

Conifer introductions decrease richness and alter composition of litter-dwelling beetles (Coleoptera) in Carpathian oak forests

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Abstract

Original oak (*Quercus*) forests in the southwestern Carpathian Mountains, Slovakia, were replaced by non-forest cover or managed stands often containing introduced non-native tree species. We compared the composition, richness, and abundance of litter-dwelling beetle (Coleoptera) communities in 30 stands across three management types: (i) reserved stands that most closely approximate the pre-clearance oak forest, (ii) managed stands of local tree species, and (iii) managed stands with introduced tree species. We collected beetle adults using a dry sieve method from litter collected monthly at eight randomly placed 25 cm × 25 cm subplots on each plot during the 2004 growing season (giving a total of 1680 samples). Overall, we recorded a total of 1291 individuals belonging to 143 species. Managed stands had different coleopteran composition, and lower total richness and abundance, than reserved stands; these differences were more pronounced in managed stands with introduced tree species. However, coleopteran richness varied with overstory composition; while managed stands dominated by oak did not differ from reserved stands, those dominated by introduced *Picea abies* were least species rich. Predators and saprophages showed contrasting patterns; predators were more sensitive to forest management than saprophages in terms of species richness, but saprophages were more sensitive in terms of abundance. Both richness and abundance tended to gradually decrease as the originally dominant oak was replaced by conifers. Our results suggest that maintaining the original overstory composition in managed forests, and setting aside forest reserves, can preserve litter-dwelling beetle communities typical of oak forests in the western Carpathians.

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1. Introduction

Beetles (Coleoptera) are the most abundant and varied group of soil-dwelling insects that inhabit soil surface and litter layers (Wallwork, 1970). Together with other soil invertebrates they have an enormous effect on the physical and chemical properties of soils, and influence almost every level of the decomposition cascade (Wolters, 2000). They modify decomposition processes directly by feeding on organic matter and indirectly by influencing microbial communities (Wolters,

1991; Shaw, 1992; Egert et al., 2003). The role of beetles as predators of other soil animals is also important (Hengeveld, 1980). Epigaeic beetles can be used as environmental, ecological, and biodiversity indicators (Rykken et al., 1997; Rainio and Niemelä, 2003). However, despite their significant role in decomposition, ecological studies of entire litter-dwelling beetle communities are rather scarce (Carlton and Robison, 1998; Rieske and Buss, 2001; Heyborne et al., 2003) as the majority of studies tends to focus only on ground-beetles (Carabidae) (e.g., Butterfield, 1997; Rykken et al., 1997; Fahy and Gormally, 1998; Magura, 2002; Poole et al., 2003).

In forest ecosystems, beetle communities respond to environmental variation imposed by heterogeneity in the overstory tree canopy (Lawton, 1983; Hunter, 1999). For example, beetle communities in forests may vary with overstory tree species composition and age (Heyborne et al., 2003). The

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species composition and abundance of litter-dwelling beetles, especially saprophages, can be particularly influenced by the quality and amount of leaf litter and coarse woody debris (Lattin, 1993; Økland et al., 1996; Magura et al., 2004; Warriner et al., 2004; Vanderwall et al., 2006). Forest management practices such as timber harvest, silvicultural treatments, and replanting of cut-over areas can significantly modify forest ecosystems. Removal of overstory trees alters post-harvest microclimate (e.g., Heithecker and Halpern, 2006) and forest understory plant communities (e.g., Halpern et al., 2005; Dovčiak et al., 2006), as well as litter layer characteristics and the amount of coarse woody debris (Freedman et al., 1996; Siitonens, 2001). Harvesting intensity and subsequent vegetation change can influence litter-dwelling beetle communities (Esseen et al., 1997; Koivula, 2002; Siira-Pietikäinen et al., 2003). As a consequence, forest management can lead to large alterations in forest beetle communities (Niemelä et al., 1993).

Forest ecosystem recovery after a timber harvest depends on the method of forest regeneration and subsequent silvicultural treatments that may favor certain local tree species or introduce new species to the ecosystem (including non-native species). Thus, the structure of the second-growth forest may differ dramatically from that of the original forest ecosystem. Litter-dwelling beetles are especially sensitive to structural and chemical properties of leaf litter (Scheu et al., 2003; Pontégnie et al., 2005), and these often differ significantly among tree species (e.g., Binkley and Giardina, 1998; Neirynck et al., 2000; Rice et al., 2004). The variation in litter chemistry among tree species and tree functional types (e.g., broadleaved versus conifer tree species) can have a considerable effect on ecosystem processes as it may influence overall soil properties such as soil acidity, fertility, and forest floor turnover rate, as well as the abundance and diversity of soil invertebrates (Reich et al., 2005). Ground-dwelling invertebrate communities may be particularly sensitive to changes from local indigenous vegetation to stands of non-native species (Samways et al., 1996). For example, non-native conifers such as Norway spruce (*Picea abies*) may negatively influence the composition and species richness of local carabid communities when compared to native beech (*Fagus sylvatica*) forest (Finch, 2005). Introduced conifer tree species may modify the forest floor environment beyond the range of adaptability of specialist beetle species such as deciduous forest specialists (Elek et al., 2001; Finch, 2005).

The main objective of this paper is to examine how past forest management and the related shift in forest composition from oak (*Quercus*) to non-native tree species influenced litter-dwelling beetle (Coleoptera) communities in the southwestern Carpathians, a historically human-dominated region. To reach this objective, we compared composition, richness, and abundance of litter-dwelling beetle communities across three distinct types of forest management ranging from reserved forest stands, to managed stands of local tree species, to managed stands containing introduced tree species. We address the following questions: (1) Does community composition of leaf-litter dwelling coleopterans progressively diverge with changes in forest management type from least to most intensive? (2) Are communities of litter-dwelling coleopterans

most species rich and most abundant in preserved forests and least species rich and least abundant in stands with introduced tree species? (3) How do these richness and abundance patterns differ between the two main trophic groups – predators and saprophages? (4) How do richness and abundance of coleopterans vary with overstory composition?

