



Vegetation of ant-hills in a mountain grassland: effects of mound history and of dominant ant species

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Abstract

Vegetation in grasslands with well-developed long-lasting ant-hills in the Slovenské Rudohorie Mts., Slovakia, was studied in relation to (i) position on the mound, (ii) ant species forming the mound, and (iii) history of the mound. Permanent plot recordings of mound size and dominant ant species started fifteen years prior the study began provided information on the history of individual mounds. The mound vegetation bears a striking similarity to vegetation in similar habitats across a large part of Europe due to presence of species such as *Agrostis capillaris*, *Dianthus deltoides*, *Polytrichum commune* agg., *Thymus pulegioides*, and *Veronica officinalis*. Out of the three major ant species-groups present at the site (*Lasius flavus*, *Tetramorium caespitium* and *Formica* spp.), *L. flavus* had the most pronounced and the most lasting effect on the mound vegetation. The dominance of the plant species listed above increased with the time span over which the mound was inhabited by *L. flavus*. The effects of other species on vegetation composition, though discernible from short-term observation, disappeared over several years. The mounds proper did not differ from the undisturbed grassland in the proportion of myrmecochorous plants or plants with specific seed size or dormancy type. However, there was a highly significant concentration of myrmecochorous plants in the grassland patches immediately neighbouring the mounds; this is likely to be due to seeds deposited there by the workers from the nest after the elaiosomes had been consumed. The mound vegetation was composed mainly of species with long stolons or rhizomes; however, there was no significant difference in formation type or length of stolons/rhizomes between mounds and the rest of the grassland or among mounds formed by different ant species.

Introduction

“Antscapes”, i.e. grassland systems with abundant ant-hills, occur in various types of temperate extensively managed grazing systems in Europe (Elmes 1991; Dean et al. 1997). In these grasslands, ants build rather regularly spaced mounds of several tens of centimetres in height and in diameter; this often happens on rather extended areas, giving the whole phenomenon landscape-wide importance. These systems are built primarily by the terricolous species *Lasius flavus*, though other ant species may contribute as well. The mounds are the places where the ant col-

onies reside; though the activity of each colony extends both deeper and wider into the soil, most of the workers, the queen and the larvae are in the mound or immediately below it. This mound-building activity generates remarkable environmental heterogeneity that underpins floristic differentiation between mound vegetation and the rest of the grassland (King 1977a). The vegetation of mounds is rather specific; though it is generally a subsample of the species that occur off the mounds as well, some species seem to be much more common on the mounds than elsewhere (King 1977a; Dean et al. 1997).

The difference in vegetation between mounds and the rest of the grassland has been attributed to three non-exclusive causes: (i) different soil environment in the mounds (King 1977a; Petal 1980; Elmes 1991; Culver and Beattie 1983; Rice and Westoby 1986), (ii) myrmecochory, i.e. seed transport by ants, and (iii) soil disturbance that generates open soil surface that is available for germination or inhibits some plants, particularly rosette species (Grubb et al. 1969; King 1977a). Of these factors, myrmecochory in grassland ant-hill systems is assumed to be less important, since *L. flavus* feeds primarily on aphids and aphid nectar belowground and does not regularly appear at the soil surface; this kind of behaviour is likely to limit its potential to carry seeds (Pontin (1978); Woodell and King 1991). Disturbance by soil transport is another likely cause of the mound vegetation specificity. Since ants carry large amounts of, they generate (Grubb et al. 1969; King 1977a). (King 1977b, 1977c; Petal 1980; Elmes 1991)

Indirect observations show that individual mounds can attain the age of more than 100 years (King 1981), though the longest direct observations are 22 years (Woodell and King 1991). Consequently, their size, structure, the amount of soil transported and vegetation composition are bound to reflect their past history and age (King 1981). Strikingly little seems to be known on the dynamics of this process. This concerns both the soil parameters (soil at the mounds seems to be richer in potassium and phosphorus, King (1977a); Petal (1980)) and of vegetation differences, either due to disturbance or myrmecochory. Available knowledge is often based on indirect data (King 1977b).

To fill this gap, we studied effects of the ant species and the history of the mound on the mound vegetation in a grazed grassland in the Slovenské Rudohorie Mts., Slovakia. There, the ant-hills occur in a species-rich, extensively grazed mountain grassland at altitudes 900–1100 m above sea level. Their vegetation differs from the remaining grassland in a similar way as in other ant-hill grasslands (King 1977a; Dean et al. 1997). The ant fauna of the site is richer than that of many other systems; regularly there are three common mound-building species groups (*Lasius flavus*, *Tetramorium caespitum* and *Formica* spp.) present at the site. This enabled us to study effects of presence of individual ant species in the past. A large permanent plot was established at the site in 1979; sizes of the mounds and of dominant ant species were recorded. Consequently, we used the infor-

mation from the permanent plot to determine how the present vegetation is affected by the history of the mound and the past and present occurrence of major ant species. In addition, we studied correlation of the plant species composition with indirect indicators of the mound age, such as mound height and diameter.

As supplementary questions we also determined differences between vegetation of mounds and of surrounding grassland, and attempted to find out whether species that either avoid or prefer mounds (i.e. are not indifferent to the mound-grassland gradient) share some important biological parameters (such as seed bank or clonal growth parameters).

Methods

Study site

The study site is located at an elevation of ca. 950 m in the summit area of Slovenské Rudohorie Mts., which is a part of the Western Carpathians range. It lies ca. 0.3 km SE of the point Obrubovanec (1020 m a.s.l.; 48° 41' N, 19° 39' E). Bedrock is formed by migmatites and amphibolites; the soils are therefore rather poor and the resulting grasslands are rather acidic. The study site lies at a grassland complex which is regularly and extensively grazed by sheep and livestock; some parts of it outside the study site itself are also mown. The grasslands can be classified as the alliance *Nardo-Agrostion tenuis* Sillinger 1933 (periodic intensive grazing may cause a shift toward *Cynosurion* Tx. 1947); dominant grass species are *Festuca rubra*, *F. pratensis*, *Agrostis capillaris*, and *Dactylis glomerata*. Further data on the locality are reported by Kovář and Kovářová (1998).

