ANT ASSEMBLAGE COMPOSITION IN A SUCCESSIONAL HUNGARIAN SAND DUNE AREA

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Abstract. In the frame of a project dealing with the succession of ant communities in sand dune areas of different geographical regions in Europe, in Kéleshalom sandy area (southern Hungary) eight study plots, representing different successional stages of vegetation, were selected for detailed sampling program. PCA analysis of the ant assemblages of study plots shows that the succession of the ant community composition follows two main pathways: one is typical to open areas, i.e. grasslands, the other is usually terminated in forests.

Comparing the successional sequence of the study plots according to their ant assemblages, vegetation composition and epigeic fauna, it is established that the initial and final successional phases are the same in each case, but there are uncoordinated successional steps in the three assemblage types in the transitional stages. The diversity of ant assemblages increases along the successional gradients, but that of the vegetation and epigeic fauna has a maximum in a transitional phase.

Microclimate, dead twigs on ground surface and vegetation architecture were identified as the main external correlates, which probably have certain role in structuring ant assemblages.

Key words: ant communities, primary succession, environmental correlates, sand dunes

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Introduction

Vegetation succession has extensively been studied from the very beginning of ecology (Clements, 1916; Cowles, 1899; Gleason, 1917). The succession of animal communities, however, is one of the most neglected fields in animal ecology. Although there is a lot of information on the composition of ant communities (see e.g. Brian, 1983; Hölldobler and Wilson, 1990; as reviewing books), we know much less about the process of organization, i.e. succession of these assemblages. The succession of the ant communities is usually studied by simultaneous comparison of several habitats representing different successional stages (Szujecki et al., 1978; Vepsäläinen and Pisarski, 1982; Boomsma and Van Loon, 1982; Zorrilla et al., 1986; Gallé, 1991; Gallé et al., in preparation) and there are much fewer long-term investigations on the successional transformation of ant populations or assemblages in a particular habitat (e.g. Gallé, 1981; Gallé et al., 1993) because of the long time

span of community dynamic processes. We use the first, comparative approach in the present paper, which is a part of a project dealing with the primary succession of ant assemblages in different sanddune areas of Europe and the Middle East, from Finland to southern Turkey. The previous papers of the series have been carried out by Gallé (1990a, 1990b, 1991) and Gallé et al (in preparation).

The field studies were done in a successional sand-dune area in Middle-Hungary in order to reveal the main attributes of ant communities of different successional stages. Three main questions were addressed, as follows:

(1) What kinds of differences and similarities exist in the composition of the ant assemblages in the study plots, which represent different successional stages of vegetation?

(2) Is there any co-ordination between the pathways of ant community succession, and that of other assemblages, i.e. vegetation and the epigeic fauna?

(3) Which external conditions (habitat proper-

ties) are correlated with the structure of ant assemblages?

Study area and methods

The study area is a complex of wind-formed sand-dunes, between the rivers Duna and Tisza in the southern part of Hungary, and it belongs to Kiskunság region near the village Kéleshalom.

For detailed studies, eight plots were selected with areas of 300 to 500 m². The plots were parts of such habitats, which represented different stages of the sand-dune vegetation succession (Fekete, 1992) from the bare sand thorough open grasslands, closed grasslands, shrubby habitat to a poplar forest. Plot 1 had a low coverage (<20%) of plants, mainly Festuca vaginata and Stipa borysthenica. Although differing in exposition and total vegetation coverage, plots 2 and 3 were similar open grasslands of denser vegetation than plot 1, predominated by Festuca vaginata, Stipa borysthenica and Koeleria glauca. The moss and lichen layer was also considerable. Litter cover was about 40%. Plot 4 was a closed grassland, predominated by Festuca pseudovina, Teucrium chamaedrys, Holoschoenus vulgaris, Galium verum and Poa angustifolia. The moss and lichen cover was also considerable. Plot 5 resembled to 3, but with a Populus alba shrubby storey (height <50 cm, coverage about 30%). Plot 6 was a shrubby habitat with Crataegus monogyna, Juniperus communis, Berberis vulgaris and Ligustrum vulgare. Thymus degenianus, Stipa borysthenica, Carex liparocarpos, Galium verum plant species were found in the understorey. Plot 7 and 8 were closed poplar (Populus alba) forests with some Robinia pseudoacacia trees. There were

shrubby storeys with *Crataegus monogyna* and *Juniperus communis. Carex flacca* was predominant in the herb layer. These two plots apperently differed in their red wood ants, therefore they were separately treated. A more detailed survey on the vegetation of the research area is given by Margóczi (1993).

