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The effects of within stand disturbance in plantation forests indicate complex and contrasting responses among and within beetle families

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Abstract

Plantation forests with timber production as the major function are highly fragmented and disturbed regarding the tree species composition and stand area. Their closed canopies also have different microclimatic conditions compared with better studied conservation areas. We studied three beetle families (click, longhorn, and rove beetles) with different ecological demands in lowland plantation forests dominated by Sessile oak and Norway spruce in the Czech Republic. Our main interest was how their species richness, abundance, diversity, body length, rarity, red-list status, species composition and individual species were driven by the main tree species, stand area and canopy openness. We analyzed 3466 individuals from 198 beetle species and the results revealed complex and contrasting responses of the studied beetle families – click beetles mostly preferred sun-exposure and spruce as the dominant tree species, longhorn beetles mainly preferred large stands, whereas rove beetles were mostly influenced by oak as the dominant tree species and increasing area. We also observed that some species had different preferences in plantation forests than is known from the literature. The main conclusions of our results are that the dominance of non-natural spruce plantations and a large stand area (both originating from artificially replanted large clear-cuts) did not affect the majority of the studied taxa as we expected. On the other hand, our results might have been influenced by other factor, such as the current small total area of the former vegetation, which in the past might have led to extinction debt; or a large area of other conifers in the surroundings that might have promoted conifer-associated fauna.

Keywords: biodiversity, canopy openness, forest ecology, Norway spruce, Sessile oak, stand area

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Introduction

European forest plantations, which are intended for timber production, are often composed of tree species that are non-native to a particular site (Bauhus *et al.*, 2010). In Europe, the tree composition generally consists of natural beech and oak stands and large areas are given over to commercial coniferous monocultures, whereas more than three-quarters of the central European forests are managed (Hannah *et al.*, 1995). The usual method of recent forest management is still clear-cutting, when the biomass of a mature forest is completely removed from the stand, followed by replanting of the same stand (Magura *et al.*, 2003). Nevertheless, forest management is mostly restricted by law – e.g. in the Czech Republic, the maximum permitted area that can be clear-cut is 1 ha and the minimum age is 80 years.

Some of the most sensitive taxa to modifications by the management of plantation forests (e.g., changes in canopy openness, tree species alterations, or clear-cutting) are arthropods, of which insects are among the most studied taxonomical groups (Horak, 2013). Beetles belong to one of the four most abundant and species-rich taxa of insects and are an important part of the forest ecosystem food chain. The intensive management of plantation forests can affect the composition of species for some beetle families.

Some authors have discussed the response of particular beetle families in forest ecology and management (Niemelä *et al.*, 1993; Sebek *et al.*, 2012; Horák & Rébl, 2013) and others have also dealt with the foraging and functional ecology of particular families (e.g., ground, rove, or bark beetles) and have demonstrated that particular species of beetle families exist in several different habitats (Lövei & Sunderland, 1996; Bussler *et al.*, 2011; Přikryl *et al.*, 2012). Some studies have investigated different aspects of ecology (e.g., habitats) of particular families or species and have concluded that variations in habitat loss and heterogeneity play a huge role in their sensitivity in terms of distribution and life cycles (Niemelä *et al.*, 1993; Driscoll & Weir, 2005). Furthermore, changes in habitat complexity can shift species richness at certain local sites (Tews *et al.*, 2004). Nevertheless, several management activities that influence beetle diversity are well known – e.g., habitat diversification and an increase in the habitat area, together with improvements in habitat connectivity via the creation of stepping stones and corridors (Kuuluvainen *et al.*, 2002; Horak, 2014).

Functional or conservation traits are still not often used for evaluation of the effect of forest management. Experiments on ecological traits have been performed regarding the invertebrates (e.g., Nota *et al.*, 2013 for springtails, Kunieda *et al.*, 2006 for Hymenopterans and Dipterans). Dupont & Nielsen (2006) suggest that body length is a proxy for body size, which is an important functional trait. Saproxylic beetles are an example of complexity in the food chain and are commonly affected by habitat fragmentation (Horak, 2014), and therefore, are at a high risk of extinction. Conservation traits could be evaluated using more approaches. Red lists serve as a useful mechanism to establish a system for the potential extinction probability of species in different geographical locations (Rodrigues *et al.*, 2006). Seibold *et al.* (2015) tested the red-list status for a phylogenetic signal and for some beetle families (e.g., Elateridae, Tenebrionidae, Melandryidae, and Buprestidae) and almost half of all species were considered to be threatened, whereas, e.g., Nitidulidae, Pselaphidae, and Staphylinidae contained a very low number of threatened species.

The stand and patch structure of plantation forests might be changed from year to year and furthermore, in more extensive and different ways than changes that are caused by natural disturbances (Horak, 2015). We were interested to understand how selected beetle families are driven by stand-level disturbance using two characteristics that reflect forest fragmentation – dominant tree species (i.e., oak vs. spruce) and stand area, and also by one patch-level characteristic that reflects microclimate – canopy light conditions. In this study, we focused on the response of three beetle families: click beetles (Elateridae), as representatives of a highly diversified group in terms of habitat requirements; longhorn beetles (Cerambycidae), as representatives of a group associated with dead wood; and rove beetles (Staphylinidae), as a highly species-rich and abundant group with a low number of specialists.

Methods

Study area

The study area consisted of more than 6000 ha of forest and was situated in the southern half of a spatially continuous area of the eastern Bohemian woodlands (Pardubice Region, Czech Republic). The area was in the past mainly covered by deciduous forests dominated by Sessile oak (*Quercus petraea*) (Neuhauselova & Moravec, 2001). For more than two centuries, most of the area has been planted by conifers (Scots pine, *Pinus sylvestris*) and Norway spruce (*Picea abies*), of which the latter is non-native in the studied area.

Study families and trapping method

We used non-attractive crossed-panel window traps. The height of the center of the trap was 1.3 m. Traps were fixed using two iron sticks and were located in the center of the stand (Loskotová & Horák, 2016). All of the traps were activated at the beginning of March and were deactivated at the end of September 2011. Traps were regularly emptied and cleaned in 2–3 week intervals.

We studied the response of three selected families; firstly, we selected a family of click beetles (Elateridae), which is intermediate in terms of species richness (Bouchard *et al.*, 2009) and its species are highly diversified with respect to their foraging behavior (predators, herbivores, saprophages, etc.), habitat requirements (soil-dwelling, hollow trees, phytophages, etc.), and a majority of species are associated with woodlands (Laibner, 2000). The second family consisted of longhorn beetles (Cerambycidae), which is a family with a medium to high species richness (Bouchard *et al.*, 2009) and the majority of species in temperate zones are associated with bast and wood of woody plants (Sláma, 1998). The third family consisted of rove beetles (Staphylinidae), which is a highly species-rich family (Bouchard *et al.*, 2009) and the majority of its species are generalist predators or feeders of decaying material (Boháč & Matějíček, 2003).

