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Species richness, abundance and diversity of beetles (Coleoptera) in relation to ecological succession

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ABSTRACT: Beetles (Coleoptera) were collected by pitfall trapping near Budapest (Hungary), in three stages of dolomitic succession from April to October in 1988. Species richness and abundance were greatest in the mature stage, in sessile-turkey oak forest. The diversity and equitability values were greatest in the medium stage, in dolomitic steppe meadow. The open dolomitic grassland was the poorest habitat. The similarity was high between the two grass-dwelling communities, but low between the forest and each of the grass-dwelling communities. The changes of diversity and equitability did not support the general theory of ecological succession.

INTRODUCTION

Succession theory has always played a central role in ecology from the beginning of the twentieth century (Clements 1916, Gleason 1926, Margalef 1968, Odum 1969, Horn 1976, Connel and Slatyer 1977, MacMahon 1980). This theory gives general trends in community development, providing an important tool for the prediction of environmental changes (Peet and Christensen 1980). The latter has a significant role in nature conservation.

The majority of succession projects dealt with plant communities (Gallé 1985). There are some further studies on birds, e.g. Shugart and James 1973, Helle and Fuller 1988, Moskát and Székely 1989 , but papers on insects are rather scarce. There are only a few papers about the succession of beetles, namely about phytophagous (Brown and Hyman 1986) and aquatic species (Nilsson 1984).

We studied species richness, species abundance and diversity of ground-dwelling beetle communities of different successional stages of a rocky vegetation in Hungary.

STUDY AREA

The study area is located on the Kutya hill in the Budai Mountains (Northern Hungary). The area lies 30 km from Budapest in NW direction (47° 35' N, 18° 90' E). The basic rock is triassic dolomite. There are rendzina in patches covered by grass vegetation, and brown soil in forested areas. We selected three study sites to represent different levels of the successional sere:

I. Open dolomitic grassland ('open habitat'). (Seseli leucospermo-Festucetum pallentis.) This is the first stage of dolomite succession after the lichen-moss communities (Jakucs 1981). Festuca pallens and Seseli leucospermum are the dominant and characteristic plant species. The rock/grass ratio is about the same.

II. Dolomitic steppe meadow 'steppe habitat'. (Chrysopogono-Caricetum humilis.) There are several steppe plant species in this phase, where Carex humilis and Chrysopogon gryllus are the dominant and characteristic species. This plant community is almost closed, the rock/grass ratio is about 5/95.

III. Sessile-turkey oak forest ('forest habitat'). (Quercetum petraea-cerris.) This forest type is mainly composed of Quercus cerris and Q. petraea. The presence of Fraxinus ornus is also pronounced. The trees are not too high (10-15 m), because of the shallow soil.

METHODS

For sampling we used altogether 324 pitfall traps, 108 for each of the 3 vegetation phases. Plastic jars were used with a mouth diameter of 9 cm. The traps contained ethylene-glycol. The project lasted for about six months, from 7th of April to 23rd of October, 1988. We visited the traps in every fortnight, altogether fourteen times, and mean values of the 14 visits were used. Only beetle data were analyzed.

We compared the beetle communities connected with the three different plant communities with the help of community structure parameters, like species richness, species abundance and species-abundance distributions. The Sorensen index was applied to measure the similarity between the habitat:

$$C = 2aJ / (A+B),$$

where A= number of species caught on site A,
B= number of species caught on site B,
J= number of joint occurrences.

If C= 1, then the two communities are identical, if C=0, then totally different (Southwood 1978).

The Shannon-Weaver's diversity index was evaluated in relation to different beetle communities. The diversity index is:

$$H = -\sum p(i) * \ln p(i),$$

where p(i) is the proportion of individuals in the i-th species (Southwood 1978).

Equitability was calculated according to the formula:

$$J = H / \ln S,$$

where S is the number of species present.

We applied agglomerative cluster analysis based on 154 species, which were collected more than one time. Squared Euclidean distance and single linkage grouping strategy was chosen. Multiple stepwise regression was also applied for the Coleoptera data. These statistical analyses were carried out by the SPSS/PC+ statistical program package (Norusis 1986).

