

# Edge effect on carabid assemblages along forest-grass transects

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During 1997 and 1998, we have tested the edge-effect for carabids along oak-hornbeam forest-grass transects using pitfall traps in Hungary. Our hypothesis was that the diversity of carabids will be higher in the forest edge than in the forest interior. We also focused on the characteristic species of the habitats along the transects and the relationships between their distribution and the biotic and abiotic factors.

Our results proved that there was a significant edge effect on the studied carabid communities: the Shannon diversity increased significantly along the transects from the forest towards the grass. The diversity of the carabids were significantly higher in the forest edge and in the grass than in the forest interior. The carabids of the forest, the forest edge and the grass are separated from each other by principal coordinates analysis and by indicator species analysis (IndVal), suggesting that each of the three habitats has a distinct species assemblages. There were 5 distinctive groups of carabids: 1) habitat generalists, 2) forest generalists, 3) species of the open area, 4) forest edge species, and 5) forest specialists. It was demonstrated by multiple regression analyses, that the relative air moisture, temperature of the ground, the cover of leaf litter, herbs, shrubs and canopy cover, abundance of the carabids' preys are the most important factors determining the diversity and spatial pattern of carabids along the studied transects.

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Forest edges are in the focus of both ecological researches and conservation purposes; with exponential destruction and fragmentation of habitats, forest edges are becoming proportionately greater relative to interiors in some areas, whereas in other regions they disappear due to recent plantations or abandonment of adjacent farmland (Saunders et al. 1991). According to the classical edge effect hypothesis the diversity is higher in ecotones than in adjacent communities (Odum 1971). The goal of our study was to test the edge effect hypothesis for carabids (Coleoptera: Carabidae) along three parallel forest-grass transects. We also examined the environmental variables that may be important to control the distribution of ground-dwelling carabids, and thus can influence edge effect on carabid beetles. Our hypothesis was that changes in carabids are

most pronounced in forest edge characterised particular environmental conditions, and that according to the classical edge effect hypothesis the diversity of carabids will be higher in the forest edge than in the forest interior. Moreover, our objectives were to assess the extent of variation in distribution of carabid species along the transects, and to relate this to habitat characteristics and to spatial distribution of co-occurring carabid species.

## Materials and methods

Sampling area was located at the North Hungarian Mountain at the Aggtelek National Park. In this region the zonal forest association is oak-hornbeam (Querco-Carpinetum),

which is the most extensive forest type in this area. On the research area three habitats were studied along the transects: 1) forest interior: oak-hornbeam forest, with dense litter layer, moderate herbaceous and shrub layer, 2) forest edge, with moderate litter layer and dense herbaceous vegetation originated from the nearby grass. The shrub layer was also dense in this habitat, consisting mainly of shrubs and saplings of the canopy trees (*Carpinus betulus*, *Corylus avellana* and *Prunus spinosa*), and 3) grass (*Polygala majori-Brachypodium pinnati*), with dense herbaceous vegetation dominating by *Brachypodium pinnatum*, *Polygala major*, *Carex montana*, *Betonica officinalis* and *Adonis vernalis*.

Three parallel transects of pitfall traps were set along the three studied habitats. To provide adequate statistical independence for pitfall samples, transects were set at least 50 m from each other (Digweed et al. 1995). There were 5 unbaited pitfall traps in each habitat (Fig. 1.). Trapped individuals were collected monthly from March to November in 1997 and 1998, so that samples covered the snow-free seasons.

We measured eight environmental variables to study whether any of the environmental measurements could predict the diversity of carabids along the transect. We measured the temperature of ground in 2 cm depth, the air temperature on the surface and the relative air moisture near each trap. Moreover, we estimated the percentage cov-

er of the leaf litter, the herbs, the shrubs and the canopy layer within a radius of 2 m around each trap. We also studied the abundance of the carabids' potential food resources (abundance of other animals, that fell in the traps; e.g. other *Coleoptera*, *Chilopoda*, *Collembola*, *Diplopoda*, *Gastropoda*, *Isopoda*, *Orthoptera*, etc.)