Study environment

We studied the influence of three important forest characteristics on mature stands (i.e., older than 80 years) in plantation forests.

The first variable was a stand-based characteristic that reflects anthropogenic disturbance and fragmentation – namely, the effect of dominant (i.e., main) tree species. This focused on the origin of the tree species, which is a potentially important factor for beetles (e.g., Bertheau *et al.*, 2009). Norway spruce (*P.*

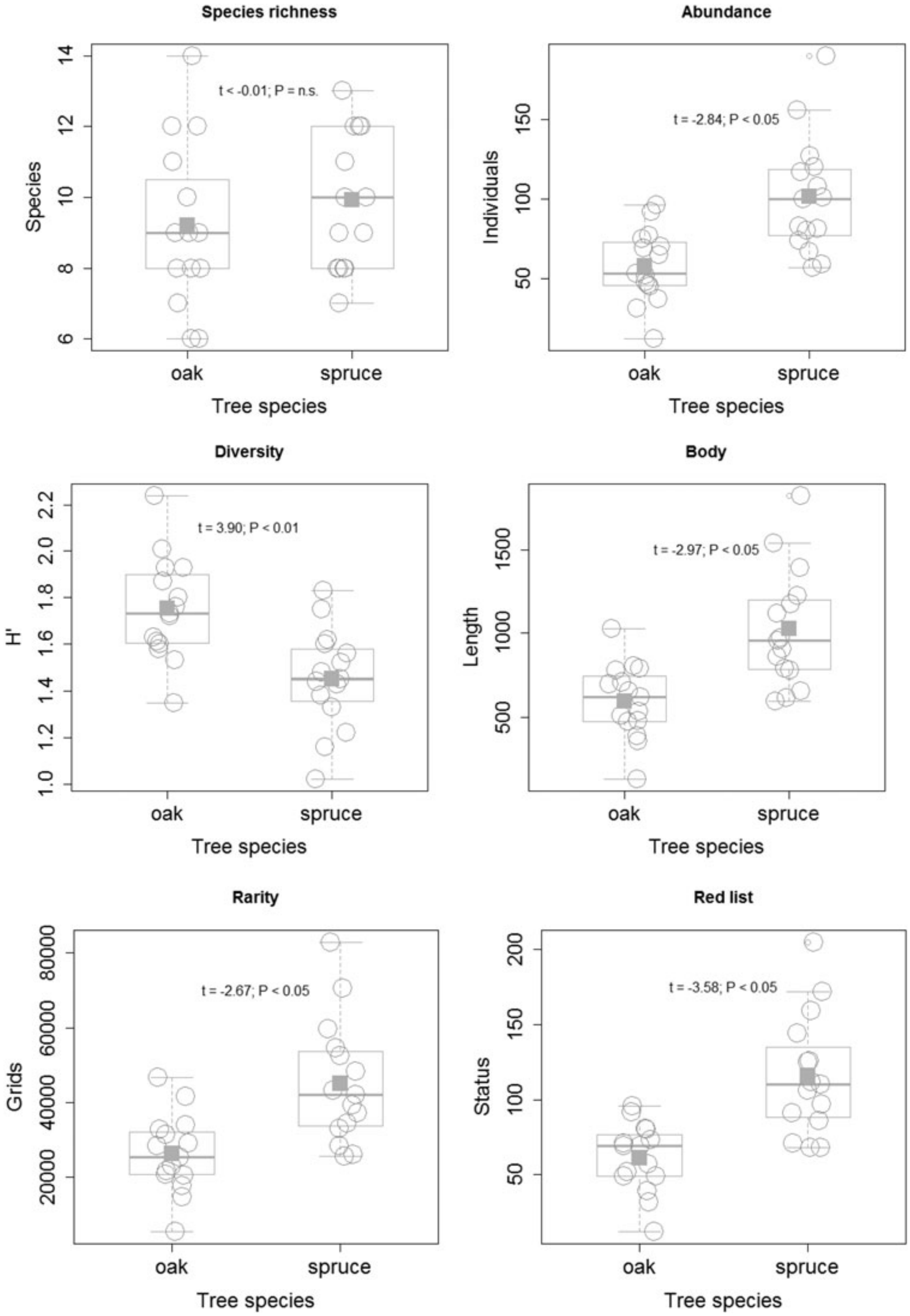

Fig. 1. Results for the comparison of species richness, abundance, Shannon diversity, body length, rarity, and red-list status of click beetles (Elateridae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – the *t* and *P* values are derived from a linear mixed-effects model (table 1); open circles show the actual values, filled squares represent the means, and thick lines show the median values.

abies), as the non-native tree to our study area (especially its intensive plantations), covered approximately the same area as native sessile oak (*Q. petraea*), which was one reason to choose spruce (instead of the widespread Scots pine) to compare the effect of dominant tree species. An additional reason was that Scots pine was potentially distributed in the study area in the past – even if only as a relict species (Neuhauselova & Moravec, 2001) and thus, it is native to the area. The final reason was that relatively few pine stands were mature in age and most were spatially clumped.

The second variable was again stand-based. Namely, the total area of the stand in hectares (mean = 2.06 ± SE = 0.15;

