2003; Viketoft, 2007; see Wardle, 2002 for an extensive review), but some soil macroinvertebrates can also perform similar effects (Laakso and Setälä, 1997).

The crucial role of shrubs in preventing desertification processes and in conservation and restoration of arid lands has been widely recognised (e.g., Burke, 2001; Maestre and Cortina, 2005; Zhao et al., 2007). Shrubs in arid ecosystems are able to modify their near environment through different mechanisms involving the effects of both the root system and the canopy, creating high nutrient patches in a low-nutrient matrix (i.e., fertile islands) with important consequences on arid land dynamics (Charley and West, 1975; Garner and Steinberger, 1989; Schlesinger et al., 1996). In addition to shrubs, ants and other animals can be important agents creating patches of higher nutrient and water availability compared with the bare soil in arid regions (Cammeraat et al., 2002; Wagner and Jones, 2006). Accumulation of litter and nutrients in these patches, affecting both resource availability and microclimatic conditions, have been shown to favour the existence of higher abundance and diversity of soil biota (microorganisms, nematodes and/or micro-arthropods) under shrubs (Pen-Mouratov et al., 2004; Goberna et al., 2007) and in ant-nest mounds (Wagner et al., 1997; Boulton et al., 2003) than in the surrounding soil.

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The effects of island microhabitats on the distribution of soil fauna have further consequences in arid ecosystems, where these microhabitats are maintained by soil macroinvertebrates (Sarr et al., 2001; Ouédraogo et al., 2004) potentially through their profound effects on feedback loops linking C, N, microbial communities, and plants (Lavelle, 1997; Wardle, 1999; Ehrenfeld et al., 2005). Thus, the distribution pattern of soil organisms considering the spatial heterogeneity created by different shrub species and animal created patches constitute an important question to understand the structure and dynamics of desert systems (Whitford, 2002). However, although differences in structure and physiology among shrub species provoke differences in their effects as fertile islands (Charley and West, 1975; Schlesinger et al., 1996; Titus et al., 2002; Li et al., 2007), differences in their influence on animal communities have been poorly explored in arid environments (Peterson et al., 2001; Pen-Mouratov et al., 2008). In addition, the high temporal variability of these environments (Doblas-Miranda et al., 2007) may interact with the spatial heterogeneity created by shrubs and animal created patches to produce a dynamic mosaic in the distribution of the soil fauna, a question not addressed in previous studies but with potentially important consequences on conservation and management of arid ecosystems.

In this paper, we analyse the effects of chamaephyte and phanerophyte shrubs varying in structure and size and *Messor* harvester ant-nest mounds on macroinvertebrate assemblages in a strongly seasonal desert location of SE Spain. In our system, the dominant shrubs provoke a facilitation effect on annuals and these or similar species have been documented as creating fertile islands in different deserts (e.g., Cannon et al., 1995; Pugnaire and Haase, 1996; Pugnaire et al., 1996; Haase, 2001; Maestre et al., 2002). Similarly, detritus mounds of *Messor* harvester ants constitute patches with increased amount of nutrients, affecting the distribution of different organisms in arid and semi-arid systems (Cammeraat et al., 2002; Boulton et al., 2003). The effect of these microhabitats on other organisms would vary due to differences in microhabitat traits and as a consequence of changing environmental conditions. Thus, we hypothesise that: (1) shrubs and ant-nests harbour higher density of taxa, abundance and biomass of soil macroarthropods than the surrounding soil; (2) macroinvertebrate assemblages vary among the different shrub species and ant-nests; (3) shrub species and ant-nest mounds affect the trophic structure of the assemblage; (4) the spatial mosaic is temporally dynamic in this extreme, strongly seasonal desert environment.

2. Materials and methods

2.1. Study system

The study was conducted at Barranco del Espartal (ca. 50 ha), a seasonal watercourse located in the arid Guadix-Baza Basin (Granada, Southeastern Spain), from June 2003 to May 2005. Potential evapo-transpiration exceeds three times the amount of annual rainfall (250–300 mm). Climate is Mediterranean continental, with strong temperature fluctuations (ranging from 40 to -14 °C), and highly seasonal. The sudden change between the hot and dry summers and the cold and rainy winters determine that autumn does not appear as a distinct season in the area (Castillo-Requena, 1989), only three seasons being actually recognizable: (1) spring, from March to May; (2) summer, from June to September; and (3) winter, from October to February.

