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Microgeographical distribution of ants (Hymenoptera: Formicidae) in coastal dune grassland and their relation to the soil structure and vegetation

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Abstract—In this paper, we investigate the microgeographical distribution of ants nests in an intensively grazed dune pasture. A total of seven species were recorded. By the application of a forward multiple logistic regression we were able to determine nesting choice for the three common species *Lasius niger, L. psammophilus* and *Myrmica specioides*. The first could be identified as a pioneer species, while the two latter species, which are typical of dry, sandy dune grounds, differ slightly in their nesting preference. The effect of nest building on soil structure was investigated for a mound-building species (*Formica cunicularia)* and for a non-mound-building species (*Lasius psammophilus*). Both species significantly decrease the thickness of the organic and water-capturing soil layer, while the mound-building species additionally affects the soil lime content (an increase) and the soil hardness (a decrease). Mound building in dense *Calamagrostis* vegetation also stimulates the germination of a characteristic and rare plant species, *Thymus pulegioides*.

Keywords: ecosystem processes; Formicidae; microgeographical distribution; populations; soil characteristics.

INTRODUCTION

The effect of mound-building ants on soil characteristics and vegetation composition has already been studied intensively. Most studies suggest a totally different soil composition in the mound than in the reference soils. The amount of organic matter,

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N, P and K content and Ca concentrations of uninhabited pedons differ significantly from formicarious mounds (Green et al., 1998; Blomqvist et al., 2000). Petal (1978) even suggests that ants may regulate the pH of the nest but Green et al. (1998) suggest a regulation by accumulation of basic calcareous material. Excavated material at the surface of the mound explains why the soil can be different from uninhabited pedons. Moreover, the surface of the mounds is often covered with a crust or mulch that can consist of sand grains, pebbles or whatever is available. As below-ground foraging tunnels of ants may extend to up to 1 m from the mound (*L. flavus*), we may also expect non-mound-building ants to influence soil characteristics (Woodell and King, 1991; Blomqvist et al., 2000). These soil properties, and the ease with which ant mounds can be detected and mapped, make them ideal subjects for studying the effects of ant activity on soil and indirectly on vegetation.

The importance of ant communities on the dispersion and distribution of myrmecochorous plants is already well studied (Huxley, 1991; Gorb and Gorb, 1995; Mark and Olesen, 1996; Andersen and Morisson, 1998; Brunet and von Oheimb, 1998; Gomez and Espadaler, 1998, 1999; Wolff and Debussche, 1999; Lopez et al., 2000). Physical and chemical soil processes can create suitable germination sites for different plant species (Caldwell et al., 1996; George et al., 1997). Also some Poaceae not classed as myrmecochoreous plants as they lack an elaiosoom, can benefit from transport of their diasporas by ants (Levey and Byrne, 1993; Seifert, 1996; Warburg, 2000). Besides influencing soil characteristics, dispersion of plants and even landscape formation, ants nests can also be a shelter for a number of other invertebrates (Seifert, 1996). Habitat preference and modification have also been extensively studied in rainforests (Levey and Byrne, 1993; Agosti et al., 2000), deserts (Gordon, 1992; Nash et al., 2001), and continental and Mediterranean pastures (Crist and MacMahon, 1992; Lopez et al., 2000).

In Flanders, sandy soils are highly favoured ant habitats and a lot of species can be found in grazed dune grassland (Lehouck et al., in press). As most of these species do not build notable mounds, the influence of this abundant ant community on soil and vegetation is probably underestimated. Additionally, we must note that new taxonomical revisions with regard to the European myrmecology were recently published (Seifert, 1992, 1996). Some new species were recently added to the Belgian fauna (Dekoninck and Vankerkhoven, 2001), and old records and information on the ecology and habitat selection of these species should be updated and rechecked. In this contribution, we aim to study (i) the microgeographical distribution of ants according to initial (not influenced by nesting) soil characteristics and vegetation structure, topography and presence of myrmecochorous plants, and (ii) to what extent dominant mound (*Formica cunicularia*) and non-mound-building (*Lasius psammophilus*) species influence in their turn the soil and vegetation at the nest location.

