



Colonization of temperate grassland by ants

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Abstract

Land-use change creates mosaics of habitats of different successional stages in landscapes. Knowledge about successional changes in species richness and community composition is essential for understanding biodiversity change in landscapes. Here we report about the community dynamics associated with the colonization of temperate grassland by ants. The study was carried out in low-intensity farming systems in Central Hesse, Germany, where the area covered by managed grasslands has continuously increased over the last decades. The simultaneous availability of grassland sites of different age allowed us to apply the 'space-for-time substitution' approach as a surrogate for a long-term study on ant succession. Our study on the community dynamics associated with the colonization of temperate grassland by ants did not reveal any drastic changes in species richness or composition in time. We nevertheless found clear differences between different phases of ant succession. Our data indicate a community driven by factors such as resistance to anthropogenic disturbance and opportunistic colonization during the initial period of ant succession. Ant composition was highly variable during early successional phases due to the strong site-specific differences in the distribution and abundance of pioneering species. Later successional phases, in contrast, showed much less variation in species composition, providing strong evidence for a rather predictable ant community in mature grasslands in this region. We found a change from ground nesting species that predominantly forage above-ground to the increasing abundance of the hypogaeic *Lasius flavus* foraging mainly below-ground. This change marks an alteration of the functional structure of the ant community.

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Zusammenfassung

Landnutzungswandel erzeugt Mosaik von Habitaten unterschiedlicher Sukzessionsstadien in Landschaften. Um Auswirkungen des Landschaftswandels auf die Biodiversität abschätzen zu können, benötigen wir Kenntnisse über Sukzessionsprozesse und deren Einfluss auf Artenreichtum und Artengemeinschaften. Diese Studie

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beschreibt den Ablauf der Kolonisierung von Grünländern in gemäßigten Breiten durch Ameisen und den sukzessiven Wandel der Ameisengemeinschaften. Sie wurde in einer landwirtschaftlichen Ungunstlage Mittelhessens (Deutschland) durchgeführt, in der die Fläche bewirtschafteten Grünlandes innerhalb der letzten Jahrzehnte kontinuierlich zunahm. Die verfügbaren Grünlandflächen waren unterschiedlich alt, was uns erlaubte, durch simultane Beprobung den Raum-für-Zeit Ansatz anzuwenden. Diese Methode dient als Ersatz für eine Langzeitstudie. Die Besiedlung des Grünlandes durch Ameisen zeigte im zeitlichen Ablauf keinen drastischen Wandel im Artenreichtum oder der Gemeinschaftszusammensetzung. Dennoch konnten klar unterscheidbare Schritte der Ameisensukzession gefunden werden. Unsere Ergebnisse zeigen, dass die Gemeinschaft in den frühesten Phasen der Sukzession durch Faktoren wie der Resistenz gegenüber anthropogenen Störungen und opportunistischer Besiedlung geprägt ist. Die Zusammensetzung der Ameisengemeinschaften ist hier sehr variabel, was auf flächenspezifische Unterschiede im Vorkommen der Pionierarten zurückzuführen ist. Spätere Sukzessionsphasen hingegen zeigten eine deutlich geringere Variabilität in der Gemeinschaftszusammensetzung. Dies weist darauf hin, dass die Ameisengemeinschaft reifer Grünländer der Region gut vorhersagbar ist. Entlang der Zeitreihe zeigte sich ein Wandel der funktionellen Struktur der Ameisengemeinschaften. *Lasius flavus*, welche ihre Nahrung hauptsächlich unterirdisch sammelt, nahm stark in ihrer Abundanz zu, wohingegen die Abundanz der oberirdisch Nahrung suchenden Arten in den späten Phasen stagnierte.

