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HABITAT CORRELATES OF ANT ASSEMBLAGES IN DIFFERENT FORESTS OF THE SOUTH PANNONIAN PLAIN

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Abstract. Ant assemblages and their potential habitat correlates were studied in 20 forests of different tree composition (oak, poplar, juniper, black locust, pine, Russian olive and hybrid poplar), age, state of isolation and anthropogenic disturbance. The forests were characterized with 148 habitat scores, grouped in five: vegetation architecture, vegetation composition, microclimate, soil properties and the number, the condition and the size of the twigs on the ground surface. A non-parametric correlation analysis was carried out between the configuration of the observed habitats in principal coordinate factor spaces obtained on the basis of their ant assemblage composition and the different groups of habitat scores. Significant correlation was revealed between ant assemblages and vegetation architecture, vegetation composition and the twigs on the ground surface. Another computation of correlation between single habitat scores and the axes of PCoA factor space of ant assemblages showed that ants correlated with vegetation cover at 5 cm height, with the average tree diameter, with all the measured parameters of twigs and with the soil pH.

Key words: ant communities, native and planted forests, habitat conditions

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Introduction

One of the classical approaches of community ecology is to seek for the relations between the composition of ecological assemblages and the properties of their habitats. The roots of such studies are traced back to the "meteorological theories", which regard physical habitat attributes, such as microclimate or soil characteristics to be responsible for the presence, density and regulation of the populations or communities in question. In ants, this kind of approach was employed by several authors (e.g. Gallé 1972a, 1972b, 1975, 1979, Doncaster 1981, Johnson 1992), emphasizing the ultimate role of soil and microclimate in structuring the ant communities. Later, however, the habitat properties were considered only as one subset of the possible external correlates of ant assemblages. Besides physical factors, the food supply is often found to be effective in structuring ant communities, as well (Brian 1964, Andersen 1983, Marsh 1986, Seifert 1986, Sommer and Cagniant 1988). The role of vegetation, especially its architecture was investigated by several authors (Majer 1972, Greenslade and Greenslade 1977, Andersen 1992, Huxley and Cutler 1991) and manifold community-level interactions were established between ants and other animals, such as birds (Haemig 1992), mammals and birds (Kelrick *et al.* 1986), aphids (Stary 1987, Molnár *et al.* 1999, Reznikova and Novgorodova 1999), the epigeic and herb layer fauna (Gallé 1991, Gallé *et al.* 1998).

In our previous paper (Alvarado and Gallé 1999) we reported the distribution of ants in Hungarian lowland forests of different tree composition and different level of disturbance. In this paper we concentrate on habitat properties (plant species composition, architecture and degradation tolerance spectrum of the vegetation, microclimate, the number and condition of dead twigs on the ground surface and soil properties) as possible external correlates of ant assemblages in the same set of habitats.

Table 1. Attributes used for the characterization of the studied forest sites

Group	Attributes	No. of categories
1. Vegetation composition	1.1 Relative frequency of predominant plant species	97
2. Vegetation architecture	2.1 Whole vegetation cover	1
	2.2 Litter cover	1
	2.3 Litter thickness	1
	2.4 Vegetation cover at 15, 30, 70, 150, 300 cm	5
	2.5 Canopy cover	1
	2.6 Cover of mosses and lichens	1
	2.7 Tree diameter average	1
3. Microclimate	3.1 Temperature of soil and of air above soil surface, above herb layer, above 30 cm and at 1.6 m.	4
	3.2 Humidity of soil surface, herb layer, above 30 cm and at 1.6 m	5
4. Dead twigs on the ground surface	4.1 Density of dead branches of various sizes and conditions	20
5. Soil	5.1 Soil humidity	3
	5.2 Soil hygroscopic values	7
	5.3 pH of soil	1
Total		148

Material and methods

Habitat types

Research was conducted in twenty sites in the South Hungarian Plain, near Szeged, approximately 200 km south-east of Budapest. The sites selected for the study included indigenous and introduced forests, and we made a note of their location, complexity, isolation and degree of anthropogenic disturbance (Table 1). They were located: on the outskirts of Szeged (3 patches); in Ópusztaszer (30 km north of Szeged, 3 patches); in Balástya (35 km north-west of Szeged, 3 patches); in Ásotthalom (25 km west of Szeged, 9 patches); in Bócsa and Bugac regions of the Kiskunság National Park (50 km north-west of Szeged, 2 patches).