2. Materials and methods

2.1. Study area

The study was conducted in the Štiavnické Vrchy Mountains Protected Landscape Area in the western Carpathians, Slovakia. This region has mean annual precipitation of 895 mm and a mean annual temperature of 7.6 °C (Hlavaček, 1985). The geology and soils of the area are of volcanic origin; rich brown soils overlaying andesite bedrock are most frequent (Konečný et al., 1998). Undisturbed forests in the region tend to be dominated by oak (mainly *Quercus petraea* Liebl.) and beech (*Fagus sylvatica* L.) (Korpel', 1989).

The region has been used intensively for mining of metals since the 13th century. Human settlement, mining, and associated intensive timber production left a large portion of this area deforested, paralleling a general decline of low elevation forests in Slovakia (Korpel', 1989) and elsewhere in Europe (Gilg, 2005). The loss of the original forests in the Štiavnické Vrchy Mountains was partially compensated for by extensive reforestation with non-native species. Norway spruce (*Picea abies* L.) and European larch (*Larix decidua* Mill.) were introduced from higher altitudinal zones in nearby regions, and Austrian pine (*Pinus nigra* Arnold.) and black locust (*Robinia pseudoacacia* L.) were introduced from outside the western Carpathians (Blattný and Šťastný, 1959; Holubčík, 1968). The vast majority of mature forests in the region are of second-growth origin, and they continue to be used for timber production, while only a few proxies of the original forests remain within small areas set aside as nature reserves.

2.2. Study design

Based on forest management plans and stand maps, we selected 30 stands within a 300–560 m elevation zone on SE, S, or SW facing slopes in mature forests belonging to one of the two forest types of beech-oak association (*Fageto-Quercetum*) with comparable mean potential overstory composition — *Quercus petraea* Liebl. (55–60%), *Fagus sylvatica* L. (20–25%), *Carpinus betulus* L. (5–10%), *Acer platanoides* L. (5–10%), and *Tilia cordata* Mill. (5%) (forest types 2305 and 2311; Hančinský, 1972). These two forest types were selected because they approximate the pre-clearance forest vegetation that is likely to have occurred across a large portion of the study area and because they are present in the reserved stands of the Kašivárová National Nature Reserve which contains the closest modern analogues of these pre-clearance forests (c.f., Korpel', 1989). By definition, these forest types have a broadly similar abiotic environment (soil and climate) regardless of the current overstory species composition (Hančinský, 1972).

The stand selection was stratified to accommodate the range of current species composition and three broad forest management types implemented within the study area: (a) reserved stands (RS) free of direct management intervention for >150 years (four plots); (b) managed stands without introduced tree species (MI−) dominated either by native *Quercus petraea* (*Q. pet.*, five plots) or by other native tree species (o. nat., five plots); and (c) managed stands with introduced tree species (MI+) – *Larix decidua* (*L. dec.*, five plots), *Picea abies* (*P. abi*, five plots), *Pinus nigra* (*P. nig.*, four plots), or *Robinia pseudoacacia* (*R. pse*, two plots). Both categories of managed stands experienced typical silvicultural treatments (e.g., regular thinning) and were of second growth origin. The individual stand types did not occur equally frequently within the landscape. We were able to locate only two stands dominated by *Robinia pseudoacacia*; we will report results for this species only to the extent that, as the only introduced broad-leaf species, it provides a considerable ecological contrast to the introduced conifers. All managed stands (MI− and MI+) were located in forests managed for timber and all reserved stands (RS) were located within the Kašivárová National Nature Reserve (Fig. 1).

2.3. Field sampling and laboratory procedures

We established a 30 m × 30 m study plot within each selected stand. The current forest composition was characterized by measuring diameter at breast height (dbh, at 1.3 m

height) of all trees (dbh > 6 cm, including both overstory and midstory trees) within each plot and calculating relative proportions (%) of the individual tree species for each plot and stand type (Table 1).

Litter-dwelling Coleoptera were sampled monthly during the snow-free period from April through October (seven sampling intervals) in 2004. A total of 240 subplots were sampled during each sampling interval by randomly placing 8 subplots (25 cm × 25 cm) within each plot and collecting most of the LFH horizon (giving a total of 1680 samples for the sampling season). Litter-dwelling beetles were extracted from the litter using the dry sieve method with a set of three sieves of 12 mm, 5 mm, and 1 mm mesh sizes (Wallwork, 1970). This method is designed to measure the abundance and composition of litter-dwelling arthropods as it targets a particular volume of leaf litter. While our methodology is designed to characterize coleopteran communities across the entire season regardless of beetle activity levels (unlike pitfall traps), it may underestimate large mobile species that are able to take evasive action during the approach of a person sampling (Spence and Niemalä, 1994). Thus, any differences in richness or abundance of the more active species (e.g., top coleopteran predators) in this study should be seen as conservative estimates of the actual trends as this potentially sensitive species group may have been under-sampled.

After sieving, samples were visually examined for adult beetles and manually sorted. Beetles were immobilized using ethyl acetate, mounted onto a paper card, and labeled. Each specimen was identified to species (if possible) using a binocular microscope with maximum magnification of 100×. Nomenclature follows Jelínek (1993) and the assignment of trophic groups follows Freude et al. (1964, 1967, 1971, 1974, 1981, 1983). Data from the eight subplots and seven sampling dates at each plot were pooled together to characterize the overall mean species composition, richness, and abundance within each plot across the whole sampling period. Richness and abundance were calculated and analyzed for all species together and separately for predators and saprophages – the two main trophic groups encountered within the leaf litter samples.

