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Nest-mounds of the yellow meadow ant (*Lasius flavus*) at the "Alter Gleisberg", Central Germany: Hot or cold spots in nutrient cycling?

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A B S T R A C T

Nests of the yellow meadow ant (*Lasius flavus*) occur at high densities in grasslands worldwide. Although many studies have shown that *L. flavus* nests influence soil nutrient contents, little is known about their effect on soil nutrient cycling rates. The aim of this study was to examine the role of nest-mounds inhabited by *L. flavus* as potential 'hot spots' for soil nutrient cycling. Six pairs of nest-mounds and control soils were selected at a grassland site at the plateau of the Alter Gleisberg (Thuringia, Central Germany). *L. flavus* significantly modified the soil environment within the nest. In comparison to the control soils, nest-mounds were characterized by slightly higher soil temperatures during the summer months. In addition, we found that nests were related to decreased potential C mineralization rates and increased potential net N mineralization rates. Nest-mound soil exhibited lower amounts of SOC, hot-water extractable DOC and DN, and higher concentrations of leachable DOC and DN. Moreover, ants promoted the enrichment of base cations in the nest. Differences in the soil environment between nests and control soils were possibly a result of the burrowing activity of ants, soil mixing, accumulation of aphid honeydew, and decreased plant-derived nutrient inputs into the nest-mound soil. In conclusion, *L. flavus* nest-mounds had a significant but element dependent effect on the soil nutrient cycling and may represent cold spots for C cycling and hot spots for N cycling. Thus, *L. flavus* nests increase the spatial heterogeneity of soil properties and create unique micro-sites within grassland ecosystems.

1. Introduction

Ants are an important component of terrestrial ecosystems due to their abundant occurrence (Folgarait, 1998). Elmes (1991) estimated that there are 5–10 ants per m^2 of dry land. The activity of ants has been shown to directly affect chemical and physical properties of soil, such as organic matter content, nutrient concentrations, water content, bulk density and particle size distribution (Cammeraat et al., 2002; Dostál et al., 2005; Holec and Frouz, 2006). Ant-mediated soil modifications indirectly affect several landscape characteristics including: soil microclimatic conditions (King, 1977a; Rosengren et al., 1987), nutrient cycling rates (Lenoir et al., 2001; Wu et al., 2013), the abundance and activity of other soil biota (Wagner et al., 1997; Boots et al., 2012), as well as plant community composition and soil seed banks (King, 1977a,b,c; Dauber et al., 2006). Therefore, ants are considered to be "ecosystem engineers" (Jones et al., 1994) that increase the spatial heterogeneity of soil properties. However, the effect of ants on soil properties is variable and depends on species specific factors, such as nest size and density, colony age, feeding and nesting strategy (Dauber and Wolters, 2000; Boots et al., 2012), as well as on properties of the surrounding soil (Frouz et al., 2003). Hence, nest-mounds might act as hot or cold spots with disproportionately high or low reaction rates in comparison to the surrounding soil (McClain et al., 2003).

European grasslands are dominated by ants of the genera *Formica*, *Lasius* and *Myrmica*. The yellow meadow ant (*Lasius flavus*) is especially common in grasslands, where nests can occur at densities of up to 0.5 nests m^{-2} forming "antscapes" (Kovár et al., 2001; Steinmeyer et al., 2012). Nests are constructed below the ground or with visible dome-shaped mounds of mineral soil (Waloff and Blackith, 1962; Schreiber, 1969) and are usually maintained for over 20 years (Woodell and King, 1991). The species lives primarily underground and forages along tunnels extending up to 1 m around the nest (Woodell and King, 1991). *L. flavus* feeds on sugar-rich honeydew excreted by root aphids as well as on the

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aphids themselves, which they cultivate in their nests (Seifert, 2007). Thus, the ants potentially fuel the cycling of labile carbon belowground.

Nests of *L. flavus* are known to influence the nutrient content of soils, but there has been little consensus on the exact nature of that influence. In this context, several studies on *L. flavus* nests in grasslands found higher concentrations of total nitrogen (TN), K, Na and P in nests compared to the surrounding soil (Frouz et al., 2003; Dostál et al., 2005; Platner, 2006; Wu et al., 2010), whereas others reported lower concentrations of total carbon (TC) and TN (Dean et al., 1997; King, 1977a; Dostál et al., 2005; Holec and Frouz, 2006). Increased levels of nutrients are commonly attributed to the accumulation of food, honeydew and organic waste material, and high numbers of nitrogen-fixing bacteria in nests (Frouz et al., 1997 cited by Frouz et al., 2003; Dostál et al., 2005; Kilpeläinen et al., 2007), while decreased nutrient contents can be explained by the burrowing activity of ants mixing upper organic with deeper mineral soil layers (Frouz et al., 2003; Holec and Frouz, 2006).

