MOSAIC STRUCTURE OF ANT COMMUNITIES (HYMENOPTERA: FORMICIDAE) IN EASTERN CARPATHIAN MARSHES: REGIONAL VERSUS LOCAL SCALES

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The ant communities of 12 habitats in four marshlands were studied in the Eastern Carpathians. Altogether 11 ant species were identified, but none of the species could be considered a specific relic species of marshlands, though characteristic species could be detected, like *Myrmica rubra*, *M. ruginodis* and *M. scabrinodis*. The sampling procedure seems to be fairly complete. The between and within region comparisons revealed that there were no regional differences in the ant communities, but differences could be attributed mostly to differences in habitat attributes like vegetation and related characteristics. The three most abundant *Myrmica* species all showed clear habitat preferences, which overlapped just to a lesser extent. The diversity analysis suggested a highly mosaic-like distribution pattern of ants in different habitats, which could be attributed to specific constraint factors acting on the ant species inhabiting mountain marshlands. Thus usually one patch is occupied and dominated by a single species. The existence of this mosaic-like pattern is also supported by the possibility of competition between *M. rubra* and *M. ruginodis*. The importance of connecting different scales to elucidate mechanisms creating the observed patterns is emphasized.

Key words: Formicidae, communities, mountain marshes, constraint factors, patchiness, competition, scales

INTRODUCTION

The general recognition of the significance of biodiversity emphasizes the importance of animal community studies revealing the mechanisms, which create the observed patterns. Considering ecological processes significant in nature conservation like extinction, recolonization, recovery, etc. it becomes essential to connect different scales, and to carry out within and between habitat comparisons (SAVOLAINEN *et al.* 1989, PUNTTILA *et al.* 1994, NIEMELÄ *et al.* 1996, PUNTTILA *et al.* 1996, GALLÉ 1999, GALLÉ *et al.* 2000, BESTELMEYER & WIENS 2001, GALLÉ 2002), in order to elucidate to what extent specific communities are exposed to threats. The connection of different scales, e.g. regional ⟹ local ⟹ patch, is of main importance, as it can help elucidate how different processes on different scales interact and produce a pattern observed on regional level (SAVOLAINEN &

VEPSÄLÄINEN 1988, BESTELMEYER & WIENS 2001, GALLÉ 2002). These studies can at least reveal how stable the qualitative-quantitative features of a specific type of animal community are in similar habitats but in different regions. The accurate analysis of the characteristics of the same type of animal community in similar habitats also offers the possibility of assessing the constraints acting on it (MABELIS 1977, PUNTTILA et al. 1994, NIEMELÄ et al. 1996, PUNTTILA et al. 1996, GALLÉ 1999, GALLÉ et al. 2000, BESTELMEYER & WIENS 2001). The knowledge of the natural variations of such features, as well as of the constraint factors acting on the community can help conservationists to elaborate appropriate protection plans for specific types of communities. This is especially important in the cases of such extremely vulnerable and unstable habitats as mountain marshes in Central and Eastern Europe, which are constantly exposed to disturbances either from the part of forestry or from tourism.

In the Eastern Carpathians there are several marshes, which are known as glacial refuges for different valuable plant species (POP 1960, KOVÁCS 1984, RUP-RECHT & SZABÓ 1999, MARGÓCZI et al. 2000). These habitats bear specific conditions, e.g.: high water level and low annual mean temperature potentially acting as strong constraint factors on the potential set of animal species inhabiting these areas. The high water level can induce higher mortality, or it can inhibit the larval development in the case of insects. The combination of these factors can also act indirectly: e.g. the scarcity of living organisms means narrower prey spectra for predators. In the case of ants one of the primary constraints is the availability of suitable nesting sites (MABELIS 1977, BOOMSMA & DE VRIES 1980, WARDLAW & ELMES 1996), as colonies need inundation-free conditions for the normal development of the larvae and pupae. Another specific limiting factor for ants is the narrow spectra of organisms serving as prey for them, which can also have a serious impact on their survivor, or on the size of the colony (MABELIS 1977, ELMES 1991, WARDLAW & ELMES 1996). Whereas a solitary animal can solely assure the continuity of its species by finding food sources, and then reproducing, in ants the colony acts as a single reproducing unit, requesting many times more food to maintain the colony population. Under these conditions ant-communities of marshlands are expected to bear specific characteristics (GALLÉ et al. 2000). Obviously these communities can be unique in several ways, e.g. (1) containing specific marshland species (VEPSÄLÄINEN et al. 2000), (2) bearing specific qualitative and quantitative characteristics (GALLÉ et al. 2000, VEPSÄLÄINEN et al. 2000), (3) having specifically strong inter- and intraspecific interactions due to the scarcity of resources (SAVOLAINEN & VEPSÄLÄINEN 1988), (4) developing suitable colony founding and dispersal strategies e.g. colony fission, and (5) adapting colony systems to long-time persistence, like polygyny.

Although the descriptive comparison of communities cannot elucidate the underlying structuring processes (VEPSÄLÄINEN & PISARSKI 1982, PISARSKI & VEPSÄLÄINEN 1989, PUNTTILA et al. 1994, 1996), as the same community structure can be reached on several routes (VEPSÄLÄINEN & PISARSKI 1982, GALLÉ 1991), but some suggestions can be formulated on the basis of their analysis. Generally it is agreed that one of the basic structuring processes is competition in ants (MABELIS 1977, VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988, PISARSKI & VEPSÄLÄINEN 1989, SAVOLAINEN et al. 1989, GALLÉ 1991, JÁRDÁN et al. 1993, PUNTTILA et al. 1994, GALLÉ 1999), although other species-specific factors as dispersal ability, habitat requirements, dependence on other species (MABELIS 1977, BOOMSMA & DE VRIES 1980, VEPSÄLÄINEN & PISARSKI 1982, PUNTTILA et al. 1994, 1996, JÁRDÁN et al. 1993, BESTELMEYER & WIENS 2001), or even stochasticity (VEPSÄLÄINEN & PISARSKI 1982, PUNTTILA et al. 1996) can also stand at the basis of the presence of a specific ant species in a given community.

This study proposes to offer answers to some basic questions regarding ant communities of some Eastern Carpathian marshland areas:

(1) Can the studied marshes be considered as refuges for habitat specialist ant species?

(2) Are there inter- or intraregional differences among the ant-communities of different sites?

(3) Does the community structure show the constraints acting on ant-communities e.g. scarcity of nesting sites?

(4) Is competition important in structuring marshland ant communities and to what extent?

Ants are also potentially ideal bio-monitoring organisms and have proven to be valuable indicators of environmental conditions and of biodiversity (GALLÉ 1991, JÁRDÁN et al. 1993, GALLÉ 1999, ALONSO 2000, ALONSO & AGOSTI 2000, KASPARI & MAJER 2000) showing how vulnerable a habitat is. The study of ant communities should help evaluate the condition of marshlands in the Eastern Carpathians.