The soil is a Gypsiric Regosol (WRBSR, FAO, 1998) characterized by a sandy loam texture, high pH, low water retention capacity and high salinity. The substrate is composed of silt mixed with gypsum sediment, and is slightly calcareous (<5% $CaCO_3$ content). Soil structure ranges from weak fine granular (in the upper centimeters of the soil) to single grain, generally with profiles showing a sequence composed of horizons A (usually 15–20 cm depth, with maximum values of organic matter <2% in the upper 1–2 cm) 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 as detritus accumulations on the soil surface around nests of *Messor* (*Messor barbarus* L. and *Messor bouvieri* Bondroit) harvester ants.

The vegetation is an arid open shrubsteppe dominated by *Artemisia* (*Artemisia herba-alba* Asso and *Artemisia barrelieri* Bess) and *Salsola* (*Salsola oppositifolia* Desf.) chamaephyte shrubs, tussock grasses (*Stipa tenacissima* L. and *Lygeum spartum* L.) and *Retama* (*Retama sphaerocarpa* L.) phanerophyte bushes. Individual plants and ant-nest mounds are spaced at enough distance (usually > 0.5 m apart) to conform discrete patches.

Analyses were carried out focusing only on soil macroinvertebrates due to the relatively low abundances of microarthropods in the study area (Gómez-Ros et al., 2006). Soil macroinvertebrates are a diverse and abundant component of the soil biota performing important roles in soil ecological processes (Lavelle, 1997; Wolters, 2000), with potentially high implications in nutrient limited desert soils (Whitford, 2000). The soil macroinvertebrate assemblage at the study site is dominated by arthropods both in terms of abundance and biomass. The most important groups are Hymenoptera (Formicidae), Coleoptera (especially Tenebrionidae and Cebrionidae larvae and Carabidae adults), Hemiptera (*Dimargarodes mediterraneus* Silvestri), Embioptera (*Haploembia palaui* Stefani), Araneae, Julida (*Julus* sp.), Geophilomorpha (*Pseudohimantarium mediterraneum* Chalande and Ribaut) and Thysanura (for a complete list of taxa see Doblas-Miranda et al., 2007), constituting 92.2% of the total abundance and 76.1% of the total biomass (unpublished data).

2.2. Sampling design

The study was conducted during 2 years, from June 2003 to May 2005. To analyse the distribution of the soil macroinvertebrates, we considered two levels in the soil: litter (which appears as a distinct layer of accumulated detritus on the soil surface) and belowground. To sample the litter level, we collected the litter (leaf litter under the shrubs or detritus of the ant-nest mound) 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 at the same spot by using a 10 cm diameter auger. Soil cores were extracted up to 50 cm depth. Maximum depth was selected based on preliminary data collected at the study site showing that all taxa and >90% abundance occurred from 0 to 50 cm depth (Sánchez-Piñero et al., unpublished data). To analyse the distribution patterns of macroinvertebrates, both litter and core samples were taken in six different microhabitats: (1) ant-nest mounds (thereafter ant-nest), (2) *Artemisia*, (3) *Retama*, (4) *Salsola*, (5) tussock grasses, and (6) bare soil matrix (devoid of litter). We collected 10 replicates per microhabitat each month (except for some months when weather conditions limited the sampling to a lower, but equal, number of replicates per microhabitat) during the 2 years of study. Replicates were arranged randomly along the study area, distances between sampled microhabitats ranging 3–50 m to ensure that samples were completely independent. In order to investigate seasonal variations, we have distinguished six sampling periods, which comprise the three different seasons over the 2 years of study (in temporal order: Summer-1, Winter-1, Spring-1, Summer-2, Winter-2 and Spring-2).

Samples were processed in the field using fine-mesh sieves (1 mm mesh size). After sieving, the litter or soil held back in the sieve was placed in 20 cm × 15 cm white pans and invertebrates