These grasslands are inhabited by colonies of several ant species. In the absence of regular mowing, these colonies form pronounced mounds (up to 40 cm in height and 70 cm in diameter, though most of them are smaller). The most common species is *Lasius flavus* (F.), which forms dense and long-lasting (~20 years or more; Kovářová et al. unpubl. data) mounds. Another common species is *Tetramorium caespitum* (L.). This species, in addition to its underground colonies, often builds fast-growing temporary mounds that are steep and of low bulk density. Other recorded species are several species of the genus *Formica* (*F. fusca* L., *F. lemni* Bondroit, *F. pratensis* Retz., and *F. rufa* L.), *Lasius niger* (L.) and *Myrmica ruginodis* Nyl.

Data collection

A large permanent plot (30 × 30 m) was established at the site in 1979. Further recordings of the permanent plot were done in 1981, 1988 and 1995. During each recording, positions of all discernible mounds were recorded, together with the longest horizontal diameter of the mound and the dominant ant species; abandoned mounds (i.e. with no living workers inside) were treated as a separate category. The position of the permanent plot was chosen to encompass a part of the grassland with well developed mounds; there were no mature trees and saplings at the plot in 1979. Since the plot was established, many seedlings established in the plot (often directly on the mounds) and parts of the plot are now covered by sparse trees of several meters in height.

In 1995, three vegetation transects were laid out in the study area. The first transect was established in a grazed grassland with no trees; the second transect was established in a grazed grassland with sparse spruce saplings, but still with no trees (except for seedlings) closer than 2 m from the transect; the third transect was established in a grassland with sparse trees approx. 20 years old. Transects 2 and 3 were established in the above permanent plot; transect 1 was established in the open grassland outside the permanent plot and thus no information on history of its mounds is available. The lengths of these transects were 50, 38 and 30 m respectively (their size was different due to constraints of the permanent plot). Transect 1 was linear, whereas transects 2 and 3 were U-shaped to fit the permanent plot.

Along the transects, 0.25 × 0.25 m sample plots were established; these plots were separated by a gap of 0.25 m, i.e. two plots were established per one meter of the transect. All plant species including bryophytes and lichens rooting in these plots were recorded; their dominance was visually assessed using a three degree scale (1 - cover < 5%, 2 - cover 5–10%, 3 - cover > 10%). Total cover of vascular plants and of the bryophytes and lichens were also recorded. If needed, bryophytes and lichens were sampled and determined in the laboratory. Further, positions of each plot, relative to the closest mound, were recorded using the three degree scale: (i) no visible mound in the plot, (ii) mound covering part of the plot, and (iii) mound fully covering the plot. This data set is further referred to as dataset I ($n = 235$).

A separate data set (dataset II, $n = 205$) was recorded at the same time to identify structure within

vegetation at the mounds. All mounds closer than 1 m to the above transects were selected for this data collection. All plants rooting at these mounds were recorded using the same three-degree scale as above. Further, the longest basal diameter of the mound, the longest diameter perpendicular to it and the height of the mound were recorded. Species of ants living at these ant-bills in 1995 were recorded by digging gently into the hills and taking samples of the workers; if no workers were present up to the depth of 20 cm, the mound was considered abandoned. Determinations of the ant species were checked by Petr Werner and Milan Dad'ourek. For the purpose of analyses of this dataset, all *Formica* species were lumped; no *Myrmica ruginodis* nest was in the studied set. A subset of the above data set that lay in the permanent plot (i.e. mounds at the transects 2 and 3) enabled additional analyses with parameters of the mound history (dataset III, $n = 98$). The following parameters were thus available for these analyses: ant species in 1981, 1988, and 1995 and longest diameter in these years.

Vascular plant nomenclature follows Flora Europaea (Tutin 1964–1980), bryophyte nomenclature follows Frahm and Frey (1992). Clonal growth form of plant species was identified using the database CLO-PLA1 (Klimeš et al. 1997; van Groenendael et al. 1996); the clonal growth types used in the database were lumped to produce the following four large groups based on spacer (i.e. stolon or rhizome) length: short-lived spacers (types *Lycopodium*, *Fragaria*, *Caltha* and *Asperula*), short spacers (types *Festuca ovina*, *Rumex obtusifolius*, *Dactylis glomerata*), long spacers (types *Rumex alpinus* and *Aegopodium*) and non-clonal species (true nonclonal and type *Trifolium pratense*) data on seed bank dynamics are based on Thompson et al. (1996), data on myrmecochory are taken from Grime et al. (1988) and from Frank and Klotz (1988). Mean seed size is taken from Grime et al. (1988).

Data analysis

Relation of the plant species composition in the sample plots to the position of the plot relative to mounds (dataset I) was determined by redundancy analysis (RDA) on covariance matrix. Redundancy analysis is a canonical form of principal components analysis; it assumes linear relations both between species and between species and environmental variables (for further description and discussion of the method, see e.g. Jongman et al. (1987)). Scale of species quantities

Table 1. Summary of species-environment relation determined by redundancy analyses of the dataset I and dataset II. Proportion of explained variation refers to residual variation after fitting covariables (if any). All variables refer to the 1995 measurements. Significance is determined by Monte Carlo randomisation tests (for details see the Methods section):**, $P < 0.01$. None of the tests ceases to be significant after a Bonferroni correction for multiple testing is made. 'position' refers to two variables describing whether the plots was on the mound, in the remaining grassland, or at the mound margin (i.e. containing both microhabitats).