To test edge effect on carabids the Shannon diversity of carabids per trap from the three habitats along the three transects were compared with each other in both years. Kruskal-Wallis non-parametric ANOVA and Tukey-type multiple comparisons were used to determine differences in the carabid diversity per trap. Multiple regression analyses were used to study the relationships between the eight environmental measurements and the diversity of carabids, and also the relationships between the environmental measurements and the abundance of each frequent carabid species. Principal coordinates analysis (PCoA) using the Bray-Curtis dissimilarity was used for abundances to assess similarities in carabid assemblages among the traps. The IndVal (Dufrene and Legendre 1997) method was used to find indicator species characterising the forest interior, forest edge and grass. The statistical significance of the species indicator values is also evaluated by IndVal using a randomisation procedure.

## Results

The abundance of the trapped species are shown by the Table 1. The non-parametric ANOVA provided that there was variation in the carabid diversity among the habitats for the transects in both years ( $F=34.69$ ,  $DF=8,44$ ,  $p<0.0001$ ; and  $F=29.72$ ,  $DF=8,44$ ,  $p<0.0001$ , respectively). By the Tukey-type posteriori test it is evident that the Shannon diversity was significantly ( $p<0.05$ ) higher in the forest edge and in the grass than in the forest interior in both years, but the differences in diversity between the forest edge and the grass were not significant (Table 2). The same diversity pattern was shown by the pooled samples of the habitats (Table 3).

Multiple linear regression analyses showed that in 1997 the relative air moisture, while in 1998 the temperature of the ground and the cover of herbs were the most important factors determining the diversity of carabids along the transects.

The result of the ordination (PCoA) shows that there was a linear gradient in the data, namely the carabid assemblage changed gradually from the forest interior towards the grass along the transects (Fig. 2). Carabid samples of the grass, the forest edge and the forest interior separated from each other along the gradient. The composition of the samples from the forest edge and the forest interior were more similar to each other than to the samples from the grass. Forest habitats (forest interior and forest edge) and grass habitat are separated along axis one. Traps from forest interior and forest edge are separated along axis two.

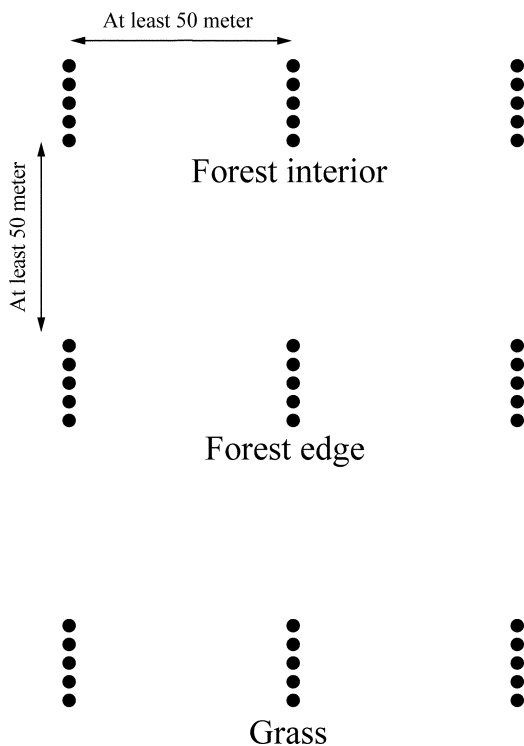


Fig. 1. Layout of pitfall traps along the transects.

Table 1. Number of individuals of collected carabids for the two-year study period.

