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Ptačí společenstva v porostech nepůvodních dřevin
Bird communities in stands of non-native trees

Ph.D. Thesis

Supervisor: doc. Mgr. Jiří Reif, Ph.D.

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

Declaration:

Hereby I declare that I worked out this thesis independently, using the listed sources and literature. I have not submitted this thesis, or any significant part thereof, for the purpose of obtaining the same or any other academic degree.

In Prague, 24. 06. 2016

Jan Hanzelka

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Table of contents

List of publications and manuscripts included in the Ph.D. thesis

Paper I **Hanzelka, J.**, Reif, J., Effects of vegetation structure on the diversity of forest bird communities in an era of plant invasions: the cases of nonnative black pine (*Pinus nigra* A.) and black locust (*Robinia pseudacacia* L.) in the Czech Republic. (submitted manuscript)

Paper II **Hanzelka, J.**, Reif, J., 2015. Responses to the black locust (*Robinia pseudoacacia*) invasion differ between habitat specialists and generalists in central European forest birds. J. Ornithol. 156, 1015–1024.

Paper III Reif, J., **Hanzelka, J.**, Kadlec, T., Štrobl, M., Hejda, M., 2016. Conservation implications of cascading effects among groups of organisms: the alien tree *Robinia pseudacacia* in the Czech Republic as a case-study. Biol. Conserv. 198, 50–59.

Paper IV **Hanzelka, J.**, Reif, J., 2015. Relativní míra predace umělých hnízd v invazních akátových a přírodě blízkých dubových porostech. Sylvia 51, 63–73.

Author's contributions

Paper I: JH performed most of the field work (mapping of birds and vegetation structure), conducted statistical analyses, and led writing of the manuscript.

Paper II: JH collected data in the field (mapping of birds), conducted statistical analyses, and led writing of the paper.

Paper III: JH participated in field data collection (mapping of birds and vegetation structure, light traps operation) and contributed significantly to writing of the paper.

Paper IV: JH performed most of the field work (placing and checking of artificial nests), conducted statistical analyses, and led writing of the paper.

The supervisor of Ph.D. thesis and the co-author of all presented papers, Jiří Reif, fully acknowledges the contribution of Jan Hanzelka as stated above.

doc. Mgr. Jiří Reif, Ph.D.

Abstract

This thesis deals with the effects of non-native tree stands on birds in the Czech Republic. Non-native plants, including trees, are known to adversely affect the biodiversity. At the same time, birds represent a widely used biodiversity indicator. The studies of bird communities in stands of non-native trees presented here show the extent to which the birds have been impacted by non-native tree stands. This knowledge can be used to evaluate the importance of non-native plants as a biodiversity threatening factor.

As the representatives of widespread non-native trees, the broad-leaved black locust and coniferous black pine were selected. In these stands I investigated possible mechanisms affecting bird communities, arising from assumed differences in vegetation structure, bird species richness, bird community composition, food supplies, and nest predation pressure compared to the stands of native oak and native Scots pine.

In general, the bird species richness positively correlates with the vegetation structure complexity. Despite the fact that the non-native stands proved to have a higher heterogeneity of vegetation structure than the native stands, bird species richness did not differ among the focal stands. The bird community composition was primarily affected by the birds' preference of coniferous or broad-leaved stands. It suggests that basic stand characteristics may play more important role than the non-nativeness of the tree species. However, the tree origin was another factor significantly affecting the bird community composition. Its influence can be seen mainly in a decline of habitat specialists in black locust stands. The numbers of these specialised bird species have declined, most likely, also due to the impoverishment of the investigated food supply, nocturnal Lepidoptera representing an important food source during the breeding season. On the other hand, species less demanding on the food source quality, habitat generalists, prevailed in the black locust stands. Finally, the predation pressure on artificial nests, expected to be lower in non-native black locust stands due to the higher vegetation heterogeneity in these stands, did not differ between both stand types. Probably, the undergrowth of non-native stands might not provide sufficient nest concealment from predators.

To conclude, certain bird species may suffer in stands of non-native trees. However, modest species are able to utilize such habitats and possibly to thrive there. Attached publications provide detailed analyses and discussions of the investigated phenomena.

Abstrakt

Tato dizertační práce se zabývá vlivy porostů nepůvodních dřevin na ptáky v České republice. Nepůvodní rostliny, včetně dřevin, jsou známy svým nepříznivým vlivem na biodiverzitu, přičemž ptáci představují její široce používaný indikátor. Zde předložené studie ptačích společenstev v porostech nepůvodních dřevin zkoumají, do jaké míry jsou ptáci nepůvodními dřevinami ovlivňováni, což může pomoci ke zhodnocení významu nepůvodních rostlin jako faktoru ohrožující biodiverzitu.

Jako zástupce rozšířené nepůvodní dřeviny byl vybrán z listnáčů trnovník akát a z jehličnanů borovice černá. V porostech těchto dřevin jsem zkoumal možné mechanismy ovlivňující ptačí společenstva, vycházející z očekávaných rozdílů ve vegetační struktuře, druhové bohatosti ptáků, složení ptačího společenstva, potravních zdrojích a míře predačního tlaku v porovnání s porosty původního dubu a původní borovice lesní.

Obecně počet druhů ptáků pozitivně koreluje se složitostí vegetační struktury. Počet druhů ptáků se však mezi zkoumanými porosty nelišil, navzdory průkazně vyšší vegetační heterogenitě porostů nepůvodních dřevin v porovnání s porosty původních dřevin. Složení ptačího společenstva se lišilo především s ohledem na rozdílnou preferenci jehličnatého a listnatého lesa u jednotlivých ptačích druhů. Z toho plyne, že základní parametry porostů mohou hrát důležitější roli než nepůvodnost dřevin. Avšak původ dřeviny byl dalším faktorem průkazně ovlivňující složení ptačího společenstva. Jeho vliv lze vidět především v poklesu habitatových specialistů v akátových porostech. Těchto specializovaných druhů ubylo pravděpodobně také kvůli ochuzení zkoumaného potravního zdroje, nočních motýlů představující důležitou součást potravy v hnízdním období. Na druhou stranu habitatoví generalisté, druhy méně náročné na kvalitu potravního zdroje, v akátových porostech převládali. V poslední řadě predační tlak na umělá hnízda se nelišil mezi oběma typy porostů, přestože byla očekávána nižší míra predace hnízd v akátových porostech z důvodu jejich vyšší heterogenity vegetace. Je možné, že podrost těchto porostů nedostatečně skrýval hnízda před predátory.

Na závěr lze konstatovat, že určité druhy ptáků mohou v porostech nepůvodních dřevin trpět. Avšak nenáročné druhy jsou schopné tyto porosty využívat a možná se jim tam může dařit. Detailní rozbor a diskuzi zkoumaných jevů přinášejí přiložené publikace.

Introduction

Non-native species are, generally speaking, those species that occur out of their natural area of distribution (Hettinger, 2012; Kolar and Lodge, 2001). Many of non-native species has been spread by human activities, whether accidentally or intentionally (Mack et al., 2000). Vast majority of non-native species do not influence the ecosystems negatively (Williamson and Fitter, 1996). However, some well-adapted and rapidly spreading species may pose a potential threat for ecosystems. If such species do have a negative impact on the environment, they are called invasive species (Ruiz and Carlton, 2003). Their impacts are often reflected in a decrease of biodiversity and in a change of ecosystem functioning (Davis, 2009), whether directly by affecting the native species by competition (Bruno et al., 2005), or by altering the physical parameters and resources (e.g. water, light conditions or soil chemistry) as a consequence of ecosystem engineering (Crooks, 2002). Invasive species are able to decrease the species richness and, in an extreme case, to participate in the extinction of a species (Sax and Gaines, 2008).

Virtually any species can become a non-native species with a possible impact on an ecosystem. However, species located on low trophic levels carrying over their effects to other, higher trophic levels (cascade effects) might have a greater potential to an extensive influence on ecosystems. For this reason, I focused on the investigation of the effects of primary producers, here represented by two species of non-native trees in the Czech Republic, on secondary consumers, here bird communities occupying the studied tree stands. Many studies investigating the effects of non-native plants on birds aimed at non-native herbs, e.g. exotic grasses (Flanders et al., 2006), goldenrod (Skórka et al., 2010), knotweed (Hajzlerová and Reif, 2014), leafy spurge (Scheiman et al., 2003), and shrubs, e.g. acacia (Rogers and Chown, 2014), barberry (Schmidt et al., 2005), honeysuckle (Gleditsch and Carlo, 2014), tamarisk (Sogge et al., 2008), far less studies focused on the impact of non-native trees on birds, e.g. Sitka spruce (Sweeney et al., 2010) or Monterey pine (Lindenmayer et al., 2002). The studies comprising this thesis thus help to enhance our knowledge about the interaction of birds and non-native trees.

The first investigated non-native tree species was the black locust (*Robinia pseudoacacia* L.). This broad-leaved tree is native in south-eastern part of the USA where it occupies disturbed forests and other open habitats (Huntley, 1990) given the fact it is strongly shade intolerant (Huntley, 1990). It was introduced into Europe in the

17th century (Slavík, 1995) and currently ranks among the top invasive plants in Europe (Kleinbauer et al., 2010). In the Czech Republic it has been grown since the beginning of the 18th century (Slavík, 1995) and nowadays it is the most widespread non-native tree species in our country (Křivánek et al., 2006). It was primarily planted as an ornamental tree species; later it was grown on dry, steep, unstable rocky slopes to contribute to their stabilisation and also as a melliferous tree (DAISIE, 2009). It is able to expand in a relatively short time and replace indigenous plants in various habitats (DAISIE, 2009). As a nitrogen-fixing species it enriches the soil (Castro-Díez et al., 2014) and thus enables a strong development of herbaceous and shrub layers with a predominance of nitrophilous plants (Vítková and Kolbek, 2010), e.g. small balsam, common nettle, greater celandine, or black elderberry. A representative of a native broad-leaved tree used to compare the effects of non-native and native stands was an oak (*Quercus* spp.). It has been widely grown as a common commercial tree species in the study area and it occurred, together with other tree species, in biotopes nowadays overgrown by the black locust.

The second non-native tree species of my interest was a black pine (*Pinus nigra* A.). This coniferous tree is native in the Mediterranean region with a scattered distribution of its population (Cseresnyés and Tamás, 2014). Unlike the black locust, it is geographically native in Europe and its closest natural occurrence to the Czech Republic is in Austria (Cseresnyés and Tamás, 2014). The black pine was introduced in the late 18th century in our country (Hejný and Slavík, 1988) and was planted as an alternative tree species and, similarly to the black locust, to control soil erosion (Hejný and Slavík, 1988). It was grown mainly in non-forest, dry, and karst areas (Hejný and Slavík, 1988) where it grows better than the native trees given its high tolerance to drought (Eilmann and Rigling, 2012). Compared to the black locust it has much lower invasive potential given the fact it is not able to reproduce clonally or to grow rapidly. Effects of stands of the black pine were compared to the effects of Scots pine (*Pinus sylvestris* L.) stands. This native coniferous tree species has been planted also in biotopes now occupied by the black pine and represents a common commercial tree species occurring across the study area.

The influence of both non-native tree species could be reflected in higher trophic levels. A look at the opposite end of the trophic chain should clarify whether the influence is really transmitted through it.

Birds are useful indicators of the habitat quality (Canterbury et al., 2000; Gregory et al., 2003; Gregory and van Strien, 2010). If the quality is decreasing, the abundances of certain bird species may decline. In forest ecosystem the decline can be caused by a decrease of habitat heterogeneity coming from a low area or absence of some vegetation layers (Heyman, 2010), and by growing the monocultures (Felton et al., 2010) or even-aged stands (Thill and Koerth, 2005). However, we should be aware that the bird abundance may be a misleading indicator of the environmental health (Van Horne, 1983). Sometimes the bird species are attracted to a poor-quality habitat in perspective of their reproduction. Such a habitat acts as an ecological trap (Dwernychuk and Boag, 1972; Schlaepfer et al., 2002). Therefore, it is necessary to turn the attention also to the species richness which more clearly mirrors the relation of birds to the habitat. In general, altering the habitat becomes evident in a change in bird community composition (Fuller, 2012). Subsequently, the community is often more homogenised and specialised species are declining, e.g. habitat specialists are replaced by habitat generalists (Clavel et al., 2011; Le Viol et al., 2012) or the cavity-nesting species are declining (Martin, 2015).

Birds in central European forests play a role of primary consumers (frugivores, granivores), but more frequently, they represent the secondary consumers (insectivores, omnivores) since the vast majority of the birds feed their nestlings by animal food (Cramp, 1977–1994). That implies the effects of the primary producers, non-native trees, could transmit via the bird food to the top of the food chain, to birds. Substantial part of the bird food during the breeding season comprises of the larvae, mostly of nocturnal Lepidoptera (Thomas et al., 2001). However, the survey of bird food was not focused on larval stages, but on the mature individuals. Their abundances well express the relative amount of the available larvae (Skórka et al., 2010) and it can be used as a proxy variable.

The last phenomenon considered in this thesis is the nest predation. The stands of non-native trees are often characterised by altered vegetation structure (Hartman and McCarthy, 2008; Knight et al., 2007; Richardson and Rejmánek, 2011; Vitousek et al., 1996), which might be the reason for an increased or decreased rate of the nest predation. To simplify the study of the nest predation I used the artificial nests. Despite the fact that the rate of artificial nest predation does not match the rate of real nest predation (Moore and Robinson, 2004; Weidinger, 2001; Zanette, 2002), it is a useful indicator of a relative rate of the nest predation in particular forest stand types (Roos, 2002).

Aims of the thesis

Based on the above mentioned assumptions I set the following aims:

- To find out whether the bird species richness and the bird community composition differ between non-native and native tree stands and to identify the effects of structural parameters of vegetation. (**Paper I+II+III**)

- To identify bird ecological traits affecting bird species richness in stands of non-native black locust. (**Paper II+III**)

- To compare the quantity of the major food supply, nocturnal Lepidoptera, between native oak and non-native black locust stands and to test its effect on the bird community composition taking the bird ecological traits into account. (**Paper III**)

- To compare the relative nest predation rate between non-native black locust and native oak stands using the artificial nests. (**Paper IV**)

Vegetation structure of forest stands

Vegetation structure is one of the key parameters affecting the composition and diversity of many animal communities. Examples of this pattern can be seen in arthropods (Litt et al., 2014), amphibians (Atauri and de Lucio, 2001), reptiles (Garden et al., 2007), mammals (Williams et al., 2002), as well as in birds (James and Wamer, 1982). The relationship between diversity of animal communities and complexity of vegetation structure used to be predominantly positive (Stein et al., 2014; Tews et al., 2004). Thus the higher is the structural complexity of the vegetation, the greater is the diversity of present animal species. Birds do not represent an exception and their species richness frequently positively correlates with habitat heterogeneity (Cody, 1981; MacArthur and MacArthur, 1961).

In forests we can define the vegetation diversity, or, more generally, the structural heterogeneity of a given stand in a vertical and a horizontal direction. Vertical structure is primarily represented by forest layers (e.g. herbaceous, shrub, and canopy layers), horizontal structure is characterised mainly by forest discontinuity (e.g. forest clearings, uneven distribution of particular forest layers, and age classes) caused by terrain morphology, soil characteristics, and also by the forest management. Both directions describing the heterogeneity of forest stands are of great importance for forest birds. Vertical structure characterises various types of suitable habitats for birds whereas horizontal structure determines the extent of the habitats. In general, bird species richness markedly responds to vegetation structure of the habitat, and the vegetation diversity, in terms of plant community composition and plant species richness, plays rather a supporting role (Díaz, 2006; Laiolo, 2002; Zhang et al., 2013).

Commercial forests are characterised rather by a lower heterogeneity of vegetation structure compared to natural or semi-natural forests (Paillet et al., 2010). The reason could be seen mainly in growing even-aged and monoculture forest stands, and in removing the dead wood and old-growth trees (Angelstam and Mikusiński, 1994; Esseen et al., 1997). Except for the commercial and semi-natural stands, the stands invaded by non-native trees or fully composed of non-native trees can be considered a special type of forest stands. Such stands may have altered vegetation structure since many non-native plants can simplify the structure of vegetation cover (Hartman and McCarthy, 2008; Knight et al., 2007) which applies to non-native trees too (Richardson and Rejmánek, 2011, 2004). Subsequently, the stands may host fewer bird species compared to non-invaded stands. However, the opposite phenomenon may also be true because some non-native plants may increase habitat complexity through the ecosystem engineering process (Crooks, 2002). We can assume that in this case the invaded but more heterogeneous habitat may support more bird species than the habitat comprised of the native vegetation. To distinguish whether the vegetation structure in our study stands consisting of non-native trees is simplified or heterogeneous, compared to the stands of native trees, I mapped and analysed the following vegetation structure characteristics in all four forest types, i.e. in non-native black locust and black pine, and in native oak and Scots pine stands: the percentage cover of the herb layer <0.5 m high, herb layer >0.5 m high, shrub layer 1–5 m high, canopy, and clearings. Further I recorded the presence of unbroken canopy, the percentage proportion of the tree layer 5–10 m high, tree layer >10 m high, trees up to 0.2 m in diameter at breast height, 0.2–0.5 m and >0.5 m, and I counted the number of fallen trees and dead trees. These stand characteristics were used in analysis of the vegetation heterogeneity of the study plots expressed as Shannon indices of diversity (Shannon, 1948) (**Paper I**).