MATERIALS AND METHODS

The following criteria were taken in account when selecting the study sites: to have (1) both large and relatively small areas, (2) marshes from different regions, (3) and different types of habitats within one marshland, like sedge meadows, marsh-forests, peat bogs etc. Upon these criteria the ant communities of four marshlands were analyzed in the Eastern Carpathians, Romania: the marshland

at Voslobeni in the Giurgeului Basin, Lacul Dracului marsh in the Harghita Mts, Fagul Rotund, and Apa Lenta marshes in the Nemira Mts.

(1) The fen area at Voslobeni (46°40'N, 25°37'E) is the remnant of a once existing large marsh-complex lying in the Giurgeului Basin near the river Mures at cca. 770 m above sea level. Nowadays this scattered marshland contains wet hayfields, peat bogs, bushes, and large fens, such as both eutrophic and oligo-mesotrophic habitats are present. This very mosaic area is one of the richest regions in relic plant species (POP 1960, MARGÓCZI *et al.* 2000). Three sampling sites were selected: (a) the core of the marsh (V1) is a peat bog of approximately 60 m diameter with sparse pines (*Carici echinatae-Sphagnetum* SOÓ (1934) 1954), where the peat moss (*Sphagnum* sp.) cover is 70–80%, (b) V2 is a sedge meadow (*Caricetum rostratae* RÜBEL, 1912) with sparse trees and shrubs (*Betula pubescens*, *Salix cinerea*, *S. pentandra*), and the presence of *Sphagnum* species is quite common in the moss layer, whereas (c) V3 is a dense marsh forest with willow and alder trees (*Alnetum incanae* BROCKMANN 1907) (GALLÉ *et al.* 2000).

(2) The Lacul Dracului marsh-complex (46°29'N, 25°31'E) is a more isolated area in a small depression in the Harghita Mts at 1180 m above sea level. It contains both eutrophic and oligotrophic habitats. Altogether four sample sites were studied. The typical peat bog is represented by LD1 (*Eriophoro vaginati-Sphagnetum recurvi* HUECK 1925), a relatively open area with sparse Scots pines and blueberry bushes. The core area of the marsh is an open sedge meadow (*Caricetum elatae* KOCH 1926, LD2 and LD3), and the nearby area (LD4) is a dense and wet forested bog with small spruces (*Piceetum sphagnoso-Polytrichetosum* SOÓ 1944) (SZABÓ A. and MÁTIS A. pers. comm.).

(3) Fagul Rotund (46°11'N, 26°21'E) is the smallest marsh of all. It lies in the Nemira Mts, one of the easternmost parts of the Eastern Carpathians, at cca. 1100 m above sea level. The first sample site (FR1) was an open peat bog (*Eriophoro vaginati-Sphagnetum* POP *et al.* 1987), whereas the second one (FR2) was a sparse Scots pine forest with a dense moss layer and blueberry bushes (*Vaccinio-Pinetum silvestris* KLEIST 1929) (KATÓ Z. pers. comm.).

(4) The Apa Lenta marsh complex (46°11'N, 26°17'E) lies also in the Nemira Mts in a valley next to Fagul Rotund (2.5–3.5 km away) at cca. 1000 m above sea level. It is a mosaic of eutrophic and oligo-mesotrophic marsh patches. The first sample-site (AL1) was an open sedge meadow (*Caricetum rostratae* RÜBEL 1912), the second area (AL2) was a peat bog with sparse birch and spruce trees (*Eriophoro vaginati–Sphagnetum recurvi* HUECK 1925), whereas the third site (AL3) was a dense willow and birch forest (*Salici pentandrae-Betuletum pubescentis* SOÓ (1934) 1955) (RUPRECHT & SZABÓ 1999). *Sphagnum* species were present in the moss layer at every site.

Ants were collected with pitfall-traps using plastic jars of cca. 5.5 cm diameter. Fifteen traps were set out at each sample site, which were arranged in a 3×5 grid, each trap being separated by 5 m from the other traps (SAVOLAINEN *et al.* 1989, PUNTTILA *et al.* 1994, 1996, NIEMELÄ *et al.* 1996, GALLÉ *et al.* 2000). Ethylene glycol was used as preserving liquid in the case of Voslobeni, and Lacul Dracului, whereas in the case of Apa Lenta, and Fagul Rotund marshes brine (saturated NaCl-solution) replaced the ethylene glycol. The samplings were carried out between 1998 and 2000, as follows: Fagul Rotund 20–27 July 1998, Apa Lenta 21–28 July 1998, Voslobeni 21–31 July 1999, Lacul Dracului between 6–13 August 2000.

The collected specimens were identified on the basis of the keys of SEIFERT (1988, 1996) and RADCHENKO *et al.* (1997). Two richness estimates were used to see how effective the collections were in every region. The first-order jackknife estimate is based on the observed species number (S_{obs}) and the number of species occurring in only one sample (L), where n is the total number of samples (LONGINO 2000):

$$S^* = S_{obs} + L\left(\frac{n-1}{n}\right)$$

The Chao2 richness estimate also incorporates the number of species occurring in two samples (M) (LONGINO 2000):

$$S^* = S_{obs} + \frac{L^2}{2M}$$

In both richness estimates S^* is the assessed number of species.

Regional differences

Principal Coordinate Analysis (distance algorithm: Wishart's similarity ratio) was used to analyze the structure of the dataset. Two steps were separated. In the first step the origin of the data was used as grouping criteria. In the second step the type of habitat was considered as possible grouping factor. It is generally known that differences between ant communities are not following the differences in the vegetation, but more likely the architectural properties of the vegetation determine the differences (JÁRDÁN et al. 1993, GALLÉ 1999, GALLÉ et al. 2000). On this basis it was more appropriate to use the following three main habitat types: (1) dense marsh-forests with alder, willow, birch and spruce, (2) typical peat-bog areas with sparse Scots pines and birches, and (3) sedge meadows. During the analysis each trap was considered as a separate unit. The computations were carried out with the SynTax computer software (PODANI 1993). The habitat preferences of the most frequent species were analyzed by comparing the number of individuals recorded in traps in different habitat types using Kruskall-Wallis ANOVA and Mann-Whitney U-test (StatSoft 1995).