	Forest interior	Forest edge	Grass
<i>Carabus arcensi</i>	1	20	28
<i>Carabus convexu</i>	3	15	13
<i>Carabus coriaceus</i>	4	39	5
<i>Carabus hortensi</i>	26	91	3
<i>Carabus intricatus</i>	4	9	3
<i>Carabus montivagus</i>	3	8	14
<i>Carabus nemoralis</i>	10	20	8
<i>Carabus violaceus</i>	23	72	77
<i>Anisodactylus signatus</i>	0	0	1
<i>Harpalus latus</i>	0	0	2
<i>Harpalus rufipes</i>	1	1	31
<i>Poecilus cupreus</i>	0	0	4
<i>Pterostichus burmeisteri</i>	131	63	1
<i>Pterostichus macer</i>	0	0	1
<i>Pterostichus melanarius</i>	2	4	114
<i>Pterostichus niger</i>	0	1	0
<i>Pterostichus oblongopunctatus</i>	538	164	0
<i>Pterostichus ovoideus</i>	0	0	22
<i>Molops piceus</i>	148	96	86
<i>Abax carinatus</i>	3	1	10
<i>Abax ovalis</i>	157	30	14
<i>Abax parallelepipedus</i>	661	400	104
<i>Abax parallelus</i>	26	3	8
<i>Symuchus vivalis</i>	0	1	34
<i>Calathus fuscipes</i>	0	0	1
<i>Agonum viridicupreum</i>	0	0	1
<i>Amara aenea</i>	0	0	1
<i>Amara aulica</i>	0	0	1
<i>Amara communis</i>	0	0	4
<i>Amara convexior</i>	0	0	1
<i>Amara littorea</i>	0	0	1
<i>Amara ovata</i>	0	1	0
<i>Panagaeus bipustulatus</i>	0	3	1
<i>Aptinus bombardia</i>	21	6	2

According to their habitat preference the collected carabid species can be divided into five groups by indicator species analyses (IndVal, Fig. 3): 1) habitat generalists that occurred numerously in all habitat types; 2) forest generalists that were recorded exclusively in the forest habitats or were the most abundant in the forest habitats (forest edge and forest interior); 3) species of open habitat (grass species) that were captured exclusively in the grass or were the most abundant in the grass; 4) forest edge species that occurred exclusively or were the most abundant in the forest edge; and 5) forest specialists that were recorded exclusively or numerously in the forest interior.

Multiple regression analyses between the distribution of carabids and the environmental variables and occurrence of other carabids were significant ( $p < 0.05$ ) for each dominant and subdominant species, except *Carabus intricatus* Linnaeus, 1761 and *Carabus nemoralis* O. F. Müller, 1764, while the multiple regression was marginally significant for *Abax parallelus* (Duftschmid, 1812). Relative cover of the leaf litter was

a significant negative predictor for two carabid species (*Abax parallelepipedus* (Piller et Mitterpacher, 1783) and *Aptinus bombardia* (Illiger, 1800)). Cover of the herbs was a significant positive predictor for *Carabus coriaceus* Linnaeus, 1758. Relationship between the cover of shrubs and the carabids' abundance was significant for two species (*Abax parallelepipedus* and *Molops piceus* (Panzer, 1793)). Canopy cover was a significant positive predictor for *Abax parallelepipedus*. Abundance of carabids' preys was a significant positive predictor for three carabids (*Carabus convexus* Fabricius, 1775, *Harpalus rufipes* (De Geer, 1774) and *Symuchus vivalis* (Panzer, 1797)). There were eleven significant relationships between the distribution of particular carabid species and the occurrence of other carabids. The majority of these relationships were positive. A notable exception was the pair *Molops piceus* (body length 11–15 mm) and *Pterostichus burmeisteri* Heer, 1841 (12–14.5 mm), which have nearly identical body sizes, similar seasonal activity and food preference. They showed significant negative association in abundance.

Table 2. Average Shannon diversity of carabids per trap (with SD) in the studied habitats. Means with different letters indicate a significant ( $p < 0.05$ ) difference by Tukey-type multiple comparison.