I revealed, rather surprisingly, higher vegetation heterogeneity in both stands of non-native trees, i.e. black locust and black pine, compared to the stands of native trees, i.e. oak and Scots pine (**Paper I**). This finding could imply that the non-native stands may host more bird species. However, a more detailed analysis showed that this was not the case and more heterogeneous stands were occupied by more bird species when the model was controlled for the effect of tree origin. In other words, bird species richness did not differ between stands of non-native and native trees. Thus some other attributes of non-native trees probably decreased the quality of the habitat so that its higher heterogeneity did not result in a higher bird species richness. I assume that food supplies may be altered in stands of non-native trees. This idea is thoroughly examined in another chapter.

Apart from vegetation heterogeneity analysis, the principle component analysis (PCA), describing the main gradients in vegetation structure of the black locust and oak plots was performed (**Paper III**). The first and the most important gradient in vegetation structure (PC1) directed from stands with tall trees and developed canopy to stands with low, thinner trees, developed shrub layer, and lots of fallen wood. This PC1 gradient corresponds to the difference between oak and black locust stands (**Paper I**). And since the PC1 gradient explained the increase of the species richness of habitat generalist birds, it shows that more habitat generalist bird species occurred in the black locust stands. This outcome was also confirmed using other data of bird richness in the black locust stands (**Paper II**). It remains to add that generalists generally thrive in heterogeneous habitats (Devictor et al., 2008), here represented also by the black locust stands, which is in accordance with aforementioned results of the analysis of vegetation heterogeneity structure. Regarding the stands of both pine species, although their structure differed in terms of vegetation heterogeneity, the difference in particular vegetation parameters was negligible (**Paper I**).

The differences in bird community composition between particular forest types were tested using a direct gradient analysis, the redundancy analysis (RDA), where the explanatory variable was a forest type – a categorical variable with four levels of black locust, black pine, oak, and Scots pine stands. The analysis showed that the community varied significantly between black locust and oak stands and negligibly between black pine and Scots pine stands (**Paper I**). Overall, the structure of bird community depended more strongly on forest type (coniferous and broad-leaved) than on tree origin (non-native and native).

Plant species richness, although not investigated, might also have an effect on surveyed birds. However, I assume it had only a little influence on them. Generally, non-native plants do not adversely affect the species richness of native plants (Thomas and Palmer, 2015), and, as mentioned above, birds respond more to the vegetation structure than to particular plant species. However, it is possible that if the undergrowth of focal stands comprises of non-native or invasive herbs and shrubs, the vegetation structure would be more simplified and negatively affect the bird species richness. Similarly, it can be assumed a negative effect of strongly simplified stands of non-native trees on birds, e.g. in eastern white pine (*Pinus strobus*) stands.

To conclude, the differences in bird species richness between stands of non-native and native trees were not proved. Nonetheless, birds can greatly differ in their requirements on the habitat quality. For this reason, the next chapter deals with the deeper analysis of bird species richness taking the birds' ecological demands into account.

Ecological traits of birds

Birds have evolved in various types of environment requiring different adaptations (Cody, 1987). They have chosen such habitats which meet their basic needs, as breeding opportunities, food supplies, or safe shelters against predators. The fulfilment of the habitat requirements mirrors in the presence and also in the abundance of a certain species. That implies the number of different habitats occupied may mirror the adaptability of a species, whereby the species inhabiting lots of habitats is more adaptable and probably less demanding than the species occupying only a few habitats. To investigate the extent to which the bird species surveyed in stands of non-native trees are adapted to this altered habitat, I focused on their habitat specialisation.

Species' habitat specialisation was evaluated using a species specialisation index (SSI) introduced by Julliard et al., (2006). This index is represented by a coefficient of variation of abundance of a given bird species across various habitats. Low values mean habitat generalists, i.e. species not highly prevailing in any habitat type, and high values mean habitat specialists, i.e. species occupying only a few habitats. The SSI values of surveyed species were obtained from Reif et al., (2010). They used data from the Breeding Bird Monitoring Programme (BBMP) in the Czech Republic (Janda and Šťastný, 1984) for the calculation of the SSI of Czech birds. Although my field research of birds was conducted on local or regional scale, I believe the usage of SSI based on whole country data is not very biased because BBMP surveys are conducted in representative biotopes across the Czech Republic.

Habitat specialisation describes, to some extent, dispersion ability of a given species and its resistance to environmental changes. To investigate the measure of adaptation to environmental changes I focused on the life history strategy of the bird species.

Life history strategy includes various traits and adaptations concerning species' reproduction (Stearns, 1992). Specifically, I focused on the position of surveyed bird species on the gradient from K-selected to r-selected species, the slow-fast continuum. The gradient used was obtained from Koleček and Reif, (2011) who performed PCA on six life history traits (body mass, egg mass, number of broods per year, laying date, clutch size, and length of incubation period) of 178 bird species breeding in the Czech Republic for its determination. Slow life history species (with larger body size, longer lifespan and lower fecundity) are expected to be more sensitive to habitat alteration than fast life history species. So the bird community in stands of non-native trees may comprise of less numbers of K-selected species compared to the stands of native trees.

The differences in the environment, e.g. vegetation heterogeneity structure, of both stand types thus could manifest in different shares of habitat generalists/specialists and species with slow/fast life history strategy. The following analyses shed light on this issue.

I focused on the differences in the abundance of the bird species between the black locust and the oak stands taking the SSI and life history strategy into consideration. The analysis was performed employing the generalized linear mixed model with Poisson structure of errors and species identity as a random factor. The abundance of each bird species summed over all plots within each forest type was the response variable, and forest type (black locust and oak), SSI, life history strategy, and the interactions of SSI × forest type and life history × forest type were the explanatory variables. Further I performed several analyses showing whether the species richness of generalists/specialists is associated with stands of black locust or oak.

The first analysis used the position of particular bird species along the gradient from black locust to oak showing their association with particular stand types. It was obtained as the position of particular bird species along the first axis of RDA, representing the gradient from black locust to oak stands. These positions of the species, species scores, were used as response variable in the phylogenetic generalized least squares model. The explanatory variables were the species traits, i.e. SSI and life history strategy.

In the second analysis I compared the numbers of bird species in several groups of generalists/specialists between both stand types. Bird species were sorted according to their SSI into two halves into groups of “specialists” and “generalists”, and into four quartiles into groups of “strong specialists”, “moderate specialists”, “moderate generalists”, and “strong generalists”. I employed simultaneous autoregressive (SAR) models to take the spatial autocorrelation of the plots and thus their possible spatial non-independence into account.

The third analysis was performed to find out whether the bird species richness in mentioned groups of habitat specialisation depended on various characteristics of the plots, including aforementioned PC1 scores, corresponding with the gradient from black locust stands to oak stands.

It proved to be a higher abundance of birds in the black locust stands and only the habitat specialisation, not the life history strategy, had a significant effect on the differences in the abundance between focal stands. Specifically, in the black locust stands the generalists prevailed over the specialists; in the oak stands the abundance was the same with regard to the habitat specialisation. A similar pattern was discovered in the analysis of species richness. Species with low SSI, the generalists, were associated with the black locust stands whereas species with high SSI, the specialists, were associated with the oak stands. However, richness of species with fast/slow life history strategy did not prove to be different among both stand types (**Paper II**).

The results of the analyses evaluating different bird groups of habitat specialisation confirmed previously mentioned patterns. “Generalists” and “strong generalists” dominated in the black locust stands while “specialists”, “moderate specialists” and “strong specialists” prevailed in the oak stands. Among various characteristics of the plots only the PC1 gradient explained significantly the species richness in all three groups of generalists. It seems the vegetation structure represents an important habitat component. By contrast, species richness of specialists was not related to PC1 gradient, but it depended on the diversity of the food, here represented by the nocturnal Lepidoptera (**Paper III**). Specialised species are thus probably limited by the food supplies in an altered habitat. To examine this assumption, the next chapter is devoted to the birds’ food supplies.

Food supplies

Birds of our focal forests represent primarily the secondary consumers, with predominance of insectivores and omnivores. Since most of the birds feed their nestlings on animal food (Cramp, 1977–1994), the arthropods are very important food source during the breeding season. However, the community composition of this group may be altered by the presence of non-native trees, given the fact that one of the main determinants of arthropod diversity is the habitat structure (Harris et al., 2004; Litt et al., 2014; van Hengstum et al., 2014). And since it has been already shown that the vegetation structure of black locust stands differs compared to the stands of native oaks (see the chapter Vegetation structure of forest stands), it may be expected that the arthropod communities are also modified. Consequently, the bird community in the black locust stands may be impoverished due to the changes in the food supply. Specifically, some specialised bird species may be missing as a result of a lack of specific food. It is also worth to mention the plant food source, namely berries and seeds, probably available in a higher amount in black locust stands having a strong undergrowth of various shrubs and herbs, compared to oak stands. However, such a food source is most likely more important outside the breeding season (Snow and Snow, 2010).

Among the arthropods, I focused on the diversity of nocturnal Lepidoptera (hereafter called moths) representing the essential part of the diet of the surveyed birds during the breeding season (Cramp, 1977–1994). However, birds predominantly feed their nestling on moths' larvae (Krištín and Patočka, 1997; Seki and Takano, 1998) which are difficult to survey in the scale of the whole study plot. Nonetheless, the richness of adults relatively well mirrors the richness of larvae (Skórka et al., 2010). For that reason, portable light traps were used to investigate the availability of food in both focal stand types.

Although all the investigated bird species were insectivores/omnivores, they differed in the way of obtaining the food at the habitat scale. Using five main categories of foraging techniques, the birds were sorted into groups of ground foragers, shrub foragers, canopy foragers, foliage gleaners, and bark foragers. Such a classification took the major foraging strata as well as the most utilised parts of vegetation for foraging into account. Then the differences in bird species richness among the particular groups of foraging techniques between black locust and oak stands were investigated. Additionally, I analysed whether the species with invertebrate, and with mixed diet prevails in some stand type.

Moth species richness, as well as the diversity of moths measured as the Shannon diversity index, was lower in stands of non-native trees (**Paper III**). It was most likely caused by the lack of moth species bound to the forest canopy layer probably having not enough time to adapt to the exotic tree (unpublished data). This impoverishment might be reflected in the species richness of birds.

Employing several simultaneous autoregressive (SAR) models where the bird species richness in particular groups of habitat specialisation was a response variable and moth diversity together with other plot characteristics were the explanatory variables, it was discovered that only the bird specialists were affected by the moth diversity (**Paper III**). Specifically, species richness of "specialists" and "moderate specialists" was increasing with the increasing moth diversity on the plots. And since the higher diversity of moths was found in the oak stands, I can conclude that more specialised birds are probably limited by the quality of the food supply in the invaded stands. The absence of this relation in "strong specialists" suggests that such species may be much more sensitive to the quality of the food supply than the rest of specialists and the diversity of moths is not a sufficient predictor of their richness. Or, there is a more prosaic explanation for it: specialised species are rather scarce and the test was not significant due to the low sample size.

The analysis of foraging techniques revealed that the bird community in black locust stands was more species-rich on shrub foragers and foliage gleaners. Apparently, the strongly developed herb and shrub layer in the black locust stands could attract them. In the oak stands, only the species richness of canopy foragers tended to be (slightly insignificantly) higher, compared to the black locust stands, probably with respect to higher canopy closure in those stands. Finally, the invertebrate or the mixed diet species did not prevail in either stand type. It implies that the limited quality of investigated food supply, here represented by moths, may be supplemented by other arthropods (e.g. spiders, beetles, and other ground-dwelling invertebrates) in the black locust stands wiping out the differences between food supplies and consequently the bird species richness in both stand types. Similarly, it has not been shown that likely more impacted invertebrate diet species thrived worse than mixed diet species using a wider variety of resources (**Paper III**).

Lower diversity and species richness of moths in black locust stands indicate less choice or lower availability of particular food. However, only the information about a complete diet in surveyed bird species would clarify the function of the food supply mechanism. In fact, it is possible that specialised birds could be limited by other (insect) food sources to a certain extent correlated to the diversity of moths.

Despite the fact that the black locust stands are impoverished in terms of moth species, it seems there is enough food for breeding. Therefore, the next chapter concerns the nesting of birds, namely nest predation, to investigate whether the black locust stands are rich on it.

Nest predation pressure

Nest success is one of critical parameters influencing the reproductive output of a given individual (Newton, 1998; Ricklefs, 1969) and, to a lesser extent, it also affects the reproductive success and abundance of the whole population (Cresswell, 2011). Still, the comparison of nest predation between habitats provides an insight on the habitats' hospitality in view of the reproduction of present bird community. Similarly to the bird species richness, the nest success may depend on the habitat structure (Chalfoun and

Martin, 2009; Martin, 1988). It can be expected that in poorly structured habitats with simplified vegetation, the nest predation pressure is higher than in heterogeneous habitats, potentially offering enough protection against the nest predators. Higher nest concealment could thus increase the nest survival rate. Looking at the nest predation in stands of non-native trees, it has been reported many times that simplified vegetation cover of those stands might often be the reason of increased nest predation in there (Borgmann and Rodewald, 2004; Ortega et al., 2006; Rodewald et al., 2010). Naturally, the nest location within the stand also plays an important role (Seibold et al., 2013).

Bird species vary in nest site preferences and the nest location itself could increase/decrease the nest predation pressure. Generally, the predation of passerines' nests located on the forest floor is lower compared to the nests located in the forest understorey (Martin, 1993). To find out whether such pattern appeared also in the black locust stands studied, the nest predation pressure was investigated both in ground and shrubs located nests. However, given the fact that studying the real nests would be highly time-consuming and laborious in the scale and numbers of our study plots, I used the artificial nests containing one quail and one plasticine eggs mimicking the small forest passerines' nests.

The usage of the artificial nests has been widely criticised due to their uncertain information value (Moore and Robinson, 2004; Robinson et al., 2005; Thompson and Burhans, 2004). Nonetheless, despite the predation rate of artificial nests does not match the predation rate of real nests (Moore and Robinson, 2004; Weidinger, 2001; Zanette, 2002) and there was a higher rate in the first case (Burke et al., 2004; King et al., 1999; Wilson et al., 1998), the artificial nests are suitable for the comparison of the relative nest predation rate between the habitats assuming that the nests are placed so as to be exposed to the same predation pressure and predators in compared habitats (Pärt and Wretenberg, 2002).

The black locust stands studied were characterised by higher vegetation heterogeneity than the native oak stands. For that reason, we expected a higher nest predation rate in the latter mentioned because the nests were probably easier to detect by a predator in there. However, I did not find a difference in the nest predation rates between both stand types. It suggests that the birds breeding in the stands of non-native black locust may not rely on a better nest concealment and their nests can be threatened similarly as in the native stands with far less extent of the understorey. The nest predation rate taking the nest position on the ground and on shrubs into account was also not different between the two stand types showing that the effect of dense understorey was rather slightly noticeable (**Paper IV**).

Similar pattern in nest predation rate would be expected by conducting the nest predation experiment in stands of non-native and native pines. Both these stand types had similarly developed undergrowth and thus the nests should be exposed to the same predation risk. I also expect the predator community composition would not differ between the two types of the pine forests, because black pine and Scots pine are closely related and probably offer similar habitat conditions. Maybe, the higher vegetation heterogeneity of black pine stands could play a role. But its effect probably did not apply in the conducted experiment in black locust stands and thus I assume it would also not show an effect in black pine stands.

The suitability of black locust stands for breeding showed to be unclear. Better understanding of the birds' performance in stands of this non-native tree could be achieved by further studies on the real nests success of the bird communities present.

Conclusions

This thesis contributes to the understanding of the relationship of birds to non-native trees. By studying the effects of stands of non-native black pine and black locust I investigated whether the vegetation structure, bird species richness, bird community composition, food supplies, and nest predation pressure have been affected.