The ant assemblages were sampled with pitfall traps. 12 traps were used in each study plot and the traps worked two times for two weeks. The same pitfall traps yielded the data on the composition of the epigeic fauna, as well. Herb layer invertebrates were collected with sweep net. 5x10 sweeps were applied in each study plot. Beside the various invertebrate groups, these samples yielded some additional information on the ant fauna of the study plots, too. All collected animals were sorted on taxonomic group level. If considerable body size differences were observed within a taxonomic group, it was subdivided into size classes.

The cover of plant species was estimated in 5 quadrates of 1 m² in every plot. Using the average values of the number of collected ant specimens, that of the other epigeic groups, and the average cover values of plant species, three resemblance matrices were set up. The percentage similarity values of Renkonen index were used in these matrices to compare the study plots according to the three different assemblages, i.e. vegetation, ants and epigeic fauna. With the help of these matrices, the possible successional sequence of study plots could be set up, because the similarity between the plots presumably represents the successional relations of them.

In order to find the main external correlates of the composition of ant assemblages, we examined

Core group	Habitat cores	No. of categories
[1] Vegetation architecture	1.1 Total plant cover	1
	1.2 Cover of mosses and lichens	2
	1.3 Mould thickness	1
	1.4 Plant cover at 0-5, 5-15, 15-30, 30-50 level	5
[2] Vegetation composition	2.1 Relative frequency of predominating plant species	65
[3] Size of plot		1
[4] Dead twigs on ground surface	4.1 Density of dead branches of various sizes and conditions	25
[5] Microclimate	5.1 Temperatures of soil, of air 2 cm above soil surface, and of air at 2 m height	3
	5.2 Soil water content	1
[6] Epigeic fauna	6.1 Frequency of various animal groups collected in pitfall traps	28
[7] Fauna of the herb layer	7.1 Freequency of various animal groups collected by sweep net	28
Total		160

Table 1. Attributes for characterization of study plots

Table 2. Frequency of ant species collected by pitfall traps (individuals/trap)

Species	Plot no.							
	1	2	3	4	5	6	7	8
Myrmica rugulosa Nyl.					1		- 13. 	*0.08
Myrmica laevinodis Nyl.							*	* 1 ¹
Myrmica sabuleti Meinert						*	+18.0	*5.66
Diplorhoptum fugax Latr.				0.09				
Tetramorium caespitum Latr.				10.27		3.58		
Leptothorax nylanderi Först.				0.18		+	*+3.41	*+1.66
Leptothorax unifasciatus Latr.						+		*0.41
Leptothorax tuberum Först.						0.58	*+1.75	+0.41
Dolichoderus auadripunctatus I							10-5-5-5-5	0.08
Tapinoma ambiguum Em				1.36		1.25		
Plagiolepis vindobonensis Lomn.	2.25	+ 8.90	+ 9.08	11.36	+11.1	0.91		+
Plagiolepis xene Starke	10000	() 545(5))	0.000000		*			
Camponotus vagus Scop						1.75		0.08
Camponotus truncatus Spin						0.08		0.08
Lasius alienus Forst	494 6	+1814	+167.0	168 1	+1391	63 33	0.08	0.16
Formica sanguinea Latr	424.0	0.27	1107.0	55 63	. 1571.	+40 58	0.00	0.10
Formica fusca Latr		0.27		00.00		0.25	4 4 1	4 50
Formica cumicularia Latr			1 83		0.33	*2 75	3.31	4.50
Formica mila Latr			1.65		0.55	2.75	0.08	10.66
Formica ruja Lati.					2 2 2		64 75	10.00
Cotorbuchia conserved tota	# 11.0	1240	1 14 92	1 2 00	16.09		04.75	4.00
Deliveryphis denescens Latr.	11.0	T 34.0	T 14.83	T 3.09	10.08			
roivergus rujescens Latr.			0.41	7	-	10	0	1.4
Total	3	4	2	1	0	13	8	14

* = sexuals collected by hand or / and pitfall traps

+ = workers collected by sweep net

their correlation with some habitat properties. We used altogether 160 habitat attribute scores for a detailed characterization of the study plots. These habitat scores were grouped in seven: vegetation architecture, vegetation composition, size of the plot, twigs on the ground surface, microclimate, epigeic fauna and faunal composition in herb layer (Table 1).