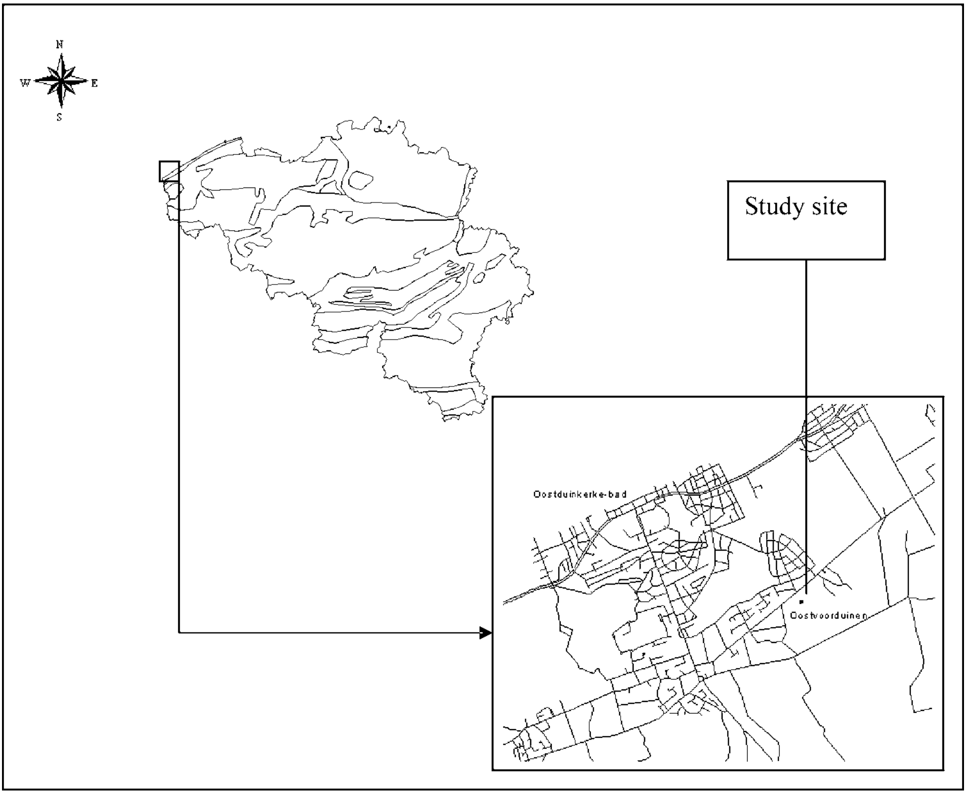

Figure 1. Location of the study area.

MATERIAL AND METHODOLOGY

Research Area (Fig. 1)

The study was conducted in an intensively grazed grey dune in Oostduinkerke (West Flanders, Belgium, 51.04°W, 2.45°N) from 24-29 June 2001. The dune area originates from the 11th century as a spit of sand dunes in the Ijzer estuary. Due to eolic processes, a landscape with distinct micro-relief was formed with a lower lime content than the younger dunes along the Flemish coast. The area has been used for pasture by local farmers for several centuries (Provoost and Hoffmann, 1996), which has resulted in floristically rich dune grassland.

EXPERIMENTAL SET UP AND FIELD MEASUREMENTS

1. Microgeographical distribution. The microgeographical distribution of ants nests was investigated in a rectangular study field measuring 22×30 m^2, which includes a humidity gradient from wet (dune valley) in the south to dry in the northern part (dune ridge). These differences in turn influence the vegetation and the soil structure in a spatially correlated way (Provoost et al., unpubl. data). The study field was subdivided into 2×2 m^2 quadrats. In these quadrats, the ants nests (sampled once) were mapped and the vegetation composition was recorded (important for the presence of myrmecochorous plants) using the Londo coverscale (Schaminée et al., 1995). Mean cover of sand, mosses and herbaceous plants was noted. The thickness of the A-horizon was measured to the nearest 0.5 cm using a hand auger. This measurement was repeated five times within the quadrat but outside the nests, and averaged.

The study field was topographically mapped using a tachymeter (Wild TC 1600), which measures with a precision of ca. 1 cm. A digital elevation model was obtained by Kriging interpolation of these points (Surfer 7, Golden Software 1999). The depth of the ground water was measured in three surrounding piezometers and the water surface in a nearby pond. Mean inclination and depth of the ground water were derived respectively from the DEM and the groundwater data in a GIS (Arcview).

Ant species were identified with Seifert (1996).

