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Impacts of non-native Norway spruce plantation on abundance and species richness of ground beetles (Coleoptera: Carabidae)

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The impacts of non-native Norway spruce plantation on the abundance and species richness of carabids were studied in the Bükk National Park in Hungary, central Europe. Pitfall catches from recently established (5 yr old), young (15 yr after planting), middle-aged (30 yr after planting), old Norway spruce *Picea abies* plantation (50 yr after planting), and a native submontane beech forest (Fagetum sylvaticae) as a control stand were compared.

Our results showed that deciduous forest species decreased significantly in abundance in the plantations, and appeared in high abundance only in the native beech forest. Furthermore, open habitat species increased remarkably in abundance in the recently established plantation. Carabids were significantly more abundant and species rich in the native forest than in the plantations, while differences were not significant among the plantations. Multiple regression between the abundance and species richness of carabids and twelve environmental measurements showed that pH of the soil, herb cover and density of the carabids' prey had a significant effect in determining abundance and species richness.

Our results showed that plantation of non-native Norway spruce species had a detrimental effect on the composition of carabid communities and no regeneration could be observed during the growth of plantations even 50 yr after the establishment. This emphasises the importance of an active nature management practice to facilitate the recolonization of the native species.

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In Hungary from 1925 to 1997 the proportion of the area covered by forest increased from 12% up to 18%. Similarly to the other countries of Europe (Butterfield et al. 1995) a rather large proportion (ca 75%) of the forests is under economical exploitation. During the years 1940–60 the ratio of non-native species increased largely (black locust *Robinia pseudo-acacia*, Norway spruce *Picea abies*, scotch fir *Pinus sylvestris*, black pine *Pinus nigra*, poplar *Populus* spp., etc.). The plantation of these non-native species, however, is influencing the surface-dwelling insects rather heavily (Magura et al. 2000). In Hungary, the Norway spruce *Picea abies* was planted most frequently, because it is a fast-growing species and producing timber preferred by industry. After the clear-cutting of the native forest usually the tree-trunks are also removed. It has a dramatic influence on the soil and the soil fauna, especially when the base rock is limestone.

We have compared the carabids of a native beech forest

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and Norway spruce plantations of different ages with special emphasis on the conservational issues. We were especially interested whether there is any regeneration of the native carabid assemblage during the ageing of the plantations.

There are just a few published data from eastern Europe concerning the carabid fauna of conifer forests (Šustek 1981, Szyszko 1983). Our case, is notably different to these studies, because Norway spruce is not native to Hungary.

Materials and methods

The study area was in the Bükk National Park in Hungary. The base rock is limestone; the climate is subcontinental. The typical native forest of the area is beech forest (Melitti-Fagetum). There were five sampling locations; four Norway spruce *Picea abies* plantations and a beech forest as a control area: 1) beech forest, 2) 5 yr old, 3) 15 yr old, 4) 30 yr old, 5) 50 yr old Norway spruce plantations. Each of the study locations was on a NW-slope; the distance between them was > 1 km, and their areas were 5–20 ha. Beetles were sampled using unbaited pitfall traps (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution. Overall, there were 80 traps; 16 in each forest during the sampling procedure. Two trapping stations were established in each forest by placing eight traps (ca 4 m apart) in a grid to provide replications. Trapped individuals were collected monthly in 1998, from the start of April to the end of November, which was the main activity period of the species. It is a snow-free period in the studied region; before this period the soil is frozen.

We measured the environmental factors that may be relevant to the distribution of the carabids. They were measured every month on a typical sunny day in the morning. The temperature of the soil at a depth of 2 cm, the temperature at the soil surface, relative air humidity, soil pH, soil compactness, $CaCO_3$ content, organic matter content were measured next to each trap. We also estimated the cover of leaf litter, herbs, shrubs and canopy around each trap in a circle within radius of 1 m. We counted the number of individuals of the following taxa: Coleoptera, Chilopoda, Collembola, Diplopoda, Gastropoda, Isopoda, Orthoptera in the traps, because they are potential preys of carabids (Sergeeva 1994).