	1997	1998
Transect 1		
Forest interior	1.5123 ± 0.1427 <sup>a</sup>	1.5215 ± 0.1264 <sup>a</sup>
Forest edge	1.8642 ± 0.1552 <sup>b</sup>	1.8176 ± 0.0963 <sup>b</sup>
Grass	1.9465 ± 0.0683 <sup>b</sup>	1.9054 ± 0.1141 <sup>b</sup>
Transect 2		
Forest interior	1.4816 ± 0.1570 <sup>a</sup>	1.5070 ± 0.1022 <sup>a</sup>
Forest edge	1.8687 ± 0.0820 <sup>b</sup>	1.8582 ± 0.0713 <sup>b</sup>
Grass	1.8454 ± 0.0265 <sup>b</sup>	1.9146 ± 0.0105 <sup>b</sup>
Transect 3		
Forest interior	1.0835 ± 0.0990 <sup>c</sup>	1.3349 ± 0.1744 <sup>a</sup>
Forest edge	1.6698 ± 0.1318 <sup>b</sup>	1.6416 ± 0.2189 <sup>b</sup>
Grass	1.7050 ± 0.1479 <sup>b</sup>	1.8222 ± 0.1869 <sup>b</sup>

## Discussion

### Edge effects on carabids

Previous studies of edge effect on carabids also demonstrated that diversity was higher in the forest edge than in the forest interior (Báldi and Kisbenedek 1994, Magura and Tóthmérész 1997, 1998). Bedford and Usher (1994) studying carabid assemblages of farmland-forest transects, also reported that open habitat and forest edge have a higher species richness than the forest interior. Our results corroborates that there is a significant edge effect on carabid assemblages. The diversity increased along the transects from the forest interior towards the grass.

Our results also suggest that the relative air moisture, the ground temperature and the cover of the herbs are the most important factors determining the diversity of carabids along the studied transects. The importance of the microclimate in structuring carabid assemblages was emphasised in previous studies (Butterfield 1997). Positive relationship between the ground temperature and the carabid's diversity can be explained by the fact that higher ground temperature may provide favourable sites for aestivation, hibernation, egg and larval development (Lövei and Sunderland 1996). The significant positive correlation between the relative air moisture and the diversity of carabids is expected because higher air moisture may produce

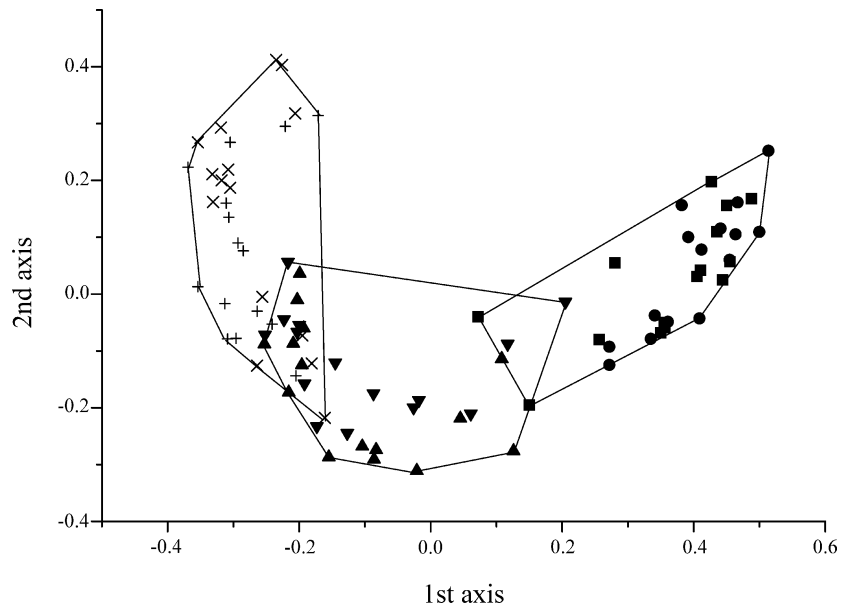
favourable microsites for carabids. Small scale spatial heterogeneity (favourable microsites) are mentioned by Niemelä et al. (1996) as important factor explaining the high carabid's diversity. The significant positive correlation between the diversity of carabids and the cover of herbs may be explained by the structure of habitats, as carabid beetles depend more on a habitat structure than on specific plant species (Spence et al. 1996). In the case of forest edge it can be stated that the herbs from the adjacent grass and the shrubs from the forest significantly contribute to the heterogeneity of the habitat and support the development and differentiation of microhabitats. With the increasing of coverage of the vascular plants (cf. habitat heterogeneity) the microclimatic conditions become more favourable for the majority of carabids and their egg and larval development. As the majority of trapped carabids are non-specialised predators, scavengers or omnivorous, percentage cover of the herbs may increase the amount of herbivorous invertebrate prey available for carabids and may provide a more uniform resource distribution in time (Niemelä and Spence 1994, Niemelä et al. 1996).