Local heterogeneity

In an ideal situation (assumed spatial homogeneity of the habitat) one would expect that animal species should be distributed evenly in space (LONGINO 2000). Consequently a sample characterizing this ideal situation should be made up of similar sample units as each species is expected to occur at the same species-specific probability everywhere (LONGINO 2000). On the basis of this logic it seems obvious that the more mosaic the species' distribution is in a given area, the bigger the differences are between the qualitative-quantitative properties of the sample units and of the sample. The Shannon-Wiener entropy is an appropriate method for characterizing communities as it implies both the richness and the evenness of the studied entity, and also emphasizes the presence of rare data types, e.g. rare species. As such it is a useful tool to assess the structure of a community. According to the above-presented logic every pitfall trap material was considered to be a small 'representative' sample unit of the studied site's community. PUNTTILA et al. (1996) suggested that individual pitfall-trap catches (separated by 5 m) should reflect the distribution of the colonies for species with short foraging ranges as Myrmica, Leptothorax, and foraging preferences of the species with wider foraging areas like Lasius or Camponotus. VEPSÄLÄINEN and SAVOLAINEN (1990) also suggested that Myrmica workers' foraging radius is equal or less than 3 m. Thus by comparing the overall diversity and evenness values with the values for single traps we should be able to characterize fairly well the spatial structure of the ant communities.

Interspecific relationships

The analysis of species distribution and abundance data also makes us possible to assume whether competition could be important in structuring these communities (MABELIS 1977, VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN et al. 1989, GALLÉ 1991, PUNTTILA et al. 1996).

Mann-Whitney U-test and Spearman rank-correlation coefficient (StatSoft 1995) was utilized to clarify the existence of interspecific relationships in the case of the most abundant species.

RESULTS

Altogether 11 ant species were identified (Table 1), each of them are widely distributed in temperate and northern Europe with the exception of *Myrmica vandeli*, which has a sporadic distribution (SEIFERT 1988), and it was first identified in Romania at Voslobeni not long ago (MARKÓ 1999). An additional parasitic species, *Harpagoxenus sublaevis* (NYLANDER, 1849), was collected at LD2 in the nest of *Leptothorax acervorum* (MARKÓ & CSŐSZ 2001), which species wasn't present in the traps.

The identified species are generally characteristic for mountain heaths, marshes, and forest clearcuts. However, no specific marshland species were detected, like *Formica uralensis*, *F. picea* (VEPSÄLÄINEN *et al*. 2000) or *Myrmica sulcinodis* (SEIFERT 1988). Generally the species number was low, it fluctuated between 3 and 7 (Table 1). Parallel to this the majority of the species showed rather uneven distribution. Besides *M. ruginodis* and *M. rubra,* only *M. scabrinodis* and *Formica lemani* showed higher constancy, and they were also more abundant than the other species. It is relevant that the most widespread species were also numerous, whereas the other species were characterized not just by sporadic distribution but also by low abundance (Table 1). The low capture efficiency of the latter species (convertible in foraging intensity) suggests that their colonies were small, probably underdeveloped. The combination of accidental occurrence and low abundance supports the hypothesis of their reduced preference for mountain marshes.

The first-order jackknife and the Chao2 richness estimates showed that approximately one species could be added to the known number of species (Table 2). In contradiction no additional species are expected to occur in marshlands when considering every region together. Thus probably one or (at most) two rare species are expected to occur in every separate region additionally, but the survey of marshland ant species can be considered fairly complete all things considered.

Ant-communities: region vs. habitat type

The result of the principal coordinate analysis did not support any clustering tendency of the ant-communities on regional level (Fig. 1). Nevertheless if we applied the main vegetation type of the given sample site as grouping criteria, there was a more or less obvious differentiation (Fig. 1). Thus the three main vegetation

Table 1. List of collected ant species: total number of specimens and number of occurrences (traps) in brackets (PB = peat bogs; SM = sedge meadows; MF = marsh–forests)

Species	Voslobeni			Lacul Dracului				Fagul Rotund		Apa Lenta		
	1 (PB)	2 (SM)	3 (MF)	1 (PB)	2 (SM)	3 (SM)	4 (MF)	1 (PB)	2 (PB)	1 (SM)	2 (PB)	3 (MF)
Myrmica rubra (L., 1758)	4 (3)	66 (8)	196 (14)	–	17 (6)	4 (2)	1 (1)	32 (7)	74 (7)	3 (2)	121 (13)	71 (11)
M. ruginodis NYL., 1846	7 (6)	3 (3)	1 (1)	24 (10)	2 (2)	10 (8)	2 (2)	60 (13)	78 (11)	3 (2)	4 (3)	8 (4)
M. scabrinodis NYL., 1846	12 (6)	87 (11)	–	–	3 (3)	5 (3)	–	1 (1)	3 (3)	10 (6)	–	–
M. vandeli BONDROIT, 1919	5 (2)	–	–	–	–	–	–	–	–	3 (1)	–	–
M. lobicornis NYL., 1846	–	–	–	–	–	1 (1)	1 (1)	–	–	–	–	–
Leptothorax acervorum (FABR., 1793)	–	–	–	–	–	2 (1)	–	3 (1)	1 (1)	–	–	–
Formica lemani BONDROIT, 1917	–	–	–	9 (2)	8 (3)	1 (1)	–	3 (3)	11 (6)	2 (2)	7 (6)	2 (2)
Lasius niger (L., 1758)	–	1 (1)	–	–	–	–	–	–	–	2 (1)	–	–
L. platythorax SEIFERT, 1991	–	–	–	–	–	–	–	1 (1)	–	1 (1)	3 (2)	–
L. flavus (Fabr., 1781)	9 (6)	5 (3)	3 (1)	–	–	–	–	–	–	–	–	–
Camponotus herculeanus (L., 1758)	–	–	–	–	–	1 (1)	2 (1)	7 (5)	6 (5)	–	–	–
Total no. of species	5	5	3	2	4	7	4	7	6	7	4	3

Table 2. Different types of richness estimates of the number of ant species occurring in the four studied marshlands

	Voslobeni	Lacul Dracului	Fagul Rotund	Apa Lenta	Altogether
No. of species	6	7	7	7	11
1st order jackknife	6.97	7.97	7.96	8.94	11
Chao2	6.5	7.25	7.5	–*	11

*M = 0, invalid formula

types, as (1) peat-bogs with sparse Scots pines and birches (61% of the peat bog samples included in the group), (2) sedge meadows (66% of the meadow samples included in the group), and (3) marsh-forests (94% of the forest samples included in the group) formed loosely defined clusters. The existence of these groups proved, nevertheless, only tendencies, for none of the three clusters was separated clearly by the others. Besides, the low value of the cumulative percentage of eigenvalues of the first two axes (35.33% and 46% for the first three axes respectively) also revealed the heterogeneity of the dataset.