RESULTS

32 families, 139 genera and 233 species are represented by a total number of 23,837 captured specimens. We recorded 13,952 individuals belonging to 153 species in the 'forest habitat', 7562 individuals of 129 species in the 'steppe-habitat', and 2323 individuals of 56 species in the 'open habitat'.

The species-abundance distributions of the three beetle communities are shown in Fig. 1. On double logarithmic scale these curves show linear relationships, but their slopes are different (Table 1).

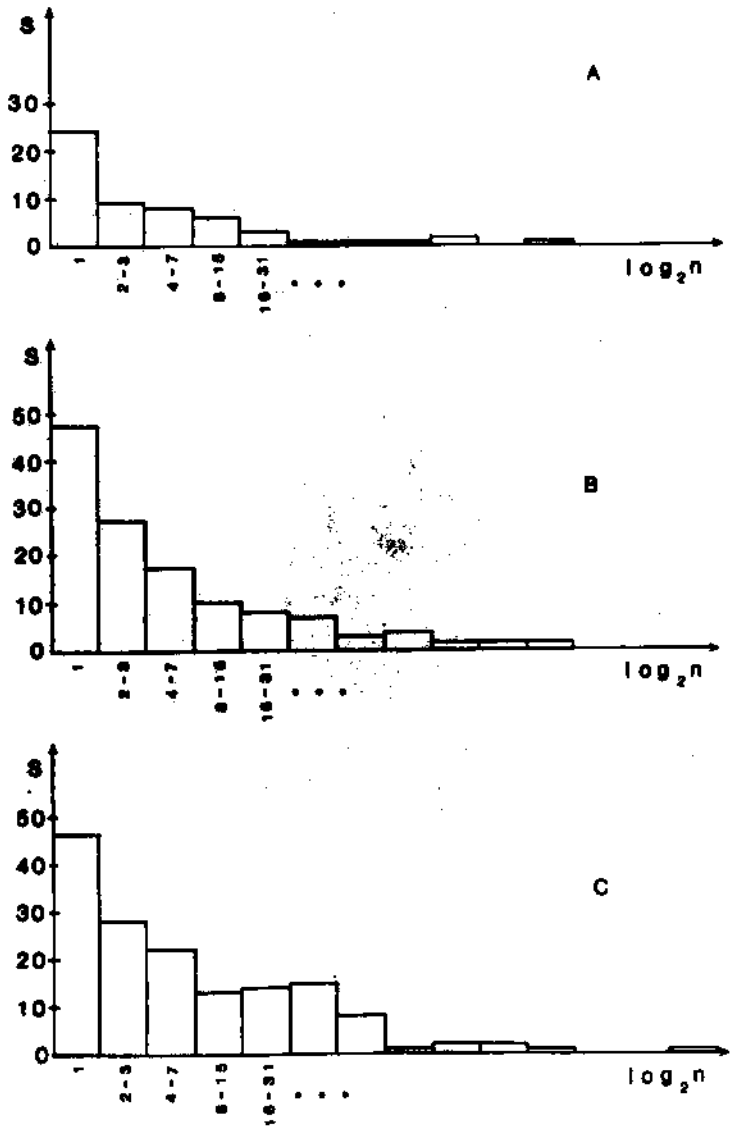

Fig. 1. Species-abundance distribution of beetles in three stages of successional sere. A= Open dolomitic grassland; B= Dolomitic steppe meadow; C= Sessile-turkey oak forest. (S is the number of species, n is the number of individuals per species)

The values of the Sorensen index indicate high similarity between the beetles of the 'steppe habitat' and the 'open habitat', and low similarities between the beetles of the 'forest habitat' and the two other phases (Table 2).