There was a linear gradient in the composition of the carabid assemblages along the transects, namely the carabid assemblages change gradually from the forest interior towards the grass along the transects. The arch effect is clear on Fig. 2; it usually represents linear gradients (Gauch 1986). Instead of the almost continuous variation of the composition of the assemblage along the gradient, carabid samples of the grass, the forest edge and the forest interior are separated from each other. The composition of the samples from the forest edge and the forest interior were more similar to each other than the samples from the edge and the grass. The analysis of indicator species also shows that all studied habitat types have characteristic assemblages of carabid species associated with them. On the studied scale the habitats are not isolated from each other and there appears to be dispersal between the adjacent habitats. The high diversity of the forest edge may be caused by dispersal processes, as carabid beetles are able to cover large distance while looking for food (Baars 1979) and movement between reproduction habitat and hibernation habitat (Wallin 1986, Andersen 1997). With decreasing of canopy cover species typical mostly of open habitats (e.g. *Pterostichus melanarius* (Illiger, 1798), *Synuchus vivalis* (Panzer, 1797), *Harpalus rufipes* (De Geer, 1774), *Carabus montivagus* Palliardi, 1825 and *Abax carinatus* (Duftschmid, 1812)) can immigrate in the forest edge increasing the diversity. Spence et al. (1996) studying carabids in a clear-cut area and in

Table 3. Shannon diversity of carabids (with SD) in the studied habitats. Means with different letters indicate a significant ( $p < 0.05$ ) difference by Hutcheson's t-test.

	Forest interior	Forest edge	Grass
1997	1.6189 ± 0.0400 <sup>a</sup>	2.0707 ± 0.0510 <sup>b</sup>	2.4477 ± 0.0557 <sup>c</sup>
1998	1.7121 ± 0.0316 <sup>a</sup>	2.0361 ± 0.0458 <sup>b</sup>	2.4163 ± 0.0616 <sup>c</sup>

Fig. 2. Ordination (PCoA by Bray-Curtis dissimilarity) of the pitfall catches within the habitats. +: Forest interior in 1997, ×: Forest interior in 1998, ▼: Forest edge in 1997, ▲: Forest edge in 1998, ●: Grass in 1997 and ■: Grass in 1998.



adjacent residual pine forest, also reported that open-habitat species can colonise the forest edge due to less canopy closure and changes in microclimate. Forest interior species (*Abax ovalis* (Duftschmid, 1812), *Abax parallelus* (Duftschmid, 1812) and *Aptinus bombardata* (Illiger, 1800)) can also move into the forest edge. This also consistent with previous observation (Spence et al. 1996) which demonstrated that forest specialists may maintain population in the forest edge. The increased variability of microsites, i.e. the increased spatial micro-heterogeneity also may support the coexistence of those species which have less competitive ability.

