STRUCTURE OF ANT ASSEMBLAGES IN A MIDDLE-EUROPEAN SUCCESSIONAL SAND-DUNE AREA

L. Gallé, L. Körmöczi, E. Hornung and J. Kerekes

Abstract. The species composition, diversity, population interactions and external correlates of ant assemblages are described in different successional plots of a sand-dune area in the Kampinos National Park, Poland. The pooled mean population densities were in the range of 0.018-0.37 colonies/m^2 and increased toward the last successional phase. The species diversity also increased, but there was a diversity decline in the last phase, probably as a consequence of the presence of red wood ant species, which are dominant in the interference competition. The range of a particular species' distribution in different ant assemblages is characterized with its position and breadth in the corresponding PCA factor space. The species number against position histogram is bimodal and differentiates the species of early successional assemblages from that of the mature, well organized communities.

The composition of the ant assemblages was found to be correlated with some structural habitat properties (architecture of vegetation, the number and condition of dead twigs on the soil surface, temperature) and the composition of epigeic fauna. In the competitive network of the early successional ant communities, *Formica cinerea* and *Myrmica rugulosa* have the same rank and both species are subordinated to *Formica truncorum*. The interference interspecific competition has an increasing significance towards the advanced successional stages.

Key words: ants, community composition, succession, diversity, interference competition

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Introduction

The possibilities of the generalization of the results obtained in particular habitats or regions are among the main conceptual and methodological problems of community ecology. A possible tool towards the generalization is the comparison of animal assemblages at different regions to reveal the similarities and dissimilarities both in their composition and in the structuring mechanisms (as illustrative examples on ants, see Andersen 1986a, 1986b, 1992a, Morton and Davidson 1988, Herbers 1989).

Most of the papers, however, that have been published on ant community succession (e.g. Boomsma and Van Loon 1982, Gallé 1981, 1991, Járdán *et al.* 1993, Szujecki *et al.* 1978, Vepsäläinen and Pisarski 1982, Zorrilla *et al.* 1986) concern only particular areas or even habitats. Therefore, it is not really known, whether the phenomena and mecha- nisms described in those papers are general proper- ties of ant community succession.

This paper reports a part of a series of comparative studies on the succession of ant commu- nities in sand-dune areas along a geographical gradient from Finland to Turkey (for the first results, see Gallé 1990a, 1990b, 1991, 1992, Járdán *et al.* 1993). The aim of this paper is to describe the struc- ture of ant assemblages in successional dune plots in Kampinos National Park (Poland). The main questions addressed are as follows: (1) What is the composition of the ant faunulas in different successional plots? (2) Is there any genetic relation between the ant assemblages of the studied succes- sional plots? (3) Are there differences in spatial patterns of ant populations and assemblages in different successional stages? (4) Is there any trend in the ant species diversity along a successional gradient? (5) Which external factors are correlated

with the distribution of ants among habitats in different successional phases? (6) What is the effect of interspecific competition on the process of organization of ant communities in early stages of succession?

Materials and methods

The field studies were carried out in the Kampinos National Park, near Warsaw (Poland). For detailed ant community surveys, we selected nine plots that presumably represented different stages of vegetation succession. One of them (plot 1) was a bare sand, almost without vegetation; plots 2 and 3 represented initial steps of vegetation succession, with mosses, lichens, some pines and very poor herb layer. The vegetation cover was less than 40%. Plots 4 and 5 were grasslands; plot 6 was a shrubby site in a transitional habitat between a grassland and a pine forest; plot 7 was a young pine plantation, which we expected to belong to the transitional successional stage between grassland and forest; and the two remaining plots were pine forests with (plot 9) and without (plot 8) a high density of red wood ant population. For detailed characterization of the study plots a set of 90 habitat scores were used, in six groups (Table 1).

The density and distribution of ant nests were estimated via grids of quadrates of 16 or 25 m^2 size. The ground was dug to a depth of 20 cm to find all ant nests in those plots which were covered by dense vegetation. Altogether an area of 1035 m^2 was sampled in this way. The position of nests and nest entrances were mapped for further analysis. Spatial distribution of nest entrances, calices and nests were studied with the distance to nearest neighbor method (Clark and Evans 1954) and with grid-pattern analysis of mapped colonies by increasing the size of sample units (Greig-Smith 1983, Körmöczi 1987).