The characteristic species of the habitats were explored by the IndVal (Indicator Value) procedure (Dufrêne and Legendre 1997). It is a new and simple method to find indicator species or species assemblages characterising groups of samples or both. The novelty of this approach lies in the way that this method combines a species' relative abundance with its relative frequency of occurrence in the various groups of samples. The statistical significance of the species indicator values is evaluated using a randomisation procedure. Indicator species are defined as the most characteristic species of each group, found mostly in a single group and present in the majority of sites belonging to that group. This duality, which is of ecological interest, is seldom completely exploited; often only the distribution of abundances in the groups is used. In these cases, species occupying only one or two sites in one habitat group and present only in that group (rare species) receive the same indicator value as species occupying all sites of that habitat group and found only in that group. However, there is an important difference between these two types of species. The first one is an asymmetrical indicator, according to the IndVal terminology: its presence cannot be predicted in all sites of one habitat, but contributes to habitat specificity. The second type of species is a true, symmetrical indicator: its presence contributes to habitat specificity and its presence can be predicted in all sites of the group. With the IndVal procedure it is possible to distinguish the two types of indicator species; species that have an indicator value > 55% are regarded as symmetrical indicator species. In many respects the IndVal approach is a quantitative characterisation of the idea of indicator species of the classical plant sociology, based on computerised randomisation procedure. This resemblance was also emphasised by McGeoch and Chown (1998). Therefore, it would be better to name the so-called indicator species as quantitative character species.

Multiple linear non-stepwise regression analysis was used to explore the relationship between the forestry management cycle (beech forest, 5 yr old, 15 yr old, 30 yr old, and 50 yr old Norway spruce plantation), the number of individuals and the number of species and the environmental variables.

Results

Altogether there were 2034 specimens of carabids in the traps, belonging to 34 species. It was indicated by ANOVA that the average number of carabid individuals per trap are significantly different ($H=37.4510$, $DF=9,79$, $p<0.0001$; Fig. 1A). The average number of individuals was significantly higher ($p<0.05$) in the native beech forest than in the Norway spruce plantations, and there were no significant differences between the average number of individuals in the case of Norway spruce plantations. The conclusion is very much the same for the species richness. ANOVA showed that the average number of species of carabids per trap was significantly different ($H=40.5887$, $DF=9,79$, $p<0.0001$; Fig. 1B). In the beech forest the average number of species of carabids was significantly higher ($p<0.05$) than in the Norway spruce plantations, and there were no significant differences between the plantations.

There were five characteristic groups of species explored by the IndVal method (Table 1): 1) characteristic species of the 50 yr old Norway spruce plantation; 2) closed canopy forest generalists that occurred in the forests with closed

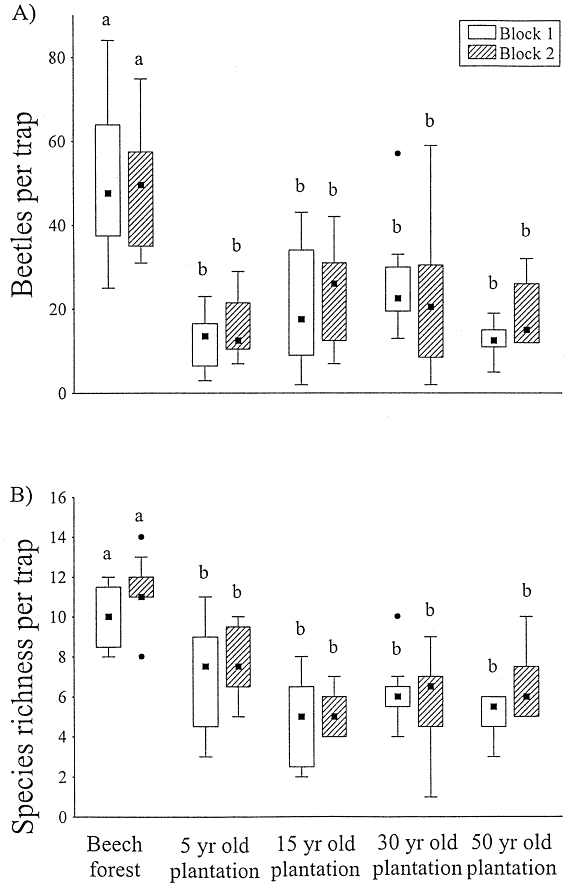

Fig. 1. Box and whisker plots of the number of carabid individuals A) and species richness B) per trap in the studied forests for the two repeated trapping stations (Block 1 and 2). Boxes represent the 25 and 75 percentiles of the data, while whiskers contain the non-outlier data; outlier data items are indicated by dots. Different letters indicate a significant (p<0.05) difference in the medians by Tukey-type multiple comparison. Legends: ■ : median, • : outlier.

