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Litter manipulation and the soil arthropod community in a lowland tropical rainforest

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ABSTRACT

Tropical soil arthropod communities are highly diverse and provide a number of important ecosystem services, including the maintenance of soil structure, regulation of hydrological processes, nutrient cycling and decomposition. Experiments in temperate regions suggest that litter dynamics are important in determining the abundance, richness and community composition of soil fauna, but there is little information for lowland tropical forests. We used a long-term litter manipulation experiment (removing, doubling and control) in a neotropical forest to investigate the consequences of changing litter dynamics on the soil arthropod community. The abundance and biomass of arthropods were reduced significantly by the removal of litter, but not affected by litter addition. Litter manipulation had no effect on simple measures of taxonomic richness or diversity, but multivariate ordination techniques revealed a significant shift in arthropod community composition with the removal, but not addition, of litter. This suggests the overall importance of top-down controls on the arthropod community in this ecosystem, with bottom-up influences only important following the removal of large quantities of litter. Of the parameters measured, the faunal composition of experimental plots was best predicted by litter depth and the concentrations of total carbon and readily-exchangeable phosphorus (in order of importance), highlighting the influential role of soil chemical properties, in addition to the physical properties of litter, in shaping soil arthropod communities. Comparison with the results of a previous study of litter-dwelling fauna in the same litter manipulation experiment suggested that the soil and litter arthropod communities are influenced by different parameters: total carbon and litter depth for the soil community, but sodium and calcium for the litter community, although phosphorus was important in both environments. We conclude that arthropod community composition is controlled by different factors in the soil than in the litter and is affected by decreasing, but not increasing, depth of litter.

1. Introduction

Estimates of the total number of extant species on Earth range from 3.6 million to over 30 million (Wilson, 2002; Hamilton et al., 2010). Many of these species are terrestrial arthropods that live in the soil for at least part of their life cycle (Giller, 1996). In fact, soil communities are thought to be amongst the most species rich components of terrestrial ecosystems (Anderson, 1975). For instance, the volume of soil beneath 1 m^2 of temperate beech woodland can contain more than 1000 species of soil animals (Anderson, 1975). Tropical soil communities are likely to be even more species rich; being home to possibly twice as many species as occur in rainforest canopies (Ruiz et al., 2008). Indeed, mature forest soils appear to have a taxonomic diversity greater than any other habitat on Earth except coral reefs (Behan-Pelletier and Bisset, 1992), perhaps as a result of the wide array of microhabitats that soil provides (Coleman, 2001; Bardgett, 2002).

These diverse soil communities provide a number of important ecosystem services; for example, soil arthropods maintain soil structure, regulate the porosity of soil, and hence influence hydrological processes and aeration (Lavelle, 1996; Ruiz et al., 2008). They also play a key role in ecosystem carbon dynamics, with a positive relationship between species richness and rates of carbon cycling, which is of significance since approximately 80% of global terrestrial carbon is stored in soils (Nielsen et al., 2011).

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Furthermore, the soil fauna is a key component of ecosystem nutrient cycling, influencing the availability of nutrients both for soil-dwelling organisms and for plants (Giller, 1996; Lavelle, 1996; De Deyn et al., 2004; Ruiz et al., 2008).

Despite the importance of soil organisms in ecosystem functioning, factors governing their ecology remain poorly understood. Current information indicates soil organisms to be partially dependent on inputs of detrital material from photosynthetic organisms (a substantial part of which is composed of plant material, such as leaves, woody debris, fruit and flowers; henceforth referred to as 'litter'), and this forms the basis for the present study.

Organic matter inputs to the soil, including leaf litter, root litter and root exudates, represent the energy base of the soil food web and are directly utilised by aerobic and anaerobic bacteria, fungi, and a variety of arthropods (Verhoef and Brussaard, 1990; Lavelle, 1996). Important arthropod functional groups include the 'litter transformers' and the 'ecosystem engineers'. Litter transformers comprise arthropods of the mesofauna (<2 mm in length) such as Collembola (Verhoef and Brussaard, 1990), as well as macrofauna (>2 mm in length) such as Isopods (Ruiz et al., 2008). Litter transformers consume the litter (including its associated microbial community), which rapidly passes through their digestive tract, producing faecal pellets. These pellets act as incubators for microbial activity and are re-ingested by the litter transformers some time after deposition, so that metabolites released by microbial action can be assimilated (Lavelle, 1996).

Ecosystem engineers comprise those organisms that are able to effectively move through the soil, like Isoptera and Oligochaeta (Lavelle, 1996; Ruiz et al., 2008). Such organisms physically modify, maintain and create habitats for other members of the community (Ruiz et al., 2008) and in doing so decrease soil density, mix soil horizons and improve aggregate structure (Knoepp et al., 2000). They are often large (generally 5–100 mm) and can develop symbiotic relationships with microorganisms in their digestive tract, enabling them to feed directly on litter. In terms of predacious groups, bacteria and fungi can be consumed directly by micropredators (like nematodes and protozoa; Lavelle, 1996), while significant secondary and tertiary predators include Araneae, Pseudoscorpiones, Chilopoda and some Acari (Wilson, 2002).