2.4. Statistical analyses

The differences in coleopteran species composition among the three forest management types (RS, MI−, and MI+) were studied using ordination techniques. Detrended correspondence analysis (DCA) with detrending by segments on presence/absence data was used to describe the general variation in species composition among study plots. Species composition was further analyzed with constrained ordination (CANOCO; ter Braak and Šmilauer, 1998). In order to avoid the distortion of the ordination space caused by a large number of zero values and the noise in the data due to rare species (Gauch, 1982), species with low dominance (<1% of total numbers) were removed from this analysis. We related community variability to the forest management types using a unimodal response model suggested by the relatively heterogeneous data and DCA

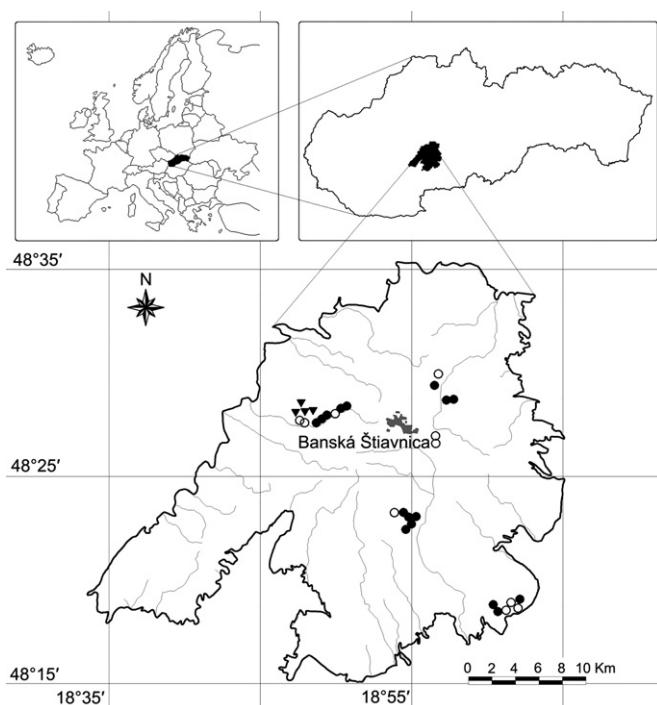


Fig. 1. Study stand locations in the Štiavnické Vrchy Mountains Protected Landscape Area in the western Carpathians, Slovakia. The Protected Landscape Area is centered on the city of Banská Štiavnica. Stands are depicted by forest management type — reserved stands (RS, ▼), managed stands without introduced tree species (MI−, ○), and managed stands with introduced tree species (MI+, ●).

Table 1

Stand composition (mean species proportion in % \pm 1 S.E.) across forest management types — reserved stands (RS), managed stands without introduced tree species (MI−), and managed stands with introduced tree species (MI+)

Tree species	RS	MI−		MI+			
		<i>Q. pet</i> ^a (n = 4)	<i>Q. pet</i> ^a (n = 5)	o. nat ^a (n = 5)	<i>L. dec</i> ^a (n = 5)	<i>P. abi</i> ^a (n = 5)	<i>P. nig</i> ^a (n = 4)
<i>Quercus petraea</i> Liebl.	86.6 \pm 7.6	74.9 \pm 15.0	35.7 \pm 5.4	19.9 \pm 6.5	5.8 \pm 2.7	14.7 \pm 11.8	1.0 \pm 1.0
<i>Quercus cerris</i> L.	—	11.4 \pm 18.3	—	7.5 \pm 4.4	—	0.8 \pm 1.2	—
<i>Fagus sylvatica</i> L.	9.2 \pm 4.5	—	1.1 \pm 1.8	—	1.5 \pm 2.3	—	—
<i>Carpinus betulus</i> L.	0.6 \pm 0.9	0.6 \pm 1.0	18.3 \pm 20.8	1.5 \pm 1.2	4.8 \pm 5.7	0.8 \pm 1.2	0.6 \pm 0.6
<i>Acer platanoides</i> L.	0.2 \pm 0.3	—	—	—	—	—	0.7 \pm 0.7
<i>Tilia cordata</i> Mill.	0.5 \pm 0.7	0.2 \pm 0.3	—	—	—	—	—
<i>Acer campestre</i> L.	—	0.1 \pm 0.2	0.3 \pm 0.4	—	—	—	3.1 \pm 0.3
<i>Cerasus avium</i> L.	—	—	—	—	—	—	13.8 \pm 2.8
<i>Fraxinus excelsior</i> L.	—	—	—	0.3 \pm 0.5	—	—	—
<i>Sorbus torminalis</i> L.	—	0.3 \pm 0.5	—	0.4 \pm 0.6	—	—	—
<i>Abies alba</i> Mill.	3.1 \pm 4.6	6.7 \pm 8.1	10.2 \pm 16.3	—	13.0 \pm 15.6	—	—
<i>Pinus sylvestris</i> L.	—	5.7 \pm 6.8	34.0 \pm 27.2	24.0 \pm 5.3	19.5 \pm 9.3	11.9 \pm 12.5	1.7 \pm 1.7
<i>Larix decidua</i> Mill. ^b	—	—	—	46.1 \pm 11.9	—	—	—
<i>Picea abies</i> L. ^b	—	—	—	—	50.8 \pm 12.7	—	—
<i>Pinus nigra</i> Arnold ^c	—	—	—	—	4.7 \pm 5.6	66.8 \pm 21.4	3.6 \pm 3.6
<i>Robinia pseudoacacia</i> L. ^c	—	—	—	—	—	5.1 \pm 7.6	75.4 \pm 2.9

^a Species dominating overstory: *Q. pet* = *Quercus petraea*, o. nat = other native species, *L. dec* = *Larix decidua*, *P. abi* = *Picea abies*, *P. nig* = *Pinus nigra*, *R. pse* = *Robinia pseudoacacia*.

^b Non-native tree species introduced from higher elevations of adjacent Carpathian mountain ranges.