canopy layer (beech forest, Norway spruce plantation of 15, 30 and 50 yr old); 3) species characteristic to the beech forest; these species were abundant only in this habitat, although they also may be present in other habitats; 4) generalists that occurred in all habitat types; 5) species of the open habitats. These species were characteristic of those habitats where the canopy layer was open; i.e. they occurred in the 5 yr old Norway spruce plantation.

It was demonstrated by multiple regression analysis between the forestry management cycle and the 12 studied environmental variables that soil pH, soil compactness and litter cover decreased significantly during the forestry management cycle (beech forest – 5 – 15 – 30 – 50 yr old Norway spruce plantation) ($F=269.2936$, $DF=12,67$, $p<0.0001$).

The multiple regression between the abundance of trapped carabids and the environmental variables revealed that soil pH and amount of potential food were the most important factors limiting the abundance of carabids. The number of individuals of carabids increased with the abundance of potential prey and with soil pH. The multiple regression between the number of species of carabids and environmental variables showed that the cover of herbs and the amount of potential food were the most important factors controlling the number of species of carabids in the studied habitats. The number of species of carabids increased with abundance of prey and with the decreasing of cover by herbs (Table 2). In the course of this study we observed that there is a significant positive correlation between the cover of herbs and the abundance of potential prey ($r_s= 0.7046$, $p<0.0001$, $n=80$).

Discussion

This study indicates that there are dramatic changes in carabid assemblages after clear-cutting of native beech forests, when non-native Norway spruce was planted in these habitats. It was also demonstrated that the number of individuals and the number of species of carabids do not increase significantly by the age of the Norway spruce plantation (Fig. 1). Studying the carabids along a beech-spruce transect, Šustek (1984) observed that the number of individuals, the species richness and the diversity were clearly lower in the spruce monoculture. Niemelä et al. (1993) also demonstrated that the increased homogeneity of the vegetation had drastic influence on the carabids, and the homogeneity contributed to the decrease in carabid diversity. Similarly to our result, Szyszko (1986) stressed that with ageing of the spruce plantation there is no regeneration observed; the carabid assemblage of the older spruce plantations was not closer to the native forest than the younger ones. Magura et al. (2000) pointed out, however, that even a limited management regime, which creates gaps and increases the number of broad-leaved trees, causes a significant increase in species richness.

During the study we demonstrated that the soil pH, the cover of herbs, and the abundance of potential prey were the most important factors to control the number of individuals and species of the carabids. The positive correlation between the number of individuals and the pH was explained by the fact that none of the species collected preferred an acidic pH (Thiele 1977). Earlier studies also stressed that the spatial distribution of carabids and the habitat preference was controlled by the soil pH (Paje and Mossakowski 1984, Butterfield 1997). This relationship is also explained by the fact that the most sensitive development stages of carabids (eggs and larvae) are very sensitive to environmental conditions (Lövei and Sunderland 1996); therefore, in habitats with unfavourable environmental conditions (extremely acid soil pH) the development may not proceed, resulting in a decreased number of individuals. Furthermore, the majority of the prey of cara-

Table 1. Two-way indicator table for the species which were present at levels of five or more individuals. The IndVal% column is the species indicator value for the habitat. ** indicates a significant (p<0.01), while "ns" not significant IndVal result. Inside columns, the first number is the number of individuals present, and the second one is the number of traps where the species was present in the habitat.