Table 1. The slopes of regression lines fitted to the double logarithmic curves of the species-abundance distributions. [p(F): significance of explained variance, slope: slope of the fitted lines, se: standard error of the slope, p: significance of regression lines]

	p(F)	slope	se	p
Sessile-turkey oak forest	0.0000	-1.388	0.1067	0.0000
Dolomitic steppe meadow	0.0000	-1.286	0.1269	0.0000
Open dolomitic grassland	0.0000	-1.245	0.1999	0.0000

Between the 'forest habitat' and the 'steppe habitat' the mean diversity values for the fourteen samples are similar (two tailed t-test, DF=26; t=1.39, n. s.), but the value of the 'open habitat' is much smaller than both the values of the 'forest habitat' and 'steppe habitat' (t=3.08, $p < 0.01$; t=4.13, $p < 0.001$, respectively)(Table 3). Equitability shows an opposite similarity due to the small diversity values. There is a significant difference in only one case, namely, between the species of the 'steppe habitat' and 'open habitat' (t= 2.53, $p < 0.05$)(Table 3).

Table 2. Values of similarity between the three stages of the successional sere, based on the Sorensen index

Sessile-turkey oak forest Dolomitic steppe meadow	0.37589
Sessile-turkey oak forest Open dolomitic grassland	0.34450
Dolomitic steppe meadow Open dolomitic grassland	0.47568

The mean number of species are similar between the 'forest habitat' and the 'steppe habitat' (t=1.35, n. s.), just like the abundance (t=1.80, n. s.). The beetle community living in the 'open habitat' highly differs from that of the 'forest habitat' in the case of species richness (t=4.99, $p < 0.001$) and abundance (t=3.84, $p < 0.001$)(Table 3). The relationships are similar between the beetles of 'open habitat' and 'steppe habitat' too (species richness: t=4.61, $p < 0.001$; abundance: t=2.70, $p < 0.05$).

Table 3. Structure parameters of beetle communities associated with the three vegetation stages. (N=14, standard deviation in brackets)

	Open dolomitic grassland	Dolomitic steppe meadow	Sessile-turkey oak forest
Species richness	8.71 (7.36)	26.6 (12.5)	34.5 (17.9)
Abundance	1.543 (1.23)	5.007 (4.64)	9.192 (7.35)
Diversity	0.98 (0.85)	2.00 (0.36)	1.78 (0.47)
Equitability	0.41 (0.33)	0.65 (0.13)	0.54 (0.18)

The number of species changed parallel between the 'forest habitat' and the 'steppe habitat' from April till October and this correlation is proved to be significant (Table 4). The abundances correlate significantly too, but this significance is not so high because of the relevant fluctuation (Table 4).

Table 4. Correlation of species richness and abundance between the three successional stages. (N=14; Pearson's correlation coefficient/one-tailed significance)

	Species richness			Abundance		
	Open dolomitic grassland	Dolomitic steppe meadow	Sessile-turkey oak forest	Open dolomitic grassland	Dolomitic steppe meadow	Sessile-turkey oak forest
Open dolomitic grassland	-	0.2762 0.170	0.3799 0.090	-	-	-
Dolomitic steppe meadow	-	-	0.8425 0.000	-0.0793 0.394	-	-
Sessile-turkey oak forest	-	-	-	0.2759 0.170	0.6344 0.007	-

There is no significant correlation between the diversity values in any of the cases (Table 5). The correlation between the equitability values of the beetles of the 'forest habitat' and the 'open habitat' is positive and significant. Between the 'forest habitat' and the 'steppe habitat' the correlation is negative and significant (Table 5).

Table 5. Correlation of diversity and equitability values between the three successional stages. (N = 14; Pearson's correlation coefficient/one-tailed significance)

	Diversity			Equitability		
	Open dolomitic grassland	Dolomitic steppe meadow	Sessile-turkey oak forest	Open dolomitic grassland	Dolomitic steppe meadow	Sessile-turkey oak forest
Open dolomitic grassland	-	0.2350 0.209	-0.3135 0.138	-	-	-
Dolomitic steppe meadow	-	-	0.1219 0.339	-0.1843 0.264	-	-
Sessile-turkey oak forest	-	-	-	0.5951 0.012	-0.5281 0.026	-

According to the results of the cluster analyses (Fig. 2) we can separate the three beetle communities into two main groups, namely, to the forest- and to the grassland-dwelling beetles.