The three most common ant species – *Myrmica rubra*, *M. ruginodis* and *M. scabrinodis* – were separately analyzed for their habitat preferences. These three
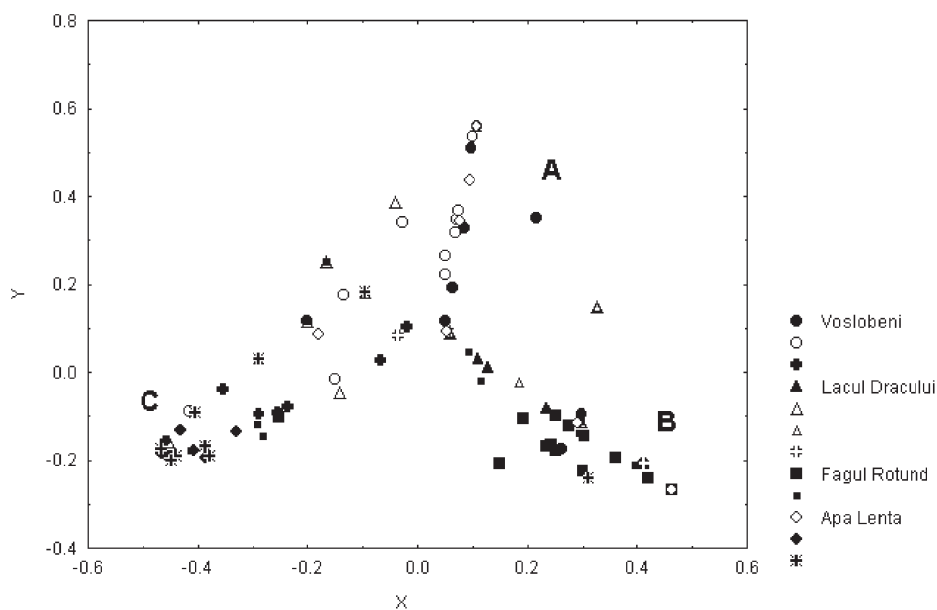

Fig. 1. PCoA–plot of the ant–communities, each dot representing a single trap: filled dots – open peat–bog habitats with sparse trees; empty dots – sedge meadows; crosses – marshland forests; A – marshland forests; B – peat–bog habitats; C – sedge meadows

Table 3. The presence of the three most frequent ant species in different types of marshland habitats

Species	Mean no. of specimens (SD)			Comparison
	peat–bog	sedge meadow	marsh forest	
Myrmica scabrinodis	1.6 (0.84) n = 10	4.56 (1.04) n = 23	–	Mann–Whitney U–test, z = –1.72
Myrmica ruginodis	4.02 (5.68) n = 43	1.2 (0.41) n = 15	1.57 (0.95) n = 7	Kruskall–Wallis ANOVA (df = 2) chi^2 = 9.16**
Myrmica rubra	7.7 (7.05) n = 30	5 (9.13) n = 18	10.3 (14.55) n = 26	Kruskall–Wallis ANOVA (df = 2) chi^2 = 6.1*

*$p < 0.05$, **$p < 0.01$

species have almost the biggest niche-overlap among other *Myrmica* species (ELMES 1991). Two of these species, namely *M. rubra* and *M. ruginodis* were present in each of the three major habitat types, whereas *M. scabrinodis* occurred only in peat bogs and sedge meadows. The presence of *M. scabrinodis* did not show any biases regarding the two habitat types (Table 3). On the contrary *M. rubra* and *M. ruginodis* showed differences in their preferences: they both preferred peat bogs and marshland forests to sedge meadows (Table 3). There were no significant differences, however, in their preferences regarding marsh forests or peat bogs (Mann-Whitney U-test, z = –0.16, p = n.s. for *M. rubra*, and z = –1.7, p = n.s. for *M. ruginodis*), though it seemed that *M. rubra* was generally more abundant in marsh forests, whereas *M. ruginodis* in peat bogs (Table 3). These results along with the PCoA-analysis showed clearly, that while in peat bogs all the three *Myrmica* species could be found in great abundance, sedge meadows were generally characterized by the presence of *M. scabrinodis*, and marsh-forests by the presence of *M. rubra* and to a somewhat lesser extent by the occurrence of *M. ruginodis*. VEPSÄLÄINEN and SAVOLAINEN (1990) also found that *M. scabrinodis* and *M. ruginodis* preferred different types of habitat (open terrains vs. forests), and they did not occur together usually.

Local heterogeneity

The data from pitfall-traps could also be used to make a fair assessment on the number of species present in the traps' range of catch. The mean species number per traps was very low which showed that generally patches were inspected by foragers of one, or in a few cases, of two species (Table 4). Thus the mean diversity values of patches were strikingly lower than the overall site diversity values in almost every case (Table 4). On the basis of the comparison of the patches' average evenness values with the evenness of the overall site diversity values (Fig. 2, Table 4)

it could be concluded that the ant fauna of the patches were clearly dominated by a few (generally one) species, while the ant community of the given site was more even in qualitative-quantitative aspects. It becomes obvious, that the structure of ant communities was very mosaic-like: foragers of mainly one species dominated the patches.

Interspecific relationships

As it was stated in the previous sections, the three most abundant *Myrmica* species showed separate habitat preferences. However, only the morphologically and behaviourally very similar *M. rubra* and *M. ruginodis* were present in every habitat type, thus it seemed obvious to investigate the probability of interspecific exclusion on finer scale only in the case of this species pair.

Only those sites were taken in consideration where both species occurred, excluding site LD1, where only *Myrmica rubra* was present, because there was no evidence whether *M. ruginodis* was missing due to exclusion by *M. rubra*, or it was absent because of other factors. We also did not consider data from traps where both species were absent, for the above-presented reasons. The Spearman rank-correlation coefficient ($r = -0.47$, $t = -5.36$, $p < 0.000$, $n = 103$) revealed a significant negative relationship between the two species that could imply the existence of
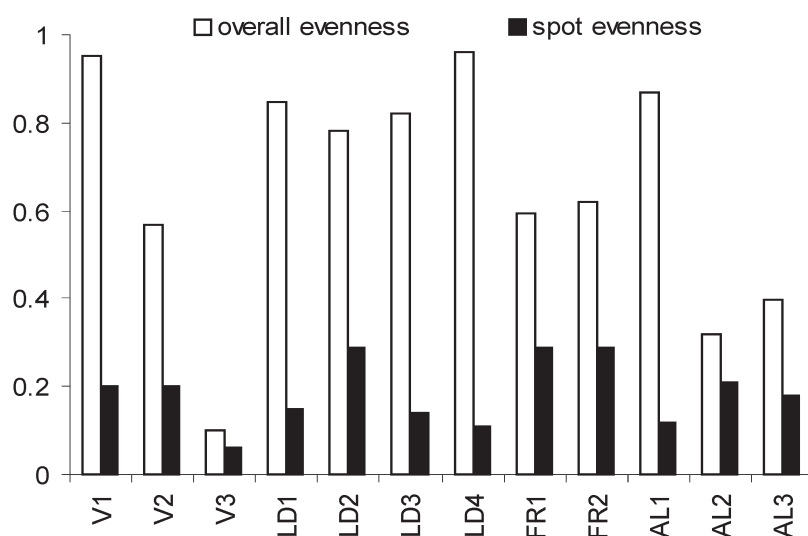