Ant sampling

Ants were sampled with pitfall traps. Traps were 6 cm diameter plastic cups, partly filled with ethylene-glycol which acted as a preservative. 3 × 5 traps at least with 3 m spacing were employed at each site. The traps worked for three consecutive 7-day periods, in May, June and July. The ants were preserved in 70% ethanol and identified by species level using standard keys and more recent reviews (Seifert 1988a, 1988b, 1992, 1996)

Habitat attributes

We used 148 habitat scores for a detailed characterization of the sites and the scores were grouped in five: vegetation composition, vegetation architecture, microclimate, number and condition of dead twigs on the ground surface and soil properties (Table 1).

The vegetation composition was established by assessing the relative frequency (percentage cover values) of the predominant plant species. One attribute group consisting of 97 scores (i.e. plant species) was obtained from this assessment. Plants were classified according to their degradation tolerance by Németh's evaluation system (Horváth *et al.* 1995). Since the plant species observed in the forests in question, belonged to three out of Németh's five categories: (1) moderately degradation-tolerant species, (2) degradation tolerant species, and (3) degradophilous species, it would tell that the sampled habitats are exposed to man-induced disturbances. Therefore we classified the sampled habitats on the basis of the assessed rate of disturbance. The disturbance degree was based on the amount of human influence or anthropogenic disturbance evident at each site. For this aim, we created a scale of four categories: nature reserve without disturbance (0); plantation with slight forester's activity (1); apparent tourist traffic, litter, etc. (2); grazing, repeated cuttings (3). The age, degree of disturbance and vegetation of the studied forests are summarized in Table 1.

In the analysis of the vegetation architecture, the total coverage values of the litter, soil, mosses, lichens and those of the higher plants at different heights (5, 15, 30, 50, 75 cm) were assessed and expressed as percentages. 12 scores, belonging to five attribute classes were obtained in this way (Table 2).

In the microclimate analysis the temperature and humidity were measured every month at each site (four times per site). Two groups containing

Table 2. Location, age, isolation, and the degree of disturbance of 20 studied forests in the South Hungarian Plain

Number	Location	Forest type	Age (years)	Disturbance	Isolation
1	Ásotthalom	poplar	100	0	medium
2	Ásotthalom	poplar	100	0	medium
3	Bugac	poplar	40	0	high
4	Ásotthalom	oak	80	2	medium
5	Ásotthalom	oak	80	1	medium
6	Bugac	oak	40	0	high
7	Ópusztaszer	oak	60	3	low
8	Ópusztaszer	oak	60	3	low
9	Bugac	juniper	30	0	high
10	Ásotthalom	black locust	50	3	low
11	Ópusztaszer	black locust	30	2	low
12	Bugac	black locust	15	0	high
13	Ásotthalom	pine	40	1	medium
14	Ásotthalom	pine	25	1	medium
15	Ásotthalom	pine	15	1	medium
16	Ásotthalom	pine	5	1	medium
17	Szeged	Russian olive	15	3	low
18	Balástya	hybrid poplar	30	2	low
19	Balástya	hybrid poplar	15	2	low
20	Balástya	hybrid poplar	15	2	low

altogether 9 categories were measured and recorded (Table 2). The soil temperature was measured at a depth of 5 cm and on the soil surface. The air temperature was measured at 30 cm and 160 cm above the soil surface. As the simultaneous measurement of all 20 places would have been impossible, data was taken from meteorological stations and used as standard reference.

The average number of dead twigs on the ground surface was estimated in 50 by 50 cm quadrates. The size and the condition (dry, fresh, rotten, only bark) of each twig were also noted. A total sample of fifteen such quadrates were taken at each site and 5819 twigs were measured in total. From the data we found oak forests having the highest, while juniper and Russian olive forests had the lowest number of twigs.

From among the soil properties, soil water content was measured every month, hygroscopic values and soil pH were also analyzed by standard methods. Three attribute groups and altogether 11 scores were recorded.

Data analysis

Since the most of our data were not of normal distribution, we employed non-parametric statistics in the majority of cases.

A principal coordinate analysis (PCoA) was performed on the basis of ant assemblage composition and each set of the above-mentioned habitat scores (five in total). NuCoSa (Tóthmérész 1993) and Syn-Tax packages (Podani 1995) were used for the computations. The resemblance matrices were set up using Sørensen's presence-absence index for the vegetation composition and Czekanowski's index for the other score groups and for ant assemblages. In order to identify the groups of external factors (i.e. core groups) that are correlated with, and therefore presumably affect the habitat differentiation of ant assemblages, we computed Spearman's rank correlation between PCoA factor spaces made on the basis of ants and habitat score groups. For the correlation analysis, the relative position of the forest sites in the PCoA spaces (i.e. the multidimensional Euclidean distances between the points representing the sites) were measured and correlated. In order to reveal the role of single factors, also Spearman's rank correlation was calculated between the PCoA axes of ant assemblages and each single factor. Successive rank correlation was computed to look for a possible statistical link between the relative frequency of ant species and the habitat scores. Most analyses produced composed statistical tables, therefore the significance values were corrected with Bonferroni's test (Bonferroni 1935, 1936).