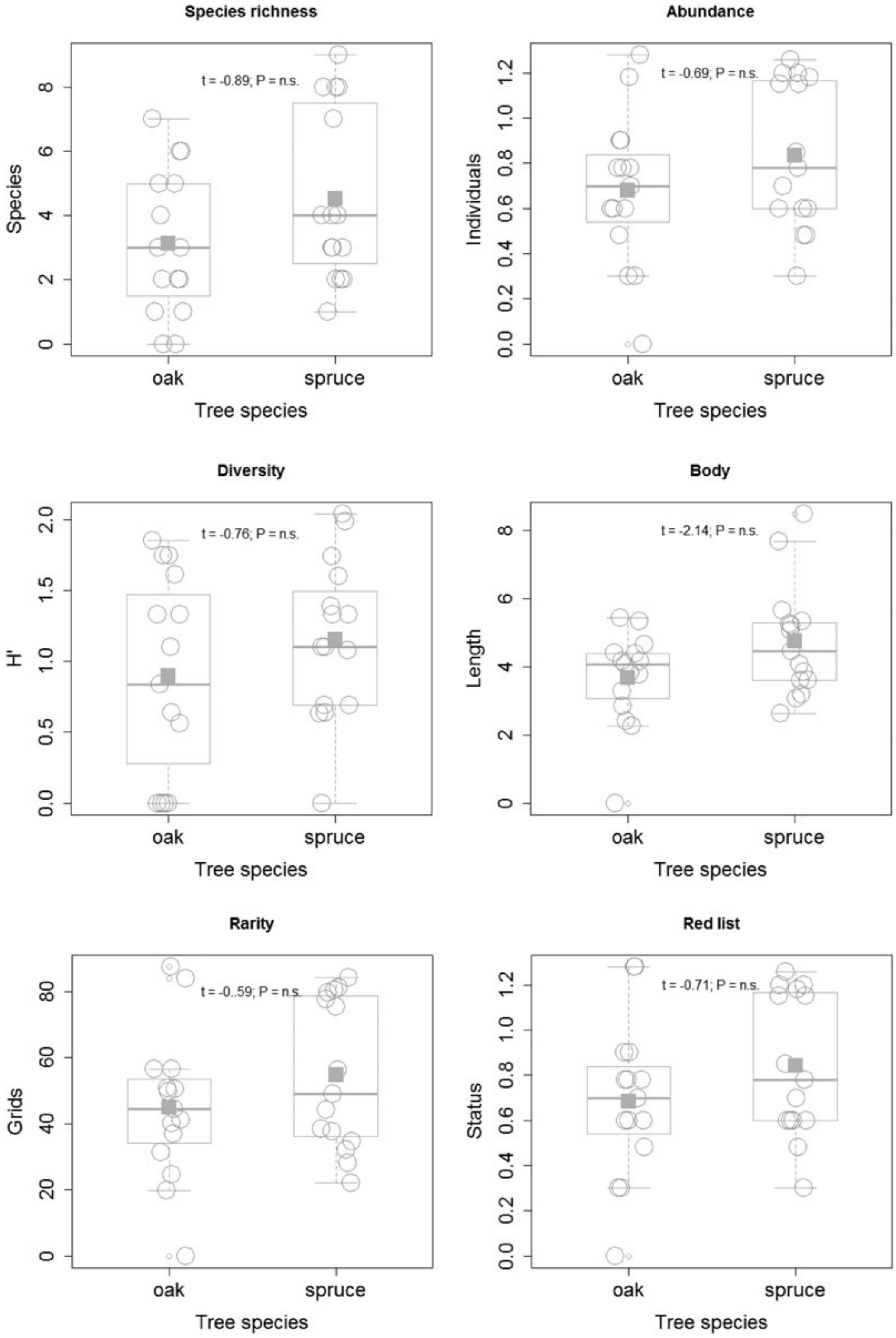

Fig. 2. Results of the comparison of species richness, abundance, Shannon diversity, body length, rarity, and red-list status of longhorn beetles (Cerambycidae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – *t* and *P* values are derived from a linear mixed-effects model (table 2); open circles show the actual values, filled squares show the means, and thick lines show the medians. Note that the length and grids are root-square-transformed, and individuals and status are log-transformed.

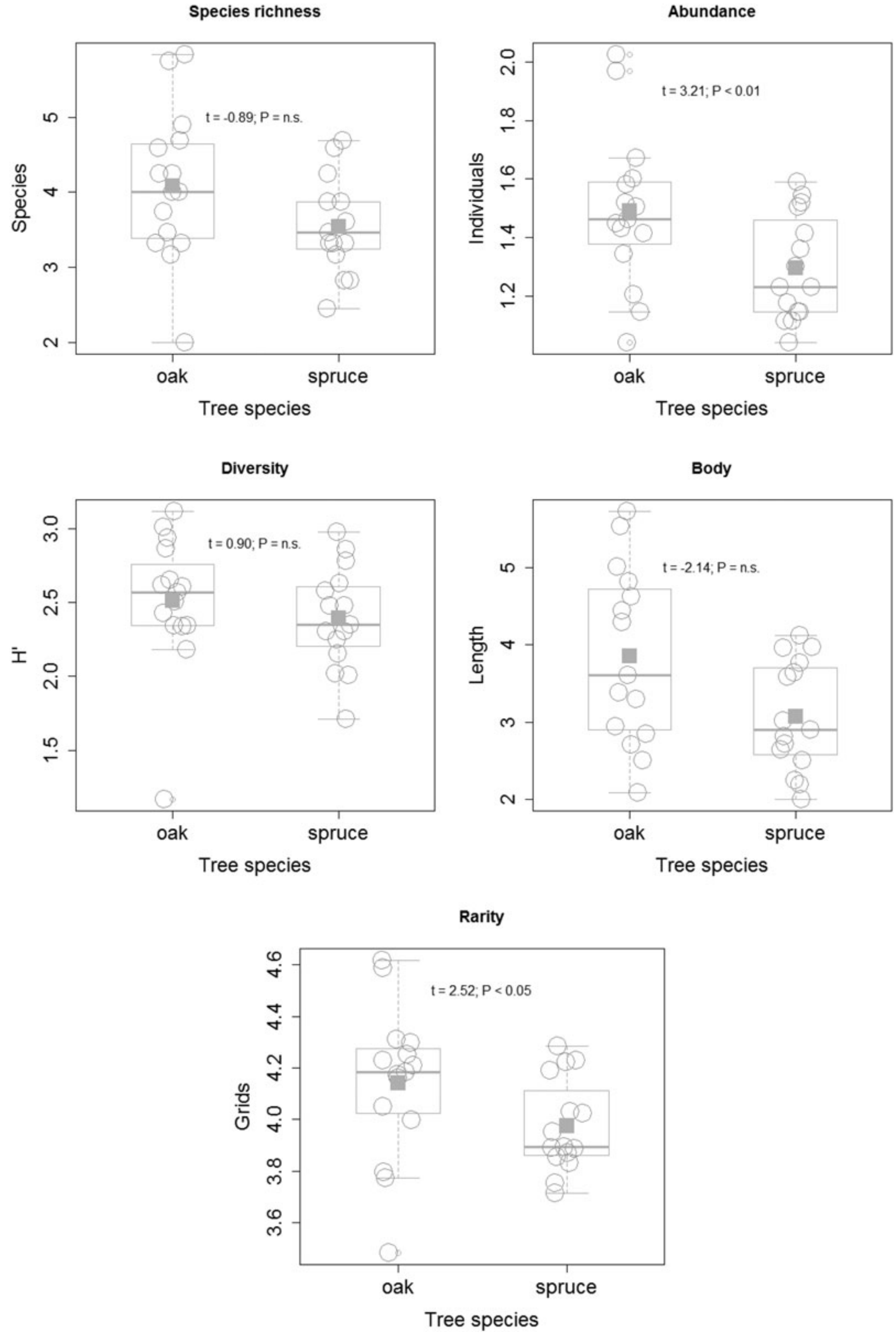

Fig. 3. Results of comparison of species richness, abundance, Shannon diversity, body length, and rarity of rove beetles (Staphylinidae) between stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests – *t* and *P* values are derived from a linear mixed-effects model (table 3); open circles show actual values, filled squares show means, and thick lines show medians. Note that species and length are root-square-transformed, and individuals and grids are log-transformed.