Fig. 2. The overall evenness vs. the evenness of the mean patch–diversity values for each sample site (V – Voslobeni, LD – Lacul Dracului, FR – Fagul Rotund, AL – Apa Lenta)

Table 4. Shannon–Wiener entropy values ($\log_2$) of the ant communities and the mean entropy values of the patches. Patch evenness was calculated as follows: mean patch diversity/$\log_2 S$

	Voslobeni			Lacul Dracului				Fagul Rotund		Apa Lenta		
	1	2	3	1	2	3	4	1	2	1	2	3
Diversity	2.21	1.31	0.15	0.84	1.56	2.3	1.9	1.66	1.6	2.43	0.63	0.62
Mean patch diversity (SD)	0.47 (0.09)	0.47 (0.15)	0.1 (0.43)	0.15 (0.18)	0.59 (0.19)	0.4 (0.06)	0.22 (0.05)	0.82 (0.17)	0.76 (0.18)	0.34 (0.05)	0.43 (0.34)	0.28 (0.28)
Evenness (%)	0.95	0.56	0.09	0.84	0.78	0.81	0.95	0.59	0.62	0.86	0.31	0.39
Patch evenness (%)	0.2	0.2	0.06	0.15	0.29	0.14	0.11	0.29	0.29	0.12	0.21	0.18
Mean no. of species in traps (SD), n=15	1.5 (0.91)	1.7 (1.3)	1.06 (0.45)	0.8 (0.67)	1.4* (0.96)	1.2** (0.69)	1.2*** (0.5)	2.06 (1.27)	2.2 (1.42)	1.07 (0.73)	1.6 (1.05)	1.1 (0.99)

*n = 10, 5 traps were destroyed; **n = 14, 1 trap was destroyed; ***n = 4, 11 traps were destroyed

competition for available nesting sites or that of innate differences in habitat requirements.

These results do not tell us precisely how clear-cut the two species are affected by the presence of the rival in their foraging activity, nevertheless the basic competitive processes are small-scale phenomena (SAVOLAINEN & VEPSÄLÄINEN 1988). The comparison of the number of individuals present in patches in the absence of the rival with the number of foragers from patches where they co-occurred offered us valuable information on this matter. Thus the number of individuals was significantly higher in patches where there was no rival both in the case of *Myrmica rubra* (Fig. 3) and *M. ruginodis* (Fig. 4), which emphasizes the probability of competition between the two species.

The relationship between the no. of individuals of other species and those of *Myrmica rubra* or those of *M. ruginodis* respectively were also negative, though the correlations were weaker (Spearman r = –0.36, p < 0.01, n = 63 for *M. rubra* vs. other species, r = –0.34, p < 0.01, n = 60 for *M. ruginodis* vs. other species), which emphasizes the importance of competition between sister species over the competition between non-related species.
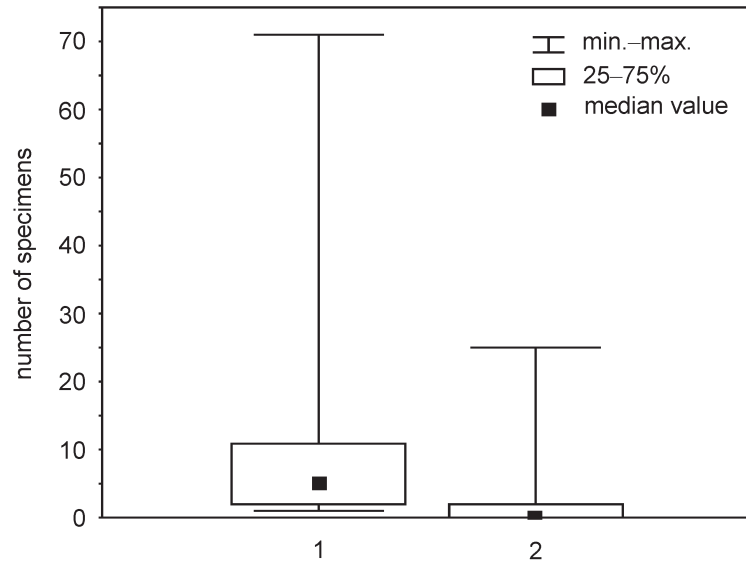
Fig. 3. Number of *Myrmica rubra* specimens in the absence (1), and in the presence (2) of *M. ruginodis* (Mann–Whitney U–test, $z = -5.15$, $p < 0.000$, $n_1 = 47$, $n_2 = 56$)
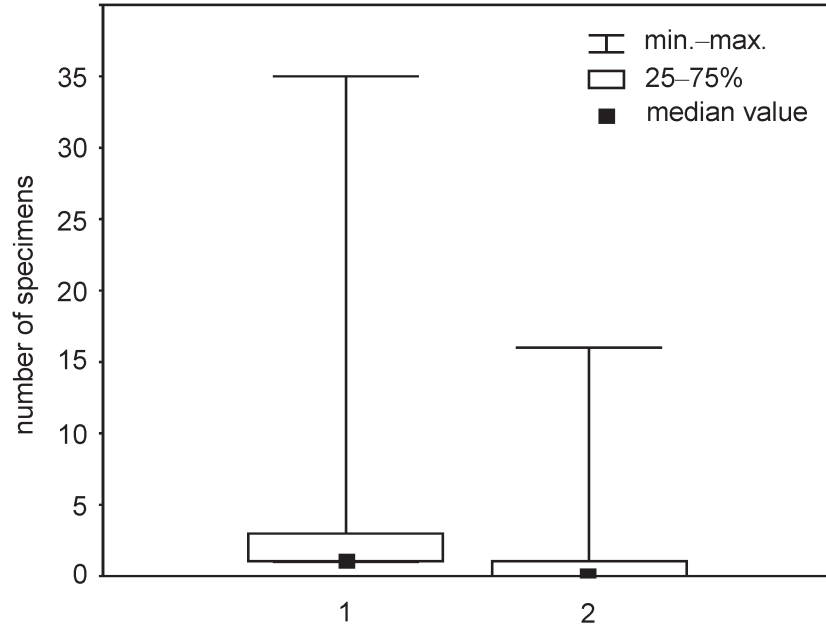