Results

Composition of ant assemblages

Altogether 36 ant species were recorded in the sampled forests (Table 3, see also Alvarado and Gallé 1999). The majority of them are typical forests species (e.g. *Leptothorax, Myrmica* spp., *Dolichoderus quadripunctatus, Camponotus* spp., with exception of *C. piceus, Formica fusca* and the mound-building *Formica* s. str. species etc.), but some (e.g. *Anergates atratulus, Camponotus piceus, Cataglyphis aenescens, Formica cunicularia, F. rufibarbis, Lasius niger, L. alienus, L. psammophilus, L. carniolicus, Myrmica schencki, Plagiolepis vindobonensis, Polyergus rufescens, Solenopsis fugax, Tapinoma ambiguum*) are more characteristical for grassland habitats in the studied region (Gallé 1972)

Table 3. List of ant species recorded in different forests in the South Hungarian Plain.

No.	Species
	Subfamily: Myrmicinae
1	*Anergates atratulus* (Schenck, 1852)
2	*Leptothorax nylanderi* (Förster, 1850)
3	*Leptothorax interruptus* (Schenck, 1852)
4	*Leptothorax unifasciatus* (Latreille 1798)
5	*Myrmica rubra* (Linnaeus, 1758)
6	*Myrmica sabuleti* Meinert, 1861
7	*Myrmica salina* Ruzsky, 1905
8	*Myrmica schencki* Emery, 1895
9	*Myrmecina graminicola* (Latreille, 1802)
10	*Solenopsis fugax* (Latreille, 1798)
11	*Tetramorium caespitum* (Linnaeus, 1758)
	Subfamily: Dolichoderinae
12	*Dolichoderus quadripunctatus* (Linnaeus, 1758))
13	*Tapinoma ambiguum* Emery, 1925
	Subfamily: Formicinae
14	*Camponotus fallax* (Nylander, 1850)
15	*Camponotus piceus* (Leach, 1825)
16	*Camponotus truncatus* (Spinola, 1808)
17	*Camponotus vagus* (Scopoli, 1763)
18	*Cataglyphis aenescens* (Nylander, 1849)
19	*Cthonolasius* sp.
20	*Formica cunicularia* Latreille, 1798
21	*Formica fusca* Linnaeus, 1758
22	*Formica polyctena* Förster, 1850
23	*Formica pratensis* Retzius, 1783
24	*Formica rufa* Linnaeus, 1761
25	*Formica rufibarbis* Fabricius, 1793
26	*Formica sanguinea* Latreille, 1798
27	*Formica truncorum* Fabricius, 1804
28	*Plagiolepis vindobonensis* Lomnicki, 1925
29	*Polyergus rufescens* (Latreille, 1798)
30	*Lasius alienus* (Förster, 1850)
31	*Lasius fuliginosus* (Latreille, 1798)
32	*Lasius niger* (Linnaeus, 1758)
33	*Lasius paralienus* Seifert, 1992
34	*Lasius platythorax* Seifert, 1992
35	*Lasius psammophilus* Seifert, 1992
36	*Lasius carniolicus* Mayr, 1861

Correlation with habitat attributes

A significant rank correlation was found between PCoA space of the ant assemblages and that of the vegetation architecture, the vegetation composition and the twigs on the ground surface, respectively. No significant correlation was noticed, however, with microclimate and soil score groups (Table 4).

Table 4. Spearman's rank correlation between PCoA spaces of different groups of the habitat cores and that of the ant assemblages. |r| = absolute value of correlation coefficient; p = level of significance already corrected with Bonferroni's test

Score groups	|r|	p
Vegetation architecture	0.361	<<0.001
Vegetation composition	0.258	0.016
Microclimate	0.124	n.s.
Dead twigs on the ground surface	0.439	<<0.001
Soil	0.005	n.s.

At the Spearman rank correlation between the first three PCoA coordinates of the ant assemblages and the various habitat scores mentioned, we found that the first coordinate correlated significantly with the number and condition of twigs on the ground surface, vegetation cover at 30 cm, percentage of mosses and lichens, and the tree diameter average measured at each place (Table 5). The second axis correlated with vegetation composition (i.e. the number of plant species present at each site) and vegetation cover at 5 and at 15 cm. The third coordinate correlated with the soil pH.