Vegetation data Analysis	Covariate(s)	Environmental variable(s)	Variation (%) explained by first axis all canonical axes	
<i>Dataset I</i> (plots differing in their positions relative to mounds), $n = 235$				
1a Plots in all transects	none	transect code	17.1**	21.1**
1b Plots in all transects	transect code	position	3.0**	3.3**
<i>Dataset II</i> (all mounds), $n = 205$				
2a All mounds	none	transect code	19.1**	27.6**
2b All mounds	transect code	mound size variables	2.8**	4.1**
2c All mounds	transect code	ant species	3.1**	4.5**
2d All mounds	transect code	mound size variables, ant species	4.0**	7.7**
2e All mounds	transect code, mound size	ant species	2.3**	3.7**

was not transformed; however, both percentage-transformed and presence-absence data yielded similar relationships (analyses not shown). Four analyses were run, one for each transect and one for all transects taken together. In the latter case a partial analysis was run with transects as covariates. Significance of the species-environment relationship was tested using Monte Carlo permutation tests; each transect was permuted independently by circular shifts. The tests are not based on the assumption of normality of data; therefore they can be applied to the current data structure.

Relation of the plant species composition of mounds to environmental variables (dataset II and dataset III) was determined by redundancy analysis on covariance matrix using non-transformed species quantity data. Two types of analyses were run: (i) Mound vegetation data from all three transects with the longest diameter, shortest diameter, height and dominant ant species as environmental variables (dataset II); different combinations of environmental variables and covariates were tested (Table 1). Dominant ant species were grouped by genera as described above. If applicable, transects were taken as covariates to screen off habitat differences among transects. (ii) Mound vegetation data from transects 2 and 3 with diameter and dominant ant species in 1981, 1989 and 1995 as environmental variables (dataset III). Due to the scarcity of *Formica* spp. in the dataset III, only presence of *L. flavus* and *T. caespitum* were used as environmental variables. Again, different combinations of environmental variables were used. No cova-

riates were used in the latter case. Stepwise form of redundancy analysis was also used for exploratory analyses aimed to identify environmental variables that contributed most to floristic variation among the mounds. A form of the F -statistic was used as a stepping criterion following Ter Braak and Šmilauer (1998).

All calculations were done by CANOCO version 4 (ter Braak and Šmilauer 1998); the ANOVAs were calculated using SPSS ver. 7.

Results

Plots along transects: vegetation of mounds vs. grassland (dataset I)

There were pronounced differences between vegetation of the mounds and remaining grassland (Table 1, analysis Table 1b, Figure 1). Several species showed marked preference for the mounds, viz. *Polytrichum commune* agg., *Thymus pulegioides*, *Rumex acetosella*, *Festuca ovina*, *Anthoxanthum odoratum*, *Dianthus deltooides*, *Veronica officinalis*, *Sieglingia decumbens*, *Agrostis tenuis*; species such as *Potentilla erecta*, *Nardus stricta*, *Festuca rubra*, *Luzula multiflora*, *Carex pallescens* or *Cruciata glabra* tended to avoid the mounds.

There was no significant relationship between the score on the first or the second canonical axis and occurrence of any of the four major types of clonal growth (short-lived spacers, short spacers, long spac-