^c Non-native tree species introduced from outside the Carpathian mountains.

results (gradient length >3.5 SD; c.f., ter Braak and Šmilauer, 1998). Partial canonical correspondence analysis (CCA) was used to test the null hypothesis that there is no difference in community composition among the management types after the effect of altitude is partialled out. The Monte Carlo permutation test (999 unrestricted permutations) was employed to assess the statistical significance of analyzed models. We based our analyses on the test on the trace.

The overall trends in coleopteran species richness and abundance across the forest management types and across stands dominated by different overstory species were tested using one-way ANOVA. For those tests that yielded significant main effects ($P \leq 0.05$), the significant pairwise differences between the group means were identified with a generalized Tukey's HSD test for unequal sample sizes (StatSoft, Inc., 2001). The homogeneity of variances between groups was tested using a Hartley F max test, the normality within groups was tested using a Shapiro–Wilks test, and the data were log-transformed when ANOVA assumptions were not met.

We used multiple regression analysis to determine which plot variables had the greatest influence on coleopteran species richness and abundance. The full set of predictor variables included the altitude, the proportion of *Quercus*, and the proportion of all conifers pooled together; none of the individual tree species occurred at significant proportions at enough plots to warrant their inclusion in the full model as separate predictors. The best models were identified by the best-subset regression method using Mallow's *Cp*. To meet the normality assumptions, *Quercus* and conifer proportions were arcsine square-root transformed, while altitude, saprophage richness, total abundance, and predator abundance were log transformed.

3. Results

We collected a total of 1291 individuals belonging to 143 species from 24 families of Coleoptera. The five most common species accounted for 53% of the total number of sampled individuals: *Atheta fungi* (20.8%), *Ptenidium pusillum* (9.1%), *Euplectus signatus* (9.1%), *Cephennium machulkai* (8.8%) and *Corticaria elongata* (5.3%). Except for *P. pussillum*, which occurred almost exclusively (94.1%) within the two stands dominated by non-native *Robinia pseudoacacia*, these species were well represented across all forest management types.

3.1. Changes in composition of beetle communities

Plots from the reserved stands and the two types of managed stands (with and without introduced species) tended to occupy different portions of the ordination space, suggesting that the composition of litter-dwelling beetle communities differed among the three forest management types (Fig. 2). Beetle community composition appeared to progressively diverge with management intensity; plots from managed stands without introduced tree species (MI−) tended to cluster closer to the plots from the reserved stands (RS) than the plots from managed stands with introduced tree species (MI+) did (question 1). The only larger deviation from this trend was the stand with a relatively open *Pinus nigra* overstory and a well developed *Quercus* understory; this stand had a beetle community very similar to those of the *Quercus* dominated reserved stands (plot 25 versus RS plots, Fig. 2).

The observed differences in beetle community composition among the three management types corresponded to significant

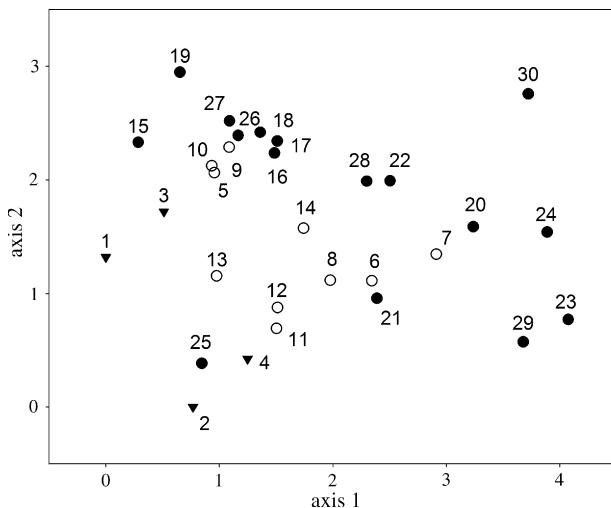


Fig. 2. DCA plot depicting overall differences in beetle species composition among stands and forest management types — reserved stands (RS, ▼), managed stands without introduced tree species (MI-, ○), and managed stands with introduced tree species (MI+, ●). The first two DCA axes explained 12.1% ($\lambda_1 = 0.746$) and 6.1% ($\lambda_2 = 0.379$) of variation, respectively. Note that the MI+ plot 25 has a well developed *Quercus* understorey under a relatively open canopy of *Pinus nigra*.

changes in the proportions of several common beetle species (CCA, $F = 3.028$, $p < 0.007$, Fig. 3.). The reserved stands had higher proportions of *Tachyporus hypnorum* and *Cryptophagus badius* than did either of the two types of managed forest.