Overall, edge effect on carabids is due in part to the presence of species characteristic of each of the adjacent habitats (forest interior and grass) plus species inhabiting the edge. These edge species may find microsites at the edge that are not present in either habitat alone, or they may require two structurally different habitats in close proximity to one another.

### Spatial pattern of carabids along the transects

The analyses of indicator species by IndVal showed that the collected carabid species had a clear habitat and microsite preferences with specific environmental conditions. In the literature, four not mutually exclusive factors are mentioned that might explain the spatial distribution of carabid beetles (Niemelä et al. 1985, 1996): 1) differences in environmental conditions (habitat heterogeneity, food resources, microclimate, etc.), 2) autecological characteristics of the species, 3) small-scale dispersal, and 4) interspecific interactions. Our analyses showed that a significant proportion of the variation in catch is associated

with a particular kind of environmental heterogeneity reflected by the cover of leaf litter, herbs, shrubs, canopy layer and by the distribution of carabids' preys. This may be a fairly general pattern among carabids because clear preferences for microsites defined by ground vegetation and litter also was detected elsewhere (Niemelä et al. 1992, Lövei and Sunderland 1996). Multiple regression analyses showed that canopy layer was a significant positive predictor for *Abax parallelepipedus*. *Abax parallelepipedus* is a habitat generalist, but significantly more individuals were captured in the forest interior than in the other habitats, suggesting the importance of microsite preference within the movement area. The significant negative association between leaf litter and *Abax parallelepipedus* and *Aptinus bombardata* is surprising. Loreau (1987) reported that *Abax parallelepipedus* is active mainly at the surface of the litter. Perhaps this species can move easier in a habitat with limited litter layer. The same may be supposed for *Aptinus bombardata*. As many carabid species are generalist predator, scavenger or omnivorous, the amount of available prey may influence location of foraging (Hengeveld 1985) and carabids can aggregate in habitats with high amount of prey (Bryan and Wratten 1984). This may explain the positive relationships between the abundance of carabids' preys and the four carabid species.

At the studied spatial scale, the occurrence of other carabids was a significant predictor of the abundance of particular dominant and subdominant species. Most of the correlation were positive, suggesting a similar respond to habitat properties. Previous works (Niemelä and Spence 1994) also reported few negative relationships. These relationships were usually between species of different body sizes or seasonal activities, or both, and are better attributed to different microhabitat preferences than to effects of