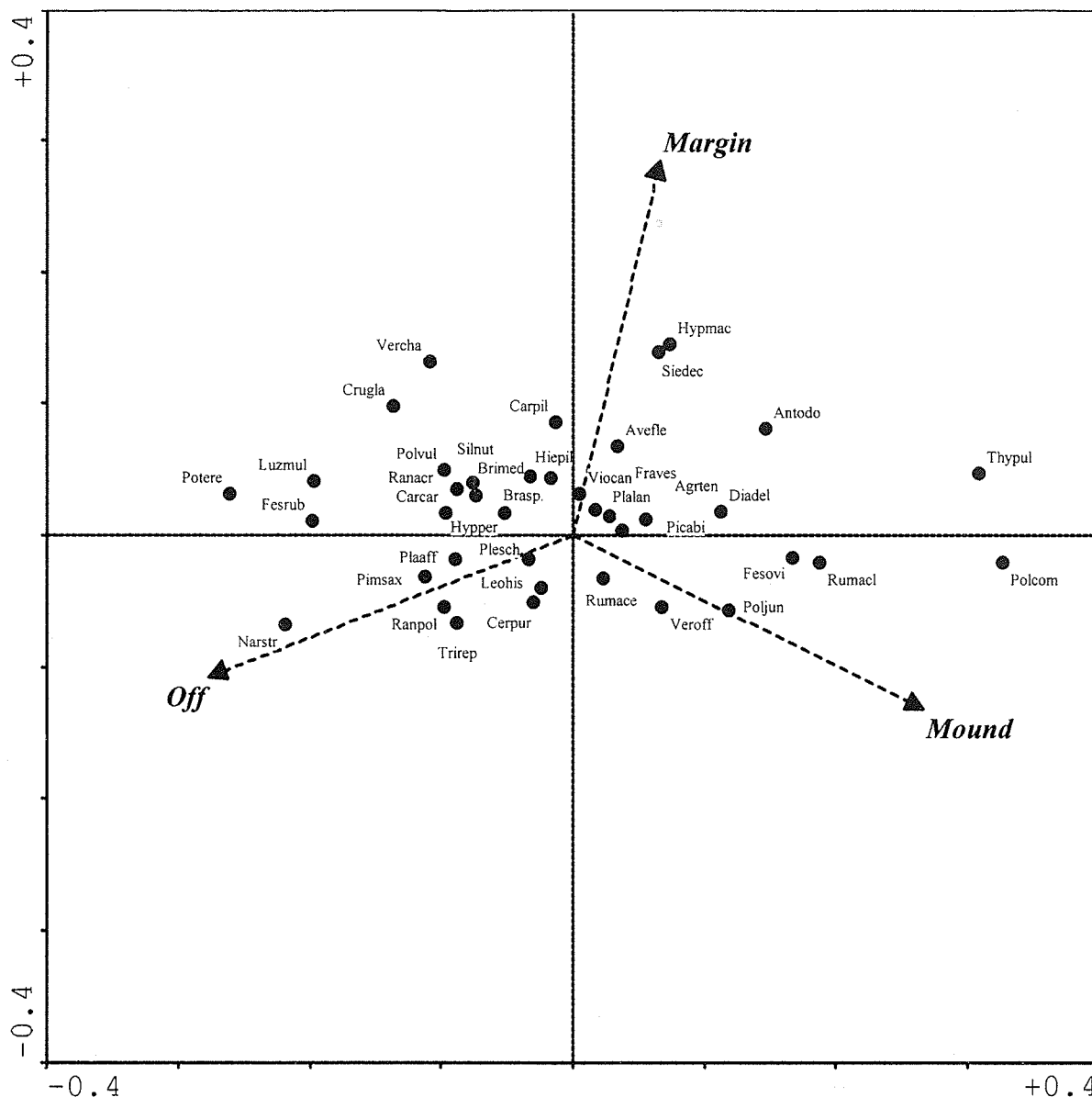


Figure 1. Canonical ordination (RDA) of plots using their position relative to mounds as environmental variables (analysis 1b, see Table 1). (a) Scores of environmental variables (MOUND; quadrats on the mounds, OFF: quadrats in undisturbed grasslands; plots lying over a border of a mound have both variables non-zero), (b) scores of species. Only species with absolute frequency higher than 5 are plotted; some points refer to more than one species. The first canonical axis (horizontal) separates quadrats lying on mounds (right side) from quadrats lying in the rest of the grassland (left side); the second canonical axis separates quadrats lying at the borderline of the mounds (upper part) from the rest. Species abbreviations (only species with frequency > 10% are shown): Agrten, *Agrostis capillaris*; Antodo, *Anthoxanthum odoratum*; Avefle, *Deschampsia flexuosa*; Brasp., *Brachythecium* sp.; Brimed, *Briza media*; Carcar, *Carex caryophylla*; Carpil, *Carex pilulifera*; Cerpur, *Ceratodon purpureus*; Crugla, *Cruciata glabra*; Diadel, *Dianthus deltoides*; Fesovi, *Festuca ovina*; Fesrub, *Festuca rubra*; Fraves, *Fragaria vesca*; Hiepil, *Hieracium pilosella*; Hypmac, *Hypericum maculatum*; Hypper, *Hypericum perforatum*; Leohis, *Leontodon hispidus*; Luzmul, *Luzula campestris* agg.; Narstr, *Nardus stricta*; Picabi, *Picea abies*; Pimsax, *Pimpinella saxifraga*; Plaaff, *Plagiomnium affine*; Plalan, *Plantago lanceolata*; Plesch, *Pleurozium schreberi*; Polcom, *Polytrichum commune*; Poljun, *Polytrichum juniperinum*; Polvul, *Polygala vulgaris*; Potere, *Potentilla erecta*; Ranacr, *Ranunculus acris*; Ranpol, *Ranunculus polyanthemus*; Rumace, *Rumex acetosa*; Rumacl, *Rumex acetosella*; Siedec, *Danthonia decumbens*; Silnut, *Silene nutans*; Thypul, *Thymus pulegioides*; Trirep, *Trifolium repens*; Vercha, *Veronica chamaedrys*; Veroff, *Veronica officinalis*; Viocan, *Viola canina*.

ers and non-clonal species). Still all the mound-inhabiting species are capable of various forms of clonal growth. Except for *Festuca ovina*, all these species form various types of long spacers; however, apart from this, there did not seem to be any specific clonal growth form type associated with the mound-inhabiting species. There were species both with root-derived spacers (*Rumex acetosella*), shoots-derived below-ground spacers (*Anthoxanthum odoratum*, *Dianthus deltoides*, *Polytrichum commune* agg.) and surface-creeping rooting stems (*Thymus pulegioides*, *Dianthus deltoides*). These types of spacers were not confined to the mound-inhabiting species; similar adaptations are found in plants that occur disproportionately outside the mounds or that were indifferent. There were very few annual or rosette species and none of them was frequent; they did not seem to be confined to either type of habitat.

There were no significant differences in the scores on the first canonical axis (i.e. between mound-inhabiting and mound-avoiding species) relative to the type of their seed bank, seed size or capacity for myrmecochory. However, there was a highly significant difference in the score on the second canonical axis (i.e. species overrepresented at the mound margins vs. the rest; Figure 1) when species were grouped by their capacity for myrmecochory ($F = 7.25$, d.f. = 1,35, $P = 0.011$ when information on myrmecochory was taken from the Frank and Klotz data, and $F = 12.45$, d.f. = 1,35, $P = 0.001$ when information on myrmecochory was taken from the Grime et al. data; cf. also Figure 2). Seed bank type and seed size were not significantly related to the second canonical axis either.

The set of species associated with the mounds changed from the open grassland (transect 1) to a grassland partially overgrown with trees (transect 3). In grassland with no trees (transect 1), the mounds were colonized specifically by *Thymus pulegioides*, *Festuca ovina*, *Anthoxanthum odoratum*, *Rumex acetosella*, *Agrostis tenuis*, *Sieglingia decumbens*. In grasslands that were partially overgrown by trees (transect 3), most mounds were covered by *Polytrichum commune*, together with *Thymus pulegioides* and other species that persisted from earlier succession stages. Floristic difference among the transects was very strong and significant when both plots (dataset I, analysis 1a) and mounds (dataset II, analysis 2a) were compared using RDA with transect code as environmental variable. Mound vegetation differed strongly among the three transects, indicating a