Besides these habitat characteristics, there was a close correlation between the second axis of the above PCoA factor space and the degree of anthropogenic disturbance of the sampled habitats ($r = 0.58$, $p<0.01$).

The following correlation was established between the frequency of the ant species and the above-mentioned habitat scores (Table 6). The frequency of both grassland (*L. alienus, L. niger, S. fugax, F. rufibarbis*) and open forest species (*C. vagus, F. fusca*) correlated with the cover of herb layer either at 5 or at 15 cm above the ground. Grassland species showed negative correlation with tree diameter, while *F. fusca*, which is one of the most typical forest species in this region, had a positive correlation. Only the frequency of *L. niger* and *Leptothorax unifasciatus* was in correlation with the litter cover, in the case of the number of twigs, however, the grassland and forest species are well separated on the basis of their correlation. *Lasius platythorax* was the only species that correlated significantly with the pH of the soil.

Discussion

In our attempt to reveal which habitat conditions are correlated with the composition of ant assemblages, we found that vegetation composition, vegetation architecture, and the number and condition of dead twigs on the ground surface presumably affect the distribution and diversity of ants. In addition to differentiation among forest types, the degree of differentiation according to

Table 5. Factors correlated with axes of PCoA ordination space of the different forest on the basis of the composition of ant assemblages. |r| = absolute value of correlation coefficient; p = level of significance; p(corr) level of significance corrected with Bonferroni test

Factors	axis	|r|	p	p(corr)
Vegetation cover at 5 cm	II	0.565	0.009	0.072
Vegetation cover at 15 cm	II	0.481	0.032	0.256
Vegetation cover at 30 cm	I	0.474	0.035	0.280
Cover of mosses and lichens	I	0.462	0.040	0.320
Tree diameter	I	0.625	0.003	0.024
Abundance of different plant species	II	0.522(?)	0.018	0.144
No of dead twigs	I	0.607	0.005	0.040
Soil pH	III	0.594	0.007	0.048

Table 6. Spearman's rank correlation between the relative frequency of ant species and habitat attributes (significant values only)

Attributes	Ant species	r	p
Litter cover	*Lasius niger*	0.45	0.08
	Leptothorax unifasciatus	0.49	0.02
Vegetation cover at 5 cm	*Lasius alienus*	0.45	0.04
	Solenopsis fugax	0.65	0.002
	Formica rufibarbis	0.62	0.006
	Lasius niger	0.45	0.08
	Camponotus vagus	0.50	0.02
Vegetation cover at 30 cm	*Myrmica sabuleti*	0.49	0.02
	Formica fusca	0.51	0.04
	Camponotus vagus	0.72	0.0003
Tree diameter average	*Lasius paralienus*	-0.48	0.03
	Tetramorium caespitum	-0.49	0.04
	Tapinoma ambiguum	-0.48	0.06
	Formica fusca	0.47	0.072
Number of twigs	*Tetramorium caespitum*	-0.56	0.02
	Tapinoma ambiguum	-0.58	0.012
	Solenopsis fugax	-0.50	0.04
	Formica rufibarbis	-0.49	0.04
	Leptothorax nylanderi.	0.76	0.0001
	Dolichoderus quadripunctatus	0.64	0.002
	Camponotus fallax	0.68	0.0009
pH of soil	*Lasius platythorax*	-0.52	0.01

"microsite" variation (Whittaker and Levin 1977) within forest types is important. It is not an "average forest" that most species require but some particular elements within the forest itself.

Brian (1964) was one of the first to establish that since ants are not randomly distributed but have acquired some relation to the pattern of habitat variation it must be presumed that two obvious mechanisms of assortment exist: the first is that queens must have some power to select the best habitat in which to live, while the second is that the colonies once established may further assort themselves through population pressure largely dependent on the success with which they exploit their immediate resources and their potentiality for aggression. He also learned from the results of PCA analysis that moisture, the nutrient status and wind were the most important factors for heathland ants.