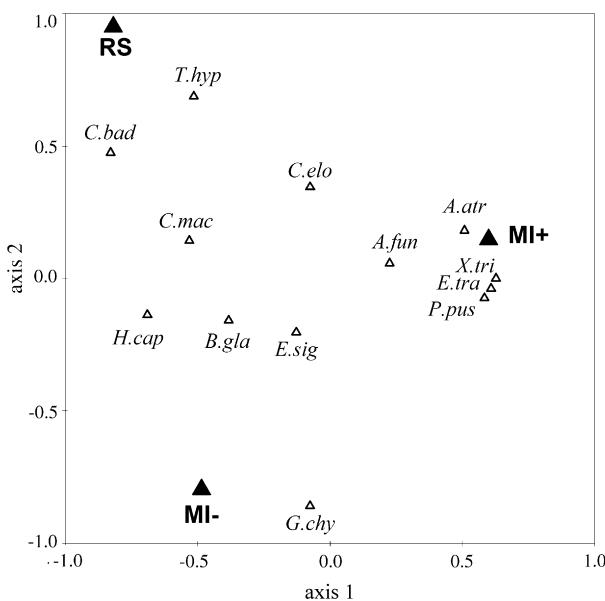


Fig. 3. CCA biplot depicting the main differences in beetle species composition among forest management types (▲) — reserved stands (RS), managed stands without introduced tree species (MI-), and managed stands with introduced tree species (MI+) ($F = 3.028$, $p < 0.007$). The first two CCA axes explained 10.8% ($\lambda_1 = 0.313$) and 4.5% ($\lambda_2 = 0.131$) of variation, respectively. Only species (△) with $\geq 10\%$ of variation accounted for by the model are displayed — *Atheta fungi* (A. fun), *Atomaria atricapilla* (A. atr), *Bryaxis glabricollis* (B. gla), *Cephennium machulkai* (C. mac), *Corticaria elongata* (C. elo), *Cryptophagus badius* (C. bad), *Enicmus transversus* (E. tra), *Euplectus signatus* (E. sig), *Geostiba chyzeri* (G. chy), *Habrocerus capilaricornis* (H. cap), *Ptenidium pusillum* (P. pus), *Tachyporus hypnorum* (T. hyp), and *Xantholinus tricolor* (X. tri).

Managed stands without introduced tree species were characterized by an increased proportion of *Geostiba chyzeri*, while managed stands with introduced tree species had increased proportions of *Atheta fungi*, *Atomaria atricapilla*, *Enicmus transversus*, *Ptenidium pusillum* or *Xantholinus tricolor*. The remaining beetle species had less clear affinities toward any single forest management type, but several of them (*Cephennium machulkai*, *Habrocerus capilaricornis*, *Bryaxis glabricollis*) appeared to be related more to the two less intensive management types (RS, MI-). These results further corroborate that beetle species composition differed among the three forest management types; while the beetle communities in managed stands with introduced tree species (MI+) were most distinct, the differences between reserved stands and managed stands without introduced tree species (MI-) were smaller, as several beetle species were represented equally well in both of these management types (question 1).

3.2. Changes in richness and abundance of beetle communities

Reserved stands contained $\sim 40\text{--}50\%$ more species of ground dwelling beetles compared to the managed stands and this difference was highly significant (Fig. 4A) (question 2). A similar trend was apparent for both predators and saprophages, but it was only significant for predators, of which there were a greater number of species (Fig. 4B and C) (question 3). Differences in beetle richness were not very large or significant between the two types of managed stands. A large portion of the considerable difference in total coleopteran richness between reserved and managed stands was due to the fact that several stenotopic litter specialists such as *Cryptophagus deubeli*, *Acallocrates denticollis*, *Mycetea subterranea*, *Plectophloeus zoufali*, and *Alevonota rufotestacea* occurred only in reserved stands (data not shown).

The trends in coleopteran abundance among the management types were similar to the differences in their species richness. Coleopteran communities were $\sim 40\text{--}45\%$ more abundant in reserved stands than in managed stands, but only managed stands with introduced species had significantly lower abundance relative to reserved stands (Fig. 4D) (question 2). Again, similar to beetle richness patterns, the differences in total abundance among management types reflected the differences in the abundance of predators and saprophages. However, unlike richness patterns, the differences in abundance among the management types were more pronounced and significant for saprophages than for predators that typically exhibit higher mobility (Fig. 4E and F) (question 3). These abundance trends emerged only after removal from the analysis of two highly outlying stands with introduced *Robinia pseudoacacia*. These stands supported saprophage beetle communities that were on average only slightly less species rich but >3 times as abundant as their equivalents in reserved stands (data not shown), probably reflecting the high palatability of leaf litter of this nitrogen fixing tree species.

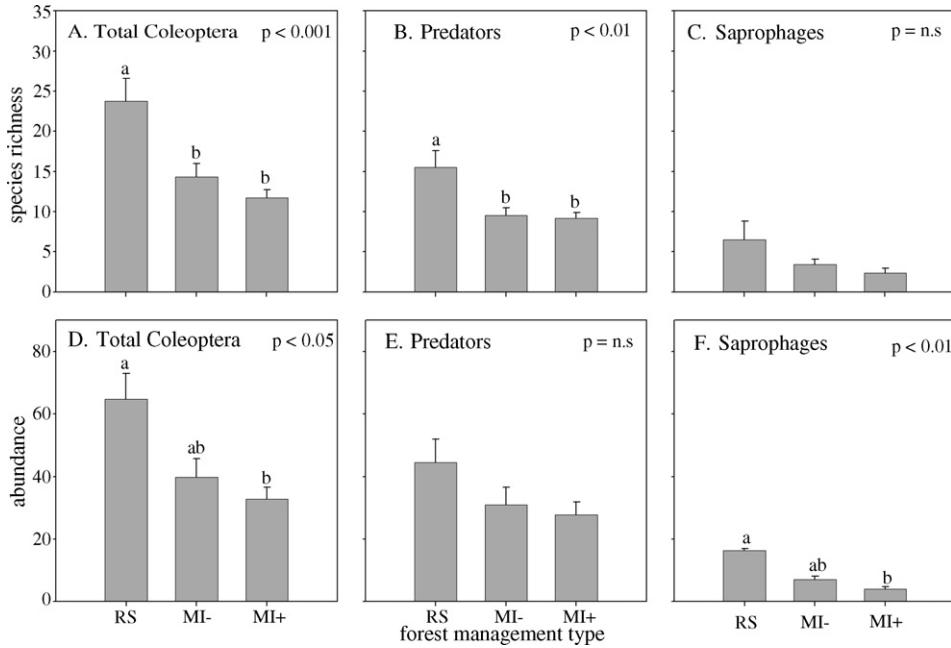


Fig. 4. Mean species richness (A–C) and abundance (D–F) of all Coleoptera and separately of predators and saprophages by forest management type — reserved stands (RS), managed stands without introduced tree species (MI–), and managed stands with introduced tree species (MI+). Different letters indicate significant differences in means ($p < 0.05$) from Tukey's HSD tests for unequal sample sizes. Error bars show +1 S.E. Note that the two highly influential outlying stands of *Robinia pseudoacacia* were not included in these analyses; their inclusion did not change trends in richness (A–C), but trends in abundance (D–F) became statistically non-significant.

