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Spatial patterns of grasses influence soil macrofauna biodiversity in Amazonian pastures

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ABSTRACT

Grasslands are often characterized by small-scale spatial heterogeneity due to the juxtaposition of grass tufts and bare ground. Although the mechanisms generating plant spatial patterns have been widely studied, few studies concentrated on the consequences of these patterns on belowground macrofauna. Our objective was to analyze the impact of grass tuft (*Brachiaria bryzantha* cv. *marandu*) spatial distribution on soil macrofauna diversity in Amazonian pastures, at a small scale (less than 9 m^2). Soil macrofauna was sampled among *B. bryzantha* tufts, which showed a variable spatial distribution ranging from dense to loose vegetation cover. The vegetation configuration explained 69% of the variation in total soil macrofauna density and 68% of the variation in total species richness. Soil macrofauna was mainly found in the upper 10 cm of soil and biodiversity decreased with increasing distances to the nearest grass tuft and increased with increasing vegetation cover. The size of the largest grass tuft and the microlandscape connectivity also had a significant effect on biodiversity. The density and species richness of the three principal soil ecological engineers (earthworms, ants and termites) showed the best correlations with vegetation configuration. In addition, soil temperature significantly decreased near the plants, while soil water content was not influenced by the grass tufts. We conclude that soil macrofauna diversity is low in pastures except close to the grass tufts, which can thus be considered as biodiversity hotspots. The spatial arrangement of *B. bryzantha* tussocks influences soil macrofauna biodiversity by modifying soil properties in their vicinity. The possible mechanisms by which these plants could affect soil macrofauna are discussed.

1. Introduction

Large-scale determinants of soil macrofauna diversity are relatively well known: climate, soil type, land-use management practices and landscape structure are among the most influential factors (Dauber et al., 2003, 2005). At smaller scales, however, there is much less agreement about the environmental factors that drive soil macrofauna diversity and distribution (Lavelle and Spain, 2001). It has been suggested that in general, grassland invertebrates are less likely to be limited by the quantity of food available, but rather by microclimate and food quality (Curry, 1994). Microclimate is very important since the body temperature of soil macrofauna varies with external conditions (thermoconformers) and the range tolerated by many species is quite narrow (Precht et al., 1973; Geiger and Aron, 2003). In addition, soil macrofauna must maintain body water content within fairly narrow limits, which creates a dependence on water. Soil macrofauna organisms are also sensitive to the nutrient content of their food because they need to maintain their internal chemical concentrations and the balance between the different nutrients of their body within a strict range (Sterner and Elser, 2002; Martinson et al., 2008). Thus elements of food quality, such as phosphorus (Kay et al., 2006; McGlynn and Salinas, 2007), nitrogen (Warren and Zou, 2002) or Ca^{2+} (Reich et al., 2005) content, can become a limiting factor. As autogenic ecosystem engineers, plants modify food quality, quantity, and the microclimate of soil macrofauna. With their associated microflora they affect the physical and chemical properties of their environment by producing and taking up organic and mineral substances, creating biopores, and producing litter (Lavelle and Spain, 2001). Plants modify the microclimate in their vicinity by cooling down the soil and air in the shade of their leaves. They also modify

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humidity by intercepting wind and rain, and by absorbing water in the ground. As a consequence, they create specific living conditions (i.e. physical habitats and available food for e.g., Jackson and Caldwell, 1993). A wealth of literature deals with the consequence of these engineering effects on microbial communities (Spetch, 1958; Northup et al., 1999) but much less is known about the relationships between vegetation cover and soil macrofauna diversity and distribution.

In Amazonian pastures, vegetation is typically dominated by large herb tufts of the genus *Brachiaria*, which clearly alternate with bare ground. The vegetation cover is highly variable, from dense to loose, which leads to heterogeneous habitats for soil organisms. Cattle ranching is the dominant activity in Amazonia in terms of land surface (Muchagata and Brown, 2003) and the major motivation for deforestation. Pastures are often characterized by a dramatic decrease in productivity after 10 years of exploitation (Costa and Rehman, 1999; Muchagata and Brown, 2003). This phenomenon is accompanied by a reduction in soil macrofauna biodiversity (Fragoso et al., 1997; Barros et al., 2002). Soil macrofauna biodiversity plays a recognized role in the productivity and soil functioning of these systems (Chauvel et al., 1999; Laossi et al., 2008), but the factors that drive its distribution are still poorly documented. In particular we lack information about the small-scale sources of environmental variability that cause local patterns of soil macrofauna biodiversity (Mathieu et al., 2004).

Our aim was to analyze the effect of vegetation spatial configuration on belowground soil macrofauna density and species richness in Amazonian pastures. We investigated the correlations between the spatial configuration of *Brachiaria bryzantha*, a very common plant in these pastures, and soil macrofauna distribution, and the relations between the spatial configuration of *B. bryzantha* and the soil macrofauna environment. In particular, we discuss the role of soil temperature and water content as factors, which structure the microenvironment, and their possible consequences on soil macrofauna diversity and abundance.