Perfecto and Vandermeer (1996) found that shade and leaf litter had a significant effect on the ant fauna in tropical agroecosystems but also probably (for indirect reasons) having to do with species interactions. Parameters belonging to the vegetation architecture are factors that are intertwined and operate together to provide ants with food and good nesting sites. Gallé and coworkers (Gallé 1991, Gallé *et al.* 1992, 1998), working in different successive stages of sand-dune areas in Southern Finland, Hungary, Poland, and Turkey, found that the vegetation architecture, the number and condition of the dead twigs on the ground surface and the composition of epigeic invertebrate fauna are assumed to be of importance in differentiating the composition of ant communities. Under more extreme climatic conditions the microclimate was also correlated with ant community composition (Járdán *et al.* 1993), but in our case no correlation was seen between microclimate and the composition of ant assemblages. The reason could be that no microclimatic extremities occur in these forests because of the shading effect produced by the canopies.

The importance of small-scale heterogeneity and variation in diversity in forest-floor invertebrates is also a very important aspect to consider and has been well documented by Niemelä *et al.* (1996). They found that a major element creating systematic variation in local assemblages is the contrast between mature and young forests. Both forest physiognomy, through its effect on microclimate, and the composition of undergrowth, through its effect on micro-habitats and litter, are presumably important determinants of this difference. Andersen (1986) established that a greater structural complexity of vegetation will increase the availability of nesting and foraging sites, the level of ground insolation, and possibly food supply as well. The complexity of vegetation architecture is one of the most important component of the habitat heterogeneity that can be responsible for the increasing diversity in ant community succession (Kondoh and Kitazawa 1984, Gallé 1991, Járdán *et al.* 1993, Gallé *et al.* 1998). A positive correlation generally exists between structural diversity of the habitat, and the abundance and diversity of ants (Culver 1974, Room 1975, Greenslade and Halliday 1983). The soil-litter complex have also been documented by Andersen (1986) as a prime parameter for cryptic predators and scavenger ants in the soil.

Seifert (1986) described the environmental background of different ant communities on the basis of plant species composition and cover in different layers. We saw that plant species composition influences ant assemblages, depending on the kind of plant taxons present in the different sites. More degraded places showed lower values of ant diversity and species richness. The site differences in species composition could then match the differences in vegetation. This is consistent with the widespread finding that distinctive ant assemblages are often associated with different vegetation types (Brian 1964, Brown 1959, Cole 1934, Gallé *et al.* 1985, Greenslade 1971, Greenslade and Greenslade 1977, Hayashida 1960, Majer 1972, Markó 1999, Room 1971, Sanders 1970, Talbot 1934, Yasuno 1963, but see Markó 1998). Mabelis, as early as 1977 established three important factors that influence ants: amount of shade, soil moisture and number of plant species. The number of plant species plays an important role in supporting plant lice which are in close connection with ant species and also offer an abundance of items for predation. More plant species means a broader spectrum of different animals as well as more diverse nesting places for the ants.

In the case of soil the only parameter that had a significant correlation was the acidity-alkalinity of the soil. The explanation is not very easy, because ants as constructing their nests have an effect on changes in soil processes, e.g. a buffering the soil pH, therefore cannot expect a strong dependence of ant populations on the pH of the soil. The effect could be reverse: the ant populations differently modify the pH of the soil, therefore this correlation could be observed. Ants modify the abundance of different microflora groups and these changes depend on the size of ant colonies and on their biomass turnover. The size of a colony generally has an inhibiting effect on the abundance of ammonifying bacteria and stimulates the abundance of *Actinomycetes*. The turnover of biomass has a positive effect on the number of ammonifying bacteria. In this connection ant constructing species have different effects on the pH and the content of exchangeable cations in the soil of nests (Petal 1980). Ant mounds also provide an environment for plants, one that has better aeration and is warmer as well as nutrient-rich (Lesica 1998). Compared with surrounding soils, ant-hills often have a significantly higher pH and cation content, which suggests that ant activities counteract leaching (King 1981). *Lasius platythorax* nests are known because they contains several internal basic elements and fungi hyphae (Seifert 1996). Therefore, this modifying role of ant nests on the soil properties could explain the high significant correlation ($p=0.01$) between *L. platythorax* and pH.

A comparison of the results presented in this article with the previous one suggests that vegetation architecture (vegetation cover at different heights, litter cover, percentage of mosses and lichens, and tree diameter), vegetation composition and the number and condition of twigs on the ground surface are the main habitat attributes which most likely play a role in structuring ant assemblages in the investigated forest patches. We think that these habitat attributes are the primary ones that count for ants in the process of choosing a place to establish themselves. After ants find a definite site, interspecific competition for food, nests and territories will also help to structure the ant assemblages and determine the way in which they interact with other ant species. Decaying wood, leaf litter, tree trunks and the presence of other plant species provide a variety of microhabitats that most probably disappear with the intensification of forestry management and dominance of exotic trees.

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