Only few studies have dealt with nutrient cycling rates to explain varying nutrient contents in soils. It is hypothesized that higher temperatures and higher amounts of easily available nutrients in nest-mounds stimulate microbial activity, leading to accelerated decomposition and mineralization of organic matter (OM), nutrient leaching and uptake by plants, and CO_2 emissions to the atmosphere (Ohashi et al., 2007; Wu et al., 2013). In this context, Dauber and Wolters (2000) observed higher C mineralization rates in nest-mounds of *L. flavus* than in the surrounding soil, which they attributed to a higher activity of soil microorganisms in nest-mounds, consequently forming a mosaic of "microbial hot spots". The results corroborate findings by Stadler et al. (2006), who tested the effect of wood ants (*Formica polyctena*) on litter solution chemistry of Norway spruce and microbial enzyme activities in litter extracts. They observed that the presence of ants resulted in significantly increased concentrations of dissolved organic carbon and nitrogen (DOC and DON) in litter solutions and higher enzyme activities in litter extracts. In contrast, Lenoir et al. (2001) and Domisch et al. (2008) observed very dry moisture conditions in nest-mounds of wood ants (*Formica rufa* group and *Formica aquilonia*), resulting in decelerated decomposition rates of OM. Thus, the mineralization of C, N and P proceeded more slowly in nest-mounds compared to the surrounding forest floor, consequently representing "cold spots" for nutrient mineralization. Both authors supposed that the decomposition and mineralization of OM are accelerated as soon as nest-mounds are abandoned and their dryness is no longer maintained by ants. Hence, abandoned nest-mounds could provide "potential hot spots" for nutrient mineralization (Lenoir et al., 2001; Domisch et al., 2008).

In this study, we characterize the carbon (C) and nitrogen (N) cycling rates and related microclimatic conditions and soil chemistry of nest-mounds and adjacent control soils located at a grassland site at the "Alter Gleisberg" (Thuringia, Central Germany). In detail, the objectives of this study are (1) to compare temperature and moisture conditions of *L. flavus* nest-mounds and the surrounding soil, (2) to compare nutrient cycling rates and related C and N contents between *L. flavus* nest-mounds and the surrounding soil, and (3) to compare base cation concentrations in soil and soil solution between *L. flavus* nest-mounds and the surrounding soil. The hypothesis is that nest-mounds represent hot spots for soil nutrient cycling by creating favorable environments for other soil biota due to a surplus of easily decomposable organic material (honeydew and organic wastes) as well as suitable temperature and moisture conditions. This environment enhances the microbial activity and therefore leads to higher rates of nutrient mineralization and nutrient leaching in comparison to the surrounding soil. Thus, it is expected that nest-mounds are characterized by lower soil nutrient contents but higher rates and higher amounts of released nutrients in the soil solution.

2. Material and methods

2.1. Study site

The study was performed at a grassland site situated on the limestone plateau of the Alter Gleisberg at 343 m a.s.l. (50°57′22″N, 11°42′11″E). The mean annual temperature in this area is 8.5 °C and mean annual rainfall amounts to 588 mm (1961–1999) (PIK, 2009). The Alter Gleisberg consists of sedimentary rocks of the Mesozoic era. The plateau and steep flanks are comprised of limestone of the Lower Muschelkalk (Lower Wellenkalk). The soils are classified as shallow and loamy Rendzic Leptosol (IUSS Working Group WRB, 2006; Wenzel et al., 2012). The vegetation of the grassland is dominated by grasses (*Arrhenatherum elatius*, *Brachypodium pinnatum*, *Bromus* sp., *Dactylis glomerata*, *Festuca* sp.) and herbs (*Euphorbia cyparissias*, *Bupleurum falcatum*, *Melampyrum arvense*, *Origanum vulgare*). Shrubs (*Cornus sanguinea*, *Crataegus monogyna*, *Prunus spinosa*, *Rosa canina*) occur along the edge of the grassland. In the last few years, the grassland was regularly grazed by sheep and mowed in autumn to prevent shrub encroachment (Wenzel et al., 2012).

Ant nest-mounds are common in this grassland, with an average density of 0.33 nest-mounds m^{-2}. Six pairs of *L. flavus* nest-mounds containing living colonies and adjacent control soils located within an area of approximately 1600 m^2 were selected for this study. To cover the site variability of the grassland, two pairs were chosen along the edge of the grassland (2, 6), two pairs in the center of the grassland (4, 5) and two pairs in the transition between grassland and shrubs (1, 3) (Fig. 1). A wide range of different nest-mound sizes were chosen encompassing mound volumes from 0.007 to 0.023 m^3 (Table 1). Control soils were approximately 1 m away from each nest-mound to exclude ant effects on soil characteristics. Compared to the controls, nest-mounds were characterized by a sparse plant cover with higher numbers of vegetation-free patches.

2.2. Microclimatic conditions

The study covered a period of 20 weeks, starting on June 8 and ending on October 25, 2012. To characterize the microclimatic conditions during the study period, the soil temperature and soil volumetric water content were measured in 10 cm depth from the mound top in the central part of all nest-mounds and control soils. The soil temperature was continuously recorded at 1-h intervals with a data logger (EL-USB-1, Lascar Electronics, Salisbury, UK). The

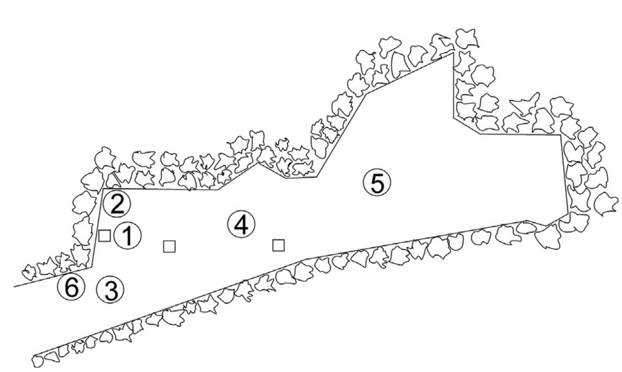

Fig. 1. Schematic drawing of the grassland site on the plateau of the Alter Gleisberg. Circles mark the position of the six selected *L. flavus* nest-mounds and control soils, rectangles mark the position of the three bulk precipitation collectors.