Ordination techniques are useful tools in successional studies (cf. Howard and Robinson 1995). Therefore, the state of each sampled ant assemblage in an assumed successional sere was established by PCA ordination and similarity analysis. Renkonen's percentage similarity function,

$$CR_{ih} = 100\sum_j \min(p_{ij}, p_{hj})$$

and an asymmetric index of similarity formally the same as Levins' function

$$CL_{i,h} = 100\frac{\sum_j p_{ij}p_{hj}}{\sum_j p_{ij}^2}$$

were employed to compute similarities of different assemblages, where $p_{i,j}$ is the relative frequency of jth species in the assemblage i.

Markov chain models are widely used to study the successional relationships of the different stages of ecological systems (Horn 1975, 1976). In the present study, we computed the transitional probabilities between the ant assemblages of the sample plots from their similarity matrix. The Markovian properties of the assemblage sequences were investigated with a chi-square test of the estimate of -2lnλ (Usher 1979, 1987).

The PCA ordination of the individual sampling units on the basis of their ants yielded information on the position and overlap of ant assemblages of the sampled habitats plots. The range of the assemblages occupied by a species, called breadth hereafter and the position of a particular species in the PCA space were computed with similar basic concepts as were employed by MacNally and Doolan (1986). Let w_i is the amount of variance explained by the ith factor and $\bar{x}$ and s_i are the mean and standard deviation of sample units which are occupied by the species in question, then the breadth (B) and the position (P) are defined by these equations:

$$B = \frac{\sum_i\{w_i s_i\}^2}{\sum_i w_i^2} \quad \text{and}$$

$$P = \frac{n\sum_i\{w_i x_i\}^2}{\sum_i w_i^2}.$$

Species diversity was computed by the means of both Shannon-Wiener (Shannon and Weaver 1949) and Simpson-Yule (Pielou 1975) indices. The former was used to characterize the diversities of different successional ant assemblages, and the latter to compute correlation between the different diversities (i.e. plants and ants, vegetation architecture and ants, etc.).

From among the habitat properties (Table 1), for the analysis of vegetation architecture and composition, the coverage values were assessed in grids of 5×5 m cells by eye at different heights and expressed as percentages. The average number of dead twigs on the ground was estimated in 50×50 cm quadrates; the size and condition of twigs were also noted. A set of ten such quadrates were taken at each site.

Soil water content was measured at depths of 5 and 10 cm. The physical composition of the soil was characterized by hygroscopic values (Balleneger 1953). Soil temperature was measured at a depth of 5 cm and that of the air at 40 cm and 200 cm above the ground surface. All temperature measurements were

Table 1. Attributes for characterization of study plots

Group	Attributes	No of categories
1. Vegetation architecture	1.1. Whole vegetation cover	1
	1.2. Cover of mosses and lichens	4
	1.3. Cover of plant debris	3
	1.4. Plant cover at 5-15, 15-30.... cm levels	4
2. Vegetation composition	2.1. Relative frequency of predominating plant species	33
3. Size of the plot		1
4. Dead twigs on the ground surface	4.1. Density of dead branches of various sizes and conditions	14
5. Soil and microclimate	5.1. Temperature of soil and of air above soil surface as a difference from air temperature at 2 m height	2
	5.2. S.d. of 5.1.	2
	5.3. Soil humidity at two depths	2
	5.4. Soil hygroscopic value	2
6. Epigeic fauna	6.1. Density of various animal groups collected in pitfall traps	22

carried out ten times simultaneously in all nine study plots on cloudless days.

Pitfall trap method was employed to establish the composition of ground surface fauna. Fifteen traps were used in each habitat plot for a week. Collected materials were preserved in ethanol (70 %) and sorted at taxonomic group levels (altogether 22 taxa).