Table 1. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, rarity, and red-list status of click beetles (Elateridae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	133.77	<0.01	n.s.
	Canopy openness		2.31	0.0395
	Area		0.96	n.s.
Abundance	**Tree (spruce)**	271.69	2.84	0.0149
	Canopy openness		2.36	0.0359
	Area		−1.58	n.s.
Diversity	**Tree (spruce)**	18.06	−3.89	0.0021
	Canopy openness		1.08	n.s.
	Area		1.48	n.s.
Body	**Tree (spruce)**	390.95	2.97	0.0116
	Canopy openness		2.03	n.s.
	Area		−1.50	n.s.
Rarity	**Tree (spruce)**	589.22	2.67	0.0203
	Canopy openness		2.45	0.0308
	Area		−1.67	n.s.
Red list	**Tree (spruce)**	276.24	3.58	0.0038
	Canopy openness		1.92	n.s.
	Area		−1.75	n.s.

Table 2. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, rarity, and red-list status of longhorn beetles (Cerambycidae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	145.51	0.89	n.s.
	Canopy openness		1.37	n.s.
	Area		0.69	n.s.
Abundance	Tree (spruce)	35.68	0.69	n.s.
	Canopy openness		1.71	n.s.
	Area		2.22	0.0462
Diversity	Tree (spruce)	76.09	0.76	n.s.
	Canopy openness		0.67	n.s.
	Area		0.31	n.s.
Body	Tree (spruce)	115.53	2.14	n.s.
	Canopy openness		0.46	n.s.
	Area		2.34	0.0373
Rarity	Tree (spruce)	255.27	0.59	n.s.
	Canopy openness		1.69	n.s.
	Area		2.27	0.0421
Red list	Tree (spruce)	35.58	0.71	n.s.
	Canopy openness		1.70	n.s.
	Area		2.35	0.0369

min = 1.00; max = 3.81 ha). This variable was measured based on actual forest management plans and was confirmed by our observations in the field and by actual aerial photographs. The relationship of area to disparate biological variables is often studied (Horák, 2016), but its use in forest insect ecology is, to the best of our knowledge, relatively limited (Webb *et al.*, 2008).

The final variable was patch-based and reflected the disturbance of canopy and microclimate. Namely, the canopy light conditions of the environment, which is very important for insects (Vodka *et al.*, 2009). Canopy openness was measured as a percentage (9.44 ± 0.36; 6.74–14.46%) during the same weather conditions in the peak of vegetation season (i.e., under the full canopy). We used a Nikon COOLPIX 995 with a Nikon FC-E8 Fish Eye converter. Each photograph of 180° was taken at the top of the trap, 1.55 m above the ground. All photographs were then evaluated using Gap Light Analyzer 2.0.

In these conditions, we found and studied 15 pairs of spruce and oak tree-dominated stands.

Statistical analyses

We used three dependent variables that are traditionally analyzed regarding biodiversity: species richness (the number of species trapped), abundance (the number of individuals trapped), and diversity (the Shannon diversity index). We also used one dependent variable that is used in functional ecology: body length (the mean of maximum and minimum value published in the entomological literature), and two dependent variables that reflected conservation traits, i.e., rarity (the total number of unoccupied grids in the Czech Republic based on Sláma, 1998; Dušánek & Mertlik, 2015 and the personal database of J. Boháč) and the red-list status (the species rank values based on the red-list index using IUCN criteria LC = 1, NT = 2, VU = 3; EN = 4 from Farkač *et al.*, 2005). Some dependent variables were transformed to reach normality (abundance of longhorn and rove beetles, click beetles' red-list value and rove beetles' rarity were log-transformed; rarity and body length of longhorn beetles, species richness of rove beetles, and their body length were square-root transformed).

To compute the relationship between the dependent variables and the variables that reflected the study environment, we used linear mixed-effect models in R (package nlme). Three independent variables we treated as fixed factors. Numbers of pairs of stands (spruce vs. oak, from 1 to 15) were used as a random factor. The species composition and the responses of individual species were analyzed in CANOCO. We used redundancy analyses (RDA) for click beetles (Detrended correspondence analysis length of gradient = 2.697) and canonical correspondence analyses for longhorn (8.460) and rove beetles (4.475). We used 9999 randomizations with pairs of stands as a split-plot design.

Results

In total, 2388 individuals from 31 species of click beetles, 194 individuals of longhorn beetles from 36 species, and 884 individuals from 131 species of rove beetles were trapped during the research in the lowland plantation forests.

The results showed that there was no significant difference in species richness between oak- and spruce-dominated stands (figs 1, 2 and 3), although the number of click beetle species significantly benefited from increasing canopy openness (table 1). The number of individuals of click and rove beetles (figs 1 and 3) was significantly positively influenced by spruce and oak, respectively. The abundance of click beetles, furthermore, was positively influenced by canopy openness (table 1), where longhorn beetles were positively influenced only by the increasing area of the stand (table 2). The diversity of click beetles was significantly higher in oak than in spruce stands (fig. 1) and the diversity of rove beetles was significantly positively influenced by the increasing stand area (table 3). Spruce stands hosted click beetles with a higher body length than oak stands (fig. 1). The body length of longhorn and rove beetles was positively significantly influenced by an increasing stand area (tables 2 and 3). Rare click beetles were significantly more abundant in spruce than in oak stands (fig. 1) and

Table 3. Results of linear mixed-effect models on the species richness, abundance, Shannon diversity, body length, and rarity of rove beetles (Staphylinidae) in lowland plantation forests; significant variables appear in bold.

Name	Variable	AIC	*t*	*P*
Species richness	Tree (spruce)	145.51	0.89	n.s.
	Canopy openness		1.37	n.s.
	Area		0.69	n.s.
Abundance	**Tree (spruce)**	18.85	−3.21	0.0075
	Canopy openness		1.37	n.s.
	Area		−0.13	n.s.
Diversity	Tree (spruce)	46.04	−0.90	n.s.
	Canopy openness		0.15	n.s.
	Area		2.33	0.0380
Body	Tree (spruce)	115.53	2.14	n.s.
	Canopy openness		0.46	n.s.
	Area		2.34	0.0373
Rarity	**Tree (spruce)**	23.09	−2.52	0.0271
	Canopy openness		1.36	n.s.
	Area		0.77	n.s.

were also positively influenced by increasing canopy openness (table 1). Rare rove beetles were more frequent in oak than in spruce stands (fig. 3) and the rarity of longhorn beetles significantly increased with an increase in area (table 2). Spruce stands hosted significantly more red-listed click beetles than oak stands (fig. 1), whereas the red-list index of longhorn beetles was positively influenced by increasing area (table 2). We did not trap red-listed rove beetles.