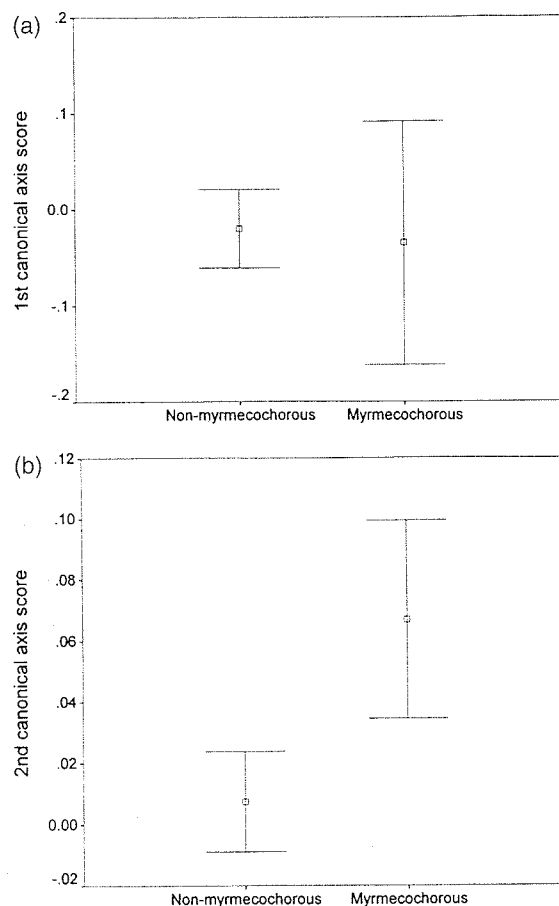


Figure 2. Score of individual species on the first (a) and the second (b) canonical axes from the Figure 1; species are divided into myrmecochorous (using either Frank and Klotz (1988) or Grime et al. (1988)) and non-myrmecochorous. The bars express 95% confidence interval of the mean.

change in the plant composition of mounds during a succession to the forest.

The number of plant species present was lower on the mound, but the difference was rather weak (though significant). It was higher in transects 2 and 3 (Figure 3) than in Transect 1.

Variation among mounds: effects of ant species and mound history (datasets II and III)

Vegetation of the mounds differed due to the dominant ant species present and due to the size and shape of the mound (Table 1; dataset II). In particular, the major direction of variation separated mounds with *L. flavus* as a dominant species from mounds with no living ant colony (Table 1; analyses 2c – 2e; Figure 4). Plants associated with the *L. flavus* mounds

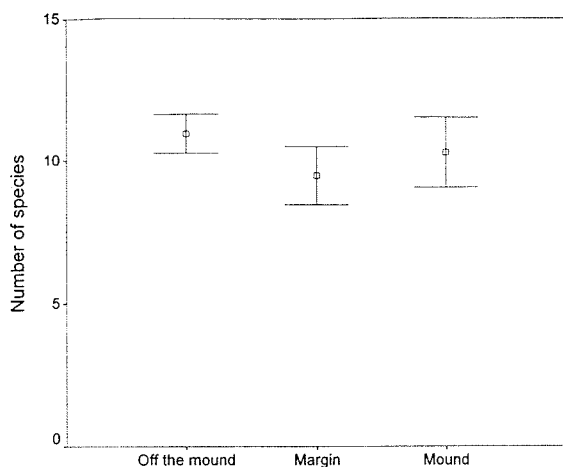


Figure 3. Number of vascular plant species in 0.25×0.25 m squares on the mound, at the mound margin and in the undisturbed grassland; 'transect' refers to the three transects used to collect the data. The bars express 95% confidence interval of the mean.

were the typical mound-inhabiting species, such as *Thymus pulegioides*, *Anthoxanthum odoratum*, *Polytrichum* spp., *Sieglingia decumbens*, *Agrostis tenuis*, *Rumex acetosella*; species that are associated with abandoned mounds were particularly species of acidic habitats such as *Potentilla erecta*, *Nardus stricta*, *Luzula albida*, *Vaccinium myrtillus*, *Hypericum maculatum*. Presence of other ant species (*T. caespitum*, *Formica* spp.) had much lesser effect on vegetation of the mounds. The inhabited mounds (particularly those with *L. flavus*) differed from abandoned mounds in their size parameters; in particular, abandoned mounds were on the average smaller. Correlation coefficients of the absence of any ant species with height and longest diameter of the mound are -0.36 and -0.25 respectively (see also analysis 2b).

The number of plant species present differed between inhabited and abandoned mounds (Table 2), but did not differ between mounds inhabited by different ant species (HSD test). The number of species was, as expected, higher on larger mounds, but was not affected independently by mound height.

If history of mounds was taken into account (dataset III), the principal direction of variation remained the same (Figure 5). A stepwise analysis with all present-time variables (1995) as covariates showed that history variables had independent extra explanatory power for the current vegetation (Table 3). In particular, initial size (diameter in 1981) and past history of colonisation by *L. flavus* (specifically in 1988) explained variation in the current floristic

composition that cannot be explained by the knowledge of current size and dominant ant species.

Discussion

Mound history, ant species and present vegetation

Mounds are long-lasting structures whose vegetation seems to integrate effects of different episodes during their existence. In the studied grasslands, they may either be inhabited by long-lived ant colonies that stay in one mound (primarily by *L. flavus*), by more ephemeral ant colonies (*T. caespitum* or *Formica* spp.), or may be uninhabited following the death of an earlier colony. The correlation of present-day vegetation and currently present ant species showed a dominant effect of *L. flavus* (analysis 2c, 2d, Figure 4) and smaller effect of *Formica* spp. and *T. caespitum*. *L. flavus*, in particular, seems to support mounds with the typical vegetation composed of longly rhizomatous species such as *Polytrichum commune* agg., *Thymus pulegioides*, *Rumex acetosella*, *Agrostis tenuis* etc. The colonies of the latter ant species are more short-lived (Petal 1978). Hills of *Formica* spp. often have only a sparse plant cover and do not favour specific plant species, as do the hills of *L. flavus*. The vegetation of the mounds colonized by the former two species is richer in bryophytes, also indicating the presence of the bare soil surface.

The effect of *L. flavus* on vegetation is indeed on-going: the first axis in Figure 5 is highly correlated with the presence of this species even in a rather distant past. Occurrence of *L. flavus* in the past has an effect on the current mound vegetation that cannot be explained by the presence of the currently occurring ant species. In contrast, history of colonisation by *T. caespitum* does not seem to affect the mound to an important degree and its effect essentially fades away faster than the recording interval (from 1988 to 1995). (Unfortunately, there are too few *Formica*-inhabited mounds in the permanent plot to permit their sensible study.)