2. Effect on soil characteristics and the presence of Thymus seedlings by a mound and non-mound building species. For the mound-building *Formica cunicularia* and non-mound-building ant *Lasius psammophilus*, nests used to determine nest soil characteristics were located outside this study site. Here, we investigated the effect of nest building on four soil characteristics which were measured in the nests and directly outside the nests on undisturbed soil as a reference: (i) thickness of the A-layer, (ii) soil pH, (iii) soil compactness, and (iv) presence of superficial $CaCO_3$. The thickness of the A-layer was measured similarly as in the first part of the study. The compactness (penetration depth) was measured by using a manual penetration meter (precise to the nearest 0.5 cm). Chalk reaction was categorically investigated in the field by observing the reaction of 2M HCl to the upper soil core. Possible reactions were 0: no reaction, no lime; 1: moderate reaction and 2: very strong reaction (high amount of lime). The soil pH was measured in the laboratory after adding and mixing 100 ml denaturised water to the same volume of soil.

Besides soil characteristics, we also observed whether *Thymus pulegioides*, a characteristic dune grassland plant species, benefits from ant nesting in what is, for *Thymus*, unsuitable habitat (*Calamagrostis epigejos* vegetation). Therefore, the presence or absence of seedlings on *F. cunicularia* mounds and the reference soil (same surface within non-influenced vegetation) was recorded.

DATA ANALYSIS

The relations between nesting place and vegetation, soil and topographical characteristics were investigated by multiple forward logistic regression where the presence of nests of the ant species in the respective quadrat was the independent variable. Mean coverage of herbs, mosses, bare sand, myrmecochorous plants (*Luzula campestris, Polygala vulgaris*), plant species richness, inclination, soil pH, depth of the water table and thickness of the organic A-layer were included as fixed dependent factors. Because all quadrats are located within the same small study site, no corrections for spatial correlations were made since ant species can independently select nesting sites. The logistic regression was preferred to minimise bias from closely located nest apertures within the quadrat, possibly belonging to the same colony. Since vegetation and soil characteristics were recorded outside the nests but within the quadrat, they are independent of ant presence. The association with myrmecochorous plants can both result from earlier ant nesting or from a direct preference for nesting close to these plants. Because ants nest location is dynamic over years (Dekoninck et al., unpubl. data) a direct dependence of nest location according to the plant location was assumed. Score statistics and the change in likelihood were used, respectively, for entering ($P = 0.05$) or removing ($P = 0.10$) variables from the model.

Direct effects of ants nest building on soil characteristics were analysed with dependent t-tests (soil hardness, soil pH, thickness of the organic A-layer) or a sign-test (chalk reaction) since samples in the nest mound were compared with those adjacent to the nest. The presence of *T. pulegioides* was investigated by comparing the number of observed nests with seedlings to the proportion of adjacent vegetation with seedlings using a Yates corrected dependent χ^2-test.

RESULTS

1. Microgeographical distribution

A total of seven ant species was recorded in the study field (Table 1). Of these, *F. cunicularia* and *M. scabrinoides* were found only at the edge of the study field, in the dense grassland vegetation. *M. sabuleti* was less common than its sister species *M. specioides* and could be found in the presence of the latter. For the three common species *L. niger, L. psammophilus* and *M. speciodes*, microgeographical distribution was investigated. The placement of *L. niger* nests could not be explained by any of the soil characteristics, but showed only a positive logistic relation with the total number of plant species in the quadrat ($\chi^2 = 6.34$; $P < 0.05$). Contrary to

Table 1.
Total number of nests found for all the species in the study field.

Species	Total number of nests
Formica cunicularia Latreille 1798	2
Myrmica specioides Forel 1913	14
Myrmica scabrinodis Nylander 1836	2
Myrmica subuleti Meinert 1860	3
Tetramorium caespitum (Linnaeus 1758)	7
Lasius psammophilus Seifert 1992	32
Lasius niger (Linnaeus 1758)	23

Table 2.
Mean values of the measured soil characteristics in and beside the nests of ant species *Lasius psammophilus* and *Formica cunicularia*.

Species	pH-nest	pH-ref	Lime-reaction nest-ref	Soil A-layer thickness-nest (cm)	Soil A-layer thickness-ref (cm)	Soil hardness-nest (cm)	Soil hardness-ref (cm)
F. cunicularia	6.79	6.59	+	3.59*	11.41*	32.41*	21.00*
L. psammophilus	7.19	7.24	=	1.00*	3.29*	20.15	19.86

* indicates a significant effect of nest-building (dependant t-test, $P < 0.01$);
+ indicates a significant positive effect for the lime reaction (sign-test).