3.3. Influence of overstory composition

Species richness of litter-dwelling beetles within the management types was clearly influenced by overstory composition (question 4). Although the richness of all

coleopterans and predators was lower in managed stands relative to reserved stands, it was significantly lower only in managed stands that were dominated by native species other than *Quercus petraea* (o. nat) and stands dominated by species introduced from higher elevations — *Larix decidua* and *Picea*

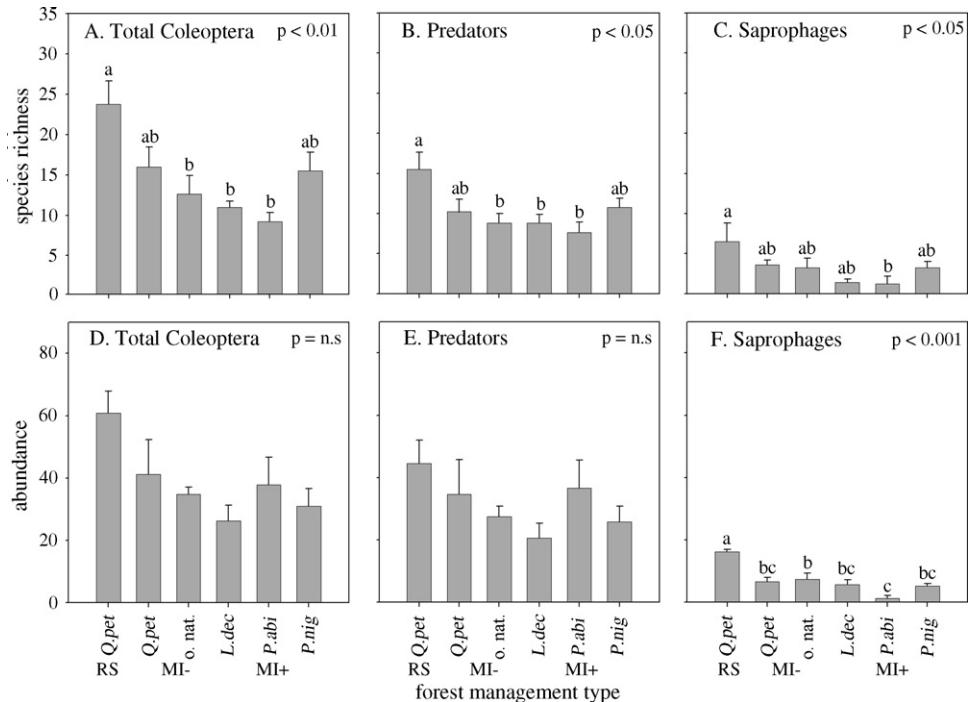


Fig. 5. Mean species richness (A–C) and abundance (D–F) of all Coleoptera and separately of predators and saprophages by stand type — reserved stands (RS), managed stands without introduced tree species (MI–) dominated by native *Quercus petraea* (Q. pet) or other native tree species (o. nat), and managed stands with introduced tree species (MI+) dominated by *Larix decidua* (L. dec), *Picea abies* (P. abi), or *Pinus nigra* (P. nig). Different letters indicate significant differences in means ($p < 0.05$) from Tukey's HSD tests for unequal sample sizes. Error bars show +1 S.E. Note that *Robinia pseudoacacia* stands were not included due to small sample size.