Vegetation structure has an important influence on the bird diversity which has also been proven in my study (**Paper I**). It has been showed that the increasing heterogeneity of vegetation structure attracted more bird species regardless of the origin of the constituent trees. The assessment of the influence of non-native tree stands on birds should thus distinguish whether a tree stand has the high vegetation structure diversity and potentially attracts many bird species, or it has a simplified vegetation structure and probably causes local impoverishment of bird communities. Nonetheless, despite the significantly higher heterogeneity of vegetation structure in stands of non-native trees I have not found higher bird species richness in those stands compared to the native tree stands (**Paper I**). The reason of this pattern can be explained by the lower diversity of nocturnal Lepidoptera in non-native tree stands, specifically in the black locust stands (**Paper III**). Limited quality of the food source can decrease the bird species richness, which I discovered in the case of habitat specialists (**Paper II+III**). It follows that apart from the vegetation structure, the sufficient quality of the food supply in non-native tree stands has to be provided. Otherwise less demanding species, like habitat generalists, can prevail in the community and often discussed homogenisation of bird communities may arise.

The bird community composition was, however, not primarily affected by the non-native trees. Since it depended more strongly on the birds' association with coniferous vs. broad-leaved forests (**Paper I**), the occurrence of a bird species in a given forest stand first results from leaf morphology and then the effect of non-native trees should be taken into account.

Black locust stands were characterised by high vegetation structure heterogeneity and also by well-developed herb and shrub layers. In relation to breeding, such attributes could reflect in a lower nest predation pressure because better nest concealment generally increases the nest success (Sloan et al., 1998; Zieliński, 2011). However, the experiment with artificial nests indicated that the undergrowth in stands of non-native trees apparently did not provide sufficient protection against predators to decrease the nest predation rate (**Paper IV**). Anyway, it would be beneficial to investigate which specific predators depredated the nests and subsequently evaluate whether the habitat composition of stands of non-native trees may somehow facilitate the nest predation.

The biodiversity does not seem to be substantially threatened by stands of non-native trees, at least from the perspective of the studied bird communities as its indicator. Nonetheless, the decline of bird habitat specialists could indicate that food sources or breeding opportunities might be altered despite the fact that the focal stands were highly structurally heterogeneous and thus constituted relatively favourable habitat. I suppose that much more simplified vegetation cover of non-native plants might significantly limit the mentioned sources and other bird species would decline, reflecting a loss of biodiversity.

Studied stands of non-native trees represent an altered habitat but they do not constitute a completely inhospitable environment for birds. They hosted considerable diversity of birds, albeit impoverished in specialised species. This pattern seems to symbolise one of the greatest threat of non-native trees to birds, potentially gaining its importance with more aggressive tree invaders.

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Attached publications

Paper I

Hanzelka, J., Reif, J., Effects of vegetation structure on the diversity of forest bird communities in an era of plant invasions: the cases of nonnative black pine (*Pinus nigra* A.) and black locust (*Robinia pseudacacia* L.) in the Czech Republic. (submitted manuscript)

Effects of vegetation structure on the diversity of forest bird communities in an era of plant invasions: the cases of non-native black pine (*Pinus nigra* A.) and black locust (*Robinia pseudacacia* L.) in the Czech Republic

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Abstract

The influence of vegetation structure on bird communities is well established; however, not sufficiently known about the effects of non-native plants. Here we surveyed bird communities and mapped the vegetation structure in stands of non-native broad-leaved and coniferous trees, black locust and black pine, in a central European country, the Czech Republic. We expected that the positive relationship between bird species richness and vegetation heterogeneity would be less pronounced in non-native stands due to an assumed negative effect of their exotic origin. Further, we tested whether the bird community composition is more impacted by tree origin (native and non-native) than forest type (coniferous and broad-leaved). We compared the bird species richness and vegetation heterogeneity between native, non-native, broad-leaved, and coniferous stands by means of spatial analysis – generalized least squares models. The bird community composition was explored by multivariate direct gradient analyses – redundancy analyses. We found that bird species richness significantly increased with increasing vegetation heterogeneity only after taking tree origin into account. Moreover, the relationship between vegetation heterogeneity and bird species richness did not differ between native and non-native stands. Since there was higher vegetation heterogeneity in non-native stands, we suggest that the potential benefits of their higher heterogeneity were suppressed by some other (unknown) characteristics (e.g. limited food supply). The most important gradient in the bird community composition was from broad-leaved to coniferous stands irrespective of tree origin. The effect of tree origin was expressed as the secondary gradient and thus less important, albeit still significant. It seems that the birds' adaptations to different leaf morphology play a much more important role in structuring bird communities than the influence of tree origin. Taken together, our results indicate that non-native trees significantly affect bird communities, but do not override the effects of more “basic” stand attributes such as leaf morphology.

Keywords: community composition; forest birds; non-native trees; species richness; vegetation heterogeneity

1. Introduction

Invasive plants are spread worldwide and have a large impact on ecosystem biodiversity (Mack et al., 2000; Pyšek et al., 2012; Vilà et al., 2011). They change the vegetation structure and composition of plant communities (Hejda et al., 2009), which is often reflected by changes in the presence of arthropods (Ballard et al., 2013; Bezemer et al., 2014; Litt et al., 2014), and vertebrates (Aslan and Rejmánek, 2010; Bateman and Ostoja, 2012; Catling, 2005; Ostoja and Schupp, 2009). It has been shown that stands of many of non-native plants have uniform and structurally simplified vegetation cover (e.g. (Hartman and McCarthy, 2008; Knight et al., 2007; Richardson and Rejmánek, 2011, 2004). On the other hand, some invasive species, including plants, can act as ecosystem engineers (Chabrerie et al., 2010; Crooks, 2002; Jones et al., 1994) and, to some extent, increase the biotope complexity (Crooks, 2002).

The structural diversity of habitat is one of the key elements determining bird diversity (James and Wamer, 1982; MacArthur and MacArthur, 1961; Tews et al., 2004). It has been frequently observed that a higher heterogeneity of vegetation structure results in higher bird species richness (Baláž and Balážová, 2012; Díaz, 2006; Ghadiri Khanaposhtani et al., 2012; Laiolo, 2002; Nájera and Simonetti, 2010), which is in accordance with theoretical predictions of the ecological mechanisms of species coexistence (Tokeshi, 1999). However, this simple relationship may be challenged by the exotic nature of some structural vegetation components

(Fleishman et al., 2003). Therefore, to understand the effects of vegetation structure on bird community diversity in the recent era of widespread plant invasions, it has to be investigated simultaneously in both native and non-native vegetation. To our knowledge, such studies are rather scarce and of limited generalization potential since they usually focus on a single non-native plant species or vegetation type.

In this study, we investigate differences in the structural diversity of non-native and native forest stands, and whether this structural diversity affects the bird species richness and community composition. Because several studies have reported important differences in bird communities between coniferous and broad-leaved forests (Díaz, 2006; Donald et al., 1998; Easton and Martin, 1998; Reif et al., 2008b), we focused on non-native coniferous stands of black pine (*Pinus nigra* A.) and stands of a non-native broad-leaved tree, black locust (*Robinia pseudacacia* L.). As representatives of native vegetation used to compare bird communities with these focal non-native tree species, we chose broad-leaved oak (*Quercus* spp.) and coniferous Scots pine (*Pinus sylvestris* L.). Such an approach allows straightforward evaluations of the effects of non-native stands on birds based on key habitat components.

Both non-native tree species studied here are among the major European plant invaders (Buchholz et al., 2015) and are the most widespread exotic trees in our study area in the Czech Republic, central Europe (Křivánek et al., 2006). Black pine was introduced in the late 18th century and widely planted as an alternative tree species, often as monoculture, in dry, non-forest, and mainly karst areas (Hejný and Slavík, 1988). It grows better than many native tree species in these areas due to its higher resistance to unfavourable conditions, especially to drought (Eilmann and Rigling, 2012). Black locust was planted from the beginning of the 18th century (Slavík, 1995). In the wild it was planted mainly on dry, rocky and steep slopes, contributing to stabilization (DAISIE, 2009). Given its ability to fix atmospheric nitrogen using symbiotic bacteria, it enriches the soil (Castro-Díez et al., 2014) and enables the development of strong shrub and herbaceous layers in its stands, with a predominance of nitrophilous species (Vítková and Kolbek, 2010). Black locust has expanded extensively in the above-mentioned biotope and often forms monocultures. Concerning the focal native tree species, Scots pine is a widely grown commercial species, and is also planted in biotopes now occupied by black pine. Oak (*Quercus* spp.) is currently grown in extensive forest stands in lowland areas, but it naturally occurred in biotopes nowadays overgrown by black locust.

Using data on bird occurrences in study plots located in stands of our four focal tree species, we tested the following hypotheses. (i) We tested whether tree origin (i.e. native and non-native) affects the relationship between bird species richness and vegetation heterogeneity. We predicted the relationship would be positive in native stands, but significantly weakened in non-native stands because the exotic origin compromises positive effect of structurally complex vegetation. (ii) We tested whether tree origin has a greater impact on bird species richness and community composition than forest type (i.e. coniferous and broad-leaved). We predicted that the outcome would depend on the relationship of a given variable with the vegetation structure. Clearly, if the tree origin affects the vegetation structure more than forest type then we would predict a greater impact on birds, and vice versa.

2. Material and Methods

2.1 Study area

We carried out the study in the Central Bohemian region, located in the western part of the Czech Republic (Central Europe). The study area is characterized by extensive woodlands as well as small forest stands surrounded by grasslands, arable fields and human settlements. Broad-leaved forests predominate, with oak, hornbeam (*Carpinus betulus*), beach (*Fagus sylvatica*), small-leaved lime (*Tilia cordata*), ash (*Fraxinus excelsior*), maple (*Acer* spp.) and black locust as the most common species. Coniferous forests are comprised mostly of spruce (*Picea abies*), Scots pine, black pine and larch (*Larix decidua*). Throughout the study area, we established 20 plots in black locust, 25 plots in oak, 20 plots in Scots pine and 20 plots in black pine stands (Fig. 1); the spatial distribution of study plots reflected the availability of suitable stands of the focal trees. Each plot was of size 100 × 100 m. Plots were located in the sloping terrain where non-native black locust and black pine were usually grown. Altitudes of the plots ranged from 210 to 510 m asl (mean 340 ± 60 SD m asl, Supplementary material Table A1), and the age of forest stands ranged between 30 and 150 years (mean 95 ± 25 SD years, Supplementary material Table A1). Any two adjacent plots were located at least 500 m apart to avoid double-counting individual birds. Most of the plots were not situated closer than 100 m from the forest edge to minimize edge effects. However, plots in black pine were located closer to forest edges (distances of ca 50 m) due to the relatively small area of these stands and the fact that black pine was often planted on formerly non-forested areas not directly adjacent to extensive forest stands.

2.2 Bird survey

A simplified spot mapping technique (Bibby et al., 2000) was used to count birds during the breeding season from April to May. An observer recorded individual birds on all black locust and 20 oak study plots in 2014, and on all black pine, all Scots pine and five oak study plots in 2015, i.e. none of the plots were counted in both years. Three visits were carried out to each study plot, in early April, at the turn of April and May, and in late May, thus sampling both early and later breeding species. All seen and heard bird individuals were recorded during a slow 20-min walk through the plot in three ca 30-m wide belts. The visits were performed in early morning between sunrise and 9:30 am during fair-weather conditions (no rain, no strong wind). From the bird species recorded we excluded species with just incidental occurrences on the study plots; i.e. all raptors and those species of which a total of only one individual was detected on all study plots together. For further analyses, the abundance of a given species on a particular plot was the maximum count from the three plot visits. For each study plot we expressed the species richness as the total number of species recorded during the visits.

2.3 Vegetation structure

We mapped the vegetation structure in detail during June, after the bird surveys. On each plot, vegetation parameters were estimated in three bands, each representing one third of the study plot, and the mean value of each parameter (except total numbers of fallen trees and dead trees) was calculated (Supplementary material Table A1). Specifically, we estimated the percentage cover of the herb layer <0.5 m high (herbS), herb layer >0.5 m high (herbT), shrub layer 1–5 m high (shrub), canopy, and clearings. Further we estimated the percentage proportion of the tree layer 5–10 m high (treesS), tree layer >10 m high (treesT), trees up to 0.2 m in diameter at breast height (trees – thin), 0.2–0.5 m (trees – med) and >0.5 m (trees – thick), and we counted the number of fallen trees and dead trees. Since these vegetation characteristics were estimated in different units, we standardized each variable to unit SDs for further analysis.

For each plot, we quantified the diversity of the vegetation structure using the Shannon-Wiener diversity index:

$$H' = -\sum_{i=1}^{S} \mathrm{p}_i \ln \mathrm{p}_i$$

where S is the number of vegetation characteristics and p_i is the proportion of the ith vegetation characteristic on each plot (Supplementary material Table A1).

2.4 Statistical analyses

2.4.1 Vegetation structure

We first compared the indices of diversity of the vegetation structure (hereafter called vegetation heterogeneity) between forest types (i.e. coniferous and broad-leaved) and tree origins (i.e. native and non-native) employing analysis of variance (ANOVA). The model included both main effects as well as the forest type × tree origin interaction. This interaction showed whether the difference in vegetation structure between native and non-native stands is more pronounced for coniferous trees than for broad-leaved trees.

In the next step, we tested whether particular stand types (i.e. black pine, Scots pine, black locust and oak) could be characterized by specific vegetation structures. For this purpose, we ran three redundancy analyses (RDA) relating all variables describing the vegetation structure (response variables) to different explanatory variables as follows. First two analyses were performed for coniferous (black pine vs. Scots pine) and broad-leaved (black locust vs. oak) forests separately. Then, a final analysis contained all stand types studied together, i.e. black locust, oak, black pine, and Scots pine.

2.4.2 Bird communities

We first focused on investigating the species richness patterns when species richness was used as a response variable in all models. The first model included tree origin (categorical explanatory variable with two levels: native and non-native) and vegetation heterogeneity (continuous explanatory variable) as well as the interaction of these variables, testing whether the relationship of bird richness to vegetation heterogeneity differs between stands of native and non-native trees. In this model we centred the vegetation heterogeneity variable to zero mean and unit variance to avoid misinterpretation of the interaction term (Schielzeth, 2010). The second model included only the main effects of variables incorporated into the previous model (i.e. no interaction terms). The third model included the main effects of the explanatory variables from the second model, i.e. vegetation heterogeneity and tree origin, and, in addition, forest type (categorical explanatory variable with two levels: coniferous and broad-leaved).

All models described above were linear models assuming independence of data points and normal distribution of errors. However, since the data may suffer from spatial autocorrelation resulting from the location of study plots, we also employed generalized least squares (GLS) models with an exponential spatial autocorrelation structure of residuals using R package ‘nlme’ (Pinheiro et al., 2015), testing for the same relationships as did the linear models. To improve the models’ fit we estimated the range and nugget parameters from semivariograms (for details see (Dale and Fortin, 2014)) based on the residuals of individual linear models. These parameters were further specified in the GLS models. Finally, we compared the Akaike information criterion (AIC) values of the linear models and GLS models to find out whether the latter improved the model fit. In all analyses, we controlled for the potential confounding effects of forest age and altitude by including these plots’ attributes into the models as fixed effects.

In the second step, we related the abundance of bird species to particular stand types using RDA in the same way as we did for the vegetation structure, i.e. we compared bird communities between black pine and Scots pine in one model, between black locust and oak stands in the second model, and the final model contained all four stand types together.

All ANOVAs, linear models and GLS models were conducted using R 3.2.1 (R Core Team, 2015); multivariate RDAs were conducted using Canoco 5 (ter Braak and Šmilauer, 2012).

3. Results

3.1 Vegetation structure

Non-native stands had higher vegetation heterogeneity, expressed as the Shannon-Wiener diversity index (mean = 2.12 ± 0.05 SE), than native stands (1.96 ± 0.05 SE; $t_{79} = 3.5$, $p < 0.001$). Moreover, coniferous stands had higher vegetation heterogeneity (1.96 ± 0.05 SE) than broad-leaved stands (1.76 ± 0.05 SE; $t_{79} = 3.7$, $p < 0.001$). Interestingly, the forest type × tree origin interaction was significant ($t_{79} = 2.1$, $p = 0.041$), indicating greater differences in vegetation heterogeneity between non-native and native stands in broad-leaved than in coniferous forests (Table 1). Comparing mean values for respective stand types supports this observation: similar values of high vegetation heterogeneity were found in non-native black pine stands (2.08 ± 0.03 SE) and black locust stands (2.06 ± 0.02 SE), whereas vegetation heterogeneity was considerably lower in native Scots pine stands (1.87 ± 0.04 SE), and the lowest values were found in oak stands (1.77 ± 0.03 SE). Comparing the linear model to the GLS model including a spatial autocorrelation structure, we found the latter did not improve the model fit (see AIC values in Table 1).