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Introduction

The area covered by managed grassland is continuously increasing in low-intensity farming systems of Europe (Stanners & Bourdeau, 1995), particularly in regions where conditions are unfavourable for arable farming ('marginal landscapes' *sensu* Baldock, Beaufoy, Brouwer, & Godeschalk, 1996). This process of land-use change creates mosaics of grasslands habitats of different successional stages in the landscapes. Therefore, knowledge about successional changes in species richness and community composition, especially of the fauna, are central to many aspects of nature conservation (Zedler, 2000). Ants provide a particularly interesting case of animal succession. Co-occurring species are similar in their ecological requirements, and competition for space and resources is as pronounced as between plants (Hölldobler & Wilson, 1990; Andersen, 1995). Considering their important role in soil engineering, distribution of plant seeds and predation (Petal, 1978; Folgarait, 1998), investigations on the community dynamics of ants will be essential for understanding biodiversity change in the cultural landscapes of Europe, despite the fact that species richness is comparatively low in many temperate regions (Golden & Crist, 2000). While dynamics of ant communities have been extensively studied, especially in Australia (Andersen, 1997), very little is known about the comparatively species poor ant communities of temperate habitats other than forests (Lynch, 1981; Boomsma & Van Loon, 1982;

Gallé, 1991). This is surprising, because some of the most fundamental studies on the factors structuring ant assemblages have been carried out in habitats such as temperate heathland (Brian & Brian, 1951; Brian, 1952; Elmes, 1971).

Here we report on the community dynamics associated with the colonization of temperate grassland by ants. The study was carried out on a chronosequence of sheep-grazed grassland sites in the Lahn-Dill-Bergland (Central Hesse, Germany). The simultaneous availability of grassland sites of different age allowed us to apply the 'space-for-time substitution' approach (Pickett, 1989) as a surrogate for a long-term study on ant succession. It is difficult to frame a clear cut hypothesis for emerging successional patterns, because although the concept of succession is one of the oldest in ecology, the underlying processes are among the least understood (Brown, Hendrix, & Dingle, 1987). Successional patterns are conspicuous, site-specific, influenced by many factors, and show a bewildering variety of patterns (Horn, 1981; Pickett & McDonnell, 1989; Morin, 1999). We expected ant species composition on the grasslands to be affected by processes of different relative importance during the colonization and maturation stages of succession (Walker & Chapin, 1987). The initial disturbance, the accessibility of the sites and the composition of the species pool were the same for all of the grasslands studied. Therefore, we expected stochastic events together with interspecific competition for nesting sites to drive species composition during the colonization stage

(Elmes et al., 1998). During the maturation stage development of vegetation cover and plant species richness should become more important by providing a higher diversity of microhabitats and food resources (Boomsma & Van Loon, 1982; Armbrecht, Perfecto, & Vandermeer, 2004). We addressed the following questions: (i) are there any clear patterns of ant succession on managed grassland? (ii) if yes, do changes in species composition lead to changes in the functional structure of the ant community?, and (iii) is there a correlation to changes in vegetation cover or plant species richness?

Materials and methods

Study sites

The study was carried out in the rural district of Steinbrücken in Central Hesse, Germany (latitude N 50° 48', longitude E 8° 20'). Poor physical soil conditions, a climate unsuitable for crops and farm sizes too small to be economically viable have resulted in considerable changes of land-use in recent decades. The proportion of arable land decreased from about 47% of the area under agricultural use in 1953 to 4% in 1998. Grassland and fallow land, in contrast, gradually increased (Waldhardt, Fuhr-Boßdorf, Otte, Schmidt, & Simmering, 1999). This created a complex spatio-temporal pattern of grassland sites of different age. Today, most of the study area is covered by moderately managed grassland, but a small fraction is still under agricultural use where wheat, oats, and potatoes are dominant crops.