From among the habitat attributes not mentioned above, the measurement of the microclimate was carried out in the usual ways. The number of dead twigs on the surface were counted in 0.5x0.5m quadrates; the lengths, widths and the condition (fresh, dry, dry with holes, wet and rotten, only husks) of the twigs were measured.

In the data evaluation, PCA ordination was employed to establish relation among the studied objects (i.e. plots, ant, invertabrate and plant communities).

Results

A total of 22 ant species were collected (Table 2). The study plots formed two main groups on the basis of the composition of their ant fauna: the ant assemblages of first three plots were predominated by *Lasius alienus*, *Plagiolepis vindobonensis* and *Cataglyphis aenescens*. These plots represented the earliest stages of ant assemblage succession, with *TISCIA 27*

low species diversity. A higher number of ant species were found in the second group of plots, especially in forest habitats (Table 2).

Ordination of the Barber trap ant data by PCA yielded the following results (Fig. 1). The ant assemblages of open habitats are positioned mainly in the "a" part of the PCA; the samples from forest plots are on the opposite part of the figure ("b"); and the angle of the pipe-like figure contains the samples of transitional stages. According to these results, it seems very possible that the succession of ant community composition may follow two main pathways: one is typical to open areas, i.e. grasslands and leading to the ant assemblages of closed grasslands, the other is characteristic to the path, which leads to the ant assemblages of the forests.

A more exact successional sequence of the plots can be set up on the basis of resemblance matrices of the ant, plant and epigeic animal communities (see Fig. 2). The plots can be arranged roughly into five successional steps in all of the three community types. It is clear that the initial and final successional stages are the same in each case, but both the position of the transitional plots and the pathways show some differences. This means that there are uncoordinated steps in the succession between the different communities.



Fig. 1. Ordination of Barber trap ant data by PCA. Traps of the same plot are encircled.



Fig. 2. Successional sequence of the study plots on the basis of resemblance matrices of the ant, plant and the epigeic animal communities.

The Shannon diversity of ant assemblages increases along the five-step successional sequence (Fig. 3.), whereas that of the vegetation and the epigeic fauna reaches a maximum in the third stage.

For the correlation analysis between ant assemblage composition and the habitat attribute scores we used the first three coordinates of each study plot in PCA factor space set up on the basis of their ant assemblage composition and the correlation were computed between these coordinates and the values of the above mentioned 160 individual habitat scores. Using this method, we found that there were 23 attributes correlated with ants, such as microclimate factors, dead twigs, some invertebrate groups and plant species (Table 3.).

There are some problems with the interpretation of these results because of the possible intercorrelation between attributes. Therefore we used also another procedure in order to determine more exactly the external correlates of ant communities. Study plots were ordinated on the basis of their ant assemblages and the different attribute groups mentioned above (Table 1.) in seven different PCA spaces. In all cases the relative position of the points representing the plots in the PCA factor spaces was measured as a set of multidimensional Euclidean distances (Pielou, 1984) from the others weighted by the variance percentage values of the PCA axes. The distances of the corresponding points in differ-

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Fig. 3. Shannon diveristy of vegetation, ant assemblages and epigeic fauna in five successional steps.

ent PCA spaces were compared with correlation analysis using non-parametric Spearman's coefficients. Close correlation between the relative position of plots computed from their ant assemblage composition and any other attribute group indicates that the attributes in question presumably affect the composition of the ant assemblages. Since this analysis resulted in a combined correlation table, the table-wide significance values were computed by the sequential Bonferroni test (Rice, 1989).

The dead twigs on ground surface, the microclimate and in less extent the vegetation

architecture were found to be significantly correlated with the composition of ant assemblages (Table 4.).