External factors that presumably affect the habitat selection and assemblage composition of ants were identified with principal component analysis. Study plots were ordinated in six different factor spaces on the basis of the following attribute groups: vegetation architecture, floral composition, number and condition of twigs on the soil surface, microclimate and soil properties, composition of epigeic fauna, and composition of ant assemblages. The relative position of points representing habitat plots in the PCA spaces were measured with multidimensional Euclidean distances (Pielou 1984), weighted by the variance of PCA axes. We then computed the similarities of the different PCA spaces on the basis of the relative position of points representing sampling plots with nonparametric Spearman's rank correlation. The contribution of single habitat properties to the axes of the PCA ordination factor space of ant assemblages was studied by simple correlation analysis.

Distribution and co-occurrence data are not always reliable for the detection of interspecific competition. Both Alatalo et al. (1986) and Hastings (1987) suggested that field experiments (reviewed by Connell 1983, Schoener 1983 and Gurevitch 1992) should be carried out to establish the presence and importance of competition. The direct competitive interactions between different species were therefore studied in bait experiments. We used honey and tinned meat to bait ants. Baits were put on small leaves which were fixed on the soil with small (ca 4×4 cm) pieces of paper sheets and pines. Altogether

285 bait recordings were made and ants were observed on baits in 180 cases. These bait experiments yielded evaluable data sets for the interaction of the *Formica truncorum* F. - *Formica cinerea* Mayr and *F. cinerea* - *Myrmica rugulosa* Nyl. species pairs. In a previous study (Gallé 1991), similar data were obtained on *F. cinerea*, *F. sanguinea* Latr. and *Lasius psammophilus* Seifert. species. In this way we have information on most possible relevant interactions of ant species on the early sand-dune successional stages in North Europe and the northern part of Middle Europe.

Results

Nest densities and species composition

Altogether 22 ant species were collected from the 9 habitat plots (Table 2). The pooled population densities varied between 0.018 and 0.37 nests/m^2. The lowest densities were found in plot 1, which had a bare sand surface, and the highest density data were observed in plot 9, which was a pine forest with a high density of foraging individuals of *Formica polyctena* Foerst.

The PCA ordination of the sampling units yielded the following results (Fig. 1). The ant assemblages of the open habitats (plots 2, 3, 4 and 5) and that of the forests (plots 8 and 9) are segregated along the first PCA axis. The central position of plot no 1 is explained by the fact that since it was an almost bare sand surface, its ant fauna mainly consisted of individuals occurring accidentally without nest. The only nesting species was *Lasius psammophilus*. This poor, single species ant assemblage could be a starting point of ant community assembly in both open and forest habitats. The transitional position of plot 6 is in accordance with its vegetation mentioned above. The ant assemblage of the young

Table 2. Density of ant colonies/100 sq m in different study plots. + only workers or * females were collected by hand or in pitfall traps

Species	Plot number								
	1	2	3	4	5	6	7	8	9
Myrmica laevinodis Nyl.			+						*
Myrmica ruginodis Nyl.	+	+	+	+		9.4	+	3.1	15.6
Myrmica rugulosa Nyl.		+	2.9	+	+	1.6	+	1.6	
Myrmica sabuleti Mein.				+					+
Myrmica lobicornis Nyl.	*				+	+	+	+	1.6
Myrmica schencki Em.	+	+		+	+	1.6			
Leptothorax acervorum (F.)						4.7	1.0	1.6	4.7
Leptothorax muscorum (Nyl.)			0.9	+		9.4			*
Leptothorax nylanderi (Foerst.)								3.1	14.1
Diplorhoptrum fugax (Latr.)		+	4.8	+	+	+	4.0	+	
Tetramorium caespitum (L.)	+	+		1.7	4.5	+	5.0		+
Stenamma westwoodi Westw.								+	*
Lasius fuliginosus (Latr.)				*					
Lasius niger (L.)				3.3	1.1		+		
Lasius alienus (Foerst.)	1.8	3.0	1.9	+	1.1				
Formica fusca L.				3.3		6.3	+	4.7	1.6
Formica rufibarbis F.	+						+		
Formica cinerea Mayr		6.0	13.3	+	+	+	13.0		
Formica rufa L.		+						+	
Formica polyctena Foerst.									0.01
Formica truncorum F.							+		
Formica pratensis Retz.	+			+	+		+		
Total	1.8	9.0	23.8	8.3	6.7	33.0	23.0	14.1	37.6