this species, *L. psammophilus* reacted negatively to the cover of herbaceous plants ($\chi^2 = 15.52$; $P < 0.001$) and to the thickness of the organic soil layer ($\chi^2 = 4.38$; $P < 0.05$), while the occurrence of *M. specioides* nests only depended negatively on the thickness of the organic soil layer ($\chi^2 = 15.75$; $P < 0.001$). Neither the presence of the three species (*L. niger*: $\chi^2_{Polygala\ vulgaris} = 0.02$, NS; $\chi^2_{Luzula\ campestris} = 0.09$, NS; *L. psammophilus*: $\chi^2_{Polygala\ vulgaris} = 3.64$, NS; $\chi^2_{Luzula\ campestris} = 0.36$, NS; *M. specioides*: $\chi^2_{Polygala\ vulgaris} = 1.58$, NS; $\chi^2_{Luzula\ campestris} = 3.45$, NS), nor the overall presence of ants nests was related to the coverage of the myrmecochorous plants present ($\chi^2_{Polygala\ vulgaris} = 0.056$, NS; $\chi^2_{Luzula\ campestris} = 1.322$, NS).

2. Effect on soil characteristics and the presence of Thymus seedlings by a mound- and non-mound-building species

The results of the influence of nest building of *L. psammophilus* and *F. cunicularia* are summarised in Table 2. In both species, superficial pH did not vary significantly between the nest mound and the reference soil. The lime content was higher on nest mounds of *F. cunicularia*.

Nest building significantly decreases the thickness of the organic A-layer in both species (Fig. 2), while the soil compactness was only altered by *F. cunicularia* (Fig. 3). There were significantly more seedlings of *Thymus pulegioides* present on nest mounds of the latter species (present on seven of the 15 investigated nests in *C. epigejos* vegetation, and absent in all adjacent vegetation; $\chi^2_{14} = 6.71$; $P = 0.01$).

DISCUSSION

Our results indicate that the dominant ant species in coastal grey dune select different nesting sites according to the cover of herbaceous plants and the thickness of the organic soil layer. Nest placement not only depends on vegetation and soil characteristics, but also influences soil and vegetation conditions, as shown for the mound-building species *F. cunicularia* and the non-mound-building ant *L. psammophilus*. Both species influence soil conditions, but in a different way: nesting of the latter influences only the thickness of the organic soil layer, while mound

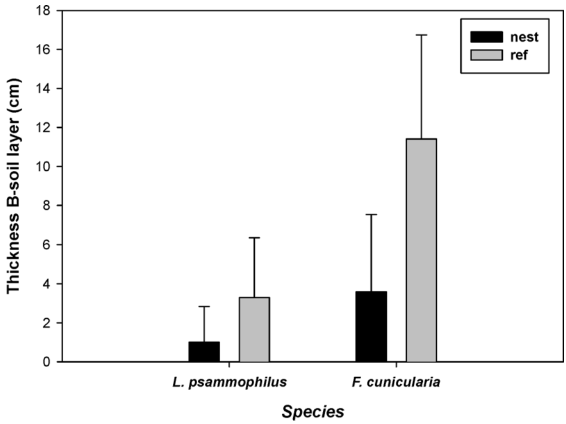

Figure 2. Effect of the presence of nests of the ants *Lasius psammophilus* and *Formica cunicularia* on the thickness of the organic (A) soil layer.

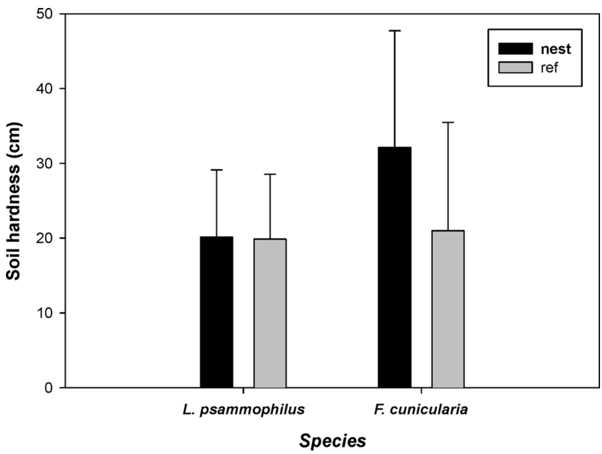

Figure 3. Effect of the presence of nests of ants *Lasius psammophilus* and *Formica cunicularia* on the soil compactness.

building additionally leads to an increase in soil lime content and a decrease of soil compactness. Nest presence is not associated with the presence of myrmecochorous plants.