Multivariate RDA of vegetation structure variables showed that stand characteristics explained only a small yet significant proportion of the variability (5.40 %, pseudo-F = 2.2, p = 0.036) between non-native and native pine stands. Both stand types were thus quite similar to each other in those characteristics (Fig. 2a). A similar analysis focused on black locust and oak showed that these stands had much more pronounced dissimilarity in vegetation characteristics (variation explained 28.83 %, pseudo-F = 15.4, p = 0.002). Specifically, black locust stands were characterized by developed shrub and higher herb layers, trees were smaller and thinner, there was a high amount of fallen trees on the ground and stands had more clearings than oak stands (Fig. 2b). Oak stands had higher canopy coverage, a more developed low herb layer, and trees were thicker, higher and more often dead than in non-native stands (Fig. 2b).

The final RDA, investigating the relationship of vegetation characteristics to all stand types, explained 23.15 % of the variability in three canonical axes. The first axis accounted for 15.09 % (pseudo-F = 14.4, p = 0.002), second axis for 6.12 % (pseudo-F = 6.3, p = 0.002) and the third axis for 1.94 % (pseudo-F = 2.0, p = 0.062) of the variability. The first axis shows the gradient going from black locust to oak stands; both black and Scots pine were located around the central position and thus independent of the gradient (Fig. 3a). The second axis shows a distinction between broad-leaved and coniferous forests, with black locust and black pine at the opposite extremes of the gradient. The third (non-significant) axis describes the gradient from black pine to Scots pine stands, with both oak and black locust located around the central position (Fig. 3b). Taken together, RDA results suggest that vegetation structure was more different between the native and non-native broad-leaved stands (the first axis) than between the coniferous and broad-leaved (the second axis) or between the native and non-native coniferous stands (third axis).

3.2 Bird communities

In total, we recorded 38 bird species, of which 32 were found in black pine stands, 29 in Scots pine stands, and 28 in both black locust and oak stands (see Supplementary material Table A2 for the bird list and abundances). Concerning the mean number of species per plot, the highest values were found in black locust stands (12.05 ± 0.67 SE), while the other stand types showed similar numbers to each other (black pine: 10.15 ± 0.72 SE, Scots pine: 10.70 ± 0.87 SE, oak: 10.80 ± 0.61 SE).

When relating bird species richness to its potential predictors by linear and GLS models, respectively, according to AIC the GLS models showed better fit than linear models, indicating the importance of taking the spatial position of study plots into account (Table 2). According to the GLS models, bird species richness was not related to either tree origin or to forest type (Table 2). However, bird species richness increased significantly with vegetation heterogeneity when tree origin was factored out (Table 2b, c). A non-significant interaction between tree origin and vegetation heterogeneity implied that this relationship did not differ between native and non-native forest stands (Table 2a). We did not observe any significant effects of stand age or altitude in the GLS models, although the latter was significantly negative in the linear models.

RDA relating the abundance of particular bird species to black pine and Scots pine stands, respectively, showed that these stands differed only slightly in bird community composition. The first canonical axis explained 3.89 % of the variability in bird abundance on study plots (pseudo-F = 1.5, p = 0.070; Fig. 4a). In contrast, RDA focused on black locust and oak stands showed significant differences in bird community composition between these stand types. The first canonical axis explained 11.92 % of the variability in bird abundance on study plots (pseudo-F = 5.1, p = 0.002), and some species showed clear associations to particular stands. The Hawfinch (*Coccothraustes coccothraustes*), the Middle-spotted Woodpecker (*Dendrocopos medius*), the Wood Warbler (*Phylloscopus sibilatrix*) and the Chaffinch (*Fringilla coelebs*) were most abundant in oak stands, while the Blackcap (*Sylvia atricapilla*), the Chiffchaff (*Phylloscopus collybita*) and the Redstart (*Phoenicurus phoenicurus*) were most abundant in black locust (Fig. 4b).

RDA investigating the relationship of bird species abundance to all four stand types together explained 17.53 % of the variability in three canonical axes. Particular axes explained 10.16 % (pseudo-F = 9.2, p = 0.002), 5.86 % (pseudo-F = 5.7, p = 0.002) and 1.51 % (pseudo-F = 1.5, p = 0.078) of the variability, respectively. The first axis describes the gradient from coniferous to broad-leaved stands, while the second axis describes the gradient from oak to black locust stands, with both black pine and Scots pine located around the central position of this gradient (Fig. 5). Bird communities are thus predominantly structured according to forest type, i.e. whether the constituent tree species are coniferous or broad-leaved irrespective of their origin, and the difference between native and non-native trees is less important.

4. Discussion

Our study demonstrates previously unrecognized patterns in the relationships between non-native trees and bird communities. Stands of our focal non-native species, coniferous black pine and broad-leaved black locust, were more heterogeneous in terms of the structural diversity of vegetation than stands of native coniferous and broad-leaved trees, Scots pine and oak. However, these differences in vegetation structure did not straightforwardly translate into differences in the species richness and composition of bird communities. First, bird species richness was positively correlated with vegetation heterogeneity, but did not differ between native and non-native stands. Second, the bird community composition was primarily driven by differences between broad-leaved and coniferous stands irrespective of tree origin, i.e. whether they were native or non-native stands. This distinction in tree origin was less important and only significant for black locust vs. oak stands, and not for black pine vs. Scots pine stands.

4.1 Bird species richness

The absence of a difference in bird species richness between native and non-native stands, despite significantly higher vegetation heterogeneity in the latter stands, may be a consequence of the exotic nature of tree species creating the heterogeneous stands. Clearly, benefits for species co-existence resulting from increased habitat heterogeneity (Tokeshi, 1999) are compromised by other characteristics of non-native tree species. Specifically, we suggest that an insufficient insect food supply, which was found in black locust stands in our recent study (Reif et al., in press) and is frequently reported in non-native plant stands due to a lack of specific herbivorous insects (Litt et al., 2014), may limit the presence of some species in these stands. In fact, we have previously found that habitat specialists are lacking in non-native stands (Hanzelka and Reif, 2015), and this may be one factor compromising the assumed positive effect of vegetation heterogeneity. On the other hand, a higher structural heterogeneity in non-native stands could explain the higher abundance of bird generalists in black locust stands compared to oak stands that was found in our previous study (Hanzelka and Reif, 2015), since generalists thrive in heterogeneous environments (Devictor et al., 2008).

In contrast, if structurally heterogeneous stands contained solely native trees, we would expect a positive effect on the number of bird species, as has been demonstrated in many studies (Díaz, 2006; Huang et al., 2014; Nájera and Simonetti, 2010; Sweeney et al., 2010; Tews et al., 2004; Zhang et al., 2013). This expectation was partly confirmed by the positive relationship between vegetation heterogeneity and bird species richness found after controlling for the effect of tree origin. However, if tree origin was the only characteristic violating the positive effect of vegetation heterogeneity on bird species richness, we would expect a significant interaction between vegetation heterogeneity and tree origin. This interaction would signify that bird communities are more species-rich as a consequence of more complex vegetation in native stands, but not in non-native stands. However, we did not detect significant differences in slopes of the species richness-vegetation heterogeneity relationship between native and non-native stands. We suggest that this unexpected pattern is caused by the overall lower heterogeneity of native tree stands and limited variability in this characteristic within native stands. If our sample had contained some particularly heterogeneous forest habitats such as lowland floodplain forests (Korňan, 2009; Storch, 1998; Tomiałojć and Wesołowski, 2004), we predict that the interaction vegetation heterogeneity × tree origin would be significant.

It is interesting that the overall bird species richness (i.e. the total number of bird species of all study plots of a given type) was higher for black pine than for all other tree species irrespective of their origin. This pattern may be explained by the different properties of some study plots located in black pine stands compared to the rest of our stands. Specifically, some of the sampled black pine stands were near forest edges or consisted of entire forest fragments, and thus birds from neighbouring habitats may have intruded to the study plots (Batáry et al., 2014; McCollin, 1998), elevating the overall richness of black pine stands. However, these events were most likely rare because local species richness did not differ between black pine and other stand types.

In all models investigating species richness patterns we controlled for unequal tree ages and altitudes of the study plots. While tree age was of negligible importance, altitude was significantly negatively related to bird species richness in the linear models, but became insignificant in the GLS models controlling for the spatial position of the study plots. These results indicate that spatial autocorrelation was responsible for this pattern: it seems that the study plots located in the lower-elevation eastern part of our study area on slopes along large rivers were more species-rich than plots located on the western higher-elevation plateau. Although several ecological theories explain declines of species richness with altitude (e.g. (Rahbek, 1995)), we suggest that our pattern is more likely to be attributed to differences in soil conditions between the western and eastern parts of our study area (nutrient-rich limestone in the east vs. nutrient-poor granite in the west; see (Ložek et al., 2005)) than to factors related to altitude *per se* given the considerably limited altitudinal range in our data. Anyway, both the effects of altitude and location were controlled for in all GLS models used for testing the ecological relationships discussed above.

4.2 Bird community composition

Bird communities differed more according to the forest type, i.e. coniferous or broad-leaved stands, than to tree origin. It thus seems that the particular characteristics driven by the exotic nature of non-native trees (see above) do not overwhelm the even deeper differences between coniferous and broad-leaved stands dictated by leaf morphology. We suggest that these differences result in specific adaptations constraining particular bird species to either coniferous or broad-leaved trees. Moreover, the effects of these adaptations arising from different leaf morphology probably also exceed the influence of vegetation structure on the bird community composition (Bergner et al., 2015; Lemaître et al., 2012). Such a dominant effect of leaf morphology on the forest bird community composition concurs with various other studies underlying this factor as a key driver of bird community structure (Donald et al., 1998; du Bus de Warnaffe and Deconchat, 2008; Hewson et al., 2011; Reif et al., 2008a), but we are not aware of any cases comparing its influence to the effects of tree origin.

After factoring out the dominant effect of coniferous vs. broad-leaved trees, a significant difference between non-native black locust and native oak stands emerged. This corresponds to our previous studies focusing solely on black locust and oak stands, which have found tree origin to be an important predictor of the bird community composition (Hanzelka and Reif, 2015; Reif et al., in press). In contrast, the difference in the bird community composition between black pine and Scots pine was insignificant. Taken together, the composition of bird communities indicates a greater similarity of coniferous stand communities than those in broad-leaved stands. This relation is in accordance with our finding of a more similar vegetation structure for coniferous than for broad-leaved stands. This also suggests that for such higher-level community structuring, vegetation structure still has a significant effect on bird communities. Nonetheless, we should note the vegetation structure differed much more between stands of native and non-native trees than did bird communities.

In other words, bird communities were less affected by tree origin than one would predict based on the differences in vegetation structure between native and non-native stands.

The minor difference between black pine and Scots pine stands in terms of both vegetation and bird community structure deserves further attention. We suggest the following explanation. Although black pine is non-native in the Czech Republic, the borders of its natural distribution are relatively close to the country: its range is scattered through the Mediterranean region in Southern Europe and the closest natural occurrence is in Austria, ca 200 km from our study area (Cseresnyés and Tamás, 2014). Therefore, this species is probably not as exotic for central European bird species as e.g. geographically much more distant North American invasive white pine (*Pinus strobus*), which nearly completely suppresses the growth of native vegetation within its stands (Härtel and Hadincová, 1998) and for which we would predict profound (although to date unreported) impacts on bird species.

Besides the measured vegetation parameters, the bird assemblage composition could also be affected by tree species composition on local scale (Díaz, 2006; Gil-Tena et al., 2007; Jansson and Andrén, 2003). We tried to cope with this influence by establishing the study plots in mostly mature and monocultural stands. But there could still have been some effects, as suggested by the occurrence of some birds preferring broad-leaved forests (e.g. the Wood Warbler, the Blackcap or the Collared Flycatcher, *Ficedula albicollis*) in stands of both pine species that had broad-leaved undergrowth (shrubs and lower trees up to 5 m height). However, this sort of bias does not change our main conclusion: that the distinction between coniferous vs. broad-leaved stands has more influence than native vs. non-native stands on the bird community composition. Indeed, without the presence of those bird species associated with broad-leaved forests at our study plots in coniferous forests, the effect of leaf morphology on the bird community composition would have been even stronger.

5. Conclusions

Although the introduction of non-native plants poses a great threat to ecosystems and often significantly decreases biodiversity (Vilà et al., 2015), the relationship in our case of interactions of birds and non-native woody plants in the Czech Republic seems to be more complex. Despite the fact that both non-native black locust and black pine had considerably more heterogeneous vegetation structure than their native counterparts, their stands did not significantly affect local bird species richness. However, increasing bird species richness with increasing vegetation heterogeneity was found after factoring out the effect of tree origin, suggesting that the exotic nature of non-native tree species compromised the potential positive effect of more heterogeneous vegetation on bird community composition. Such a ‘hidden impact’ of non-native trees on bird communities was also revealed in our analysis of the bird community composition. Leaf morphology (i.e. coniferous vs. broad-leaved forests) was the dominant driver of differences in the bird community composition, and the difference between non-native and native stands was less important, though still significant. Taken together, these patterns indicate that the ‘basic’ characteristics of forest stands like vegetation heterogeneity and coniferous vs. broad-leaved trees are more important for birds than the tree origin. However, non-native trees can be an effective environmental filter to certain species such as habitat specialists. Further studies are needed to confirm whether the relationships established in this study are also generally applicable to other cases of non-native woody plant invasions.

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Conflict of interests

The authors declare no conflict of interest.

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Figure captions

Fig. 1 Map showing the locations of black pine (×), black locust (+), Scots pine (Δ) and oak (○) study plots.

Fig. 2 Ordination diagrams of redundancy analyses, each showing the relationships of vegetation structure variables (arrows) to (a) non-native black pine and native Scots pine stands (triangles) and (b) non-native black locust and native oak stands. See the 2.3 Methods section for definitions of particular vegetation structure variables.

Fig. 3 Ordination diagrams of a redundancy analysis showing the relationships of vegetation structure variables (arrows) to non-native black pine, native Scots pine, non-native black locust and native oak stands (triangles) as expressed (a) by the first and second ordination axes and (b) by the third ordination axis. Particular vegetation characteristics are defined in the 2.3 Methods.

Fig. 4 Ordination diagrams of redundancy analyses each showing the relationships of particular bird species abundance (arrows) to (a) black pine and Scots pine stands (triangles) and (b) black locust and oak stands (triangles). See Supplementary material Table A2 for full species names.

Fig. 5 Ordination diagrams of a redundancy analysis showing the relationships of particular bird species abundance (arrows) to non-native black pine, native Scots pine, non-native black locust and native oak stands (triangles). See Supplementary material Table A2 for full species names.