pine plantation (plot 7) differs from the older, natural forests and situated among the open habitats in the PCA scattergram. The second axis is responsible for the differentiation of grassland ant assemblages from that of other open habitats (Fig. 1).
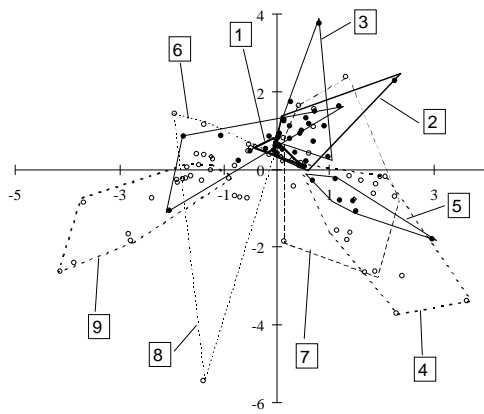

Fig. 1. Scattergram of the pitfall trap sample units of different plots along the two principal axes of PCA factor space on the basis of the species composition of their ant collection.

No significant correlation was observed between the position (P) and the breadth (B) values of the ant species (Spearman rank correlation $r = -0.36$, $n = 21$, $p>0.05$). The species number against P histogram is bimodal (Fig. 2). The species which have lower position values are usually early successional species

(e.g. *Tetramorium caespitum* L., *Formica cinerea*, *Diplorhoptrum fugax* Latr., *Lasius psammophilus*). or belong to the transitional assemblages (e.g. *Myrmica lobicornis* Nyl., *Myrmica rugulosa*) and only two species of the third column are the members of "mature", competitively organized ant communities (i.e. *Formica pratensis* Retz. and *Formica fusca* L.) as a rule, but in Kampinos they occupy early successional habitats, too. The most of
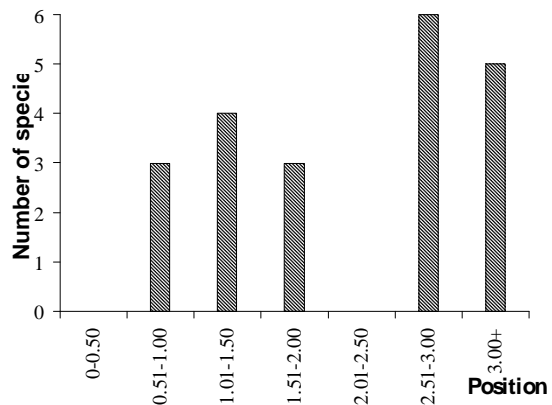

Fig. 2. Number of species plotted against n-dimensional position (see text)

the species having high P values and hence more extreme position in the PCA scattergram (last two columns in Fig. 2) are the members of mature grassland or forest ant communities (e.g. *Myrmica*

Table 3. Factors correlated with PCA axes of ordination of ant communities. |r| = absolute value of coefficient of correlation, p = level of significance

Factors	axis	|r|	p
Total plant cover	I	0.69	<0.05
Dead dicotyledon cover	I	0.75	<0.02
Dead monocotyledon cover	II	0.89	<0.01
Dead pine needle cover	II	0.65	<0.05
Plant cover at 5-15 cm level above soil surface	III	0.67	<0.05
Plant cover at 15-30 cm level	I	0.77	<0.02
Plant cover at 30-50 cm level	III	0.79	<0.02
Dead twigs of different sizes	I	0.74-0.96	<0.05-<0.01
Dead twigs of different conditions	I	0.62-0.84	<0.1-<0.01
One condition class of twigs	II	0.67	<0.05
Soil temperature	I	0.65	<0.06
Temperature in herb layer	I	0.64	<0.07
Four different plant species contributing markedly to herb layer structure	I	0.64-0.71	<0.1-<0.05
Different shrubs and trees	II	0.77-0.89	<0.02-<0.01
Five other plant species	III	0.61-0.71	<0.1-<0.05
Diplopoda	I	0.92	<0.001
Blattodea	I	0.64	<0.06
Gastropoda	II	0.65	<0.07
Chilopoda	II	0.86	<0.01
Heteroptera	III	0.70	<0.05