GIS-supported stereoscopic analysis of black and white aerial photographs from the period 1945–1997 showed that apparently homogeneous grassland areas are composed of a mosaic of different age classes (Fuhr-Boßdorf, Waldhardt, & Otte, 1999). Based on this analysis, sites belonging to five phases of grassland age (time since last cultivation before the survey was carried out in 1999) were selected: phase 1 (3 years), phase 2 (11–27 years), phase 3 (28–38 years), phase 4 (39–46 years), and phase 5 (>46 years). In addition to the grassland sites, sites on arable land (phase 0) were included as a reference for the initial conditions of the successional process (Pickett, 1989). Three replicate sites per phase were selected. The average size per site was about 0.2 ha. Thirteen of the sites were situated within an 18 ha area on a south-facing slope, and the remaining 5 sites were situated on neighbouring slopes with identical aspect. Elevation of the sites

ranged between 370 and 390 m a.s.l. The replicate sites were interspersed on the slopes and independent from each other. A map of the study area is presented in Purtauf, Dauber, and Wolters (2004). The acidic soils (pH 4) varied between regosol and cambisol on a small spatial scale. The mean annual temperature was 6.6 °C, mean annual precipitation was 1100–1200 mm. The grassland sites have been moderately grazed by sheep since 1973 and were mulched once a year. There has been no fertilizer application since abandonment of cultivation. The sites of phase 1 had the lowest richness of plant species with high relative abundance of the sown species *Lolium perenne* and *Trifolium repens* (Waldhardt & Otte, 2003). With a total vegetation cover of 65% and growth height less than 40 cm this phase showed a distinctly sparser vegetation with lower canopy height than the later phases. In all following phases vegetation cover reached about 80% with *Agrostis tenuis* and especially *Festuca rubra* gaining in relative abundance. Species richness of plants in the later phases was about two times higher than in phase 1. Vegetation changed along the successional phases from an early stage on abandoned fields to ruderalized grassland vegetation, to oat-grass meadows and finally to red fescue-bent grass meadows (for further details see Waldhardt & Otte, 2003).

Sampling

Data on species richness and nest abundance of ants were collected from June to August 1999 at 10 randomly chosen 2 m² plots at each of the 18 sites. A minimum of 5 m was left between the plots to avoid an overestimation of patchily distributed species in seemingly homogeneous habitats (Andersen, 1990). In addition, at least 2 m were left between the plots and the border zones of the sites to avoid possible edge effects (Dauber & Wolters, 2004). All ant nests within the plots were counted. Ant nests without conspicuous mounds on the soil surface were recorded by raising the turf of the whole study plot with a small chisel. Up to 10 worker ants were collected from each nest and fixed in 70% ethanol immediately. The recording of ant hills in all microhabitats within a specific area is the most appropriate method for the assessment of the nest abundance of ants (Seifert, 1986). Samples of 10 m² are suggested as suitable for the assessment of the number of small nests occurring at high concentration like those of the genus *Myrmica* (Petal & Pisarski, 1993). A comparison of the data obtained with nest densities of temperate-zone ant communities described by Seifert (1986) indicates

that the sampling method was suitable and that the ant fauna was observed exhaustively. Only soil living ant species with very small colonies from the genus *Myrmecina* or *Ponera* might have been overlooked. Taxonomic determination is based on Seifert (1996). Species were assigned to functional types (epigaeic = species foraging predominantly above ground vs. hypogaeic = species foraging predominantly below ground) according to Seifert (1996).

Data analyses

Nest density of all species (D_M) and of individual species (D_I) is given as the number of nests occurring on a 20 m² area of each site. Two different measures of species richness were calculated: total number of species found on the three replicate sites of each phase (S_T) and number of species found per site (S_M). The effect of time (phases 0–5) on S_M and D_M was tested by means of a one-way ANOVA. Whenever necessary, data were log_e-transformed prior to statistical analyses to achieve homogeneity of variance. Correlation of changes in ant species richness and abundance with changes in vegetation cover and plant species richness was tested using Pearson's product moment correlation. All statistical analyses were performed using the STATISTICA for Windows package (StatSoft Inc., Tulsa, USA). A detrended correspondence analysis (DCA) was carried out

using the CANOCO 4 software package (ter Braak & Smilauer, 1998) to analyse general trends in ant community structure along the phases of the chronosequence. Three species with records of a single nest only were omitted from the DCA.