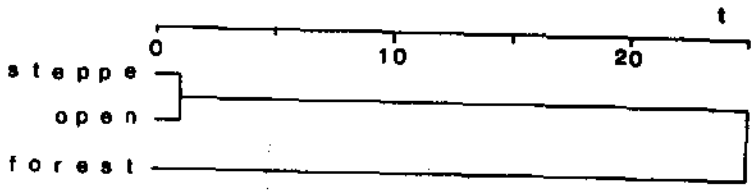

Fig. 2. The dendogram of three stages of succession, based on the squared dean distance t . Open: Open dolomitic grassland; Steppe: Dolom steppe meadow; Forest: Sessile-turkey oak forest

Discussion

The succession of plants living on dolomite is well known (Jakucs 19 The first stage is the lichen-moss phase, followed by the open dolomitic gr land community (I.), which becomes more and more closed during the successic process. The next stage is the dolomitic steppe meadow phase (II.), which c tains many species from the previous stage. This is a closed, or almost clo vegetation. In the present study the forest is the climax community, the en the ecological succession (sessile-turkey oak forest (III.)).

The two grassy communities of these successional stages are much mor similar to each other than the forest community to any of them. The present study pointed out great differences between the community structure paramet of the beetle communities associated with these vegetation phases, but the tent of these differences are relative, somewhat depending on the methods ap plied.

The number of species, species abundances and the diversity values we more similar between the beetles of the forest and steppe phases, than any c them compared to those of the 'open habitat'. This differs from the botanica results, where the two grassy communities are the most similar ones (Jakucs 1981). The 'open habitat' consists of a great portion of bare rocks, but the other two sites are covered by soil and unbroken vegetation.

High similarity occurred when beetles of the 'forest habitat' and the 'steppe habitat' were quantitatively compared. Qualitatively the similarity low, because of the low number of common species. The latter was high in the case of the 'steppe habitat' and the 'open habitat'.

The 'open habitat', which is at the beginning of the ecological succession, contains only a few species and individuals of plants and beetles. next stage is the dolomitic steppe meadow having developed from the open dol

Table 6. Expected changes of community structure parameters during the ecological succession based on the general theory, and the observed changes in the case of beetles

	Successional stages					
	Expected		Observed			
	Developmental	Mature	Developmental		Mature	
Species richness	low	high	low		high	
Abundance	low	high	low		high	
Diversity	low	high	low	high	medium	
Equitability	low	high	low	high	medium	

mitic grassland. These two stages contain a lot of common species of plants (Jakucs 1981) and Coleoptera. This plant community is almost closed, therefore, its diversity and abundance are greater than those of the previous stage. Due to the increasing value of cover and diversity of plant community, the diversity value of beetle communities also increased in the case of ground-dwelling species (Buse 1984) and the aquatic ones (Nilsson 1984). Beley et al. (1982) found the same relationship between the vegetation structure and the whole arthropod community. Brown and Hyman (1986) found such a trend only in the early stages of succession in phytophagous beetles. The sessile-turkey oak forest is the mature stage having developed from the grassy communities after a long period of time. The long time and the stages between the steppe and forest phases are the reasons for the small portion of common species, though the species numbers and abundances are similar to those of the Coleoptera community of the steppe meadow.

The classical theory of succession (Margalef 1968, Odum 1969, Price 1984) gives predictions to the changes of a lot of ecological characteristics, for example to the species richness, abundance, and diversity. These features are supposed to increase during succession. Some of the studies on arthropods also supported these results (Beley et al. 1982, Nilsson 1984, Hendrix et al. 1988). Our results showed some deviations from these expected changes in the case of diversity, and equitability (Table 6). The lower values of diversity, and equitability in the mature community are due to the extreme abundance of a few species: Geotrupes vernalis, Carabus convexus and Nicrophorus vespillo.

There are many differences in the results of ecological succession studied at different groups of animals and in different habitats. The abundance generally increases during the succession of vertebrate communities (Mehlhop and Lynch 1973, Schwartz and Whitson 1986), but not always the highest in the climax stage (Glowacinski 1981). In phytophagous beetles Brown and Hyman (1986) found that the middle stages showed the highest diversity values. Their findings in phytophagous beetles and our results concerning ground-dwelling Coleoptera revealed that the classical model of ecological succession cannot be applied to beetles.