schencki Em., *Lasius niger* L. and *Formica rufibarbis* F. or *Formica rufa* L., *Formica polyctena*, *Leptothorax nylanderi* (Foerst.), *Leptothorax acervorum* (F.) and *Stenamma westwoodi* Westw. respectively), where the interspecific competition has an important structuring effect (cf. Gallé 1986, 1992).

External correlates

The first three PCA axes of the ant assemblages are correlated with the cover of living and dead plants, the components of the plant architecture, the properties of the dead twigs on the ground surface, the cover of some plant species that contribute markedly to the structure of the herb layer, different shrubs and trees and some epigeic animal groups (Table 3). In addition to the figures in Table 3, slight correlation was found with soil and herb layer temperature, Staphylinoidea, Blattodea (axis I), *Festuca ovina*, and Gastropoda (axis II).

Although these above mentioned factors might be intercorrelated, therefore not all of them are necessarily related with ant assemblages, on the basis of their correlation with PCA axes, we might expect the vegetation architecture, the dead twigs on the soil surface, the physical habitat properties (microclimate and soil), the vegetation composition and the composition of the epigeic animal assemblages, to be those groups of habitat scores that affect the composition of ant assemblages in some ways. These expectations agree with the results of the rank correlation analysis of the relative position of study plots in different PCA spaces in few cases only. It seems that ant assemblage composition is correlated

with three groups of habitat scores, i.e. the architecture of vegetation, the dead twigs on the ground surface and the composition of the epigeic invertebrate fauna (Table 4). A table-wide $p<0.05$ significance level is maintained if we ignore the non-significant values in Table 4 (sequential Bonferroni-test, Rice 1989).

Table 4. Rank correlation between PCA spaces of different groups of habitat scores and ant assemblages

Score groups	r	p
Vegetation architecture	0.33	<0.05
Dead twigs in the ground surface	0.69	<0.001
Vegetation composition	0.23	n.s.
Soil and microclimate	0.22	n.s.
Composition of epigeic fauna	0.38	<0.02

Successional pathways and their directionality

The ant assemblages of the different habitat plots can be arranged into a successional sequence on the basis of the PCA ordination (Fig 3). This sequence is supported by the similarity analysis: the similarity values marking the possible successional relations and pathways (continuous lines in Fig 3) or any subset of them are significantly greater than the corresponding remainders (*t*-test, $p<<0.001$ in all cases). The chi-square test of the Markovity of these successional seres is also significant if the p.c. similarity values are used (either *CR* or *CL*) in the tally matrix ($\chi^2 = 2036$, $p<0.001$ and $\chi^2 = 224$, $p<0.001$, respectively). If *CR* and *CL* values are employed as decimals, however, the test result is
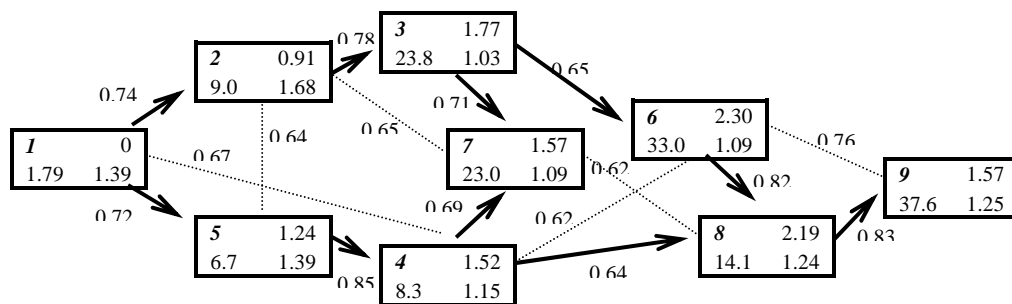
Fig. 3. Probable successional sequence of ant assemblages sampled in different study plots. Upper row in the blocks from left to right: plot number and diversity of ant assemblage; lower row: pooled density of ant colonies and R values of nearest neighbour analysis, respectively

insignificant, because the function $2\ln\lambda$ depends on the absolute values of the elements of the tally matrix. These absolute values are not independent of the investigator's decision, therefore, we do not regard this technique as a powerful tool to test the directionality of presumed successional graphs.