While the differences between individual ant species were important, the major effect seems to be due to the fact whether the mound is currently inhabited or not. Disappearance of the maintaining colony seems to trigger an array of changes such as changes in soil moisture and aeration, mineral transport, disturbance etc. (Petal 1980). As a result of such changes, abandoned mounds are physically smaller

Table 2. Analysis of variance of number of vascular plant species as determined by mound vs off-mound position (dataset I) and mound parameters (dataset II). ¹) Abandoned mounds recorded as a separate category.

Source	Sum of Squares	df	Mean Square	F	Significance
dataset I					
Transect	1144.090	2	572.045	81.085	.000
Position to mound	52.905	2	26.453	3.750	.025
Interaction	65.508	4	16.377	2.321	.058
Error	1594.410	226	7.055		
dataset II					
Mound diameter	109.544	1	109.544	10.589	.001
Mound height	2.223	1	2.223	.215	.643
Ant species ¹)	66.320	2	33.160	3.205	.043
Transect	889.631	1	889.631	85.998	.000
Species*Transect	48.000	2	24.000	2.320	.101
Error	2037.917	197	10.345		

(see also King (1977b)) and host different vegetation. This process takes several years or a decade: while the vegetation of the mounds uninhabited in 1995 differed conspicuously from that on the living ones, the fact that a mound was uninhabited in 1981 mattered little for its present vegetation (Figure 5).

A conspicuous process following the disappearance of the ant colony is the invasion of acidophytic vegetation to the mound. The proportion of these acidophytic plants is actually much higher on the abandoned mounds than in the grassland off the mounds. There are several literature reports on nutrient leaching and decrease of nutrient levels from abandoned mounds (King 1977b; Petal 1980; Elmes 1991), but this is always interpreted as a process during which the mounds return to the state of the rest of the grassland. Petal (1980) reports that mineral composition of *Myrmica* mounds will return to that of the undisturbed grassland within two years; in the studied locality, the process seems to lead to a different type of vegetation that is more acidophytic than the vegetation off the mounds. Using the correlative data available, this is hard to separate from the overall acidification at the site that occurs during the succession toward the spruce forest.

Another important carryover effect was related to the mound size in the past. The present day vegetation was correlated with the mound size and height (analyses 2b, 2d); importantly, size in the past explains additional variation in vegetation that was not accounted for by the present-day size parameters. One feasible explanation is the effect of a 'critical mound size' in the past. Though the current data cannot demonstrate it, there may be an important founder effect

in the vegetation structure of the mounds; initial mound size may direct the course of the colonisation that ultimately leads to the current vegetation. Unfortunately, very little is known on the vegetation development at the early stages of the mound development (Pontin 1960; King 1981) when the founder effects should take place. It should be noted here that *L. flavus* mounds are on average bigger than mounds inhabited by other species; the founder effect may thus be a combination of the effect of initial size and of the species-specific effect of *L. flavus*.

Biology of mound-inhabiting plant species

As in other similar systems, there are conspicuous differences between the mound and off-the-mound vegetation. The current data provide some evidence on (i) disturbance due to soil transport, and (ii) myrmecochory.

The disturbance due to the colony's building activity presumably affects the vegetation by filtering out the species that are unable to cope with the continuous soil transport to the mound. The mound-inhabiting species are typically those able to form long rhizomes or stolons, either above-ground (*Thymus pulegioides*, *Veronica officinalis*, *Dianthus deltooides*) or below-ground (*Polytrichum* spp., *Agrostis capillaris*, *Dianthus deltooides*). Still there does not seem to be a simple morphological feature that would separate the mound-inhabiting species from the species thriving in rest of the grassland, since species with a similar type of clonal growth occur off the mounds as well (e.g. *Festuca rubra*, *Prunella vulgaris*, *Ajuga reptans*) and the overall rarity of rosette-forming spe-