Since litter forms a substantial part of the foundation of the soil food web, any process that modifies the rate of litter inputs to the forest floor has the potential to directly influence the soil community. Short-term variation in forest litter dynamics occurs naturally (e.g. over an annual cycle), but longer-term changes can result from anthropogenic perturbations such as climate change (Cao and Woodward, 1998; Zak et al., 2003) and forest fragmentation (Sizer et al., 2000). Litter manipulation experiments are an excellent way to investigate the influence of changes in litterfall on soil-dwelling organisms and previous work has shown litter quantity to be an important factor in determining arthropod abundances (Wardle, 2002). Removal of litter generally leads to a decline in the abundance of soil-dwelling arthropods (Pearse, 1943; Gill, 1969; David et al., 1991; Ober and DeGroote, 2011), whereas the addition of litter leads to a slight increase in soil arthropod abundance (Poser, 1990; David et al., 1991; Arpin et al., 1995), although this is not nearly as pronounced as the effect of litter removal. Litter manipulation can also change the community composition and population dynamics of soil-dwelling arthropods (Ponge et al., 1993; Osler et al., 2006), and shifts in soil fauna have been attributed to the importance of the physical presence of litter (Pearse, 1943; Gill, 1969; Uetz, 1979; Judas, 1990) such as the role of litter as a microclimatic buffer (David et al., 1991) or as a protective barrier from terrestrial predators (Pearse, 1943). Little is currently known concerning the influence of chemical parameters on soil fauna.

It is notable that all the above studies are from temperate ecosystems and there has been little research in tropical forests. A previous manipulative study focussing on litter-dwelling arthropods (Sayer et al., 2010) found that arthropod abundance was best explained by forest floor mass, while arthropod diversity was best explained by phosphorus, calcium and sodium concentrations in the litter horizons. However, to our knowledge, the impact of large-scale litter manipulation upon communities of soil-dwelling arthropods remains largely unknown. To address this, we examined the influence of experimental litter manipulation in a lowland tropical forest in Panama on the soil arthropod community. We measured arthropod abundance, biomass, taxonomic richness, diversity, and community composition, and focussed predominantly on faunal responses to chemical changes in the soil as a result of long-term litter manipulation.

2. Methods

2.1. Site description

Samples were taken from long-term, large-scale litter manipulation plots located on the Gigante Peninsula of Barro Colorado Nature Monument (9°06′N, 79°54′ W), Republic of Panama. Nearby (~5 km) Barro Colorado Island (BCI) has an annual average temperature of 27 °C. Potential evapotranspiration and average rainfall are 1440 mm and 2600 mm per year, respectively, and 90% of rainfall occurs during a rainy season lasting from May to December (Windsor, 1990). Soils at the study site are moderately acidic (pH 4.8–6.1) Endogleyic Cambisols to Acric Nitrisols (FAO classification; Koehler et al., 2009).

The Gigante Litter Manipulation Project was established in 2000 and consists of 15 plots measuring 45 m × 45 m. All plots were trenched to a depth of 50 cm to minimise transport of nutrients and water by roots and mycorrhizas. The trenches were double-lined with plastic and back-filled. Starting in January 2003, all litter was removed from five plots once a month (L− plots) and immediately spread over five plots (effectively doubling the litter standing crop; L+ plots); five plots were left undisturbed as controls (see Sayer and Tanner, 2010 for a detailed description of the experiment).

2.2. Soil and arthropod sampling

Five sets of three cores (5 cm diameter, 10 cm depth) were taken at equal distances along one transect in each plot during July/August 2010. At each sampling site, the depth of litter was measured and then cleared to expose the mineral soil prior to soil sampling. An equal number of plots per treatment were sampled on each collection date.

Immediately upon returning from the field, soil samples were transferred to Berlese–Tullgren funnels lined with 4 mm wire mesh. Arthropods were extracted for 48 h (by which time the soil samples were dry) and stored in 80% ethanol. Samples were weighed immediately after arthropod extraction.

Since Berlese–Tullgren funnels have been reported to have a relatively low sampling efficiency (<50%) for some taxa including Acari, Oligochaeta, Collembola, Diplura and Diptera (Levings and Windsor, 1982), sub-samples of the soil were examined under a binocular microscope to determine efficacy of arthropod extraction; a near-zero abundance of arthropods remaining in the soil demonstrated that the extraction method was effective.

2.3. Soil analysis

Soil samples for nutrient analysis (0–10 cm depth) were collected from the five marked transect points in each plot in