The value of correlation between the successional graphs of the ant communities and that of the vegetation is $r=-0.0098$ (n.s.). Uncoordinated steps between the successional sequence of the vegetation and that of the ant communities were likewise found in other areas (cf. Gallé 1991, Margóczi 1993, Járdán et al. 1993).

Diversity

The Shannon-Wiener diversity increases towards the mature stages of ant community succession (Fig 3), but there is a decline in plot 9, representing the last phase. This probably is a consequence of the high density of an aggressive red wood ant species, *Formica polyctena*. The diversity of ant communities is correlated with that of the vegetation architecture ($r=0.66$, $p<0.05$); the vegetation composition ($r=0.87$, $p<0.01$); and the epigeic animal communities ($r=0.55$, $p<0.1$).

Spatial patterns

Nearest neighbor analysis indicates that the distribution of ant nests for all species is of random type in plots 3, 4, 6 and 7, which represent grassland, forest edge and young forest successional stages and it is of regular type in the earlier and more advanced phases (Fig. 3). No clear trend in the changes of spatial patterns could be observed in the successional sequence of Kampinos ant assemblages either for the single species populations: the R values vary between 0.65 and 1.85; the majority of them lie in the range of random or regular distribution, and they are independent of both ant species and successional stages.

Interference competition on baits

The direct interactions could be studied on three species, *Formica truncorum*, *F. cinerea* and *Myrmica rugulosa*, from the results of bait experiments. As it may be seen in Table 5, the baits were occupied by ants in the majority of observations (180 observations, >63%). The encounters of different species were recorded in 70 cases (38% of the above 180 recordings). *Formica truncorum* was the most aggressive species, dominating the ant community. It excluded other ant species from the baits in 27 out of 30 cases, and it was excluded only once. No direct interference was observed between *Formica cinerea* and *Myrmica rugulosa*. They coexisted without aggressive interactions on baits.

Discussion

The composition of the Kampinos dune fauna is similar to those found in other successional sandy areas in North and Middle Europe (Boomsma and Van Loon 1982, Gallé 1980, 1986, Járdán et al. 1993). The early successional species (*Formica cinerea* and *Lasius psammophilus*) are the same as in the Tvärminne district, Finland (Gallé, 1991), and the similarity between the two total ant faunas is 0.58.

The total densities of ant colonies in the Kampinos study plots are rather low in comparison with other open areas or Polish habitats (Baroni-Urbani and Pisarski 1978, Gallé 1978, 1980, Doncaster 1981, Krzysztofiak 1985, Seifert 1986, Petal and Kusinska 1994). In the Tvärminne dunes, Gallé (1991) found densities between 0.018 and 0.37 nests/m^2. These are surprisingly same as those described in this paper from the Kampinos dunes (also 0.018-0.37 nest/m^2). The average for the different study plots in Tvärminne was slightly lower (0.12 nest/m^2), because more early successional plots with lower densities were sampled in Tvärminne than in Kampinos.

An enormously high density of *Formica cinerea* was found in some early successional study plots (nos. 3 and 7, and other plots in the Kampinos National Park, not involved in this paper), where the densities of this species reached 0.13 colonies/m^2, and the average number of nest entrances was as high as 1.79/m^2. In these sites, the large colonies of *F. cinerea* dominated the whole surface area. Such a high density of F. cinerea was also found in Finland (Gallé 1991 and unpublished). In all these cases, *F. cinerea* was the only or absolutely predominating ant species, without competitors. Under similar conditions, a very high density of *Cataglyphis aenescens* Nyl. was found in the Fülöpháza dune region, Hungary (Gallé, unpublished). The type of the colony pattern represented by F. cinerea is well documented for some *Lasius* species (Brian *et al.* 1966, Levings and Traniello 1981, Traniello and Levings 1986, Gallé 1991, Gallé *et al.* 1993) and it has also been stated that such colony pattern is advantageous, because it reduces the loss of prey (Traniello and Levings 1986) and contributes to the effectivity of food collection of *Lasius* species, which forage both on soil surface and on root aphids (Gunn and Cherrett 1993). Such high density of ant nests and entrances also promotes the infiltration of the soil and probably improve its quality for further successional development (Eldridge 1994, Lobry de Bruyn and Conacher 1994).