Discussion

It has been demonstrated by several authors that diversity of different ecological communities shows an increasing trend during succession (Odum, 1969; Bába, 1980; Rey, 1981; Andersen, 1986; partially Boomsma and Van Loon, 1982; Györffy and Körmöczi, 1987; but not quite by Kondoh and Kitazawa, 1984). A decline of the diversity brought about by the high density of red wood ants at the final successional stages was demonstrated by Gallé et al. (in preparation) in Kampinos region, Poland. In the present study, however, the density of red wood ants was not so high in the forest plot that it could decrease the diversity of ant assemblages.

We found a negative correlation between the density of the pioneering ant species (i.e. Lasius alienus) and the ant community diversity (r= -0.76, p< 0.05) as Boomsma and Van Loon (1982) described it, likewise Gallé et al (1985) and Gallé (1991).

The above results suggest that the vegetation

Table 3. Factors correlated with PCA axes of ordination of ant assemblages. |r|= absolute value of coefficient of correlation; p = |eve| of significance

Factors	axis	r	р
Plant cover at 5-15 cm level	II.	0.811	< 0.02
Mould thickness	I.	0.980	< 0.001
Frequency of two plant species	11		
Cratacgus monogyna	I.	0.761	< 0.05
Carex flacca var. cuspidata	I.	0.737	< 0.05
Microclimate			
Soil temperature	I.	0.820	< 0.02
Surface temperature	I.	0.836	< 0.01
Soil water content	I.	0.906	< 0.01
Dead twigs of different sizes in different	I.	0.713 - 0.983	< 0.05 - < 0.001
conditions		5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5 5	
Epigeic invertebrates			
Acaridea	Ι.	0.740	< 0.05
Acridoidea	1.	0.727	< 0.05
Araneidea II.	I.	0.839	< 0.01
Chilopoda	III.	0.718	< 0.05
Cicadinea	I.	0.749	< 0.05
Diplopoda	II.	0.920	< 0.01
Isopoda	Ι.	0.775	< 0.05
Mollusca	I.	0.976	< 0.001
Invertebrates in the herb layer	1000		
Gastropoda	II.	0.904	< 0.01
Araneidea II.	I.	0.719	< 0.05
Diptera	III.	0.717	< 0.05
Acaridea	III.	0.762	< 0.05
Collembola	III.	0.903	< 0.01
Cicadinea	Ι.	0.849	< 0.01
Coleoptera I.	I.	0.903	< 0.01

Table 4. Spearman's rank correlation between PCA spaces of different groups of habitat scores and ant assemblages. | r | = absolut value of coefficient of correlation; p = level of significance

Score groups	r	р	
Vegetation architecture	0.376	< 0.05	
Vegetation composition	0.196	n.s.	
Microclimate	0.683	< 0.001	
Dead twigs on ground surface	0.721	< 0.001	
Composition of epigeic fauna	0.199	n.s.	
Fauna of the herb layer	0.199	n.s.	

architecture is an important factor differentiating ant assemblages. It accords with the results of Boomsma and De Vries (1980), Johnson et al. (1983), Seifert (1986), Gallé (1991) and Gallé et al (in preparation). The complexity of the vegetation architecture is a component of the habitat heterogeneity that can be responsible for the increasing diversity during ant community succession (Kondoh and Kitazawa, 1984; Zorrilla et al., 1986; Gallé, 1991).

Both previous studies (Gallé, 1991; Seifert, 1986) and the present results suggest that the dead twigs on the ground surface have an important effect on the composition of ant communities. The role of microclimate (Brian, 1964; Gallé, 1975, 1991) is not so equivocal.

In contrast to Johnson et al. (1983) and Seifert (1986), but according with Gallé (1991) we found that the vegetation composition does not play a significant role in structuring the composition of examined ant assemblages.

Making a comparison between the present results from Kéleshalom study site and the results of similar previous studies from other sand-dune areas studied in the course of the present project (Gallé, 1990a, 1990b, 1991; Gallé et al., in preparation) on the environmental factors which possible affect the composition of ant assemblages (Table 1.), there are some good agreements, e.g. regarding the correlation with vegetation architecture, the dead twigs on ground surface and the composition of epigeic fauna, but there are some differences, too. The comparative results of the present study with the previous ones, suggest that the microclimate has an increasing importance toward the southern geographical regions in the determination of the composition of sand-dune ant assemblages.

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