	IndVal %		Beech forest	5 yr old	15 yr old	30 yr old	50 yr old
					spruce plantation		
50 yr old spruce plantation							
Pterostichus oblongopunctatus (Fabr.)	51.04	**	9/8	2/1	3/2	21/10	49/12
Forests with closed canopy (beech forest, 15, 30 and 50 yr old plantations)							
Carabus hortensis (Linn.)	83.64	**	57/12	3/3	81/15	91/16	31/13
Beech forest							
Carabus violaceus (Kraatz)	76.72	**	67/16	14/9	5/3	5/4	9/6
Pterostichus melanarius (Illig.)	71.95	**	118/16	13/8	46/11	53/11	0/0
Aptinus bombarda (Illig.)	65.73	**	29/11	1/1	0/0	0/0	1/1
Pterostichus anthracinus (Illig.)	50.68	**	30/10	5/5	0/0	6/5	0/0
Carabus convexus (Fabr.)	47.60	**	21/11	6/2	3/3	7/5	0/0
Carabus nemoralis (O. F. Müll.)	44.85	**	29/8	0/0	5/3	3/3	2/2
Cychrus caraboides (Linn.)	42.19	**	11/9	0/0	0/0	3/2	8/6
All habitats							
Abax parallelepipedus (Pill. et Mitt.)	93.75	ns	308/16	34/13	174/16	139/15	38/15
Molops piceus (Panz.)	60.00	ns	50/15	34/15	3/2	0/0	79/16
Abax parallelus (Duftschm.)	51.25	ns	36/13	11/5	8/6	52/14	4/3
Carabus glabratus (Payk.)	40.00	ns	20/11	12/8	5/5	1/1	16/7
5 yr old spruce plantation							
Harpalus rufipes (De Geer)	53.57	**	3/3	20/9	1/1	0/0	0/0
Pterostichus niger (Schall.)	44.28	**	3/3	37/9	23/10	9/6	5/4
Carabus coriaceus (Sokol.)	38.46	**	8/5	10/8	1/1	1/1	2/2
Amara communis (Panz.)	25.00	**	0/0	4/4	0/0	0/0	0/0
Harpalus latus (Linn.)	25.00	**	0/0	4/4	0/0	0/0	0/0
Platyderus rufus (Duftschm.)	15.63	**	0/0	5/3	0/0	0/0	4/2

bids are also very sensitive to soil pH which could further affect the abundance and species richness of carabids.

The negative correlation between the species richness of the carabids and the cover of herbs is somewhat unexpected. It was demonstrated by Niemelä et al. (1994), studying boreal forests, that the decreasing of the cover of herbs resulted in the decreasing of the potential prey abundance, which may result in the decreasing of the number of species and the number of individuals of the carabids. We found significant positive correlation between the cover of herbs and the abundance of potential prey. On one hand there was a direct influence of herbs producing more prey animals. On the other hand, there were indirect effects of herb density and cover: the high density of the herbs decreased the number of species of the carabid assemblage. A dense cover of herbs may prevent the movement and food capture of the forest species, because these species are not adapted to such conditions. Similar arguments were used by Guillemain et al. (1997) explaining that a thick litter layer resulted in a decreased abundance and number of species of the carabids.

Our study implies that the number of individuals and species richness of carabids are determined not only by abiotic environmental factors, like soil pH and cover of herbs but also by biotic factors, like the abundance of the carabids' prey. The significant effect of prey availability on carabids has been emphasised only recently (Guillemain et al. 1997). It stresses the importance of a synthesis in carabid ecology, which integrates the influence of biotic and abiotic ecological factors on carabids. A uniform resource distribution over time with a higher abundance of prey, through the smaller resource-overlap and the decreased intra- and interspecific competition (Loreau 1990), may explain the observed significant positive correlations. These relationships may be rather complex. The carabid larvae may be more specialized with respect to diet than the adults (Thiele 1977). Moreover, competitive invertebrates, like Chilopoda or Opiliones, might have influence on the composition of carabid assemblages.

The characteristic species groups of carabids have different environmental preferences. The 5 yr old Norway spruce plantation was characterised by species which prefer

Table 2. Relationship between the number of individuals, the number of species per trap and the studied environmental variables by multiple linear regression. "ns" : not significant, * : $p<0.05$ and *** : $p<0.001$.