The ant species diversities described in this paper are very close to the diversity figures of the ant assemblages in Tvärminne dune area (Gallé 1991). The ant diversity was zero in the first successional stage in Tvärminne, too, and the highest diversity was likewise found in a forest without a high density of red wood ants (2.50 in Tvärminne and 2.19 in the present study). The mean diversities of the transitional stages are also very similar (1.15, 1.86 and 2.26 in Tvärminne, and 1.12, 1.163 and 1.93 in Kampinos, respectively). In both cases, the diversities of ant communities are correlated with those of some structural properties of the habitats (e.g. vegetation architecture). This is in accordance with the results of Withford and Gentry (1981), who also found some relations between the structural heterogeneity of the habitat and the ant community diversity.

The decline of the diversity in the last stage of the studied Kampinos successional series is probably due to the presence of *Formica polyctena,* which is a dominant species in the competitive hierarchy. The top position of this species has been reported by Vepsäläinen and Pisarski (1982), Mabelis (1984), Savolainen and Vepsäläinen (1988), Pisarski and Vepsäläinen (1989) in other areas, too. It was shown by Karlson and Jackson (1981) that the existence of a

competitive hierarchy generally decreases the species diversity. In the case of ants, Higashi and Yamauchi (1979), Gallé (1981), Rosengren (1986), Andersen (1992b) and Cammell *et al.* (1996) documented the role of the top species in the reduction of the species diversity. At the same time, we can expect an association between the top competitors and those species that have different life history strategies or body sizes and therefore different niches (cf. Maynard Smith and Brown 1986). Such species are *Leptothorax acervorum* and *L. nylanderi*, which are also typical forest ants in Kampinos, but, since they are very small relative to red wood ants, no competition can be expected between them and *Formica rufa* group species. *Leptothorax* species and *F. polyctena* are correlated in their co-occurrence in Kampinos habitats (r= 0.63 and 0.98 p<0.05 and <0.001 respectively). In accordance with these findings, Savolainen and Vepsäläinen (1988), also described a close association between *F. polyctena* and *Leptothorax* spp.

The spatial distributions of populations usually reflect the presence or absence of interaction either among the units (e.g. individuals or certain groups of individuals) of the population in question (see Brian 1965, Gallé 1978, 1980, Ryti and Case 1980, 1992, Nielsen 1986, Deslippe and Savolainen 1995, Pontin 1997 for some examples on ants), or between different populations (Shorrocks and Rosewell 1988). No definite trend could be concluded in the present study from the slight differences in the spatial distribution of ant nests between Kampinos habitats, either in the case of single populations, or when all species were considered together. This is in contradiction with the results of the studies in the Tvärminne district (Gallé 1991), where a slight tendency from random towards an arranged distribution was described.

Besides the random spatial colony arrangements, from the low density and co-occurrence rates on both the soil surface and the baits, Gallé (1991) concluded that interspecific interference competition was insignificant in the organization of ant communities in the initial phases of their succession in the Tvärminne dune area. In Kampinos, we have not studied the possibilities of the interspecific competition by observation of the coexistence of foragers on ground surface, but on the basis of low densities we cannot expect high encounter rates and strong interference competition in the early phases of succession. From the data in Table 5, it can be seen that the rate of co-occurrences was low (less than 25 %), even in a site selected for study of the interactions of different populations, which had denser ant populations relative to other successional