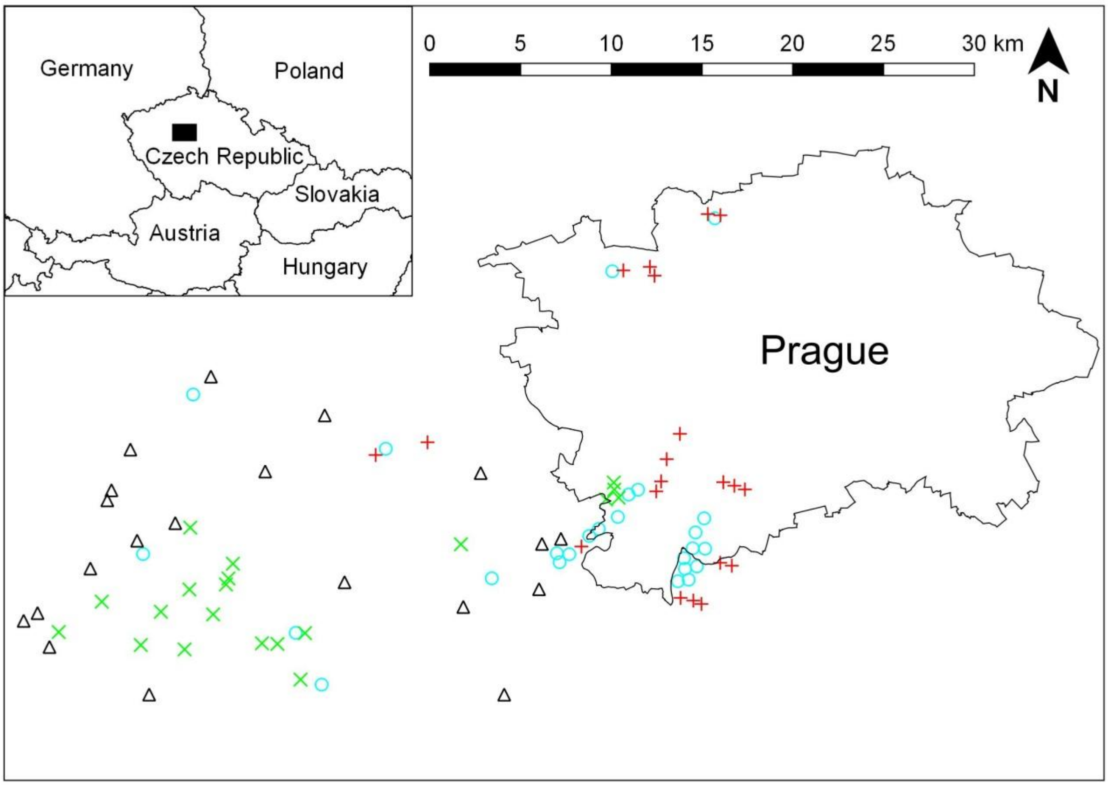

Germany
Poland
Czech Republic
Slovakia
Austria
Hungary
0
5
10
15
20
25
30 km
N
Prague

Fig. 1

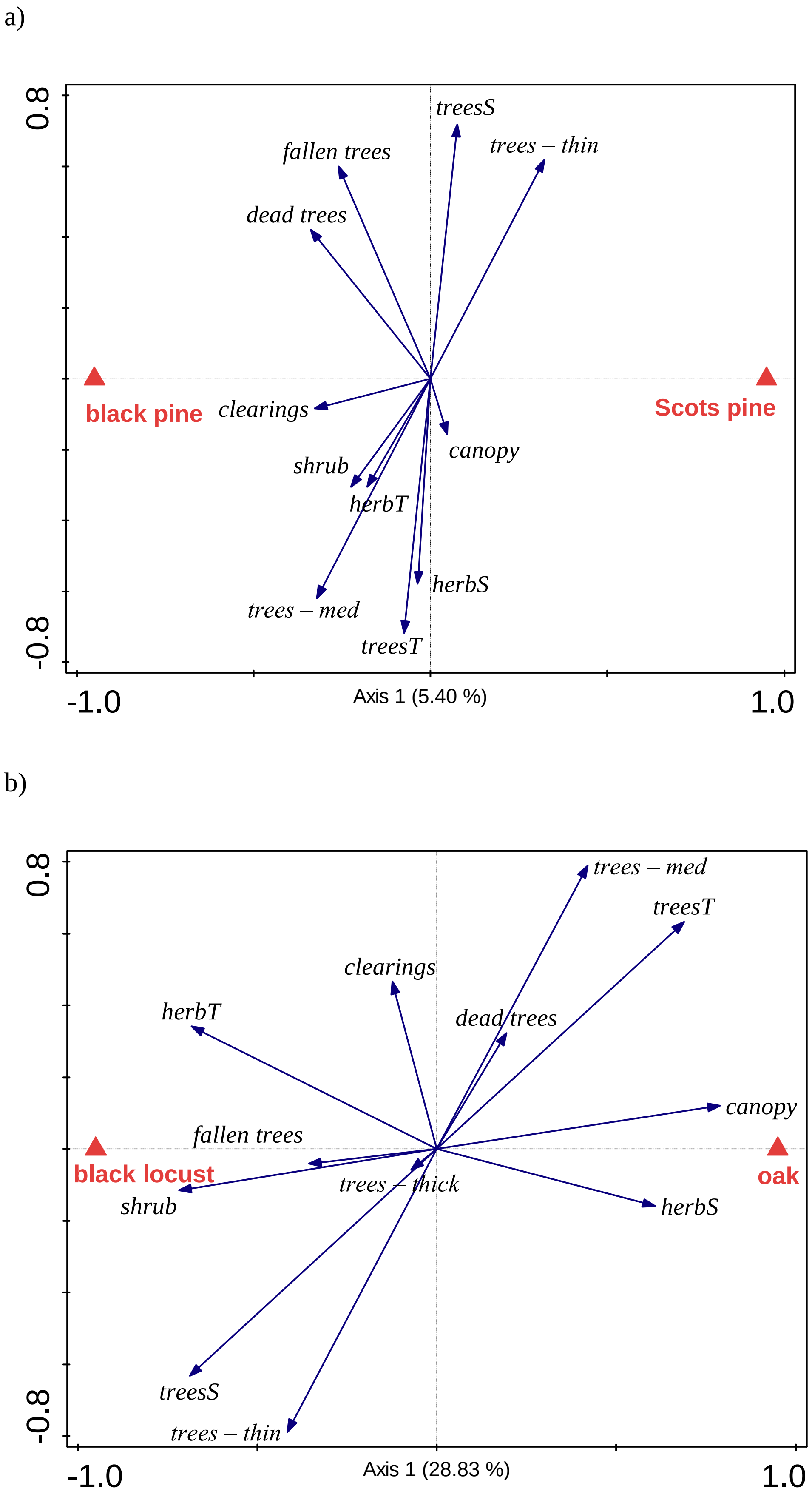
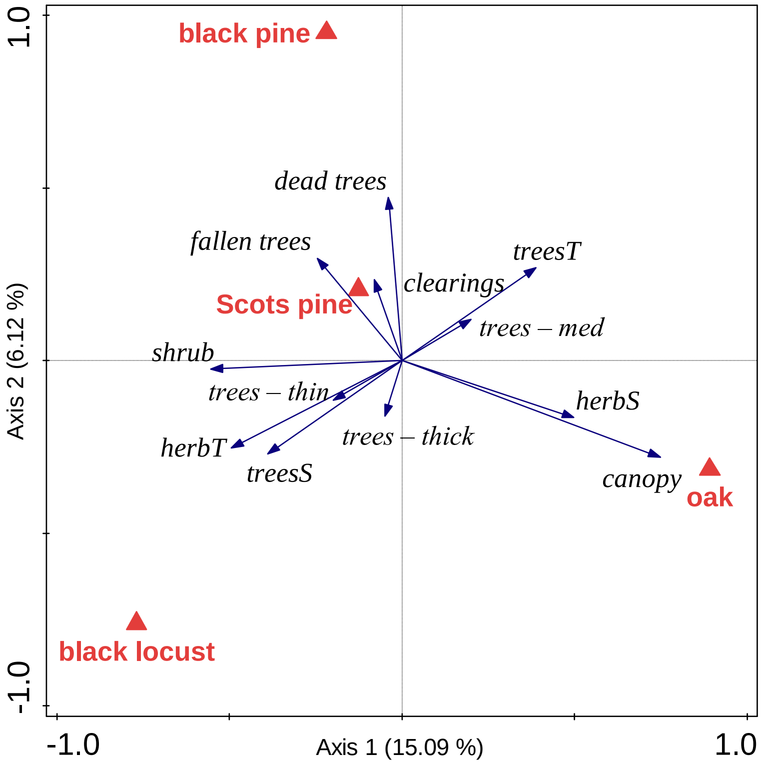

a)
0.8
-0.8
-1.0
1.0
Axis 1 (5.40 %)
treesS
trees – thin
fallen trees
dead trees
black pine
clearings
Scots pine
canopy
shrub
herbT
herbS
trees – med
treesT
b)
0.8
-0.8
-1.0
1.0
Axis 1 (28.83 %)
trees – med
treesT
clearings
herbT
dead trees
canopy
fallen trees
black locust
trees – thick
oak
shrub
herbS
treesS
trees – thin

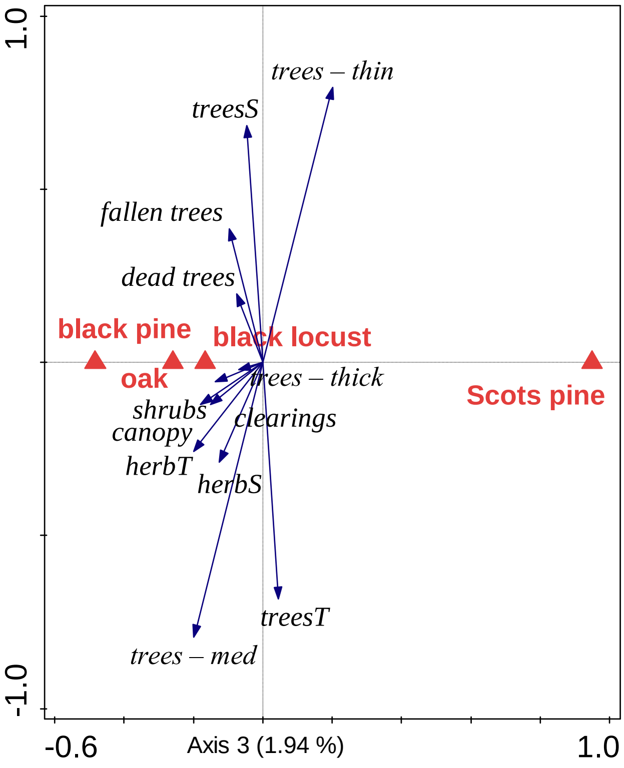
Fig. 2

676 a)



677

678 b)



679

680 **Fig. 3**

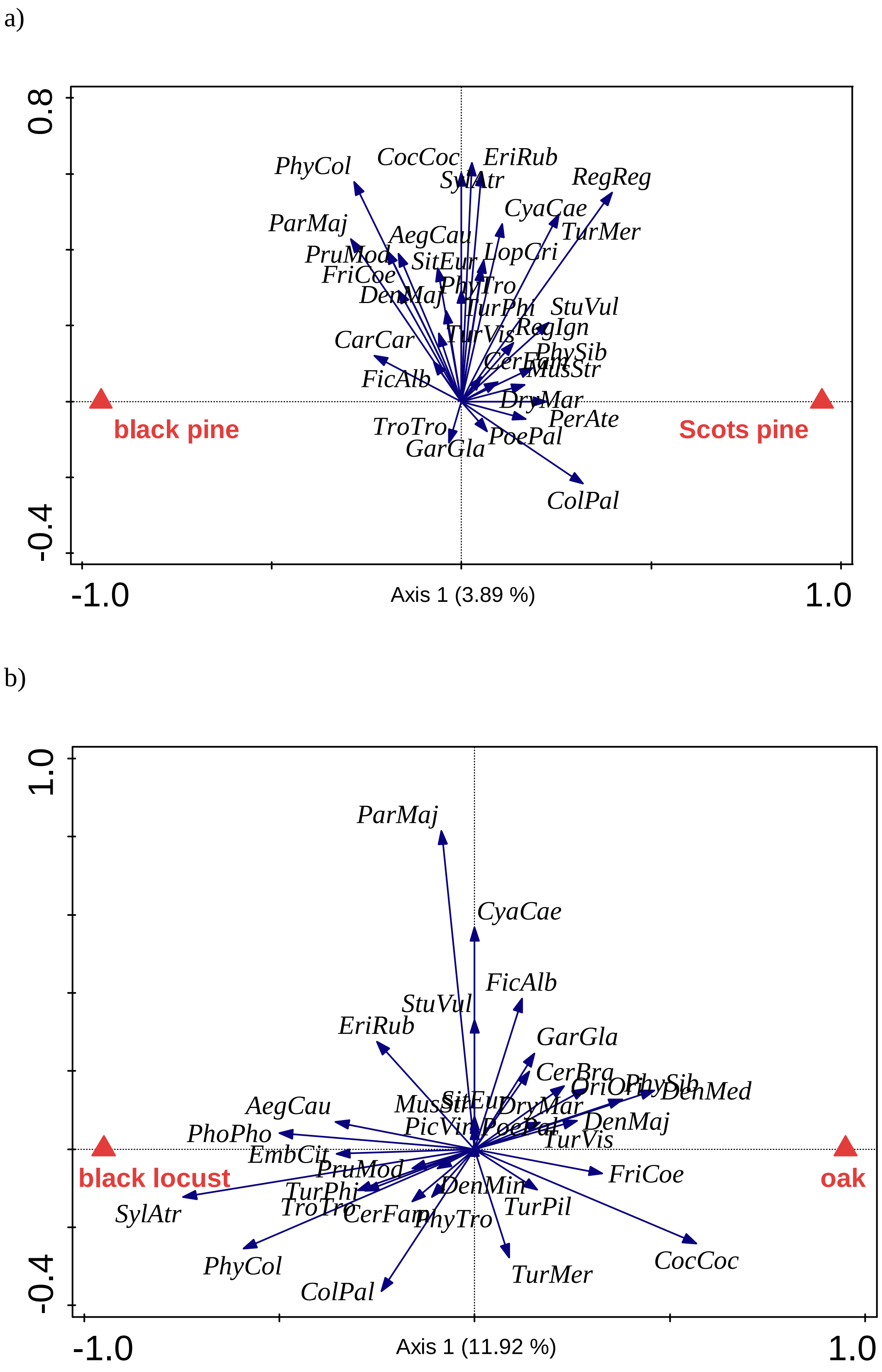

a)
0.8
-0.4
-1.0
1.0
Axis 1 (3.89 %)
black pine
Scots pine
PhyCol
CocCoc
EriRub
SylAtr
RegReg
CyaCae
TurMer
ParMaj
AegCau
PruMod
SitEur
LopCri
FriCoe
DenMaj
PhyTro
TurPhi
StuVul
CarCar
TurVis
RegIgn
PhySib
CerFam
MusStr
FicAlb
DryMar
PerAte
TroTro
PoePal
GarGla
ColPal
b)
1.0
-0.4
-1.0
1.0
Axis 1 (11.92 %)
black locust
oak
ParMaj
CyaCae
FicAlb
StuVul
EriRub
GarGla
CerBra
OriOri
PhySib
DenMed
AegCau
MusStr
SitEur
DryMar
DenMaj
PhoPho
PicVir
PoePal
TurVis
EmbCit
PruMod
FriCoe
TurPhi
DenMin
SylAtr
TroTro
CerFam
TurPil
PhyTro
PhyCol
CocCoc
TurMer
ColPal

Fig. 4

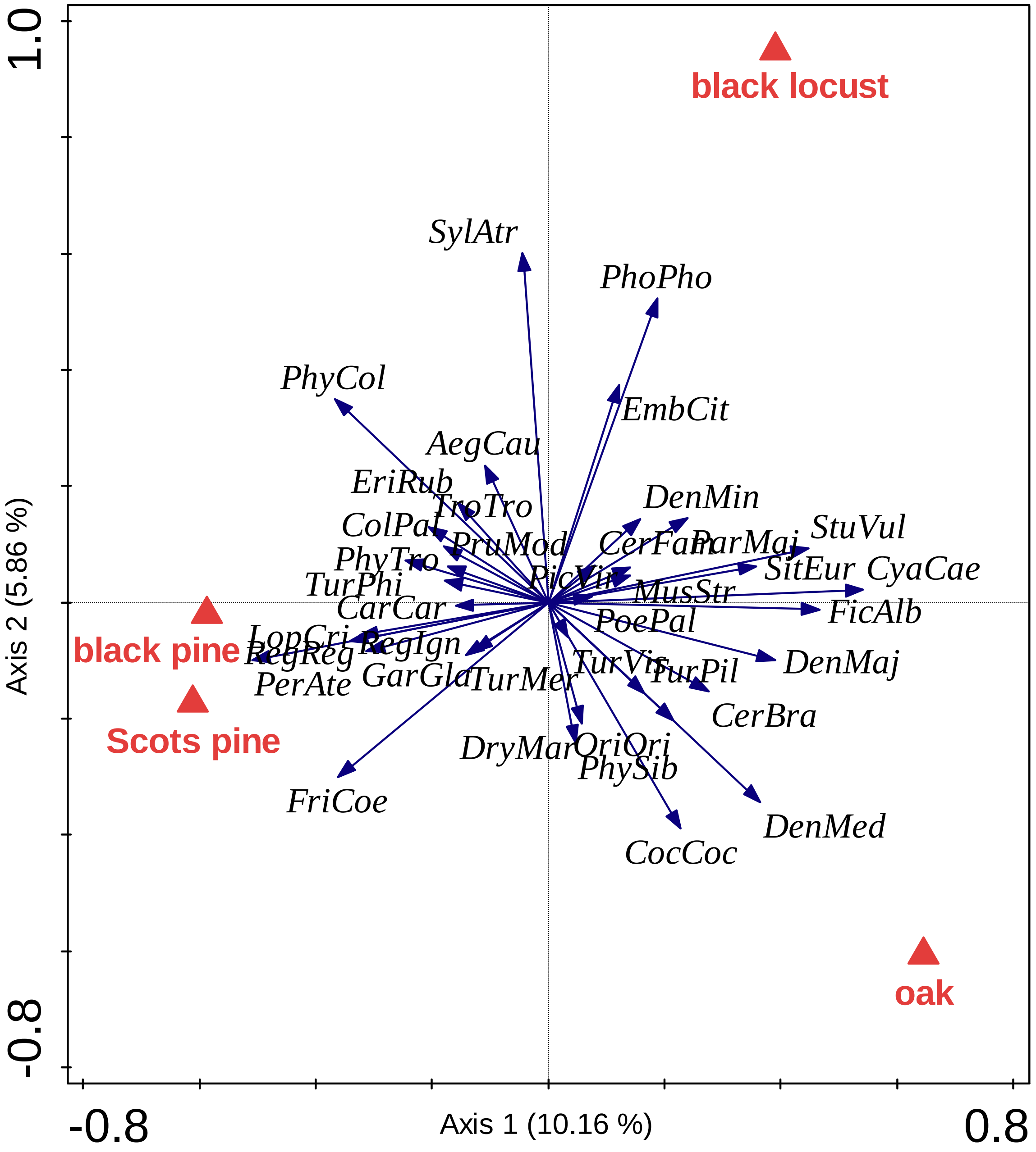

1.0
-0.8
-0.8
0.8
Axis 1 (10.16 %)
Axis 2 (5.86 %)
black locust
black pine
Scots pine
oak
SylAtr
PhoPho
PhyCol
EmbCit
AegCau
EriRub
TroTro
DenMin
ColPal
PruMod
CerFam
ParMaj
StuVul
PhyTro
PicVir
SitEur
CyaCae
TurPhi
MusStr
CarCar
PoePal
FicAlb
LopCri
RegIgn
RegReg
DenMaj
PerAte
GarGla
TurMer
TurVis
TurPil
CerBra
DryMar
OriOri
PhySib
FriCoe
DenMed
CocCoc

Fig. 5

Table 1 Estimates of the effects of stand attributes on vegetation heterogeneity (i.e. diversity of vegetation structure quantified by Shannon index, see 2.3 Methods) as revealed by a linear and a generalized least squares (GLS) model. Forest type estimates show the difference between broad-leaved and coniferous forests, and tree origin estimates show the difference between non-native and native forests. The model controls for the effects of plots' altitude and stand age. Significant values (p < 0.05) are printed in bold.