	Number of individuals	Number of species
F	10.3404	11.1902
DF	12,67	12,67
r^2	0.6494	0.6671
p<	0.0001	0.0001
Soil temperature	ns	ns
Surface air temperature	ns	ns
Relative air humidity	ns	ns
Soil pH (24.5°C)	+*	ns
Soil compactness	ns	ns
$CaCO_3$ content of soil	ns	ns
Organic content of soil	ns	ns
Cover of leaf litter	ns	ns
Cover of herbs	ns	–*
Cover of shurbs	ns	ns
Canopy cover	ns	ns
Number of carabid prey	+***	+***

the partially open habitats and the microclimatic conditions of these open habitats (*Harpalus rufipes*, *Pterostichus niger*, *Carabus coriaceus*, *Amara communis*, *Harpalus latus*, *Platyderus rufus*). These species usually disappear by the time of the closure of the canopy or have fallen in abundance. Baguette and Gérard (1993) also published data on the abundance of carabid species in spruce plantations of different ages, and they also found the following species characteristic for the young plantation: *Pterostichus niger*, *Amara communis*, and *Harpalus latus*. In our study *Carabus coriaceus* was characteristic of the 5 yr old plantation, while Baguette and Gérard (1993) found it characteristic of old plantations. However, it was also frequent in the beech forest, suggesting that this species survives in the young plantation after the clear-cutting. Niemelä et al. (1993) and Spence et al. (1996) also reported that forest specialist species may survive in lodgepole pine *Pinus concordata* – white spruce plantations *Picea glauca*.

The forest specialist species characteristic of the beech forest (see Table 1) require the microclimatic conditions specific to the forests with closed canopy, therefore they also appeared in the plantations where the canopy was closed. Generalists of closed forests also require a closed canopy regardless of the species of the canopy layer.

The result of the indicator species analysis showed that the species composition of the carabid assemblages changed significantly during the forestry management cycle: 1) the clear-cutting of the natural forest and the plantation of the Norway spruce monoculture resulted in the complete disappearance or a dramatic reduction of the number of individuals of the characteristic species of the native beech forest. 2) In the young plantation with open canopy layer there were species typical of the open habitats. They either disappeared after the closure of the canopy or remained with abundance reduced significantly. 3) In the older monocultures only habitat generalists and closed-canopy forest generalists occurred. We would like to stress that in these areas we did not find there any species characteristic of the closed-canopy Norway spruce plantations. It may be explained by the fact that Norway spruce is not native in Hungary. It was in the 50 yr old plantation, where *Pterostichus oblongopunctatus* was most frequent. This species is a typical generalist species in the forests of Hungary; high abundance in the old Norway spruce plantation is explained by the fact that it tolerates the rather acid soils, as was demonstrated by laboratory experiments (Paje and Mossakowski 1984).

The changes in the species composition of the carabids during a forestry management cycle are similar to those observed by Niemelä et al. (1993, 1994). Studying mature lodgepole pine – white spruce forest and five age categories of the forest developed after the clear-cutting they concluded that: 1) mature forest specialists disappear from the young forest or their abundance decreases heavily, 2) after clear-cutting, the number of individuals of the species characteristic of the open habitats increases in the young forests, 3) the changes do not influence significantly the forest generalists. These conclusions were supported by a great many other field studies (Šustek 1981, Magura et al. 1997).

The plantation of non-native species (so-called introduced patch, see Forman and Godron 1986) may cause serious damage to the native fauna through the elimination of the original habitats. They also may cause problems in an indirect way through fragmentation (Niemelä et al. 1993, 1994). Our studies demonstrated that the clear-cutting of the native beech forest and the plantation of Norway spruce monocultures in these areas resulted in a dramatic change in the environmental factors. The number of species, the number of individuals and the composition of the carabid assemblages also changed significantly. The changes in the carabid assemblages can be explained by the changes of abiotic and biotic factors, which control the distribution and composition of carabids. Our results demonstrated that the number of individuals and the number of species of the carabid assemblages did not increase significantly with the age of the plantation. The composition of the carabid assemblages of the old plantations were not closer to the native beech forest than to that of the younger ones. During the studied forestry management cycle there is no regeneration of the carabid assemblages. It means that the regeneration of the native carabid assemblages need active nature management. Magura et al. (2000) showed that creating gaps in the Norway spruce plantations and facilitating the re-establishment of the native herbs and shrubs enhances the regeneration of the native carabid assemblage.

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