New taxonomic insights suggest a new look at the ecology of some recently separated species (Seifert, 1996; Seifert, 1997; Boer, 1999; Dekoninck and Vankerkhoven, 2001). *Lasius psammophilus* was formerly often considered as *Lasius alienus*. The former is a common ant in Flanders on sandy soils, while *L. alienus* is only found on chalky soils (Dekoninck, unpubl. data). These new insights suggest a clear and justified ecological description of the species (Seifert, 1992, 1996; Boer and de Gruyter, 1999; Dekoninck and Vankerkhoven, 2001). *Lasius niger* is often catalogued as a pioneer species and a species characteristic of disturbed areas and without a clear ecological preference (Mabelis, 1976; Seifert, 1991, 1992;

Boer and de Gruyter, 1999, Dekoninck et al., in press). This corresponds well with the fact that the species in our study only reacts with the total number of higher plant species. In coastal grasslands, an increase of higher plant species is related to intensive management (mowing, grazing), and hence a high amount of disturbance (Provoost and Hoffmann, 1996). *Lasius psammophilus* and *Myrmica specioides* prefer the same field conditions. They are both found in open, sparse vegetation. Our results indicate that *L. psammophilus* is somehow more critical in its habitat choice, since its nest location was significantly correlated with a lower vegetation cover in combination with a more sandy soil layer (less developed organic A-layer), while *M. specioides* only reacts negatively to the soil development.

Contrary to the findings of Oostermeijer (1989), neither the presence of the dominant ant species, nor the overall presence of ants nests was related to the coverage of the myrmecochorous plants *Luzula campestris* and *Polygala vulgaris*. This can possibly be explained by a fast relocation of ants nest under a high grazing pressure, as stated by Green et al. (1998). *Lasius psammophilus* is indeed a typical species for stable habitats, and relocates its nest quickly when disturbed. Grazing disturbance is therefore often considered as negative for the presence of a diverse ant fauna in sandy habitats (Mabelis, 1976; Lambrechts et al., 2000). The relation of nest placement with the presence of myrmecochorous plants can thus be cryptic and should be studied at a larger temporal scale.

The influence of ant activity on soil characteristics has been well documented for mound-building species (Nielsen, 1986; Blomqvist et al., 2000). In our study we compare the effects of a mound-building species (*F. cunicularia*) with a non-mound-building species (*L. psammophilus*) on soil characteristics. Probably because both species prefer different microhabitats, we found different activity effects for both species. Nesting activity of both species affects the thickness of the organic A-soil layer. The soil pH remains constant for both species, but the mound-building *F. cunicularia* significantly affects the superficial lime content and soil compactness.

These results correspond more or less with other studies. The increase in superficial lime content has already been documented by Levan and Stone (1983), who found that formicarious mounds showed lime enrichment in comparison with those inhabited. Other studies, however, found no effect or a decrease in Ca content by ant activity (Woodell and King, 1991). For the Yellow ant *L. flavus*, Blomqvist et al. (2000) found that mounds were drier and had a lower bulk density than the surrounding matrix (also reported in King, 1981; Woodell and King, 1991; Dean et al., 1997), but that pH was significantly higher. Our results confirm these findings for both species since nesting activity had a negative effect on the thickness of the organic A-layer, which is positively related to soil humidity and bulk density (Krabbenborg et al., 1983; Aggenbach and Jalink, 1999). The loose soil (reduced soil hardness with *F. cunicularia*) is the result of construction of tunnels and chambers, which in turn leads to drier conditions as a result of a higher rate of evaporation (Woodell and King, 1991).

Ant nesting activity thus drastically affects the soil structure. In coastal dune grasslands, soil humidity, lime content and the thickness of the organic soil influence the presence of typical plant species (Aggenbach and Jalink, 1999). Soil disturbance due to digging activity affects the presence of typical r-selected short-lived species, especially winter annuals and perennials, which are capable of growth through heaped soil (King, 1977; Woodell and King, 1991). Our results also indicate that *Thymus pulegioides* benefits from ant activity, possibly through aeration of the soil and surficial lime enrichment, which enhance ideal germination circumstances. The presence of *T. pulegioides* seedlings on ant mounds in dense unsuitable grasslands where mature plants are absent indicates not only the creation of suitable habitats (light competition) but also the fact that ants collect and transport seeds to their nests, in which they can germinate easily. As Nielsen (1986) stated for *Lasius flavus*, mounds which last for many generations and occur in high densities can increase the diversity of the flora compared to areas without nests, because the microclimate on and in the mounds is so different from that of the surrounding area that a great number of plants are associated with them.

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