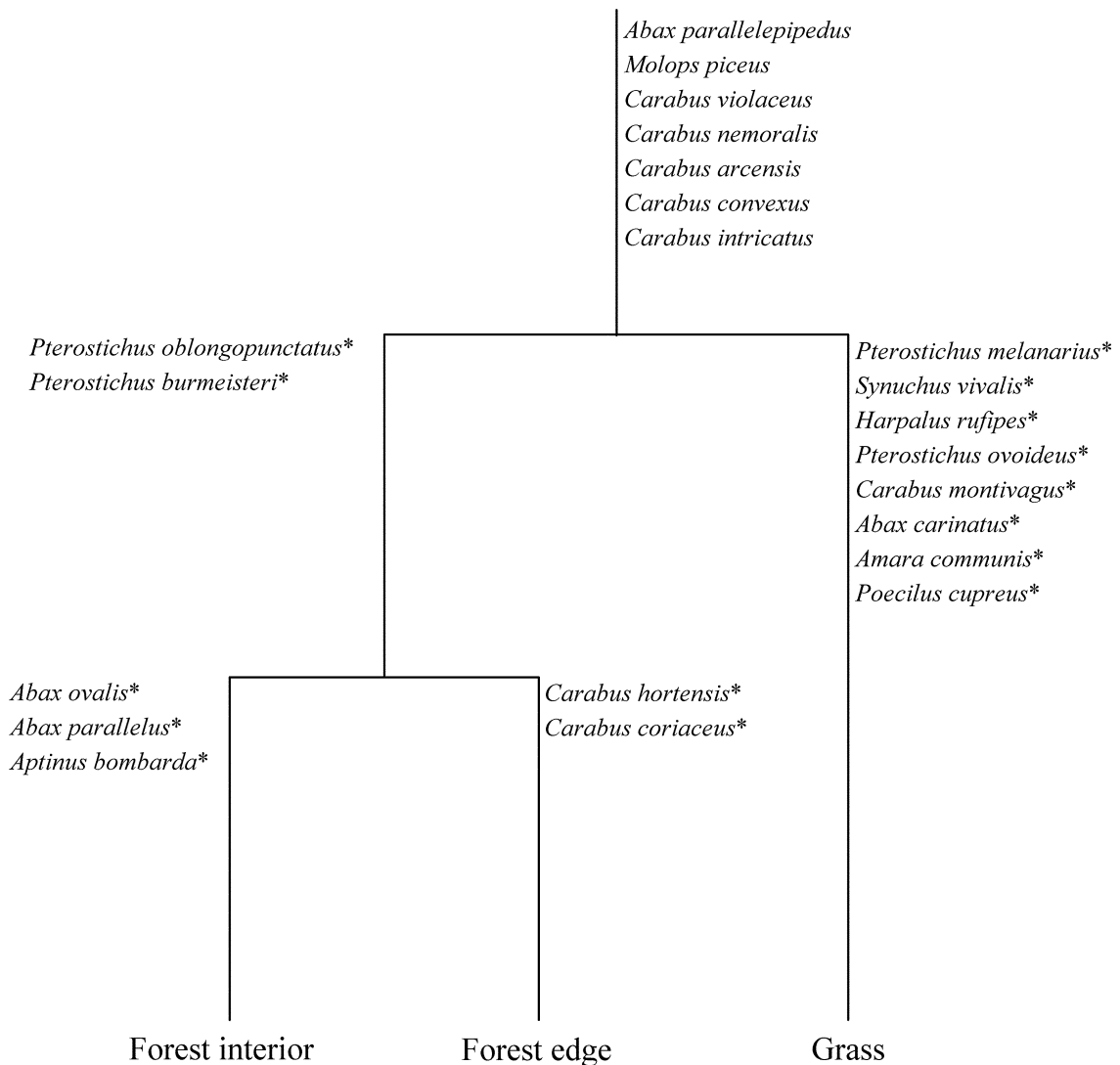


Fig. 3. Dendrogram presenting the indicator species identified by IndVal. Significant indicator species are denoted by \* ( $p < 0.05$ ). Only species represented by ten or more individuals are shown.

interspecific interactions. In our study there was a negative relationship in spatial distribution between the small *Synuchus vivalis* and the much larger *Carabus arcensis* Herbst, 1784 which also showed maximum activities at different period of the season. For similar reason, interspecific competition is not a likely explanation for the other pairs of species showing a significant negative relationship: *Carabus arcensis* and *Harpalus rufipes*; *Carabus montivagus* Palliardi, 1825 and *Harpalus rufipes*.

Interspecific competition may contribute to the negative relationship between *Molops piceus* and *Pterostichus burmeisteri* which are of similar size, they show similar habitat preference, similar patterns of seasonal activity and food preference. Other data sets (Magura and Tóthmérész 1997, Magura et al. 1997, 2000) suggest that negative interaction is not a gen-

eral feature of these two species. Niemelä and Spence (1994) also reported two carabid species with similar size and seasonal activity which showed negative interaction in a forest habitat, while these species in different forest associations showed a high overlap in spatial distribution and in seasonal activity (Niemelä and Halme 1992) or there were no correlation between the occurrence of the two species (Niemelä et al. 1993). These facts suggest that the relationships between the occurrence of carabids may be not a general feature, the interactions can vary among habitat types with different environmental attributes. Our study implies that distribution of carabids is determined not only by abiotic environmental factors but also by biotic factors. The result stresses that a synthesis is needed rather, which integrates competition with other abiotic and biotic ecological factors.

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