Fig. 4. Number of *Myrmica ruginodis* specimens in the absence (1), and in the presence (2) of *M. rubra* (Mann–Whitney U–test, $z = -5.14$, $p < 0.000$, $n_1 = 29$, $n_2 = 74$)

DISCUSSION

From regional to local level

None of the species can be considered to be specific relic species of the Carpathian marshes, though the two most abundant *Myrmica* species, *M. rubra* and *M. ruginodis,* and even *M. scabrinodis* can be regarded as core species of marshland ant communities. VEPSÄLÄINEN *et al*. (2000) report *M. scabrinodis* to be a typical peat bog species in Finland, whereas in Romania this species is generally quite frequent in mountain open areas (GALLÉ *et al.* 2000). It is interesting that GALLÉ *et al.* (2000) did not find *Myrmica rubra* and *M. ruginodis* to be common in the hayfield-marshland complex at Voslobeni. Nevertheless the high constancy of these two species in the studied marshes indicates that these species can be handled as characteristic species of Eastern Carpathian mountain marshes. The low frequency and low abundance of other species emphasizes the restrictive character of these habitats for ants. Although territorial *Formica s. str.*, *Raptiformica* and *Coptoformica* species occur in the surroundings of marshes (GALLÉ *et al.* 2000, GALLÉ *et al.* unpubl.), none of these species was detected in the studied areas. According to VEPSÄLÄINEN *et al.* (2000) virgin and early succession ditched bogs are unsuitable habitats for wood ants due to the microclimate, but the lack of large aphid colonies can also lead to the absence of these obligate aphid-tending species. Nevertheless the low abundance of their host *Serviformica* species (or their lack in the case of Voslobeni) can solely diminish the possibility of colonization. The distance to the nearest inhabited patches, or the degree of isolation from these areas can also account for the colonization probability in the case of *Formica s. str*. species (MABELIS 1994, MABELIS & KORCZYŃSKA 2001). The lack of these territorial species causes changes in the competitive hierarchy: species considered to be submissive (BRIAN *et al.* 1966 in SAVOLAINEN & VEPSÄLÄINEN 1988, VEPSÄLÄINEN & PISARSKI 1982, PISARSKI & VEPSÄLÄINEN 1989, PUNTTILA *et al.* 1996) become top species of these communities, overruling in abundance the lower ranked, but aggressive species, like *Lasius niger*, or *Camponotus herculeanus*, which occur sporadically and in low abundance.

The lack of regional differences clearly supports the idea of strong constraints acting on the set of ant species, which could inhabit these areas, and as the species pool is small and constant there is no possibility to develop specific communities. There is though some evidence that the habitat type can slightly differentiate among ant communities (MABELIS 1977, JÁRDÁN *et al.* 1993, NIEMELÄ *et al.* 1996, GALLÉ *et al.* 2000, VEPSÄLÄINEN *et al.* 2000) on local level. GALLÉ *et al.* (2000) emphasizes the importance of the vegetation's architecture in structuring

the ant communities of the hayfield-marshland complex around Voslobeni. Alike the vegetation (MARGÓCZI *et al.* 2000), the water content of the soil can be one of the major differentiating factors in ants (MABELIS 1977, JÁRDÁN *et al.* 1993, NIEMELÄ *et al.* 1996). The segregation of habitat preferences learned in the case of the three most abundant *Myrmica* species also support the possible effect of vegetation and factors related to it.

The key factor of being successful in marsh habitats generally characterized by shortage in nesting sites can be the efficiency of the applied dispersal strategy. The success of *Myrmica* species over Formicines can be attributed to the smaller size of their colonies, which allows them to inhabit smaller suitable patches, than Formicines (BRIAN *et al.* 1976 in VEPSÄLÄINEN & SAVOLAINEN 1990). It is clear that ant species, which use colony fission can more successfully colonize the available nesting sites, and parallel to this the presence of other species, which disperse exclusively by queens, can become more accidental. BANSBACH and HERBERS (1999) report that *Myrmica punctiventris* can expand its colony's territory via polydomy, thus it seems appropriate to suggest, that these *Myrmica* species, which are also well-known for the existence of polygynous colonies (ELMES 1991, WARDLAW & ELMES 1996, WALIN & SEPPÄ 2001), use colony fission as dispersal strategy (BRIAN & BRIAN 1955 in PUNTTILA *et al.* 1994, ELMES 1991, WARDLAW & ELMES 1996, WALIN & SEPPÄ 2001). It is also known in *M. punctiventris* that colonies frequently move (BANSBACH & HERBERS 1999), which was also observed in *M. ruginodis* in forests (MARKÓ and KISS pers. obs.) and in *M. gallieni* (PETAL pers. comm.). This suggests that if a nesting place becomes unsuitable the whole colony could move onto another site (ELMES 1991) even in marshes.

The resistance to occasional risings of water level can also lead to the dominance of both *Myrmica* species, and even to the noticeable presence of the *M. scabrinodis*. As stated by BOOMSMA and ISAAKS (1982) *M. rubra* and *M. scabrinodis* tolerate inundations in sandy coastal plains surviving for several weeks. The ants usually prefer well-aerated *Festuca* mounds (BOOMSMA & ISAAKS 1982), which elevate 1–2 m from the sea level. MABELIS (1977) also reports that usually *M. rubra* and *M. ruginodis* are the two ant species present in forests with high water level. In accordance *Myrmica* colonies are generally found in *Sphagnum* mounds in marshes, and *M. rubra* was found to survive the inundations in Voslobeni and in other regions, too (GALLÉ unpubl.). Contrary to *M. rubra*, *Lasius flavus* is considerably vulnerable to rising water (BOOMSMA & ISAAKS 1982), which, combined with its endogeic life style of tending root aphids (not too frequent in marshes), could also explain why this species, otherwise abundant on mountain heaths, has a low occurrence in marshes.

The low annual mean temperature of the marshlands can also interplay in the success of some species. VEPSÄLÄINEN and SAVOLAINEN (1990) suggest that *Myrmica scabrinodis* and *M. ruginodis* are predominantly low-temperature species. Other factors, as differences in larval development among species can cause biases in community structure additionally. It is known that in *M. ruginodis* the larval development is the fastest among all other European *Myrmica* species (ELMES & WARDLAW 1983), which makes possible the development of larger colonies in shorter period, than needed by the other species. This advantage over the other species is even more emphasized by the relatively short warm period in mountain areas.

From local to patch level

The low availability of nesting sites combined with other restricting factors like narrow prey spectra causes a mosaic-like structure of the ant communities: suitable patches are monopolized by mostly one species, and these patches are rarely visited by other species. This is clearly supported by the low evenness values of the patches. As a result the foraging territories of different species are well separated, the probability of overlapping is reduced. VEPSÄLÄINEN *et al.* (2000) also reports patchy distribution of three *Myrmica* species on ditched bogs in Finland, which leads us to the presumption that this is a general feature of the marshland ant communities.