The analyses of the species composition of click beetles showed that there was significant discrimination between species preferences for oak- and spruce-dominated stands (fig. 4), similar to for longhorn beetles (fig. 5). Analyses of the species composition of rove beetles showed that there was no significant discrimination between species preferences for oak- and spruce-dominated stands ($R^2 = 3.17\%$; $F = 0.92$; $P =$ n.s.). Species composition analyses of click beetles also showed that the species that were associated with spruce stands were more influenced by canopy openness and area than those associated with oak-dominated stands, which is demonstrated by a higher clustering of spruce associates to the second axis in RDA visualization (fig. 4). Species of longhorn beetles showed a higher preference for spruce or oak stands, which is illustrated by more color-pure pies (fig. 5).

Two species (*Agriotes acuminatus* and *Athous haemorrhoidalis*) and four species (*Athous subfuscus*, *A. zebei*, *Ectinus aterrimus*, and *Sericus brunneus*) of click beetles were significantly associated with oak- and spruce-dominated stands, respectively (table 4). Two longhorn beetles (*Prionus coriarius* and *Pyrrhidium sanguineum*) preferred oak stands, whereas one (*Stenocorus meridianus*) preferred spruce stands (table 5). Three rove beetles (*Gabrius breviventer*, *Liogluta granigera*, and *Oxytelus rugosus*) preferred oak stands (table 6). Two click beetles (*A. acuminatus* and *Athous vittatus*) were negatively affected by, and four species (*Ampedus balteatus*, *Ampedus nigrinus*, *A. subfuscus*, and *S. brunneus*) thrived on canopy openness (table 4). Five longhorn beetles significantly responded to canopy openness (table 5). Four longhorn species preferred open stands (*Molorchus minor*, *Paracorymbia maculicornis*, *Rhagium mordax*, and *Stenurella melanura*), whereas *Oplosia cinerea* was more abundant in shaded stands. Three rove beetles (*Atheta fungi*, *L. granigera*, and *O. rugosus*) preferred conditions of low canopy openness (table 6). Three species of click beetles responded to the area of the stand (table 4) – *A. vittatus* and *Melanotus castanipes* preferred an increasing area of mature stands, whereas *Dalopius marginatus* showed the opposite relationship. Only one longhorn beetle responded to the area of the stand (table 5) – *S. melanura* was more abundant in large stands. Four rove beetles (*Amarochara umbrosa*, *Atheta celata*, *Atheta elongatula*, and *Omalium rivulare*) were negatively affected by an increasing stand area (table 6).

Discussion

Our results revealed several different and contrasting responses among three studied beetle families: click beetles responded mainly to the dominant tree species and insolation of stands, whereas longhorn beetles were influenced by the stand extent and rove beetles were most influenced by the dominant tree species and stand area.

We also observed that the responses of individual species within the studied beetle families in plantation forest stands dominated by oak and spruce were in many cases complex and highly diverse and that some species indicated contrasting patterns compared to the literature (e.g., the preference of *S. meridianus* for conifer-dominated stands).

The response of click beetles as a highly diverse family

Click beetles revealed relatively interesting and partly contrasting responses regarding the dominant tree species. Even when their species richness did not show a significant response, the number of individuals, their length, rarity value, and red-list status was higher in spruce plantations than in oak stands. This appears to be a surprising result that might be explained by the positive influence of increasing openness in canopies (Vodka *et al.*, 2009; Horák & Rébl, 2013) in the case of abundance, but not for the other studied variables. From this point of view, it appears that click beetles represent a group that is more adaptable than is mentioned in the literature (Laibner, 2000). On the other hand, one of the factors that potentially influenced our results might be the long-term presence of Scots pine in our study area – even if this fact is questionable (Neuhauselova & Moravec, 2001). The higher adaptability of click beetles to conifer vs broadleaved tree stands rather than to particular tree species might also be relevant. Further explanations might reside in the species composition, i.e., species that were associated with oak stands were more significantly bound to it than species that preferentially occurred in spruce plantations. Another potential explanation might be that the current presence and extent of mature oak stands is below the threshold area and fragmentation caused by isolation that is acceptable for the successful development of populations of oak-associated click beetles (Alexander, 2002). This appears to be well reflected in the fact that only two relatively common species (Loskotová & Horák, 2016) significantly preferred oak stands, whereas four species were associated with spruce plantations. The opposite relationship was observed for diversity and, thus, we concluded that tree species that is not native in the studied area can negatively influence the diversity of the family; however, why the other traits responded differently remains unclear (Loehle, 2003).

The response of *Limonius poneli* that preferred closed oak stands is different to the literature – this species prefers steppes and forest steppes where adults occur on vegetation (Mertlik, 2008). This contrasts with species such as *M. castanipes*, which prefer spruce-dominated stands (Laibner, 2000). This

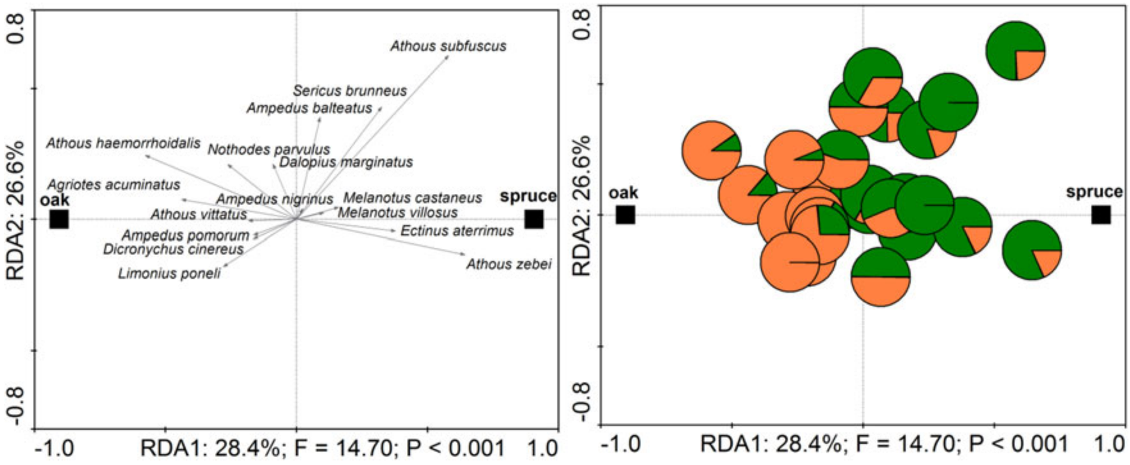

Fig. 4. Visualization of individual click beetle (Elateridae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests using redundancy analysis. The explained variance, *F* and *P* values are derived from redundancy analysis; species with fewer than ten individuals were suppressed in the left species-environmental biplot; light-brown represents individuals on oak trees and green represents individuals captured in spruce-dominated stands in the right pie plot.