Results

Ten ant species belonging to three genera were recorded at the 18 study sites (Table 1). All species are ground-nesting and can be classified as being predominantly hypogaeic or epigaeic according to their foraging strategy. Total species richness (S_T) and mean species richness (S_M) closely paralleled each other (Fig. 1). The total number of species per successional phase (S_T) rapidly increased to seven species in phase 2 and remained constant thereafter. No phase of the chronosequence had the full complement of species (Table 1). Mean species richness (S_M) significantly increased from phases 0 to 3 ($F_{5,12} = 8.2$; $P < 0.001$). Ant species richness was neither correlated to vegetation cover ($r = -0.06$; $P = 0.86$) nor to plant species richness ($r = -0.12$; $P = 0.71$).

Mean nest density (D_M) significantly increased over the whole chronosequence ($F_{5,12} = 28.5$; $P < 0.0001$) (Fig. 2). This increase resulted from two different processes: (i) the mean nest density of epigaeic species increased during early successional phases and reached a constant level at phase

Table 1. Mean nest density D_I (per 20 m²) of ants at different phases of grassland succession (0–5; $n = 3$ for all phases)

	fs	0	1	2	3	4	5
<i>Formica cunicularia</i> Latr. 1798	e						0.3 (0.6)
<i>Lasius flavus</i> (Fabr. 1781)	h			1.3 (1.2)	6.7 (5.1)	9.7 (3.8)	16.0 (5.3)
<i>Lasius niger</i> (L. 1758)	e		0.3 (0.6)	3.3 (3.5)	0.7 (0.6)	0.7 (1.2)	0.7 (0.6)
<i>Myrmica lobicornis</i> Nyl. 1846	e				1.3 (0.6)	2.7 (1.2)	3.3 (1.2)
<i>M. rubra</i> (L. 1758)	e	0.7 (0.6)	0.3 (0.6)	2.3 (2.1)	4.3 (3.1)	1.0 (1.7)	
<i>M. ruginodis</i> Nyl. 1846	e			0.3 (0.6)			
<i>M. rugulosa</i> Nyl. 1846	e			0.3 (0.6)			
<i>M. sabuleti</i> Meinert 1860	e		0.3 (0.6)	0.7 (0.6)	0.3 (0.6)	1.3 (1.5)	2.7 (2.5)
<i>M. scabrinodis</i> Nyl. 1846	e		1.0 (1.0)	3.0 (1.7)	4.7 (1.5)	2.7 (1.5)	2.3 (2.1)
<i>M. schencki</i> Viereck 1903	e				2.0 (2.7)	3.7 (2.5)	1.3 (0.6)

Standard deviations are given in parentheses. fs: predominant foraging stratum; e = epigaeic, h = hypogaeic.

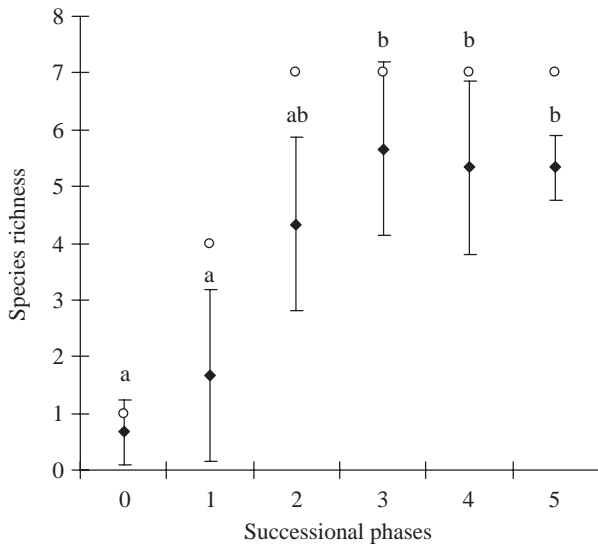


Figure 1. Mean species richness (S_M ; diamonds) of ants per 20 m² and total species richness (S_T ; circles) at different phases of grassland succession ($n = 3$). Bars represent standard deviations. Values with identical letters are not significantly different at the $P < 0.05$ level (Tukey HSD-Test).