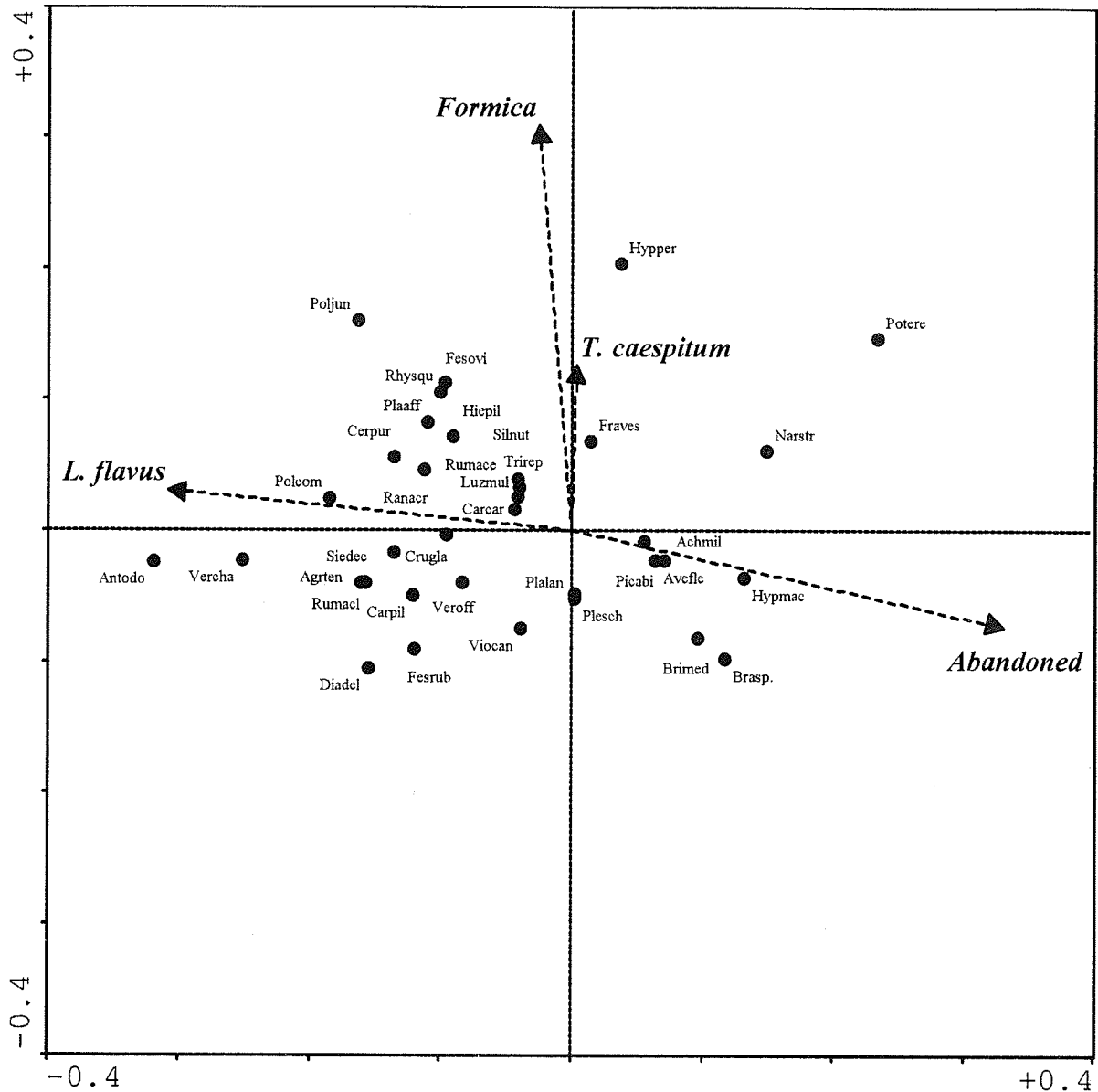


Figure 4. Canonical ordination (RDA) of mounds with the dominant ant species as environmental variables. (a) correlation of environmental variables with canonical axes; (b) species scores on the canonical axes. Only species with absolute frequency higher than 5 are plotted. Abandoned mounds are recorded as a separate category. For species abbreviations see Figure 1.

cies precluded confirming their absence from the mounds. The ability to persist on an active mound may require the capacity to respond fast enough to disturbance generated by ants by induced formation of elongated spacers, a feature not necessarily present in all species that produce elongated spacers at some point of their lives.

The set of adaptations that may enable plants to survive in ant-hills seems to be rare enough since the

flora of *L. flavus* mounds across Europe shares quite a lot of common species in spite of wide differences in the source communities (Gaspar 1972; King 1977a, 1977d; Dean et al. 1997). Clearly, the mound represents an extreme habitat that can be colonized by a specific subset of species common in the grasslands only; a few species may take advantage of it and increase their population density, but the overall species pool of species having this capacity seems to be rather

Table 3. Stepwise selection of parameters of the mound history that contribute most to floristic variation within mounds (dataset III, $n=98$). Stepwise form of redundancy analysis is used. Variables not listed failed to meet the F -criterion for inclusion into the regression equation. As in all stepwise procedures, significances are approximate. Abbreviations of independent variables: Abandoned95 - no ant species present in 1995, Diameter81 - longest diameter of the mound in 1981, Lasius88 - presence of *Lasius flavus* in 1988, Tetramorium95 - presence of *Tetramorium caespitum* in 1995. All 1995 variables: mound diameter and presence of *Lasius flavus*, *Formica* spp., and *Tetramorium caespitum* in 1995.

Step No.	Covariates	Variables selected	F -criterion
1	None	Abandoned95	5.74**
2		Diameter88	2.93**
3		Lasius88	1.83*
4		Tetramorium95	1.99*
5		Diameter81	1.71*
Variation explained by the first axis		7.1%	
Variation explained by all canonical axes		13.7%	
1	All 1995 variables	Lasius88	2.02**
2		Diameter81	1.66*

low. The difference in species pools between mounds and the remaining grassland may underlie also the low species richness of the mound vegetation relative to the rest of the grassland (Pärtel et al. 1996; Zobel 1997).

The classical study of King (1977a, 1977c) also reports a higher proportion of annual species in the mounds; this is also interpreted as a result of disturbance and opening of the sward by the building activity of the colony. In our system however, there are very few annual species in either type of microsite and none of them is common (*Myosotis arvensis*, *Euphrasia* sp.; few annuals were found also e.g. by Dean et al. (1997)).

By generating disturbance, activity of ants resembles to that of other animals generating soil disturbance (Platt 1975; Shachak et al. 1991). These disturbed sites may eventually reach a stable species composition as a result of selecting species that are able to survive the disturbance. They help to establish a mosaic of microhabitats that, on the larger scale, supports more plant species than the individual parts of the mosaic.

As in many earlier reports on temperate grassland systems with ant-hills, there is no indication here that the myrmecochory/seed collecting by ants has an important effect on the vegetation of the mounds themselves; i.e. the proportion of myrmecochores there does not differ from that in the rest of the grassland. Quite strikingly, however, myrmecochorous species are significantly non-randomly distributed in the grassland outside the mounds: they are typically con-

finned to plots that lie at the margins of the mounds. This pattern has rarely been reported from grassland vegetation (for data on individual species, see e.g. Kjellsson (1985); Oostermeijer (1989)), though there are lot of reports from other temperate and tropical systems (Beattie 1985). Presumably this is due to ants collecting the seeds with elaiosomes and depositing the seeds stripped of the elaiosomes in some sites close to the mounds (Kjellsson 1985; Oostermeijer 1989). At present we cannot say which ant species is involved in this activity. The dominant species, *L. flavus*, does not forage regularly at the soil surface where most of the seeds are deposited (Pontin 1978); however, up to 60 seeds of *Veronica officinalis* were recorded in 10×10×10 cm from the upper layer of *L. flavus* nests at the locality (Kovář and Kovářová 1998), though these may represent a leftover from some other species inhabiting the mound earlier. Indeed, a significant proportion of the mounds had episodes in which they hosted a colony of a species other than *L. flavus* (Kovářová and Kovář, unpubl. data). *T. caespitum* may collect seeds, perhaps both as the building material for the nests and for food storage (Kovář and Kovářová 1998; Oostermeijer 1989); *Formica* species may also collect seed as a building material for the nests and may collect seeds with elaiosomes (Gorb and Gorb 1995, 1996). Then the pattern that is found today may be a result of combined effects of several species present at the site; the data available now cannot help to resolve the issue.