On the level of patches this mosaic-like structure can be supported by interspecific competition, which is generally considered to be of main importance in structuring ant communities (MABELIS 1977, VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988, PISARSKI & VEPSÄLÄINEN 1989, SAVOLAINEN *et al.* 1989, GALLÉ 1991, BANSBACH & HERBERS 1999, VEPSÄLÄINEN *et al.* 2000). The different types of shortages specific for marshes can enhance even more the probability of inter- and intraspecific conflicts. The two most abundant species of marshes, namely *Myrmica rubra* and *M. ruginodis* are not just morphologically very close to each other, but their ecological requirements also overlap (MABELIS 1977, SEIFERT 1988, RADCHENKO *et al.* 1997, VEPSÄLÄINEN *et al.* 2000, CZECHOWSKI *et al.* 2002). Both species live in forests at low altitudes; *M. rubra* generally prefers oak-forests in plains, lowlands, while *M. ruginodis* can be found in forests of the hilly regions (SEIFERT 1988, RADCHENKO *et al.* 1997, ALVARADO & GALLÉ 2000, CZECHOWSKI *et al.* 2002). In mountains *M. rubra* generally inhabits wet pastures, and marshes. Its sister species occurs on pastures, marshes, and in spruce forests. Though they seem to replace each other, they can also be found together. The colonial properties of both species are also similar (SEIFERT 1988, ELMES 1991, WARDLAW & ELMES 1996), nevertheless *M. rubra*

has usually larger colonies (ELMES 1991). ELMES (1991) suggests that displacement between *M. rubra* and *M. ruginodis* is high. PUNTTILA *et al.* (1996) detected negative relationship between coexisting *M. ruginodis* and *M. sulcinodis* in Finnish taiga clearcuts, whereas MABELIS (1977) found the same relationship in the case of *M. rubra* and *M. ruginodis* species pair. Thus the mere possibility of coexistence of the two abundant *Myrmica* species having similar ecological requirements raises questions on the existence and nature of interspecific relationship, and suggests that they should form a locally improbable species pair (VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988). Although the study of competition on the basis of distribution patterns has been criticized many times, because many processes or combination of processes may lead to an observed pattern (VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988) in the case of these two *Myrmica* species we believe that the statistical analysis of the distribution data could indirectly detect the mere possibility of competition due to the above-presented similarities of the species. The results show that interspecific competition can indeed well occur between the two most abundant *Myrmica* species, which is also valid for the relationship between these species and the other species to a lesser extent. Potential coexisting competitors should exhibit resource partitioning, which could be reflected especially by habitat, time and food type partitioning (SAVOLAINEN & VEPSÄLÄINEN 1988). In this case the results support only the existence of habitat partitioning, but other types of partitioning cannot be excluded. However, these datasets refer only indirectly to the spatial pattern of the distribution of the ants, and since direct evidences for negative interactions are not available, these results should be handled carefully (SAVOLAINEN & VEPSÄLÄINEN 1988, PUNTTILA *et al.* 1996). In addition there is no available data on the role of intraspecific competition in this case, though it is known to exist and to be of relevant importance in *Myrmica* species (ELMES 1991, MARKÓ unpubl.).

Connecting different scales

The absence of regional differences proves the uniformity of regional species pools in great lines. Nevertheless there can be specific species, as *Myrmica vandeli*, which appear only sporadically, but their presence in marshes is generally negligible. The presence or absence, and the dominance of specific ant species mostly depend on their dispersal abilities, as well as on their colony foundation strategies. The differences among ant communities of major marsh habitat types are probably caused by differences in the vegetation as well as other factors connected to it, like shadiness and water level. The restrictive nature of these factors, one of which is most probably the nesting site shortage, causes a mosaic structure

of ant communities, supported then by the competition on the level of patches. Consequently it would be a mistake to consider that competition is the only factor structuring these communities. As presented previously the combination of several species-specific factors, as well as stochastic processes (VEPSÄLÄINEN & PISARSKI 1982, SAVOLAINEN & VEPSÄLÄINEN 1988, PUNTTILA *et al.* 1994, PUNTTILA *et al.* 1996, VEPSÄLÄINEN *et al.* 2000) and certainly competition, too, can shape the ant-communities of marshes. These different processes, and factors act on different scales, but all are important on their turn contributing to the community formation process.

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REFERENCES

ALONSO, L. E. (2000): Ants as indicators of biodiversity. Pp. 80–88. In: AGOSTI, D., MAJER, J. D., ALONSO, L. E., SCHULTZ, T. R. (eds): *Ants: standard methods for measuring and monitoring biodiversity.* Smithsonian Institution Press, 2000, Washington.

ALONSO, L. E., AGOSTI, D. (2000): Bidodiversity studies, monitoring, and ants: an overview. Pp. 1–7. In: AGOSTI, D., MAJER, J. D., ALONSO, L. E., SCHULTZ, T. R. (eds): *Ants: standard methods for measuring and monitoring biodiversity.* Smithsonian Institution Press, 2000, Washington.

ALVARADO, M. & GALLÉ, L. (2000): Ant assemblages associated with lowland forests in the southern part of the Great Hungarian Plain. – *Acta zool. hung.* **46**(2): 79–102.

BANSBACH, V. S. & HERBERS, J. M. (1999): Nest movements and population spatial structure of the forest ant Myrmica punctiventris (Hymenoptera: Formicidae). – *Ann. Entomol. Soc. Am.* **92**(3): 414–423.

BESTELMEYER, B. T. & WIENS, J. A. (2001): Local and regional-scale responses of ant diversity to a semiarid biome transition. – *Ecography* **24**: 318–392.

BOOMSMA, J. J. & DE VRIES, A. (1980): Ant species distribution in a sandy coastal plain. – *Ecol. Entomol.* **5**: 189–204.

BOOMSMA, J. J. & ISAAKS, J. A. (1982): Effects of innundation and salt on the survival of ants in a sandy coastal plain. – *Ecol. Entomol.* **7**: 121–130.

CZECHOWSKI, W., RADCHENKO, A. & CZECHOWSKA, W. (2002): *The ants (Hymenoptera, Formicidae) of Poland.* Museum and Institute of Zoology, Polish Academy Sciences, Warsaw, 200 pp.

ELMES, G. W. (1991): The social biology of Myrmica ants. – *Actes Coll. Insectes Sociaux* **7**: 17–34.

ELMES, G. W. & WARDLAW, J. C. (1983): A comparison of the effect of temperature on the development of large hibernated larvae of four species of Myrmica (Hym. Formicidae). – *Insectes Sociaux* **30**(1): 106–118.