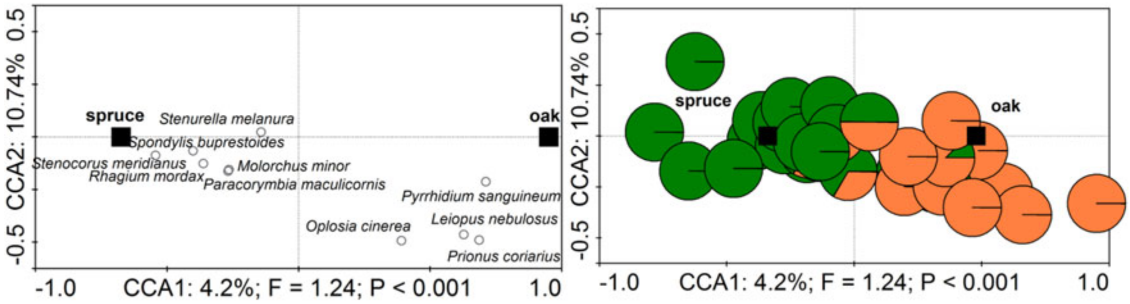

Fig. 5. Visualization of individual longhorn beetle (Cerambycidae) species preferences in stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*) in lowland plantation forests by canonical correspondence analysis. The explained variance, *F* and *P* values are derived from canonical correspondence analysis; species with fewer than five individuals were suppressed in the left species-environmental biplot; light-brown represents individuals on oak trees and green represents individuals captured in spruce-dominated stands in the right pie plot.

preference was also observed for *S. brunneus*, which mostly prefers pine stands (Laibner, 2000). Thus, this relationship might indicate that species that are associated with disparate conifer stands might use stands containing different conifer tree species as a supplementary habitat. The species *E. aterrimus* might represent an example of contrasting preferences to those known in the literature. This click beetle prefers broadleaved forests (Laibner, 2000), but in this study, was significantly associated with spruce stands. As mentioned above, most of the studied click beetle traits were favored by the insolation of stands. However, we observed some species that were associated with a closed canopy (e.g., *A. acuminatus*). An open canopy was preferred by two *Ampedus* species (*A. balteatus* and *A. nigrinus*) that are known to be associated with conifer stands, whereas *A. nigrinus* is also associated with mountainous areas (Laibner, 2000). The stand area was not one of the most important variables in determining the distribution of click beetles, although some species showed a significant relationship with stand area – e.g., *D. marginatus* showed a negative relationship and *M. castanipes* a positive relationship to increasing area of stand. A positive response is unsurprising, but the negative response of *D. marginatus* appears to be difficult to interpret, because this species is a typical forest-dwelling species.

Longhorn beetles as representatives of a saproxylic family

Except for the species composition and the individual species, the group of longhorn beetles did not change according to the dominant tree species. This is on one hand surprising, because many species are specialized either on the wood of conifer or deciduous trees and Japanese research has shown that longhorn beetles were negatively affected by the conversion of deciduous forest stands to conifer plantations (Makino *et al.*, 2007). On the other hand, our results might have been influenced by the fact that the stands were not absolutely pure in terms of tree species and this might also be influenced by the surrounding stands. The species composition and particularly, the abundance of three species were influenced by the dominant tree in the tree species composition. The explained variance in the tree species composition was relatively low, but the majority of species were present only in one type

Table 4. Individual click beetle (Elateridae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; t and P values ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$) are derived from species response curves; species with fewer than ten individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Adrastus rachifer	1				
Agriotes acuminatus	44	0.18*		−0.07*	
Agriotes obscurus	1				
Agriotes pilosellus	1				
Agrypnus murinus	9				
Ampedus balteatus	167			10.67**	
Ampedus erythrogonus	1				
Ampedus nigrinus	17			5.15***	
Ampedus pomorum	49				
Ampedus sanguineus	5				
Ampedus sanguinolentus	6				
Anostirus castaneus	2				
Anostirus purpureus	2				
Athous haemorrhoidalis	212	0.86*			
Athous subfuscus	1068		2.32*	10.89*	
Athous vittatus	21			−4.19*	4.25*
Athous zebei	257		0.89*		
Cardiophorus nigerrimus	6				
Cardiophorus ruficollis	4				
Dalopius marginatus	134				−0.05*
Denticollis linearis	6				
Dicronychus cinereus	15				
Ectinus aterrimus	137		0.41*		
Limonius poneli	40				
Melanotus castanipes	19				3.10*
Melanotus villosus	101				
Nothodes parvulus	16				
Paraphotistus nigricornis	1				
Pheletes aeneoniger	6				
Selatosomus aeneus	1				
Sericus brunneus	39		0.13*	5.82*	

of stand. With respect to the individual species, the preference of *P. coriarius* and *P. sanguineum* for oak trees is not surprising, whereas the preference of *S. meridianus* for spruce plantations is difficult to explain. This species is known to be associated with broadleaved trees in lowland forests (Sláma, 1998). Furthermore, this species was present in nine stands and thus, this result cannot be influenced by a clumped distribution in one or a few spruce stands, due to the circumstantial presence of a piece of oak dead wood.

Longhorn beetles appear to be more connected to the forest environment, because of their dependence on dead wood biomass for larval development (Sláma, 1998). However, recent research has shown that adults are more abundant in forest edges and open forests or larvae can even develop on solitary trees (Wermelinger *et al.*, 2007; Vodka *et al.*, 2009). Thus, their dependency on dead wood does not necessarily mean that this taxon is associated with forests and it is relatively surprising that longhorn beetles did not respond to canopy openness. Nevertheless, four out of five species that significantly responded to canopy openness were more associated with an increasing canopy openness. Only *O. cinerea* was associated with very shaded stands (for thresholds, see, e.g., Müller *et al.*, 2010), which contrasts with the known preference for avenues and solitary trees from the literature (Sláma, 1998). This suggests that plantation forests are still an understudied habitat type and might lead to different results than traditionally studied forest habitats such as old-growth forests or ancient woodlands (Vodka *et al.*, 2009; Horák & Rébl, 2013).