Model parameters	Linear model				GLS model			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	**1.957**	**0.143**	**13.7**	**<0.001**	**1.957**	**0.143**	**13.7**	**<0.001**
Forest type (broad-leaved)	**−0.182**	**0.049**	**−3.7**	**<0.001**	**−0.182**	**0.049**	**−3.7**	**<0.001**
Tree origin (non-native)	**0.161**	**0.047**	**3.5**	**<0.001**	**0.161**	**0.047**	**3.5**	**<0.001**
Forest type × Tree origin	**0.140**	**0.067**	**2.1**	**0.041**	**0.140**	**0.067**	**2.1**	**0.041**
Altitude	−0.001	0.001	−1.5	0.131	−0.001	0.001	−1.5	0.131
Age	0.001	0.001	1.9	0.061	0.001	0.001	1.9	0.061
AIC	−44.2				−40.2			

Table 2 Estimates of the effects of tree origin (native and non-native), forest type (coniferous and broad-leaved) and vegetation heterogeneity (diversity of vegetation structure quantified by Shannon index, see 2.3 Methods) on bird species richness as revealed by linear and generalized least squares (GLS) models. (a) Model includes interaction between tree origin and vegetation heterogeneity, (b) model including only main effects of these variables and (c) model including main effects of tree origin, forest type and vegetation heterogeneity. Tree origin estimates show the difference in bird species richness between non-native and native forests, and forest type estimates show the difference in bird species richness between broad-leaved and coniferous forests. Note that in (a) the vegetation heterogeneity estimate is a slope of regression line describing the relationship of bird species richness to vegetation heterogeneity in native stands and the interaction term shows the difference in slopes of regression lines describing the relationship of bird species to vegetation heterogeneity in native and non-native forests. All models control for the effects of plots' altitude and stand age. Significant values ($p < 0.05$) are printed in bold.

a)

Model parameters	Linear model				GLS model			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	**16.912**	**2.944**	**5.7**	**<0.001**	**14.602**	**3.423**	**4.3**	**<0.001**
Tree origin (non-native)	−0.702	0.992	−0.7	0.481	−1.164	0.869	−1.3	0.184
Vegetation heterogeneity	4.202	2.996	1.4	0.165	5.129	2.743	1.9	0.065
Tree origin × Vegetation heterogeneity	−3.530	5.288	−0.7	0.506	0.433	4.989	0.1	0.931
Altitude	**−0.017**	**0.006**	**−2.7**	**0.009**	−0.010	0.008	−1.3	0.187
Age	0.003	0.015	0.2	0.828	0.006	0.015	0.4	0.703
AIC	452.3				444.5			

b)

Model parameters	Linear model				GLS model			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	**10.778**	**5.337**	**2.0**	**0.047**	4.460	5.617	0.8	0.430
Tree origin (non-native)	−0.890	0.949	−0.9	0.351	−1.151	0.844	−1.4	0.177
Vegetation heterogeneity	3.072	2.463	1.2	0.216	**5.266**	**2.215**	**2.377**	**0.020**
Altitude	**−0.017**	**0.006**	**−2.7**	**0.009**	−0.010	0.008	−1.3	0.182
Age	0.003	0.015	0.2	0.822	0.006	0.015	0.379	0.706
AIC	455.9				447.5			

c)

Model parameters	Linear model				GLS model			
	Estimate	SE	t	p	Estimate	SE	t	p
Intercept	10.646	6.259	1.7	0.093	4.482	6.014	0.8	0.423
Tree origin (non-native)	−0.892	0.956	−0.9	0.354	−1.142	0.848	−1.3	0.182
Forest type (broad-leaved)	0.037	0.911	0.0	0.967	−0.335	1.000	−0.3	0.738
Vegetation heterogeneity	3.106	2.618	1.2	0.239	**5.127**	**2.289**	**2.2**	**0.028**
Altitude	**−0.017**	**0.008**	**−2.2**	0.032	−0.011	0.008	−1.3	0.194
Age	0.003	0.015	0.2	0.834	0.008	0.016	0.487	0.628
AIC	456.2				447.6			

Table A1 Vegetation parameters estimated on study plots; the percentage cover of the herb layer <0.5 m high (herbS), herb layer >0.5 m high (herbT), shrub layer 1–5 m high (shrub), canopy, and clearings; the percentage proportion of the tree layer 5–10 m high (treesS), tree layer >10 m high (treesT), trees up to 0.2 m in diameter at breast height (trees – thin), 0.2–0.5 m (trees – med) and >0.5 m (trees – thick); number of fallen trees and dead trees; vegetation heterogeneity expressed as the Shannon-Wiener diversity index calculated from standardized values (unit SD) of particular vegetation characteristics on each plot; age of stands in years; altitude of the middle of the plot in m asl.

Study plot	herbS	herbT	shrub	canopy	clearings	treesS	treesT	trees – thin	trees – med	trees – thick	dead trees	fallen trees	vegetation heterogeneity	age	altitude
Black locust 01	50	20	65	55	1	25	75	35	65	0	0	11	2.11	100	280
Black locust 02	75	10	50	60	1	55	45	55	45	1	0	6	2.16	80	280
Black locust 03	25	70	65	65	0	60	40	55	45	0	0	0	2.00	60	280
Black locust 04	45	40	55	60	5	5	95	10	90	0	0	10	2.04	90	320
Black locust 05	35	45	35	50	0	55	45	55	35	10	0	6	1.97	90	360
Black locust 06	10	85	80	55	0	10	90	35	65	0	0	3	1.91	100	290
Black locust 07	40	10	1	50	0	55	45	80	20	0	0	30	1.94	80	310
Black locust 08	20	50	45	20	0	85	15	80	20	0	0	34	2.05	80	340
Black locust 09	25	60	85	30	0	50	50	25	75	0	1	9	2.12	120	250
Black locust 10	30	45	90	20	0	80	20	35	65	0	3	77	2.16	110	280
Black locust 11	10	90	10	40	3	0	100	10	90	0	1	23	1.92	100	330
Black locust 12	10	85	20	35	6	5	95	10	90	0	17	21	2.12	90	340
Black locust 13	10	90	80	45	10	35	65	80	20	0	0	22	2.15	80	320
Black locust 14	45	30	40	55	0	60	40	65	35	0	0	2	2.03	100	250
Black locust 15	40	35	75	15	0	65	35	55	45	0	0	21	2.14	100	270
Black locust 16	20	80	35	55	0	30	70	60	40	0	0	21	2.07	80	270
Black locust 17	20	50	80	30	6	10	90	15	85	0	1	0	2.06	80	260
Black locust 18	40	30	95	20	6	90	10	95	5	0	9	3	2.12	100	280
Black locust 19	20	20	85	50	4	45	55	70	30	0	0	10	2.15	100	250
Black locust 20	40	45	80	35	0	70	30	80	20	0	0	1	2.02	100	210
Black pine 01	10	10	40	55	7	5	95	35	65	0	5	24	2.13	100	260
Black pine 02	35	0	80	40	3	5	95	35	65	0	19	67	2.15	100	300
Black pine 03	5	5	90	40	4	5	95	25	75	0	16	24	2.10	90	290
Black pine 04	30	10	60	45	1	2	98	30	70	0	15	7	2.07	90	320
Black pine 05	60	5	15	35	0	10	90	15	85	0	0	2	1.78	120	380
Black pine 06	35	10	15	35	6	40	60	35	65	0	2	6	2.20	110	360

Black pine 07	40	10	50	45	3	5	95	50	50	0	10	17	2.20	70	430
Black pine 08	25	70	85	25	2	95	5	10	90	0	2	7	2.04	100	410
Black pine 09	30	65	70	40	10	5	95	20	80	0	1	1	2.08	90	420
Black pine 10	60	15	75	35	5	5	95	65	35	0	29	37	2.21	100	390
Black pine 11	15	10	35	45	11	0	100	40	60	0	23	75	2.13	100	410
Black pine 12	35	10	25	40	3	5	95	65	35	0	9	11	2.16	120	330
Black pine 13	35	5	70	35	4	70	30	10	90	0	9	33	2.23	110	340
Black pine 14	20	65	65	30	16	15	85	55	45	0	11	25	2.25	110	320
Black pine 15	25	15	25	45	2	0	100	15	85	0	10	24	2.07	120	330
Black pine 16	80	20	25	55	0	0	100	15	85	0	13	47	2.04	100	470
Black pine 17	10	15	10	50	2	10	90	65	35	0	6	56	2.11	80	380
Black pine 18	45	35	20	50	2	5	95	5	95	0	3	9	2.01	110	380
Black pine 19	5	0	0	45	0	0	100	70	30	0	4	135	1.64	90	350
Black pine 20	30	60	5	40	4	2	98	10	90	0	5	5	2.01	100	380
Oak 01	60	5	15	80	2	5	95	10	90	0	0	2	1.75	120	300
Oak 02	90	2	0	80	1	0	100	10	90	0	3	4	1.67	100	300
Oak 03	45	20	3	70	2	0	100	5	95	0	1	23	1.84	140	310
Oak 04	95	0	5	80	5	0	100	5	95	0	8	0	1.77	100	280
Oak 05	95	5	0	75	5	0	100	10	85	5	3	0	1.90	120	320
Oak 06	80	0	0	75	0	0	100	5	95	0	3	0	1.52	130	370
Oak 07	35	0	0	65	5	0	100	35	65	0	15	0	1.85	100	330
Oak 08	20	0	0	65	1	0	100	10	90	0	14	33	1.81	80	300
Oak 09	80	0	0	65	0	40	60	65	35	0	2	0	1.78	80	270
Oak 10	70	25	10	70	0	0	100	10	90	0	0	0	1.67	80	350
Oak 11	35	0	0	70	0	5	95	25	75	0	0	0	1.52	90	350
Oak 12	80	0	0	65	0	20	80	30	70	0	0	0	1.66	100	340
Oak 13	90	0	0	70	3	5	95	25	75	0	9	4	1.88	120	330
Oak 14	60	0	0	75	0	5	95	80	20	0	0	0	1.53	90	290
Oak 15	75	20	40	75	0	10	90	30	70	0	0	0	1.86	130	320
Oak 16	25	75	15	75	1	0	100	9	90	1	1	0	1.88	120	260
Oak 17	70	5	80	65	2	5	95	20	80	0	0	1	1.89	130	290
Oak 18	10	1	20	75	0	5	95	75	25	0	4	20	1.81	120	320
Oak 19	80	5	10	70	1	2	98	10	90	0	0	0	1.67	100	340
Oak 20	70	10	10	65	2	10	90	70	30	0	3	11	2.02	100	360

Oak 21	5	0	50	75	0	95	5	90	10	0	4	10	1.72	140	350
Oak 22	65	25	0	70	10	0	100	50	50	0	0	1	1.86	140	350
Oak 23	90	0	0	70	2	5	95	95	5	0	1	0	1.63	80	380
Oak 24	45	15	0	65	4	20	80	60	40	0	3	7	2.05	100	350
Oak 25	85	10	25	70	0	0	100	0	100	0	0	1	1.61	110	400
Scots pine 01	60	15	10	50	1	0	100	45	55	0	1	17	1.97	50	390
Scots pine 02	20	10	70	40	0	0	100	25	75	0	0	1	1.77	60	350
Scots pine 03	10	5	35	50	0	10	90	65	35	0	0	3	1.80	50	350
Scots pine 04	3	0	5	35	0	60	40	70	30	0	11	22	1.97	40	260
Scots pine 05	20	0	10	55	0	15	85	30	70	0	13	68	1.99	90	310
Scots pine 06	10	10	35	60	0	5	95	90	10	0	3	2	1.77	50	460
Scots pine 07	10	0	60	30	0	25	75	40	60	0	0	0	1.83	100	290
Scots pine 08	50	0	0	45	3	10	90	10	90	0	5	13	1.92	100	440
Scots pine 09	45	50	0	45	3	0	100	85	15	0	1	0	1.85	50	430
Scots pine 10	5	0	80	35	1	10	90	20	80	0	8	13	1.98	100	360
Scots pine 11	55	20	55	45	15	5	95	80	20	0	0	2	1.99	40	390
Scots pine 12	10	5	5	35	0	15	85	15	85	0	8	12	1.91	120	350
Scots pine 13	60	15	5	50	0	5	95	90	10	0	0	4	1.73	30	470
Scots pine 14	15	0	0	50	0	0	100	95	5	0	0	2	1.35	30	440
Scots pine 15	70	15	60	40	1	0	100	5	95	0	2	4	1.90	100	420
Scots pine 16	65	25	65	35	5	5	95	5	95	0	3	4	2.07	90	510
Scots pine 17	0	0	0	40	0	90	10	95	5	0	17	95	1.71	80	380
Scots pine 18	70	15	55	35	1	5	95	25	75	0	9	5	2.10	80	340
Scots pine 19	10	90	45	40	1	5	95	60	40	0	1	0	1.95	50	360
Scots pine 20	10	0	5	30	3	100	0	95	5	0	15	39	1.87	150	340

Table A2 Bird species and their abundance recorded in studied forest stands.