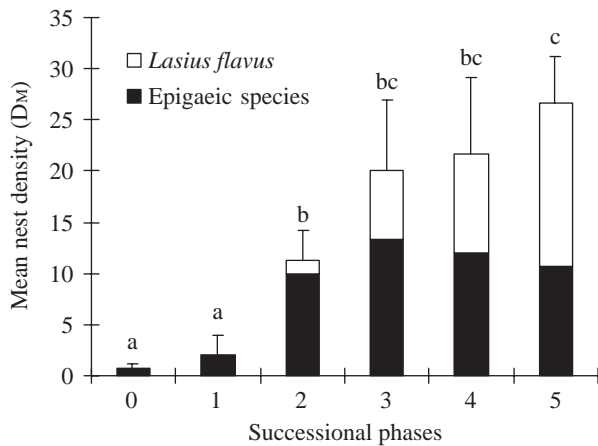


Figure 2. Mean nest densities (D_M) of ants per 20 m² at different phases of grassland succession ($n = 3$). Bars represent standard deviations. Comparison of means is confined to mean nest density of all species. Columns with identical letters are not significantly different at the $P < 0.05$ level (Tukey HSD-Test).

3, and (ii) the nest density of the hypogaecic *Lasius flavus* (Fabricius, 1781) continuously increased starting from phase 2 and into the late successional phases (Fig. 2). Thus, a shift in community structure occurred along the chronosequence. Nest density of *L. flavus* and plant species richness were significantly correlated ($r = 0.59$; $P < 0.05$). No other significant correlation between density parameters of ants and vegetation cover ($r = 0.18$;

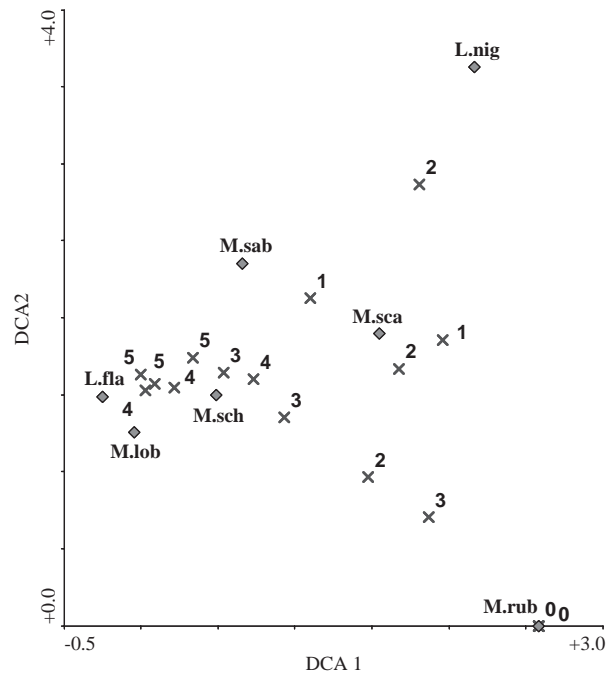


Figure 3. DCA ordination diagram with sites (x-marks) and species (diamonds). Numbers indicate the six phases of grassland succession (0–5); L.flu = *L. flavus*; M.lob = *M. lobicornis*; M.sch = *M. schencki*; M.sab = *M. sabuleti*; M.sca = *M. scabrinodis*; M.rub = *M. rubra*; L.nig = *L. niger*. One site of phase 0 and phase 1 each are not included, because no ants were found at these sites.

$P = 0.58$) or plant species richness ($r = 0.44$; $P = 0.15$) was found.