Stenurella melanura also showed a high preference for large open stands. This species is widespread throughout most of central Europe, which might be consistent with the occurrence of this species on blossoms (Sláma, 1998). Nevertheless, its distribution might be different in southern Europe, where *S. melanura* was found to be more abundant in oak forests, which generally have closed canopy (Peris-Felipo *et al.*, 2011). This difference is probably because insects can find a suitable ambient temperature in warmer climates, even under the closer canopy.

The effect of isolation caused by fragmentation in forests is understudied in comparison to non-forest habitats (Krauss *et al.*, 2004; Webb *et al.*, 2008; Horák, 2015) – and when studied, isolated forest fragments are usually only compared with different land uses (Pavuk & Wadsworth, 2013). In this study, the abundance, body size, rarity, and red-list status of longhorn beetles all increased with an increase in the area of the stand. Our results indicate that larger mature stands are highly significant not only for the total number of individuals, but also for indices that are important from the point of view of conservation biology (i.e., rare and threatened beetles) and functional ecology – larger and thus, more conspicuous longhorn beetles are associated with large stands (note that the mean value of our stand area was approximately 2 ha). The habitat area of saproxylic organisms is often characterized by the amount of dead wood or the diameter of the studied tree (Horak *et al.*, 2014; Buse *et al.*, 2016). However, the amount of dead wood in plantation forests is generally low (Kirby *et al.*, 1998); thus,

Table 5. Individual longhorn beetle (Cerambycidae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; *t* and *P* values (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) are derived from species response curves; species with fewer than five individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Acanthocinus griseus	1				
Alosterna tabacicolor	1				
Anaglyptus mysticus	1				
Callidium aeneum	2				
Clytus arietis	4				
Clytus lama	1				
Cortodera femorata	1				
Cortodera humeralis	1				
Gaurotes virginea	4				
Leiopus nebulosus	6				
Leptura quadrifasciata	2				
Menesia bipunctata	1				
Molorchus minor	13			2.66**	
Obrium brunneum	1				
Oplosia cinerea	5			−1.72*	
Oxymirus cursor	1				
Paracorymbia maculicornis	5			2.65*	
Pedostrangalia revestita	1				
Phymatodes testaceus	2				
Pogonocherus fasciculatus	3				
Pogonocherus hispidus	1				
Prionus coriarius	14	0.60*			
Pyrrhidium sanguineum	8	0.62*			
Rhagium bifasciatum	4				
Rhagium inquisitor	3				
Rhagium mordax	6			2.39*	
Saphanus piceus	1				
Spondylis buprestoides	10				
Stenocorus meridianus	12		0.47*		
Stenostola dubia	3				
Stenurella bifasciata	1				
Stenurella melanura	70			1.13***	0.03*
Tetropium castaneum	2				
Tetropium fuscum	1				
Tetropium gabrieli	1				
Xylotrechus antilope	1				

we conclude that the stand area could easily contribute to the amount of dead wood available for saproxylic organisms in studies on plantation forests.

What was the response of a rove beetle family?

Rove beetles are one of the families with the highest species richness and also one of the most complicated groups for identification to the species level (Brunke *et al.*, 2012). Previous studies have identified them as potential indicators (Boháč, 1999); although recent findings have indicated that they are probably generalists at the habitat level, at least in semi-natural forests (Parmain *et al.*, 2015).

The generalist habitat state of rove beetles appeared to be confirmed by the absence of threatened species in this study. However, we observed significantly more rare species in oak stands. We predicted that oak stands promote most of the studied dependent variables, but this was only true for the diversity of click beetles. Therefore, the greater number of rare species and total abundance of rove beetles was relatively unexpected, especially because the hypothesis concerning higher biodiversity values in stands with prevailing native vegetation was confirmed by the taxon that is currently considered to be that with the greater number of generalists or opportunists. Setting aside the problems outlined above concerning generalist taxa, rove beetles occasionally responded positively to oak stands mainly because they avoid conifer plantations (Buse & Good, 1993). Another reason might be because even if they do not appear to show habitat preferences in general (Parmain *et al.*, 2015), it is known that individual species occupy a relatively large number of microhabitats (Caballero *et al.*, 2007) – and disparate microhabitats are mostly more common in stands with native vegetation (Winter & Möller, 2008).

Rove beetles did not respond to the canopy openness gradient; however, their diversity and body length increased with increasing stand area, which was a similar response to that of longhorn beetles. Nevertheless, considering individual species responses, we found that three species were promoted by the native vegetation, three species were negatively influenced by canopy openness and four species were affected by an increasing stand area. On the other hand, the species that showed a response (e.g., *A. fungi*, *G. breviventer* or *O. rugosus*) are mostly associated with non-specific habitats, in leaf litter or decaying plant, fungal or animal residues (Boháč & Matějíček, 2003).

Potential implications for management

Oaks that were dominant in the study territory in the past (Neuhauselova & Moravec, 2001) are mostly no longer present

Table 6. Individual rove beetle (Staphylinidae) species preferences for stands dominated by Sessile oak (*Quercus petraea*) and Norway spruce (*Picea abies*), canopy openness and area in lowland plantation forests; *t* and *P* values (*$P < 0.05$; **$P < 0.01$) are derived from species response curves; species with fewer than ten individuals were not analyzed.

Species	Individuals	Oak	Spruce	Canopy openness	Area
Acidota crenata	1				
Acidota cruentata	1				
Aleochara bipustulata	1				
Aleochara sparsa	4				
Aloconota sulcifrons	3				
Amarochara umbrosa	24				−0.07*
Amischa analis	67				
Anotylus nitidulus	5				
Anotylus rugosus	5				
Anotylus tetracarinatus	15				
Atheta aeneicollis	1				
Atheta amicula	3				
Atheta celata	11				−2.60*
Atheta crassicornis	3				
Atheta elongatula	11				−0.05*
Atheta fungi	91			−5.05*	
Atheta livida	2				
Atheta malleus	2				
Atheta melanocera	6				
Atheta nigripes	2				
Atheta pittionii	1				
Atheta ravilla	3				
Atheta subtilis	1				
Atheta triangulum	3				
Atrecus affinis	3				
Autalia rivularis	2				
Bibloporus minutus	3				
Bisnius fimetarius	3				
Bythinus burrelli	5				
Bythinus macropalpus	3				
Carpelimus bilineatus	2				
Carpelimus elongatulus	7				
Carpelimus obesus	2				
Carpelimus rivularis	5				
Elonium striatulum	1				
Euplectus decipiens	2				
Euplectus karsteni	1				
Euplectus punctatus	21				
Gabrius breviventer	12	2.32**			
Gabrius nitritulus	8				
Gabrius osseticus	1				
Gabrius splendidulus	1				
Gyrophaena boleti	1				
Haploglossa puncticollis	4				
Heterothops dissimilis	2				
Kenothus laevicollis	5				
Lathrobium laevipenne	1				
Lathrobium terminatum	1				
Leptusa pulchella	7				
Lesteva longoelytrata	48				
Liogluta granigera	15	0.47**		−3.20*	
Lordithon lunulatus	4				
Lordithon trimaculatus	1				
Meotica exilis	8				
Mycetoporus corpulentus	4				
Mycetoporus erichsonanus	1				
Mycetoporus lepidus	19				
Mycetoporus splendidulus	1				
Ocalea badia	1				
Ocalea picata	1				
Omalium caesum	10				
Omalium rivulare	17				−2.82*
Oxypoda abdominalis	1				
Oxypoda acuminata	1				
Oxypoda brevicornis	2				
Oxypoda opaca	4				