Abbreviation	Scientific name	Bird abundance			
		Black locust	Black pine	Oak	Scots pine
AegCau	Aegithalos caudatus	6	6	0	2
CarCar	Carduelis carduelis	0	2	0	0
CerBra	Certhia brachydactyla	2	1	8	0
CerFam	Certhia familiaris	7	4	7	5
CocCoc	Coccothraustes coccothraustes	4	10	32	10
ColPal	Columba palumbus	7	4	3	12
CyaCae	Cyanistes caeruleus	36	11	50	14
DenMaj	Dendrocopos major	14	8	25	7
DenMed	Dendrocopos medius	0	0	11	0
DenMin	Dendrocopos minor	2	0	1	0
DryMar	Dryocopus martius	0	1	4	2
EmbCit	Emberiza citrinella	7	1	0	0
EriRub	Erithacus rubecula	27	25	21	27
FicAlb	Ficedula albicollis	15	2	24	1
FriCoe	Fringilla coelebs	16	46	39	39
GarGla	Garrulus glandarius	5	9	9	11
LopCri	Lophophanes cristatus	0	4	0	5
MusStr	Muscicapa striata	5	1	5	3
OriOri	Oriolus oriolus	0	0	3	0
ParMaj	Parus major	49	40	54	28
PerAte	Periparus ater	0	8	0	14
PhoPho	Phoenicurus phoenicurus	12	1	0	0
PhyCol	Phylloscopus collybita	23	29	3	18
PhySib	Phylloscopus sibilatrix	0	1	6	4
PhyTro	Phylloscopus trochilus	1	3	0	2
PicVir	Picus viridis	1	0	1	0
PoePal	Poecile palustris	5	2	6	5
PruMod	Prunella modularis	1	3	0	1
RegIgn	Regulus ignicapilla	0	4	0	7
RegReg	Regulus regulus	0	1	0	16
SitEur	Sitta europaea	26	12	32	14
StuVul	Sturnus vulgaris	18	0	21	2
SylAtr	Sylvia atricapilla	37	16	5	17
TroTro	Troglodytes troglodytes	7	9	2	8
TurMer	Turdus merula	23	25	32	35
TurPhi	Turdus philomelos	8	11	6	11
TurPil	Turdus pilaris	0	0	3	0
TurVis	Turdus viscivorus	4	5	7	4

Paper II

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ORIGINAL ARTICLE

Responses to the black locust (*Robinia pseudoacacia*) invasion differ between habitat specialists and generalists in central European forest birds

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Abstract Biological invasions are among the most important threats to global biodiversity. However, bird species differ in their ability to resist the invasions, and it is thus important to investigate which species' traits account for their sensitivity to the invasions' consequences. Here we focused on predictors of such sensitivity by using central European birds in oak forests invaded by the exotic black locust (*Robinia pseudoacacia*). We performed a detailed mapping of bird occurrence on plots located in the native oak stands and the invaded stands, respectively, controlling for stands' age. Using multivariate analysis, we quantified bird species' reliance on the native versus invaded forest stands. In the next step, we tested the hypotheses explaining species' position along this gradient. We predicted that the species more closely associated with the invaded forest stands will be (1) habitat generalists and (2) species with fast life history strategies. The phylogenetic generalized least squares analysis showed that only the first prediction was supported. Moreover, species' habitat specialization significantly affected differences in species' abundance between the invaded and native forests: habitat generalists were more abundant in the black locust stands than in the oak stands, which was not the case of habitat specialists. Our study implies that the spread of invasive plants may contribute to the frequently reported replacement of specialist species by habitat generalists in local bird communities.

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Keywords Forest birds · Habitat specialization · Life history strategy · Invasive tree

Zusammenfassung

Bei mitteleuropäischen Waldvögeln unterscheidet sich die Reaktion auf die Invasion der Robinie (*Robinia pseudoacacia*) zwischen Habitatspezialisten und –generalisten

Biologische Invasionen gehören zu den bedeutendsten Gefahren für die weltweite Biodiversität. Vogelarten unterscheiden sich jedoch in ihrer Fähigkeit, den Invasionen zu widerstehen, weshalb es wichtig ist zu untersuchen, welche Eigenschaften von Arten ihre Anfälligkeit für Folgen von Invasionen beeinflussen. Hier haben wir uns auf Prädiktoren solcher Anfälligkeit konzentriert, indem wir mitteleuropäische Vögel in Eichenwäldern mit eingewanderten Robinien (*Robinia pseudoacacia*) betrachtet haben. Wir haben das Vogelvorkommen in einheimischen Eichenbeständen und invadierten Beständen im Detail kartiert, unter Berücksichtigung des Alters der Bestände. Mit Hilfe einer multivariaten Analyse haben wir die Abhängigkeit der Vogelarten von den einheimischen bzw. invadierten Beständen quantifiziert. Im nächsten Schritt haben wir die Hypothesen getestet, welche die Position von Arten entlang dieses Gradienten erklären. Wir haben vorhergesagt, dass die stärker mit den invadierten Beständen assoziierten Arten (i) Habitatgeneralisten sein und (ii) schnelle life history-Strategien haben sollten. Die phylogenetische generalisierte Analyse der kleinsten Quadrate stützte lediglich die erste Hypothese. Zudem hatte die Habitatspezialisierung der Arten einen signifikanten Einfluss auf die unterschiedliche Abundanz der Arten in den invadierten und einheimischen Beständen:

Habitatgeneralisten waren in den Robinienbeständen häufiger als in den Eichenbeständen, was für Habitatspezialisten nicht der Fall war. Unsere Studie deutet darauf hin, dass die Ausbreitung invasiver Pflanzen zu der in lokalen Vogelgemeinschaften häufig beobachteten Ersetzung spezialisierter Arten durch Habitatgeneralisten beitragen könnte.

Introduction

Biological invasions rank among top threats to global biodiversity (Butchart et al. 2010). Invasive species interact with native species as predators, competitors, or parasites (Vilà et al. 2011). These interactions result in altered species composition and ecosystem function of indigenous communities (Pyšek et al. 2012), leading to global extinction of the most sensitive species in the extreme cases (Mack et al. 2000). It is thus important to investigate which species' traits account for their sensitivity to the consequences of biological invasions.

As the traits potentially characterizing such sensitive species can be considered high ecological specialization and slow life history strategy. It was already shown that habitat specialists are vulnerable to human-induced alteration of biotopes due to processes such as urbanization (Devictor et al. 2008) or agricultural intensification (Shultz et al. 2005) leading to their large-scale declines (van Swaay et al. 2006; Le Viol et al. 2012) and global threat (Davies et al. 2004). Slow life history is another trait contributing to the elevated extinction risk (Owens and Bennett 2000; Koleček et al. 2014). Species with low population productivity and long generation time are less capable to compensate increased mortality caused by environmental changes (Purvis et al. 2000; Sæther et al. 2005). However, consequences of these traits for their holders were not sufficiently studied in the context of biological invasions to date, although they were often implicitly assumed to be negative (e.g. Skórka et al. 2010; Rogers and Chown 2014).

The black locust (*Robinia pseudoacacia*) is an invasive tree species having serious impacts on native species and ecosystems (Dzwonko and Loster 1997; Rice et al. 2004; Nascimbene et al. 2012; De Marco et al. 2013). In central Europe, the black locust was planted in the seventeenth century on dry rocky slopes with shallow soil (Hejný and Slavík 1997). It escaped from cultivation in the late nineteenth century, and nowadays it occupies various habitats where it replaces indigenous plant species (Hejný and Slavík 1997). In forests, the black locust is able to colonize the gaps created by spontaneous tree falls or forest management, and it is thus able to expand over large areas in relatively short time (Reiterová and Škorpík 2012). It is a strong competitor being able to alter chemical conditions in soils (Nasir et al. 2005) thus reducing habitat suitability for plants resulting in low plant species richness of invaded habitats (Benesperi et al. 2012). Such a negative impact probably scales up the food chain leading to impoverished communities of invertebrate fauna (Alvarado and Galle 2000), although some insect groups quickly adapted to the new host plant (Matosevic and Melika 2012). At the same time, it remains unknown whether such impacts are also detectable in higher-level consumers such as birds.

Birds play an important role in natural ecosystems supporting seed dispersion and controlling abundance of invertebrate herbivores (Sekercioglu 2006; Sharam et al. 2009). At the same time, they are the most species-rich from terrestrial vertebrate classes and show a vast diversity of life styles and ecological adaptations (Bennett and Owens 2002). Here we aimed to identify ecological traits predicting sensitivity of bird species to black locust invasion. For this purpose, we counted birds in central European forests invaded by the black locust and in control stands of the native oak species (*Quercus* spp.), which forms indigenous forest vegetation in the study area. Using these data, we ordinated bird species according to their association to invaded versus native forest stands and related their positions along this gradient to the ecological traits to test the following predictions.

First, we predict that habitat generalists will be less susceptible to the invasion of the black locust than habitat specialists. Generalist species are adapted to use various kinds of habitats (Gaston et al. 1997), and thus the replacement of the native habitat by a new habitat created by the invasive plant should be less detrimental for such species than for habitat specialists. Second, we predict that species with fast life histories will be more frequently associated with invaded habitats than species with slow life histories. The species with fast life histories have higher vital rates and thus more individuals available to colonize new environment than the species with slow life histories (Stearns 1992).

Materials and methods

Study area and sampling

Our study was carried out in the central part of the Czech Republic (central Europe). Study plots were located on the periphery of the city of Prague (lat. 49°53′–50°07′N; long. 14°09′–14°27′E, elevation 200–400 m a.s.l.) in a forested area of 20 × 30 km. The area is characterized by vertically heterogeneous relief created by streams of the Vltava river and its tributaries. Forests are dominated by the sessile oak (*Quercus petraea*) and the English oak (*Quercus robur*), often mixed with the hornbeam (*Carpinus betulus*) and, to a lesser extent, with the small leaved lime

(*Tilia cordata*) and the ash (*Fraxinus excelsior*). Some parts of this native vegetation were replaced by extensive stands of the invasive black locust scattered throughout the study area.

To sample bird communities, we established 30 study plots of size 100 × 100 m each; 15 plots were located in oak stands and 15 plots in black locust stands. All study plots were randomly chosen within predefined forest units of at least 50 ha. However, we sampled only those stands with homogeneous tree species composition, i.e. those consisting solely from black locust and oak trees, respectively, and avoided stands with variable proportion of these tree species. The age of the forest stands was 60–80 years in all cases. The minimum distance between two adjacent plots was 500 m to avoid double counts of the same birds. Moreover, the plots were not located within the 100 m belt of the forest edge to avoid bias due to edge effects.

Birds were counted using simplified spot mapping technique (Bibby et al. 2000) during the peak breeding season from April to June 2013. Three visits were carried out on each plot by the same observer (JH), once in each month to sample both early and late breeders. The order of plot visits differed among particular months to randomize the daytime of bird surveys. During one visit, the observer went slowly through the plot in five 20 m wide belts and mapped the birds for ca. 20 min. We are convinced that such an intensive mapping ensured precise detection and minimized the double counting of bird individuals occurring in a given plot. On each plot all seen and heard bird individuals were recorded. The visits were always conducted in early morning between sunrise and 9:30 a.m. under favourable weather conditions (no rain, no wind).

As the abundance estimate of a given species at one plot we used the maximum count from all visits. This approach is frequently used in studies based on bird monitoring data because the maximum count probably better approximates the (unknown) real abundance than the mean count (e.g. Jiguet et al. 2007; Šizling et al. 2009; Reif et al. 2011b). Since the data were collected in the peak of the breeding season, we assume that our counts provide an estimate of the number of breeding individuals of particular species.

Bird species traits

Species' *habitat specialization* was quantified using a species specialization index (SSI) introduced by Julliard et al. (2006). It is a coefficient of variation of abundance of a given species across several habitat types. High values indicate habitat specialists, low values habitat generalists. We obtained SSI of particular species (Appendix 1) recorded on our study plots from Reif et al. (2010) who used data from a national breeding bird monitoring scheme for its calculation. The scheme covers representatively the whole area of the country (Reif et al. 2013), suggesting that the values of SSI are not affected by any regional or habitat biases. Moreover, the bird monitoring scheme providing data for SSI calculation is based on fine-scale point counts and a detailed discrimination of habitats into eight classes at the census points (Reif et al. 2010). Therefore, these data on SSI mirror local bird-habitat associations, which make them suitable for purposes of this study.

Species' *life history strategy* was expressed as its position along a gradient from "K-selected" to "r-selected" species describing the slow-fast continuum (Appendix 1). The gradient was extracted from Koleček and Reif (2011) who used principal component analysis (PCA) on six life history traits (body mass, egg mass, number of broods per year, laying date, clutch size, length of incubation period) for its calculation. This PCA was performed using all 178 bird species regularly breeding in the Czech Republic and thus covers whole diversity of bird life histories in the region.

Statistical analyses

We first assessed the strength of the association of particular bird species with the black locust and oak stands, respectively, using redundancy analysis (RDA) in CANOCO 5 statistical software (ter Braak and Šmilauer 2012). RDA is a multivariate direct gradient analysis method quantifying the linear dependence of multiple response variables on explanatory variables (ter Braak and Šmilauer 2012). In our case, abundances of particular bird species on study plots were the response variables and forest type was the explanatory variable with two levels (black locust and oak). This analysis ordinated particular bird species along the canonical axis representing the forest type. On one side occurred species the most strongly associated with the oak stands; on the opposite side were the species with the tightest association with the black locust stands. The species' scores along this axis can be thus viewed as a quantification of each bird species' preference for the black locust and oak stands, respectively. These scores were used as a response variable in further analysis. The axis represented by the forest type is the first (canonical) axis, the other (non-canonical) axes expressed using RDA represent the other gradients in bird community composition (sorted in descending order of importance) not explained by the forest type. We report the results for three non-canonical axes to compare the importance of the focal canonical axis to the other gradients.

In the next step, we related the positions of bird species along the first RDA axis (i.e. the response variable) to their traits (i.e. SSI and life history—explanatory variables) by the means of phylogenetic comparative analysis performed across species. We applied the phylogenetic generalized least-squares regression (PGLS) in statistical software R v3.0.2 (R Core Team 2013) with the packages 'ape' (Paradis et al. 2004) and 'caper' (Orme et al. 2013). We constructed the model simultaneously testing the main effects of SSI and life history. Phylogenetic tree was extracted from Jetz et al. (2012) by using http://www.birdtree.org application (Appendix 2).

Finally, we focused on comparison of the abundance of particular bird species between the black locust and oak stands taking their SSI and life history into account. For this purpose, we employed a generalized linear mixed model (Poisson family and log link function) using the package 'lme4' (Bates et al. 2014) in statistical software R v3.0.2 (R Core Team 2013). We used the abundance of each species summed over all plots of a given forest type as a response variable and forest type (a factor with two levels: black locust and oak), SSI, and life history as explanatory variables with fixed effects. The model included the SSI × forest type interaction, and the life history × forest type interaction. These interactions provide the information whether the relationship between species' abundance and forest type depends on their SSI and life history strategies, respectively. In this analysis, we used species identity as a random factor.

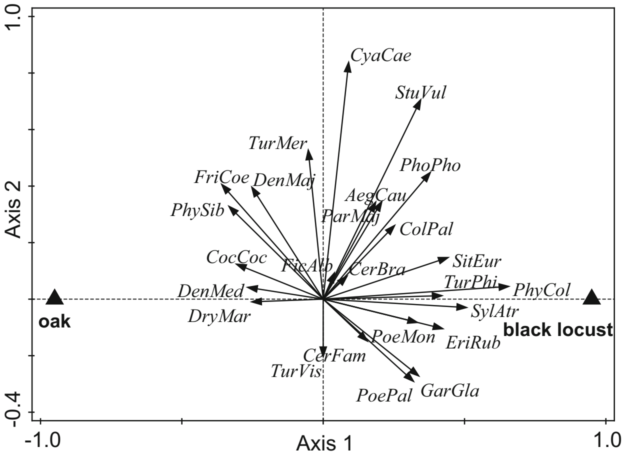

Fig. 1 Redundancy analysis (RDA) ordination plot showing the relation of the observed bird species (*arrows*, full species names are in Appendix 1) to the forest type (*triangles*) of the study plots, where the impacts of black locust invasion on birds in the native oak forests were studied. The horizontal axis is the first canonical axis expressing the strength of bird species' association with the oak stands and with the black locust stands, respectively, and the positions of particular species can be thus viewed as indicator of their susceptibility to the black locust invasion. These positions were used as a response variable in further analysis. The vertical axis is the next most important gradient in bird community composition revealed by RDA not explained by the forest type

Table 1 Characteristics of the phylogenetic generalized least squares model relating the strength of bird species' association with the native oak stands and with the invasive black locust stands, respectively, expressed as scores from the redundancy analysis (see Fig. 1), to their habitat specialization (SSI) and life history

Model term	Estimate	SE	*t* value	*p* value
Intercept	0.23	0.36	0.64	0.531
SSI	**−0.28**	**0.11**	**−2.49**	**0.021**
Life history	0.06	0.13	0.49	0.631

Significant results are printed in bold

Results

The first canonical axis revealed by RDA expressing the strength of bird species' association with the oak stands and with the black locust stands, respectively, explained 9.8 % of the variability in bird community composition among the study plots. This part of variability in bird community structure accounted by the black locust invasion was statistically significant (pseudo-$F = 3.04$, $p < 0.01$) and provides evidence that the black locust invasion alters species composition in forest bird assemblages. The species most tightly associated with the oak stands were, for example, the middle-spotted woodpecker (*Dendrocopos medius*), the black woodpecker (*Dryocopus martius*), the wood warbler (*Phylloscopus sibilatrix*), or the hawfinch (*Coccothraustes coccothraustes*). By contrast, species such as the chiffchaff (*Phylloscopus collybita*), the blackcap (*Sylvia atricapilla*), or the song thrush (*Turdus philomelos*) were those the most tightly associated with the black locust stands (Fig. 1). The other most important gradients in bird community composition, which were not explained by the forest type, were represented by the three non-canonical axes. The variability in species composition of bird communities among study plots accounting for these three axes were 21.8, 17.2, and 11.3 %, respectively.