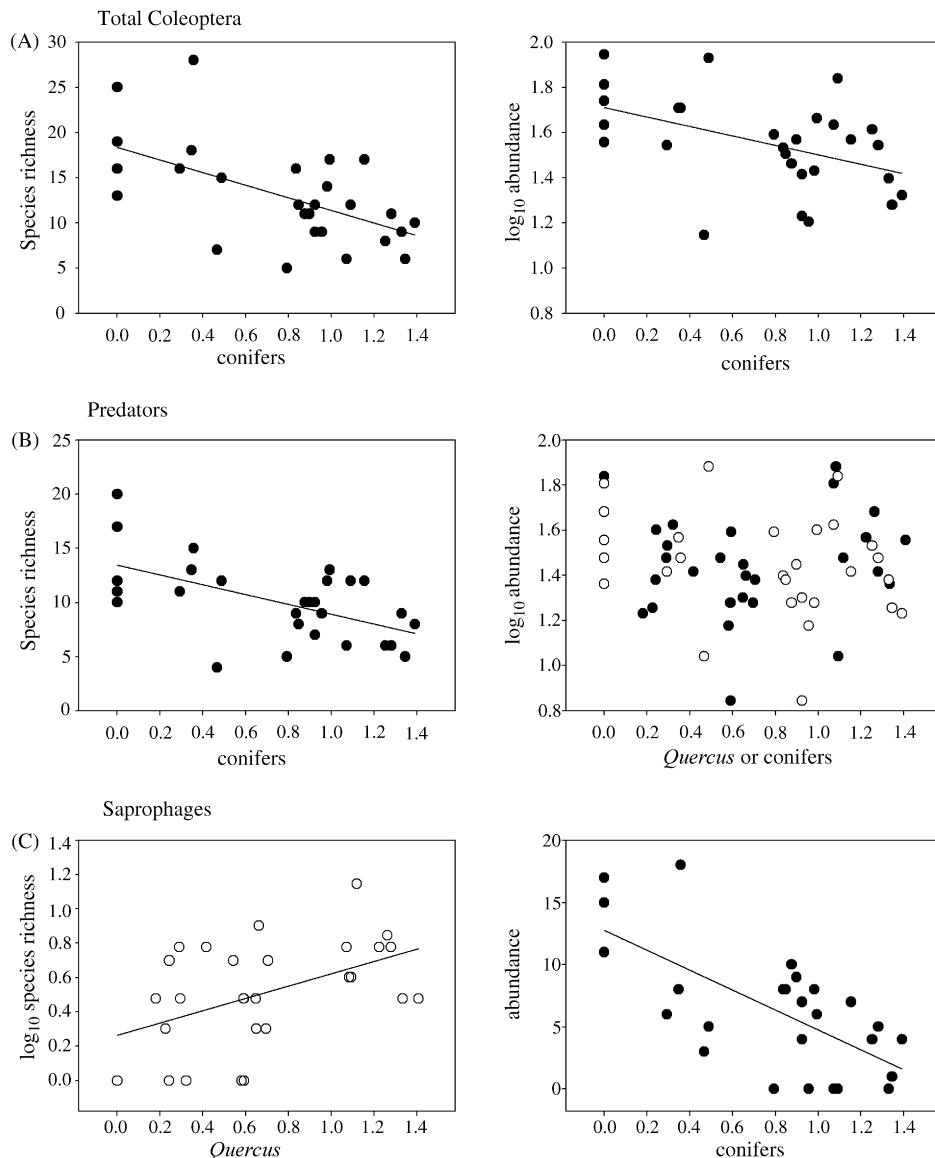


Fig. 6. Overstory influence on species richness and abundance of all Coleoptera (A), predators (B), and saprophages (C). Significant overstory predictors were either conifer (●) or *Quercus* (○) proportions (arcsine square-root transformed %). Model summaries are in Table 2.

abies (Fig. 5A and B). Saprophage richness was also lower in managed versus reserved stands, but it was statistically significantly lower only in stands dominated by *Picea abies* (Fig. 5C).

Overstory species composition did not appear to significantly influence the total abundance of all Coleoptera or the abundance of predators (Fig. 5D and E), but it had a very distinct impact on the abundance of saprophages (Fig. 5F). Saprophages were clearly most abundant in *Quercus petraea* dominated reserved stands and least abundant in stands dominated by introduced *Picea abies*, thus paralleling trends in saprophage richness.

Across all stands, the total and predator richness were negatively related to the proportion of conifers in the overstory, while saprophage richness was positively related to the proportion of *Quercus* (Fig. 6, Table 2). Both the total and saprophage abundances were negatively related to conifers,

saprophage abundance more so than total abundance. The total abundance integrated a lack of response to overstory by predator species (Fig. 6, Table 2). The proportions of *Quercus* and conifers were negatively correlated ($r = -0.91$) as the introduced conifers completely or partially replaced the *Quercus* that dominated the original stands.

4. Discussion

Our results suggest that the composition of leaf-litter dwelling coleopterans progressively diverged from their composition in reserved stands as forest management became more intensive and incorporated introduced tree species (question 1). In addition to compositional changes, litter-dwelling coleopteran communities were less species rich and less abundant in managed forests than in reserved stands, especially when managed forests incorporated introduced

Table 2

Best models for species richness and abundance of total Coleoptera, predators, and saprophages^a

Response variable	Predictors ^b	β	S.E.	R ²	P
Species richness					
Total Coleoptera	Conifers	-0.59	±0.16	0.35	<0.001
Predators	Conifers	-0.57	±0.16	0.32	0.002
Saprophages ^c	<i>Quercus</i>	0.47	±0.17	0.22	0.012
Abundance					
Total Coleoptera ^c	Conifers	-0.47	±0.17	0.22	0.012
Predators ^c					n.s.
Saprophages	Conifers	-0.71	±0.14	0.51	<0.001

^a Best models were determined using best subset multiple regression approach.

^b Arcsine square-root transformed proportions (%).

^c Log₁₀ transformed.

conifers (question 2). Trends in richness and abundance differed by trophic group — predatory beetles represented more species, and their richness was more sensitive to management than was the richness of saprophages. On the other hand, the abundance of less species rich and less mobile saprophages was very sensitive to forest management, while abundance of predators was not (question 3). However, these trends were not absolute, as the impacts of introduced tree species were varied; replacement of *Quercus* with conifers, especially with *Picea abies*, appeared to have the most pronounced effects (question 4).

4.1. Role of forest reserves

Our results provide further evidence that species richness of ground-dwelling invertebrates tends to be highest in native forest ecosystems when compared to semi-natural managed forests and plantations (Samways et al., 1996; Bonham et al., 2002; Finch, 2005). High species richness may increase ecosystem stability (e.g., Tilman et al., 1996), and, conversely, long-term ecosystem stability may promote and maintain biodiversity (Fjeldså et al., 1997). The reserved stands in our study could be characterized by such long-term ecosystem stability; in contrast to the surrounding managed stands, reserved stands did not experience silvicultural treatments or tree species introductions and they were generally free of direct human intervention for >150 years (Korpel', 1989). Such continuity and stability in reserved stands allows for the development of high habitat complexity through gradual accumulation of litter and deadwood in various decomposition classes and through gradual increase in canopy complexity (Similä et al., 2003; Lassau et al., 2005). The more complex environment in old-growth forests increases available micro-habitat, food, and shelter, and thus increases the diversity of ground-dwelling beetles (e.g., Niemelä, 1997). The stability and diversity of environmental conditions in reserved stands is especially important for the occurrence of a number of specialist forest species that tend to be more affected by forestry practices (Niemelä et al., 1993; Koivula, 2002). In our study, a large proportion of the high richness in the reserved stands was due to stenotopic litter specialists characterized by a low dispersal capability and by their absence from the managed

stands; this group of species tends to be frequently constrained to natural undisturbed ecosystems (Eyre et al., 1996; Finch, 2005).