GALLÉ, L. (1991): Structure and succession of ant assemblages in a north European sand dune area. – *Holarctic Ecology* **14**: 31–37.

GALLÉ, L. (1999): Composition and structure of primary successional sand-dune ant assemblages: a continental-scale comparison. Pp. 67–74. In: TAJOVSKÝ, K. & PIŽL, V. (eds): *Soil zoology in Central Europe.* České Budějovice, Czech Republic.

GALLÉ, L. (2002): Flood-plain research at different spatial scales. – Ecological aspects of the Tisa River Basin. – *Tiscia Monograph Series* **6**: 7–16.

GALLÉ, L., GALLÉ, R., MARKÓ, B., MIKÓ, I. & SÁRKÁNY-KISS, A. (2000): Habitat correlates of ground invertebrate assemblages in a flood plain landscape complex. – Pp. 31–36. In: GALLÉ, L. & KÖRMÖCZI, L. (eds): *Ecology of river valleys.* Szeged, Hungary.

JÁRDÁN, CS., GALLÉ, L. & MARGÓCZI, K. (1993): Ant-assemblage composition in a successional Hungarian sand dune area. – *Tiscia* **27**: 9–15.

KASPARI, M., MAJER, J. D. (2000): Using ants to monitor environmental change. Pp. 89–98. In: AGOSTI, D., MAJER, J. D., ALONSO, L. E. & SCHULTZ, T. R. (eds): *Ants: standard methods for measuring and monitoring biodiversity.* Smithsonian Institution Press, 2000, Washington.

KOVÁCS, S. (1984): Rezervaţii şi monumente ale naturii din judeţul Covasna. – *Aluta* **16**: 127–138.

LONGINO, J. T. (2000): What to do with data. Pp. 186–204. In: AGOSTI, D., MAJER, J. D., ALONSO, L. E., SCHULTZ, T. R. (eds): *Ants: standard methods for measuring and monitoring biodiversity.* Smithsonian Institution Press, 2000, Washington.

MABELIS, A. A. (1977): Artenreichtum von Ameisen in einigen Waldtypen. Pp. 187–208. In: TÜXEN, R. (ed.): *Berichte der Internationalen Symposien der Internationalen Vereinigung für Vegetationskunde.* Vaduz.

MABELIS, A. A. (1994): Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae). – *Memorabilia Zoologica* **48**: 147–170.

MABELIS, A. A. & KORCZYŃSKA, J. (2001): Dispersal for survival: some observations on the trunk ant (Formica truncorum Fabricius). – *Netherlands J. Zoology* **51**(3): 299–321.

MARGÓCZI, K., DRĂGULESCU, C. & MACALIK, K. (2000): Vegetation description of representative habitat complexes along the Maros (Mures) river I. The upper section (Vasláb/Voşlobeni). – Pp. 23–29. In: GALLÉ, L. & KÖRMÖCZI, L. (eds): *Ecology of river valleys.* Szeged, Hungary.

MARKÓ, B. (1999): New ant taxa (Hymenoptera: Formicidae) in the Romanian fauna. – *Entomologica romanica* **4**: 95–98.

MARKÓ, B. & CSŐSZ, S. (2001): Nine new ant species in the Romanian fauna (Hymenoptera: Formicidae): morphology, biology, and distribution. – *Entomologica romanica* **6**: 127–132.

NIEMELÄ, J., HAILA, Y. & PUNTTILA, P. (1996): The importance of small-scale heterogeneity in bo-real forests: variation in diversity in forest-floor invertebrates across the succession gradient. – *Ecography* **19**: 352–368.

PISARSKI, B. & VEPSÄLÄINEN, K. (1989): Competitive hierarchy in ant communities (Hymenoptera, Formicidae). – *Annales Zoologici* **42**: 321–329.

PODANI, J. (1993): *Syn-Tax version 5.0 – User's Guide*. Budapest, 104 pp.

POP, E. (1960): *Mlaştinile de turbă din Republica Populară Romînă*. Academia R.P.R., Bucureşti, 514 pp.

PUNTTILA, P., HAILA, Y., NIEMELÄ, J. & PAJUNEN, T. (1994): Ant communities in fragments of old-growth taiga and managed surroundings. – *Ann. Zool. Fennici* **31**: 131–144.

PUNTTILA, P., HAILA, Y. & TUKIA, H. (1996): Ant communities in taiga clearcuts: habitat effects and species interactions. – *Ecography* **19**: 16–28.

RADCHENKO, A., CZECHOWSKI, W. & CZECHOWSKA, W. (1997): The genus Myrmica Latr. (Hymenoptera, Formicidae) in Poland – A survey of species and a key for their identification. – *Annales Zoologici* **47**(3–4): 481–500.

RUPRECHT, E. & SZABÓ, A. (1999): A Lassúág-völgy lápjainak vegetációja. – *Múzeumi Füzetek* **8**: 94–109.

SAVOLAINEN, R. & VEPSÄLÄINEN, K. (1988): A competition hierarchy among boreal ants: impact on resource partitioning and community structure. – *Oikos* **51**: 135–155.

SAVOLAINEN, R., VEPSÄLÄINEN, K. & WUORENRINNE, H. (1989): Ant assemblages in the taiga biome: testing the role of territorial wood ants. – *Oecologia* **81**: 481–486.

SEIFERT, B. (1988): A taxonomic revision of the Myrmica species of Europe, Asia Minor, and Caucasia (Hymenoptera, Formicidae). – *Abh. Ber. Naturkundemus. Görlitz* **62**(3): 1–75.

SEIFERT, B. (1996): *Ameisen: beobachten, bestimmen*. – Naturbuch Verlag, Augsburg.

STATSOFT, INC. (1995): *STATISTICA for Windows (Computer Program Manual)*. Tulsa.

VEPSÄLÄINEN, K. & PISARSKI, B. (1982): Assembly of island ant communities. – *Ann. Zool. Fennici* **19**: 327–335.

VEPSÄLÄINEN, K. & SAVOLAINEN, R. (1990): The effect of interference by Formicine ants on the foraging of Myrmica. – *J. Anim. Ecol.* **59**: 643–654.

VEPSÄLÄINEN, K., SAVOLAINEN, R., TIAINEN, J. & VILÉN, J. (2000): Successional changes of ant assemblages after ditching of bogs. – *Ann. Zool. Fennici* **37**: 135–149.

WALIN, L. & SEPPÄ, P. (2001): Resource allocation in the red ant Myrmica ruginodis – an interplay of genetics and ecology. – *J. Evol. Biol.* **14**: 694–707.

WARDLAW, J. C. & ELMES, G. W. (1996): Exceptional colony size in Myrmica species (Hymeno-ptera: Formicidae). – *The Entomologist* **115**(3): 191–196.