The two factors extracted by the DCA together explain about 68% of the total variance (Fig. 3). The first axis (DCA 1; variance explanation: 45%, eigenvalue: 0.41) represents the shift in community structure with increasing grassland age. Younger sites (incl. arable land) are plotted on the right of the DCA diagram and older sites are plotted on the left. *Myrmica rubra* (L. 1758), *Lasius niger* (L. 1758) and *M. scabrinodis* Nylander 1846 are associated with younger sites and *M. sabuleti* Meinert 1860, *M. schencki* Viereck 1903 and *M. lobicornis* Nylander 1846 are associated with older sites. The same is true for *L. flavus* although it already occurred in phase 2, but it had exceptionally high abundance in the latest phase. The second axis (DCA 2; variance explanation: 23%, eigenvalue: 0.21) reflects the degree of spatial heterogeneity in species composition and abundance. Younger sites show a large variation along this axis due to the strong site-specific differences in the distribution and abundance of pioneering species at this stage of grassland establishment. Replicate sites of later phases, in contrast, show much less variation in species composition along this axis.

Discussion

Our study on the community dynamics associated with the colonization of temperate grassland by ants did not reveal any drastic temporal changes in species richness or composition. This is consistent with results from investigations on grasslands in Spain which showed that ant succession is characterized by gradual change in relative abundance rather than by a rapid replacement of species (Acosta, Zorrilla, Lopez, & Serrano, 1992). We nevertheless found clear differences between different phases of ant succession. Following the established scheme of stages devised for successional processes (colonization, maturation, senescence; e.g. Walker & Chapin, 1987), a few *Myrmica* species and *L. niger* almost solely characterize the earliest colonization stage (phase 1). The higher species richness in phase 2 marks the transition towards the maturation stage, although spatial heterogeneity in species composition and abundance is very high during both phases 1 and 2, reflecting colonization stochasticity. The maturation stage (phases 3–5) is characterized by an increase in the relative abundance of *L. flavus*, a shift in species composition, and a decrease of spatial heterogeneity. Total species richness and nest densities of epigeaic species remained fairly constant during the 'late phases' of grassland development, although certain shifts in the nest densities of the single species were noticeable (Table 1). A senescence stage, where factors governing senescence and mortality predominate, would a priori not be expected in a temperate-zone grassland, as disturbance generally prevents a community reaching the senescent stage (Walker & Chapin, 1987). Therefore, it seems most likely that the ant community stayed in a stage of maturation due to the continuous management of the grassland sites. This is consistent with the conclusion that managed grasslands are in a state of dynamic equilibrium between succession and opposing forces, of which management is the most important (Morris, 2000). We will explore the basic patterns of ant succession observed in greater detail in the following paragraphs.

The heterogeneous distribution of the community during the initial phase of ant succession indicates an opportunistic mode of colonization, which is in accordance with the pattern reported by Corbet (1995) for several insect groups and plants. The dominance of *Myrmica* species like *M. rubra* and of *L. niger* at phase 1 of our chronosequence suggests a long-lasting effect of arable farming on ant communities. Both taxa are epigeaic, resistant to anthropogenic disturbance (Seifert, 1993), and

able to persist even in intensely managed meadows (Petal, 1976). Yet, nest densities of *L. niger* and *M. rubra* in the young grasslands are quite low (Table 1), leaving potential nest sites unoccupied which allows colonization by other species from the surrounding landscape. Elmes et al. (1998) stated that if a new patch of habitat is created within an area containing mature ant populations, the new habitat will be colonized rapidly by fragments of surrounding colonies. This is corroborated by the high abundance of *M. scabrinodis* on young grassland sites, suggesting a significant impact of source populations in the surrounding landscape matrix on the course of ant succession. *M. scabrinodis* is one of the most abundant species in grasslands of the region (Table 1; Dauber & Wolters, 2000, 2004). Our contention of an important role of the species pool on the establishment of ant communities is supported by the findings of other authors for different habitat types (Serrano, Acosta, & Lopez, 1993; Roth, Perfecto, & Rathcke, 1994; Bestelmeyer & Wiens, 1996).