We recorded predominantly the ground-dwelling beetles by pitfall trapping, which is only a part of the beetle community of the woodland. There are only a few records in our data about the leaf- and tree-dwelling species of the forest (for example: Cryptarcha strigata). On the other hand, the pitfall trapping for grassland-dwelling beetles gives samples from the whole community, so our comparison mainly concerns the ground-living beetles.

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REFERENCES

Beley, J.R., Ditsworth, T.M., Butt, S.M. and Johnson, C.D.(1982): Arhtropods, plants and transmission lines in Arizona: community dinamics during secondary succession in a Pinyon-juniper chaparral habitat. - The Southwestern Naturalist, 27: 325-333.

Brown, V.K. and Hyman, P.S. (1986): Successional communities of plants and phytophagous coleoptera. - Journal of Ecology, 74: 963-975.

Buse, A. (1988): Habitat selection and grouping of beetles Coleoptera . - Holarctic Ecology, 11: 241-247.

Clements, F.E. (1916): Plant succession: an analysis of the development of vegetation. - Carnegie Inst. Wash. Publ. 242: 1-512.

Connel, J.H. and Slatyer, R.O. (1977): Mechanisms of succession in natural communities and their role in community stability and organization. - American Naturalist, 111: 1119-1144.

Gallé, L. (1985): Some peculiarities of succession of animal communities. - In: Fekete, G. ed. : Problems of the coenological succession. p. 135-163. Akadémiai Kiadó, Budapest. [In Hungarian].
Gleason, H.A. (1926): The individualistic concept of the plant association. - Bull. Torrey Bot. Club, 53: 7-26.
Glowacinski, Z. (1981): Stability in bird communities during the secondary succession of a forest ecosystem. - Ekologia Polska, 23: 73-95.
Helle, P. and Fuller, R.J. (1988): Migrant passerine birds in European forest succession in relation to vegetation height and geographical position. - Journal of Animal Ecology, 57: 565-579.
Hendrix, S.D., Brown, V.K. and Dingle, H. (1988): Arthropod guild structure during early old field succession in a new and old world site. - Journal of Animal Ecology, 57: 1053-1065.
Horn, H.S. (1976): Succession. In: May, R.M. (ed.). Theoretical ecology: Principles and applications. p. 187-204. Blackwell, London.
Jakucs, P. (1981): Magyarország legfontosabb növénytársulásai. In: Hortobágyi, T. and Simon, T. (eds.). Növényföldrajz, társulástan és ökológia. p.225-267. Tankönyvkiadó, Budapest.
MacMahon, J.A. (1980): Ecosystems over time: succession and other types of change. In: Waring, R.H. (ed.). Forests: Fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis.
Margalef, R. (1968): Perspectives in ecological theory. Univ. Chicago Press, Chicago.
Mehlhop, P.M. and Lynch, J.F. (1986): Bird/habitat relationship along a successional gradient in the Maryland Coastal Plain. - The American Midland Naturalist, 116: 225-239.
Moskát, C. and Székely, T. (1989): Habitat distribution of breeding birds in relation to forest succession. - Folia Zoologica, 38: 363-376.
Nilsson, A.N. (1984): Species richness and succession of aquatic beetles in some kettle-hole ponds in northern Sweden. - Holarctic Ecology, 7: 149-156.
Norusis, M.J. (1986): SPSS/PC+. Advanced statistics. SPSS Incorporation, Chicago.
Odum, E.P. (1969): The strategy of ecosystem development. - Science, 164: 262-270.
Peet, R.K. and Christensen, N.L. (1980): Succession: a population process. - Vegetatio, 43: 131-140.
Price, P.W. (1984): The concept of the ecosystem. In: Huffaker, C.B. and Rabb, R.L. (eds.). Ecological entomology. p. 19-53. John Wiley and Sons, New York.
Schwartz, O.A. and Whitson, P.D. (1986): A 12-year study of vegetation and mammal succession on a reconstructed tallgrass prairie in Iowa. - The American Midland Naturalist, 117: 240-249.
Shugart, H.H. and James, D. (1973): Ecological succession of breeding bird populations in Northwestern Arkansas. - Auk, 90: 62-77.
Southwood, T.R.E.(1978): Ecological methods. Chapman and Hall, London.

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