Table 6. (*Cont.*)

Species	Individuals	Oak	Spruce	Canopy openness	Area
Oxypoda vicina	2				
Oxypoda vittata	1				
Oxyporus rufus	1				
Oxytelus insecatus	4				
Oxytelus migrator	2				
Oxytelus rugosus	20	2.78**		−2.50*	
Philhygra elongatula	2				
Philonthus atratus	7				
Philonthus carbonarius	34				
Philonthus cognatus	23				
Philonthus decorus	6				
Philonthus fumarius	1				
Philonthus laevicollis	6				
Philonthus laminatus	11				
Philonthus quisquiliarius	3				
Philonthus rectangulus	1				
Philonthus rotundicollis	2				
Philonthus tenuicornis	2				
Philonthus umbratilis	1				
Philonthus varians	12				
Phleopora testacea	2				
Phloeonomus planus	1				
Phloeonomus pusillus	1				
Phloeopora testacea	43				
Plataraea interurbana	1				
Platydracus fulvipes	1				
Platystethus nitens	7				
Plectophloeus fischeri	32				
Plectophloeus nitidus	3				
Quedius boopoides	1				
Quedius boops	2				
Quedius fuliginosus	3				
Quedius nitipennis	1				
Quedius xanthopus	1				
Rugilus mixtus	4				
Rugilus rufipes	2				
Rugilus scutellatus	2				
Scaphisoma agaricinum	11				
Scaphisoma assimile	3				
Scaphisoma boleti	9				
Scopaeus cognatus	1				
Scopaeus laevigatus	7				
Scopaeus minutus	1				
Sepedophilus pedicularius	1				
Staphylinus erythropterus	1				
Stenus clavicornis	1				
Stenus comma	1				
Stenus fossulatus	1				
Stenus humilis	2				
Syntomium aeneus	1				
Tachinnus subterraneus	1				
Tachinus corticinus	1				
Tachinus signatus	2				
Tachyporus chrysomelinus	7				
Tachyporus hypnorum	34				
Tachyporus nitidulus	3				
Tachyporus obtusus	3				
Tachyporus solutus	5				
Trimium brevicorne	2				
Trimium carpathicum	1				
Tyrus mucronatus	2				
Xantholinus linearis	6				
Xantholinus longiventris	16				
Zyras cognatus	2				
Zyras limbatus	4				

as a dominant species (Loskotová & Horák, 2016). One potential reason why oak stands did not lead to the expected promotion of the majority of the studied taxa was that total area of broadleaved stands was relatively low and isolation was high compared with in conifer plantations (Loskotová, 2013). Therefore, one recommendation for forest management is to at least preserve indigenous broadleaved tree species, which would help to regenerate, create, and connect new islands of deciduous trees (Webb *et al.*, 2008). Although the natural regeneration of oak trees is occasionally considered complicated (Annighöfer *et al.*, 2015), it is preferred for the maintenance of beetle diversity.

Another important point for management is that legal forestry restrictions appear to be strict in most countries in central Europe. For example, clear-cuts in the Czech Republic can be performed in most cases only up to 1 ha, whereas some beetle families and their studied traits responded to an increasing area of the forest stand in our research area and the largest stand exceeded 3 ha. In Scandinavia, clear-cuts of a larger area are allowed, although with particular conservation-oriented amendments (e.g., the retention of green trees and dead wood), which might protect biodiversity (Vanha-Majamaa & Jalonen, 2001). This also appears to be important in the context of the first-mentioned management implication – i.e., an increase in the total area of broadleaved islands. To conserve the initial insect fauna, it is necessary to increase size of the broadleaved stands (Webb *et al.*, 2008), including the fragmented patches of native oaks, which are generally found in the lowland forests of the central Europe (Neuhauselova & Moravec, 2001). On the other hand, conifer plantations also supported several beetle species of conservation interest and therefore, specific forest management applications (such as support of diversified tree species composition) should be applied to avoid the loss of biodiversity and also to conserve rare and threatened species (Roder *et al.*, 2010). This is also highly connected to the fact that the majority of large forest plantations were subjected to the forest management of closed canopy stands, which is predicted to be more resistant to wind breaks (Vicena *et al.*, 1979). Therefore, larger scales of present and future harvesting with veteran tree retention (Alexander *et al.*, 1996) might also introduce a level of mosaic structure to the stands. Moreover, if natural regeneration is applied to the new clear-cut area, beetle diversity indices and traits can benefit from the newly created ecosystem heterogeneity, as has been observed for other insects (Véle *et al.*, 2016).

One of the well-known patterns in biogeography is that a large surface area of suitable habitats (i.e., stands, in this case) also means a higher species richness. Even if in this case it is rather a patch-matrix model than application of theory of island biogeography, the implication for management remains the same. The above-mentioned legal acts are oriented toward sustainable management (e.g., Gossner *et al.*, 2013); however, they might limit the further biodiversity-oriented management implications in the plantation forest stands. When we consider the maximal nature regeneration, one of the important issues regarding the future of clear-cut stands is the fact that the heterogeneity of tree species composition would be potentially higher in larger areas compared with in small cuts (Yasuhiro *et al.*, 2004).

The positive effect of spruce monocultures on certain families and species of click beetles was relatively surprising. This was probably because abundance of two native conifers of Scots pine and Silver fir together with Norway spruce in our research area could promote abundance of click beetles. The study area in total had a very low level of canopy openness (a mean light penetration of only 9%), which possibly negatively affected the final number of captured beetle species. Another explanation for the positive response to Norway spruce is that conifer plantations were more disturbed by abiotic factors in the past (spruce mainly by wind), which increased the insolation of stands compared with undisturbed oak-dominated stands. Regarding the improvement of conditions in native vegetation, any type of forest management of oak stands (e.g., the thinning of young trees or the intermediate felling of older and shelterwood cuttings in mature stands) can lead to a more open site canopy, to which many beetle species react positively (Vodka *et al.*, 2009), since the temperature of the stand is increased by the amount of sunlit space (e.g., Iverson *et al.*, 2008).

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