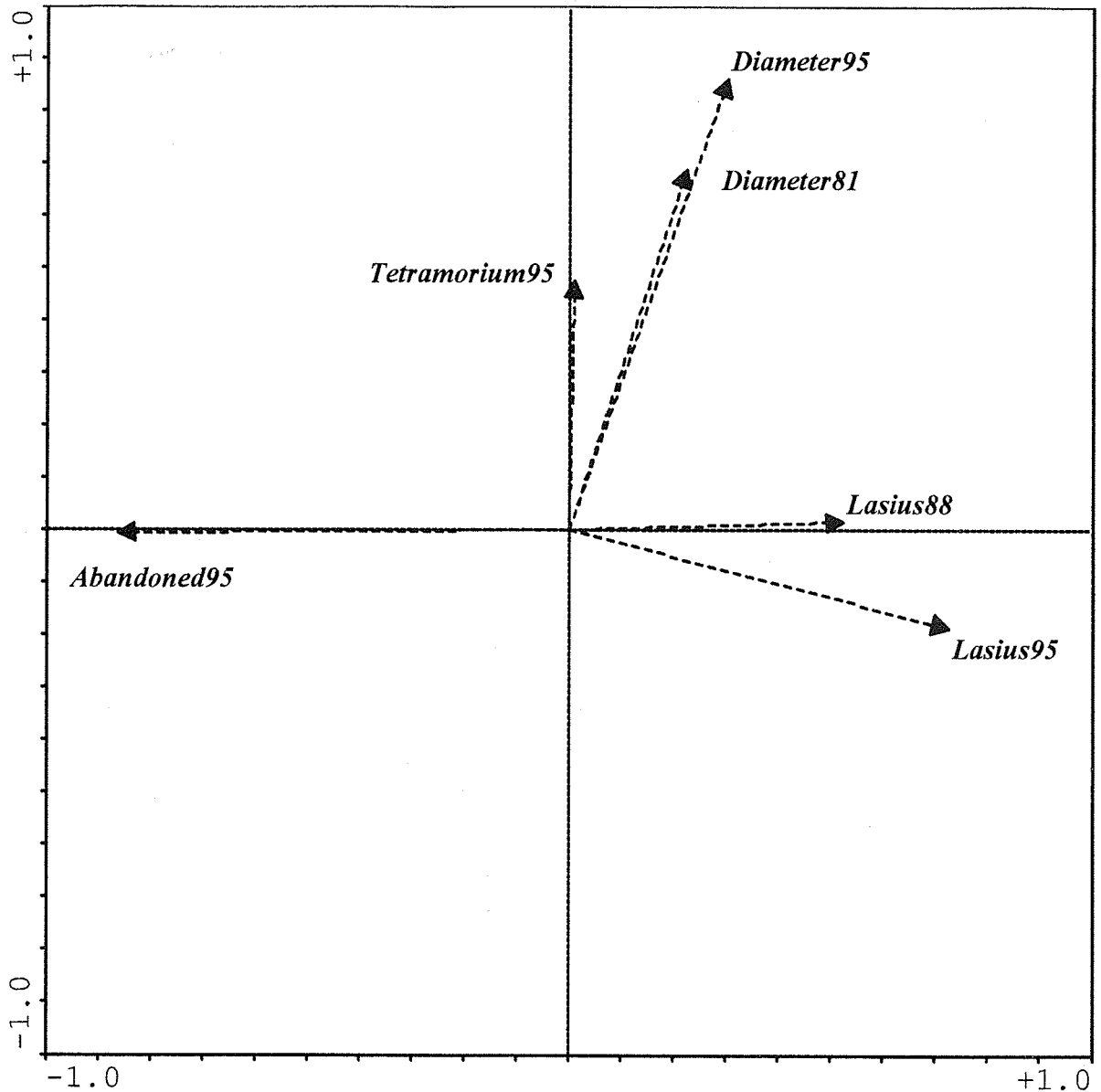


Figure 5. Canonical ordination (RDA) of the mound vegetation in 1995 with the dominant ant species and size through time as environmental variables. Only variables significant in a stepwise analysis were used (see the first analysis in Table 3. Diameter - mound diameter, Tetramorium - colony of *Tetramorium caespitum*, Lasius - colony of *Lasius flavus*, Abandoned - no ant species present. Two-digit figures refer to the year when these environmental variables were recorded; all vegetation data were taken in 1995.

Ant-hills and succession in the grasslands

In the region studied, the ant-hill vegetation is developed over rather large areas of grasslands. Most of these grasslands are moderately grazed; in areas that are regularly mown for hay the mowing prevents development of extensive ant-hill systems. This constitutes a positive feedback: once a grassland begins to bear a significant number of well-developed mounds,

it can hardly be mown again by the machinery commonly available. The grazing conducted in the area seems to support the specificity of mounds, since the sheep and livestock trample almost exclusively off the mounds while they graze preferably on the mounds, increasing the soil differences between the two (King 1977a). However, the grazing pressure is not strong enough to prevent young spruce trees from establishing. Spruce recruitment takes place almost exclu-

sively on the mounds. There are more spruce seedlings establishing on mounds than those establishing out of the mounds. The difference is often substantial, particularly when the low relative cover of the mounds (5–20% of the total area) is taken into account (Jana Raabová unpubl. data; cf. also the positive loading of *Picea abies* on the first RDA axis in Figure 1). As a result, many of the mound-rich grasslands are often being overgrown by the spruce forest under the current low-intensity farming. This is demonstrated by the vegetation development at the permanent plot (Kovář and Kovářová unpubl. data); many young spruce forests in the region indeed contain remnants of the abandoned mounds (pers. obs.). The high soil and vegetation heterogeneity generated by the activity of ants thus seems to be a temporary, though lasting several decades, phenomenon in these mountain grasslands.

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