The maturation stage of ant succession is characterized by a continuous increase of *L. flavus* nest density starting at phase 2. Since this hypogaeic species is resistant to anthropogenic disturbance (Seifert, 1993) and dispersal barriers are no issue here, establishment and population growth of *L. flavus* during the early period of grassland development must have been constrained by other factors. We hypothesize that *L. flavus* was limited by the low availability of its major food source: root aphids and the honeydew produced by these insects. The positive effect of increasing plant species richness on the nest density of *L. flavus* shown in our study might thus be a consequence of the increasing abundance of root aphids with plant cover and root biomass (Pontin, 1978). This conclusion is supported by Seifert (1993) who reports that a pauperization of plant diversity reduces food availability to *L. flavus* by reducing root aphid diversity. In a similar vein, Boomsma & Van Loon (1982) explain the increasing abundance of *L. flavus* in successive coastal dune valleys with changes in the availability of potential prey below ground. The lack of significant relationships between all other aspects of ant succession and vegetation change taken into account contrasts with Morrison's (1998) results, who found indications of a direct impact of the vegetation on the occurrence and abundance of ant species in natural systems. Considering that plant effects on ant communities are largely mediated by vegetation structure and microhabitat availability (Gallé, 1990), our result might be explained by the fact that the structural diversity of the vegetation in

managed grassland is significantly different from that of natural habitats and much less complex.

A second important aspect of ant community dynamics in the maturation stage was that total species richness rapidly reached a level of saturation. This level was identical to the average number of ant species occurring on other grassland sites of the Lahn-Dill-Bergland (compare Dauber & Wolters, 2000, 2004). This suggests a strong limitation of the number of ant species coexisting in managed grasslands even in temperate regions. The limitation, together with the decrease in spatial heterogeneity and an increase of predictability of community patterns at the later phases (Fig. 3) indicates the existence of a rather deterministic system governing the ant community pattern. The possible mechanisms lying behind the pattern development described are summarized by Corbet (1995): The first species colonizing a site will be wide-ranging and tolerant. They have the ability to colonize effectively and site-to-site differences will depend largely on site history. In our study, the occurring patterns depend on the dominance of either *M. rubra* or *L. niger* in an arable field (see Elmes et al., 1998 for a description of the competition between the two species). With an increasing number of species and individuals, dispersal ability and tolerance will become less important, and competition will favour species well suited to local habitat conditions. In fact late colonizers like *M. schencki* and *M. lobicornis* are more specialized and have smaller colonies compared to *M. rubra* (Seifert, 1996). Differences in community composition in later successional stages largely depend on habitat type and therefore mature communities of one habitat type should be more characteristic of a region than young communities (Corbet, 1995). Elmes et al. (1998) stated that due to strong competition once one or more *Myrmica* species have colonized an area, invasion of other species is unlikely unless physical conditions of the habitat are changed. Albrecht & Gotelli (2001) also emphasize the crucial role of competitive interactions for structuring ant communities (but see also Ribas & Schoereder, 2002).

To conclude, the question concerning clear patterns of ant succession on managed grassland posed in the introduction section has to be answered positively. Our data indicate a shift from a community driven by factors such as resistance to anthropogenic disturbance and opportunistic colonization during the initial period of ant succession to an increasing dominance of biotic interactions during the period of maturation. This finding is in line with conventional theories on the course of secondary succession in plants (Walker & Chapin,

1987). Although ant composition was highly variable during early successional phases it was quite constant later, giving strong evidence for a rather predictable ant community in mature grasslands of the region. The change from ground nesting species that predominantly forage above ground to the increasing abundance of the hypogaeic *L. flavus* foraging mainly below ground marks an alteration of the functional structure of the ant community. Potential consequences include higher predatory pressure below ground (Pontin, 1961) and increased bioturbation (Dlussky, 1981). The impact of the vegetation on this change seems to be rather indirect, i.e. by triggering the population growth of *L. flavus* via changes in below-ground food availability or by providing 'open gaps' to late colonizers. This probably is a consequence of the reduced structural diversity of the vegetation in managed grassland. The consistent patterns observed in our study make us quite confident that we have identified the most important elements of ant succession on temperate managed grassland. However, the space-for-time substitution approach has some shortcomings concerning the comparability of the study sites (Pickett, 1989). For example, it cannot be excluded that the different sites started from different conditions caused by differences in the amount of fertilizer applied at the times of conversion from arable land to grassland and that the composition of the species pool has changed with time.

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