2. Materials and methods

2.1. Site

This study was carried out in a community of smallholders in south-east Amazonia, at the Benfica Field Station (5°16′ S and 49°50′ E, Pará, Brazil). We surveyed three, 6 years old pastures of 20 ha on average, planted with the perennial African grass *B. bryzantha* cv. *Marandu*, the most common species used in this area. Pastures mainly served for cattle ranching. *B. bryzantha* forms massive tufts reaching 0.8 m in diameter that can locally have a fairly even spatial distribution and are separated by bare ground, leading to a heterogeneous vegetation cover (Fig. 1 shows an average configuration). In the pastures under study, grasses were planted individually when the pasture was established. The climate is tropical humid with an annual rainfall of 1800 mm and an average temperature of 26 °C. The rainy season generally starts in November or December and ends during May or June. Clayey Ferralsol soils (Isss, 1998) are dominant with varying thicknesses of aggregated, macroporous and permeable horizons, above compact alterites (subsoil). They are acid (pH = 5.8) and contain 12.7 g kg^{-1} of C, 1.8 cmolc kg^{-1} of Ca^{2+}, 5.0 mg kg^{-1} of P on average in the 10 upper cm.

2.2. Sampling design and procedures

2.2.1. Soil macrofauna

The soil macrofauna was sampled by taking 60 evenly distributed samples along 6 transects in 3 pastures (2 transects per pasture, 10 m between each sample). The sampling design was part of a wider campaign to sample soil macrofauna at the landscape level (Mathieu et al., 2005). Soil macro-organisms were collected following the tropical soil biology and fertility method (Anderson and Ingram, 1993). At each sampling point, an area of 25 × 25 × 30 cm deep was excavated and the surface cover directly above the sample was either classified as "bare ground" or "microsite"(when there was a grass tuft or dead tree trunk on the ground). The corresponding variable is hereafter referred to as "Sample Type" (ST). The litter layer and soil were quickly removed before the macroinvertebrates were hand-sorted and preserved in 4% formalin solution. In the laboratory, adult invertebrates were classified into 7 broad taxonomic groups: earthworms, termites, ants, spiders, coleoptera, centipedes and millipedes and identified at the species level with the help of a number of taxonomists. Individuals of other groups were pooled as a single group called "others". Samples were taken at the end of the rainy season in 2002 when communities were presumed to be at peak abundance and biomass (Anderson and Ingram, 1993). Macrofauna extracted from soil and litter layers was combined in the analyses.

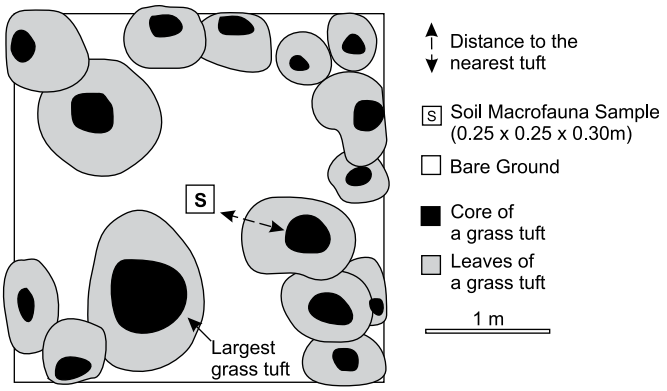

Fig. 1. A typical 9 m^2 map of the vegetation cover illustrating how the configuration of the grass tufts results in a micro-landscape. Grass tufts can be separated into two sections: the core of the tufts (i.e. the basal area), and the area occupied by the leaves (i.e. the canopies. Only the basal areas were used for calculating micro-landscape metrics.

2.2.2. Quantifying the vegetation spatial organization

The vegetation cover around each sample was described within a squared area of 9 m^2 centered on the sample (Fig. 1). Strings were attached to the ground to form a regular grid of 0.3 m × 0.3 m and the soil cover was mapped at a scale of 1:20 to show grass tussocks, grass canopies and the presence of micro-habitats such as dead wood, cattle dung and termite mounds. The maps were then digitalized and rasterized (resolution: 0.1 m × 0.1 m per pixel). This produced simple micro-landscape maps with 2 strata: bare soil (matrix) and grass tufts (patches). The resulting "micro-landscapes" were described by four classical landscape metrics (Giles and Trani, 1999): the percentage of soil occupied by vegetation (PL), the area of the largest grass tuft in the area (LPI, m^2), the Edge Density (ED, m m^{-2} i.e. the length of the vegetation boundary, in meter, per square meter of area) and the Patch Density (PD, ind m^{-2}, i.e. the number of grass tufts per unit area). Only the central part of the tufts (corresponding to the stems, or "basal area", Fig. 1) was considered because these vary considerably less with time compared to the whole leaf system which is grazed by cattle. The distance between the soil macrofauna sample and the nearest grass tuft was also measured. The metrics were calculated using Fragstats (McGarigal and Marks, 1995). In addition we evaluated visually the amount of dead wood on the ground within the area of 9 m^2, and classified it as 0: no wood, 1: some twigs and branches, 2: big branches or trunk. We will refer to this variable as WOOD here in.