Table 5. Statistics of bait experiments

Observations	Species				Total
	F.truncorum	F. cinerea	M.rugulosa	T.caespitum	
No of observations					285
No of positive observations*	97	70	19	6	180
Without coexistence	67	33	7	3	110
Encounters with *F. truncorum*	--	26	2	2	30
Excluded by *F. truncorum*	--	25	1	1	27
Aggression by *F. truncorum*	--	17	1	1	19
Encounters with *F. cinerea*	26	--	10	1	37
Excluded by *F. cinerea*	1	--	0	0	1
Aggression by *F. cinerea*	0	--	1	0	1
Encounters with *M. rugulosa*	2	10	--	0	12
Excluded by *M. rugulosa*	0	0	--	0	0
Encounters with *T. caespitum*	2	1	0	--	3
Excluded by *T. caespitum*	0	0	0	--	0

habitats. It is probable that, at the beginning of the ant community succession, the habitat properties have prior effects on the composition and structure of the ant assemblages (cf. Savolainen and Vepsäläinen 1988).

When co-occurrence was observed, the following hierarchical sequence was found for three species of Tvärminne ants: *Formica sanguinea* (top competitor) - *Lasius psammophilus* (middle-rank species) - *Formica cinerea* (subordinate to both former species). From the results of the bait experiments carried out in this study, it is obvious that *Formica truncorum* is the top competitor among the three species investigated in Kampinos. Both *F. cinerea* and *Myrmica rugulosa* are on the same, subordinated rank. The bottom position of *Myrmica rugulosa* was also shown by Czechowski (1979), who studied the mechanisms of competition between *Lasius niger* and *M. rugulosa*. In the studies that concern the competitive hierarchy of ant species (e.g. Pisarski 1978, Czechowski 1979, DeVroey 1979, Reznikova 1980, Vepsäläinen and Pisarski 1982, Mabelis 1984, Haering and Fox 1987, Czechowski and Pisarski 1988, Andersen and Patel 1994), the interference competition is emphasized, and in some publications even the life history strategies of ant species are classified on the basis of their relation to the top competitors (see Andersen 1986a). In the present study, the existence of an interference competition is obvious in the relation of red wood ants (*Formica polyctena* and *F. truncorum*) to other species. For the *Formica cinerea - Myrmica rugulosa* species pair, only a possibility of exploitation competition can be concluded from the absence of direct interactions on baits.

It is predicted that larger species are more successful in the interference competition (Persson 1985). This prediction accords with our present results on the relation between red wood ants and other species, but in some species pairs (e.g. *Formica cinerea* and *Lasius psammophilus* in Tvärminne; Gallé 1991) the larger species are subordinated because of their avoidance behaviour on baits (see also Fellers 1987). It is also a general opinion that the scarcity of resources promotes interference competition (Schoener 1982). On this basis we should expect the most intensive interference in the very early successional stages (e.g. plots 1, 2, 3, and 5), with the lowest food supply. However, since the density of forager ant workers and their encounter rates are low, in such places, the different ant populations can effect each other's success mainly by influencing their common prey (see also Gallé 1991), i.e. by exploitation competition.

The vegetation architecture, the number and condition of the dead twigs on the ground surface and the composition of the epigeic invertebrate fauna are assumed to be of importance in differentiating the composition of ant communities in this study. The same habitat properties were found to be probably effective in the Tvärminne district (Gallé 1991). In sand dune areas of southern regions in Hungary and Turkey, however, under more extreme climatic conditions, the microclimate was also correlated with ant community composition (Járdán *et al.* 1993, Gallé unpublished). Both the architecture of the vegetation and the number and condition of the twigs are important components of habitat complexity and heterogeneity. The influence of the vegetation architecture and/or habitat structural heterogeneity on the composition of ant communities is well known and has been discussed by several authors (Culver 1974, Room 1975, Withford and Gentry 1981, Andersen 1983, 1986a, Majer *et al.* 1984, Gallé 1991, Bestelmeyer and Wiens 1996). The main effects of the vegetation architecture are probably indirect through modification of the microclimate, the influence on nesting sites and determination of

the food supply (see also Andersen 1986a), but there might also be direct effects, e.g. during the habitat selection of fertilized females.

Acknowledgment

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