4.2. Impacts of forest management

Overall, changes in litter-dwelling beetle communities in our study followed the differences in forest management type — coleopteran species composition diverged, and richness and abundance decreased in managed stands, but more so in stands with introduced tree species (c.f., Similä et al., 2003; Finch, 2005). These changes corresponded to the replacement of stenotopic or rare beetle taxa typical of undisturbed forest ecosystem of the reserved stands with more frequent eurytopic species. Silvicultural practices in managed stands tend to simplify stand structure and microhabitat features (Koivula and Niemelä, 2002; Magura et al., 2004; Pontégnie et al., 2005). In extremely altered forest stands, for example in plantations of non-native trees, often only habitat generalists and forest generalists can maintain abundant populations while litter-specialists that require microclimate and litter characteristics specific to native forests may be extremely rare or missing (Elek et al., 2001; Magura et al., 2003).

In our study, species richness and abundance decreased as the proportion of the originally dominant *Quercus* decreased and the proportion of conifers increased. Conifers generally represent a foreign element in the natural composition of the studied forest types (Hančinský, 1972), and they are likely to influence negatively the structure and composition of litter-dwelling communities (c.f., Fahy and Gormally, 1998; Similä et al., 2003). Although the negative effects of altering the composition of forest ecosystems tend to be generally more pronounced when native deciduous forest ecosystems are transformed to conifer plantations (Finch, 2005), our results indicate that overstory species may potentially vary in their impacts on litter-dwelling beetle communities. Different overstory tree species frequently differ considerably in their litter quality, and they influence properties of soil environment and associated communities of soil invertebrates (Neirynck et al., 2000; Scheu et al., 2003; Reich et al., 2005).

4.3. Responses of saprophages

Saprophage richness progressively decreased in managed stands as oak was replaced by conifers (especially *Picea abies*), but saprophage abundance was much more sensitive to overstory composition than richness was. Saprophages are directly trophically limited by the quality and quantity of leaf litter and woody debris which serve as food substrate in addition to their role as a habitat (Pontégnie et al., 2005). Saprophage distribution and substrate utilization and decomposition is directly influenced by structural, physical, and nutrient characteristics of leaf litter, especially by leaf toughness, nitrogen and lignin concentrations, carbon/nitrogen and lignin/nitrogen ratios (Berg et al., 1993; Perez-Harguindeguy et al., 2000; Lavelle and Spain, 2001; Hättenschwiler et al., 2005). Moreover, some groups of saprophages such as isopods

and millipedes preferentially feed on certain types of litter (Cárcamo et al., 2000; Zimmer and Topp, 2000). Although oak litter is relatively unpalatable, oak stands tend to form relatively open canopies associated with copious understories of tree saplings of species with highly palatable leaf litter such as maple (*Acer*), hornbeam (*Carpinus*), or lime (*Tilia*) (Pontégnie et al., 2005). As oak is replaced by conifers, and especially by shade tolerant spruce which prevents the development of copious broad-leaved undergrowth, the character of the leaf litter is likely to change toward less palatability.

In addition to these direct trophic relationships, saprophages are characterized by their relatively low mobility, which makes them more susceptible to the negative impacts of forest management on the abundance of small woody debris that provides suitable microhabitat (Wallwork, 1970; Magura, 2002; Warriner et al., 2004). For example, saproxyllic beetles tend to be most abundant and species rich in native forests with large variety and abundance of deadwood (Similä et al., 2003). The conspicuous decrease of saprophage abundance in managed stands in our study may be indicative of other associated changes in ecosystem properties that depend on saprophage abundance; for example, litter decomposition may be further slowed down and nutrient cycling and soil properties altered (c.f., Reich et al., 2005).

4.4. Responses of predators

As opposed to saprophages, responses of predators cannot be explained by direct trophic linkages to leaf litter; instead, they are related to overstory structure, available habitat, and quality and quantity of prey (Hengeveld, 1985; Magura et al., 2001). Over time, introductions of conifers homogenize vertical stand structure (see discussion of saprophage responses) and influence characteristics of the forest floor. Litter under conifers is usually formed by a homogeneously thick and dense needle layer that can provide only a little shelter for large predatory beetles, which, as a consequence, tend to be more abundant in broadleaf litter (Scheu et al., 2003). In addition, we have shown that the abundance and richness of saprophages decreased in managed stands relative to reserved stands proportionately with the proportion of introduced conifers. Thus, at least a part of the trophic base for at least some of the predators was affected, and the changes in predator richness induced by forest management suggest a progression of negative effects through the food chain. Interestingly, while species richness of predatory beetles was clearly negatively affected by forest management in our study, the overall predator abundance was not. This suggests that higher extirpation rates may have occurred in rare predator species rather than in the presently abundant predators that tend to dominate the abundance response. Generally, rare species of forest organisms may be more sensitive to forest management, and responses in species richness may thus precede responses in abundance (Dovčiak et al., 2006). In addition, extirpation of some predatory species inherently increases the available niche space for the remaining species, which in this case may have been able to increase in abundance and thus compensate for an initial loss of total abundance.

5. Conclusions and management implications

The results of this study emphasize the role of strict forest reserves as a refuge for rare specialized litter-dwelling beetle species typical of oak forests and disappearing from surrounding managed landscapes. Beetle communities in reserved forests were most species rich, indicating greater habitat complexity (Lassau et al., 2005), and likely also greater stability (Tilman et al., 1996; Fjeldså et al., 1997), relative to the managed forest ecosystems. Litter-dwelling beetle communities in managed stands had a different species composition and a considerably lower species richness which decreased as the proportion of introduced conifers increased and the proportion of originally dominating oak decreased. The only beetle species able to maintain viable populations in these altered ecosystems were habitat generalists and forest generalists (c.f., Elek et al., 2001; Magura et al., 2003). The negative effects of forest management, especially the effects of conifer introductions, affected saprophage and predator communities differently. Thus, monitoring only the total coleopteran response, or monitoring only certain taxonomic groups within the Coleoptera, may mask serious impacts that forest management may incur on subgroups that may differ in their ecological roles in a forest ecosystem. The adverse effects of introduced conifers on litter-dwelling beetle communities in oak-dominated forest ecosystems underscore the importance of maintaining the original overstory composition in managed forests if preserving forest biodiversity is one of management goals.

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