In the next step, we explored the effects of the traits, i.e. SSI and life history strategy, potentially explaining the species' susceptibility to the black locust invasion (expressed by RDA scores along the first axis, see above) using phylogenetic comparative analysis. The multiple regression analysis revealed that SSI proved to be significant, while the life history strategy was not (Table 1). This means that species with the lowest SSI are mostly associated with the black locust stands, whereas the species with the highest SSI are mostly associated with the oak stands (Fig. 2).

Finally, we tested whether the forest type (i.e. oak and black locust stands, respectively) has a detectable effect on bird abundance. The generalized linear mixed model revealed that the relationship between species' abundance and SSI was significantly affected by the forest type (Table 2). Specifically, the relationship was significantly

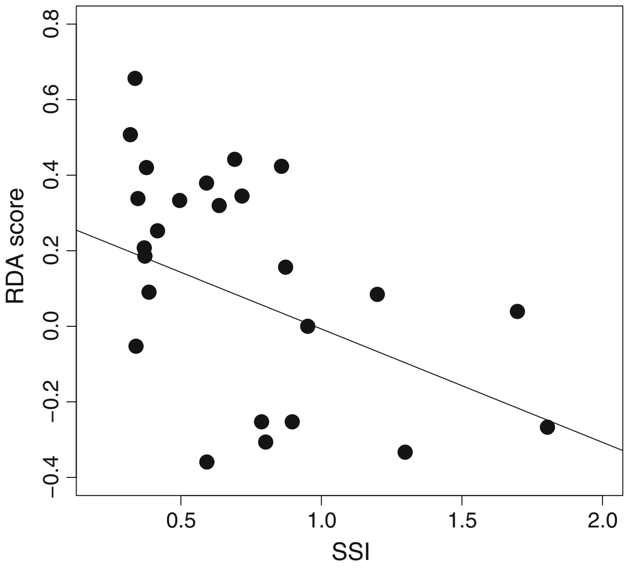

Fig. 2 The relation of the strength of bird species' association with the native oak stands (negative values on the *y* axis) and with the invasive black locust stands (positive values on the *y* axis), respectively, expressed as scores from the redundancy analysis (RDA, see Fig. 1), to their habitat specialization (SSI)

steeper in the black locust than in the oak stands, i.e. the difference in abundance between habitat generalists and habitat specialists was more pronounced in the black locust stands than in the oak stands (Table 2). In other words, habitat specialization influences significantly the difference in species' abundance between the forest types, when the higher abundance in the black locust stands than in the oak stands is typical for habitat generalists, but not for habitat specialists. By contrast, the forest type did not have any effect on the relationship between the abundance and life history strategy (Table 2). The generalized linear mixed model also revealed that bird species, after accounting for their habitat specialization or life history, had generally higher abundance in the black locust stands than in the oak stands (Table 2).

Discussion

Invasion of the black locust resulted in significant changes in bird community composition. Bird species differed in the level of tolerance to the plant invader and we investigated what species' traits are responsible for these differences. We found that the habitat specialization was a substantive predictor of the bird species' sensitivity to the plant invasion: habitat generalists were associated with the invaded forest stands, whereas habitat specialists tended to occur more frequently in the native oak stands. By contrast, birds' life history strategy, expressed as species' position along the slow-fast continuum, proved to be less important. Higher habitat specialization of species avoiding invaded tree stands supports the idea that the specialists are unable to occupy the habitats altered by exotic plants over the long term. This idea was implicitly assumed in several recent studies describing invasive plant impacts in various regions and ecosystems including temperate grasslands (Skórka et al. 2010), riparian vegetation (Hajzlerová and Reif 2014), Mediterranean forests (Matosevic and Melika 2012), or woodland savannah (Rogers and Chown 2014). What are the causes of this pattern? Below we evaluate several possible mechanisms.

The invasion of the black locust could alter availability of nesting sites for birds in forests. For example, some specific sites such as tree cavities or dead wood are generally scarcer in forests under human impact than in old-growth forests (Wesołowski 2007), and this would also apply to the case of the black locust invasion. However, this explanation probably does not apply here. Although two cavity nesters, the middle-spotted woodpecker and the black woodpecker, were among the habitat specialists most tightly associated with the native oak forest and were virtually absent from invaded forests, other cavity nesting species such as the great-spotted woodpecker (*Dendrocopos major*) or the collared flycatcher (*Ficedula albicollis*) did not discriminate between invaded and native forest

Table 2 The relationship between bird abundance on study plots and forest type (native oak and invasive black locust), bird species' habitat specialization (SSI), and life history strategy as revealed by the generalized mixed model with species' identity fitted as a random factor

Model term	Estimate	SE	*z* value	*p* value
Forest type: black locust (mean of the logarithm of abundance)	**1.84**	**0.92**	**2.01**	**0.044**
Forest type: oak (difference in the mean of the logarithm of abundance from black locust)	**−1.53**	**0.57**	**−2.67**	**0.008**
SSI (slope in black locust)	−1.08	0.60	−1.81	0.070
SSI × forest type (difference in slope between black locust and oak)	**0.89**	**0.37**	**2.41**	**0.016**
Life history (slope in black locust)	0.66	0.55	1.21	0.228
Life history × forest type (difference in slope between black locust and oak)	0.47	0.30	1.57	0.116

The model included the SSI × forest type interaction, and the life history × forest type interaction testing whether the relationship between species' abundance and forest type depends on their SSI and life history strategies, respectively. Significant results are printed in bold stands, and the blue (*Cyanistes caeruleus*) and great tit (*Parus major*) indeed more frequently occurred in black locust stands than in oak stands. This observation indicates that the black locust invasion has different ecological consequences than other types of human impacts on native forests such as timber harvesting and establishment of the same-age tree plantations, where the cavity nesters are limited by a low supply of potential nest holes (Cockle et al. 2011).

We suggest that the principal cause of the inhospitableness of the invaded habitat for habitat specialists would be connected to food supply (Holland-Clift et al. 2011). However, underlying mechanisms are probably quite complex. The simplest possibility is the overall reduction of the total amount of food available for birds as a consequence of biological invasion, by which means the exotic plant does not provide sufficient resources for invertebrates (Vilà et al. 2011), the key food for temperate birds during the breeding season (Ashmole 1963; Jetz et al. 2008). Under these circumstances, we should expect reduced species richness and total bird abundance in the invaded forest stands due to lower energy availability (Honkanen et al. 2010). Such a lack of birds' invertebrate prey was observed in temperate grasslands invaded by exotic goldenrods (*Solidago* spp.), causing seriously reduced bird species richness (Skórka et al. 2010). However, this possibility does not seem to play a role in our study system, because the total number of bird individuals was higher in the black locust than in the oak stands. This suggests that the total invertebrate biomass should not be reduced in the invaded habitat (Matosevic and Melika 2012). Instead, it is likely that the black locust stands lack some specific food types required by the habitat specialists. This might be caused by reduced diversity of plant species in these invaded habitats (Benesperi et al. 2012). Since the black locust alters soil character by increasing the amount of nitrogen (Rice et al. 2004) and also produces substances toxic for various other plants (Nasir et al. 2005), it is possible that some insect species dependent on the plants suppressed by the black locust can be missing in invaded habitat. This makes it unsuitable for specialist birds despite the nest site availability or accessibility remain unchanged. This mechanism assumes that the habitat specialists are also the diet specialists at the same time, which is supported by several recent studies on birds (Belmaker et al. 2012; Pearman et al. 2014).

By contrast, the black locust stands frequently hosted habitat generalists such as the chiffchaff, the blackcap, the blackbird, the song thrush (*Turdus philomelos*), or the robin (*Erithacus rubecula*). These originally forest species have recently colonized highly urbanized landscapes suggesting their ability to occupy novel environments (Evans et al. 2010; Reif et al. 2011a). Indeed, broad habitat niche was recently recognized as a key trait enabling such urbanization in birds (Evans et al. 2011), and, in turn, it also most likely facilitates the presence of such species in invaded forest stands. However, high abundance of these generalist species in invaded habitat may not be a good indicator of its suitability for these birds. Specifically, in the case of the black locust in central Europe, Remeš (2003) showed that a high breeding density of the blackcap on the invaded study plot coincided with increased nest predation leading to extremely reduced breeding performance. As a result, the black locust served as an ecological trap for this species and its breeding population must have been supplied by individuals from neighbouring native oak forests (Remeš 2003). Based on our data, we cannot decide whether or not this may be the case of the black locust stands on our study plots.

Finally, we should note that the gradient in bird community composition explained by the type of the forest stand (i.e. black locust and oak, respectively) was not the strongest gradient revealed by RDA, since the other (non-canonical) RDA axes accounted for a larger amount of variability in bird species abundance on the study plots than the axis corresponding to the forest type. Therefore, we should bear in mind that there are also other factors than the black locust invasion structuring forest bird communities in the study area. These factors can include tree height, canopy closure, or tree bark structure, which we did not measure. On the other hand, the performance of the other gradients attributable to the unknown habitat variables (explaining 10–22 % of variability in bird community structure) was comparable to the performance of our focal forest type (almost 10 %). Moreover, our study plots were of the approximately same tree age, so this factor was controlled for by the sampling design. Therefore, we can conclude that the black locust invasion is not the strongest, but significant factor affecting abundance of forest birds in the breeding season in the study area.

Conservation implications

In conclusion, results of our study imply that the invasive black locust strongly influences individual species of native higher-level consumers, here represented by birds, and this influence can be predicted by their ecological specialization. We can thus speculate that biological invasions may significantly contribute to the widespread replacement of specialist bird species by habitat generalists in local communities (Le Viol et al. 2012), together with more frequently cited effects of urbanization, agricultural intensification or climatic changes (Shultz et al. 2005; Reif et al. 2011a; Davey et al. 2012). Specifically, this could be the case of the habitat specialist forest birds in the central part of the Czech Republic examined in this study. If these species should not become regionally threatened, we recommend reducing the stands of the invasive black locust by conservation management and replacing them by the native trees typical for indigenous oak forests.

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Appendix 1

See Table 3.

Table 3 Characteristics of bird species observed on the study plots

Abbreviation	Scientific name	Bird abundance		RDA	SSI	Life history
		Black locust	Oak			
AegCau	*Aegithalos caudatus*	2	0	0.19	0.37	1.32
CerBra	*Certhia brachydactyla*	2	1	0.08	1.20	1.45
CerFam	*Certhia familiaris*	3	1	0.16	0.87	1.51
CocCoc	*C. coccothraustes*	1	9	−0.31	0.80	0.84
ColPal	*Columba palumbus*	3	0	0.25	0.42	0.66
CyaCae	*Cyanistes caeruleus*	43	39	0.09	0.39	1.70
DenMaj	*Dendrocopos major*	13	21	−0.25	0.79	0.95
DenMed	*Dendrocopos medius*	0	2	−0.27	1.80	0.98
DryMar	*Dryocopus martius*	0	3	−0.25	0.90	−0.09
EriRub	*Erithacus rubecula*	18	6	0.42	0.86	1.56
FicAlb	*Ficedula albicollis*	9	8	0.04	1.70	0.87
FriCoe	*Fringilla coelebs*	10	19	−0.36	0.59	1.49
GarGla	*Garrulus glandarius*	8	1	0.34	0.35	0.66
ParMaj	*Parus major*	48	38	0.21	0.37	1.82
PhoPho	*P. phoenicurus*	7	0	0.38	0.59	1.15
PhyCol	*Phylloscopus collybita*	12	1	0.66	0.34	1.53
PhySib	*Phylloscopus sibilatrix*	0	3	−0.33	1.30	1.01
PoeMon	*Poecile montanus*	3	0	0.33	0.50	1.08
PoePal	*Poecile palustris*	5	0	0.32	0.64	1.48
SitEur	*Sitta europaea*	30	16	0.44	0.69	0.87
StuVul	*Sturnus vulgaris*	18	1	0.34	0.72	1.01
SylAtr	*Sylvia atricapilla*	21	1	0.51	0.32	1.25
TurMer	*Turdus merula*	25	27	−0.05	0.34	1.59
TurPhi	*Turdus philomelos*	6	0	0.42	0.38	1.74
TurVis	*Turdus viscivorus*	5	5	0.00	0.95	0.92

Abundance in black locust and oak plots, respectively; RDA, species' scores expressed using redundancy analysis (RDA) describing the strength of species' association with the native oak stands (negative values) and with the invasive black locust stands (positive values), respectively (see Fig. 1); SSI, species specialization index from Reif et al. (2010); life history, species' position along the gradient from "K-selected" to "r-selected" species from Koleček and Reif (2011)

Appendix 2

See Fig. 3.

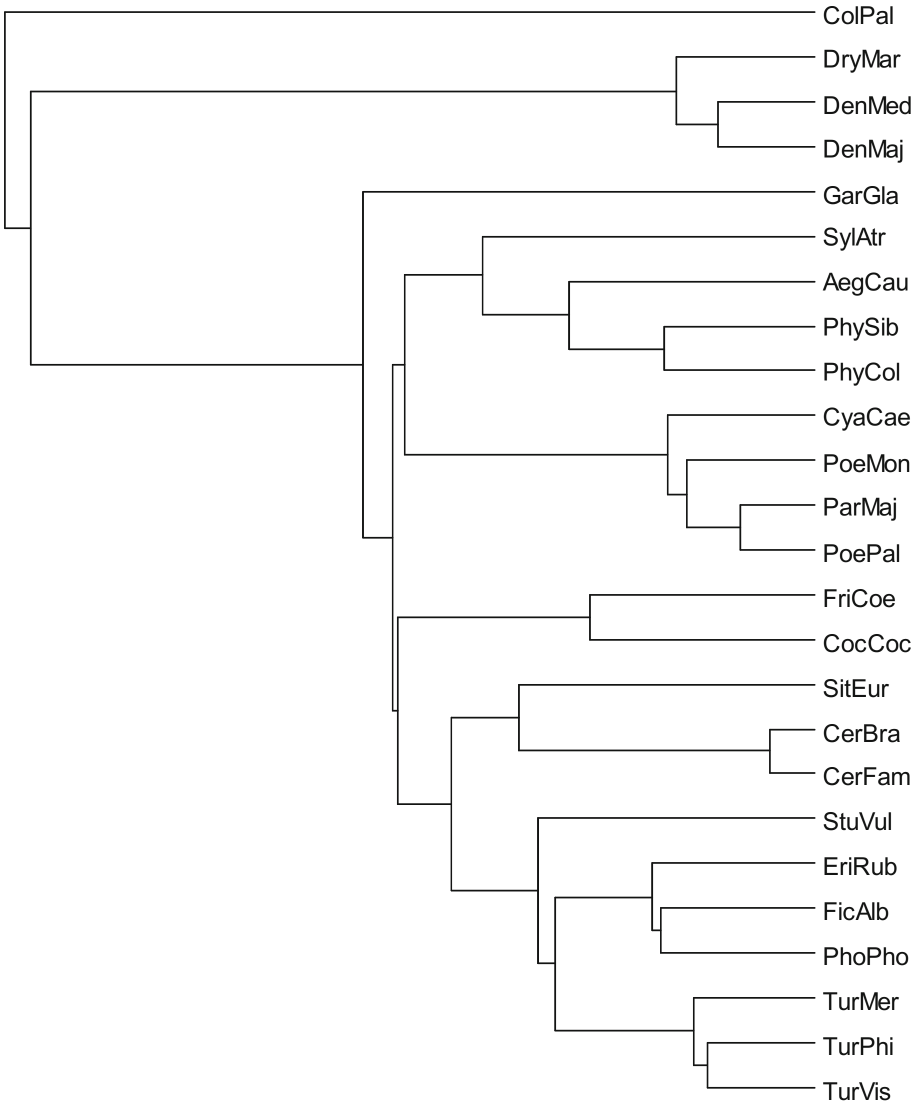

Fig. 3 Phylogenetic tree of the observed bird species compiled according to Jetz et al. (2012) by using http://www.birdtree.org

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Paper III

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Conservation implications of cascading effects among groups of organisms: The alien tree *Robinia pseudacacia* in the Czech Republic as a case study

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ABSTRACT

Invasions of non-native plants often result in impoverished local communities; however, their cascading effects along food chain remain unknown. Here we investigated how the alteration of food resources and habitat structure due to the invasion of an alien tree affects the species richness of habitat specialist and generalist birds. During 2014, we sampled forest stands of the invasive *Robinia pseudacacia* and control stands of native trees in the Czech Republic (central Europe). Specifically, we performed intensive breeding bird counts and assessed moth diversity as a key food resource for breeding birds and, described the habitat structure of sampled stands. Compared to native tree stands, stands of *R. pseudacacia* had a lower species richness of habitat specialist birds, a higher species richness of habitat generalist birds, a lower diversity of moths, a less continuous canopy and a more developed shrub layer. Then we related bird species richness to moth diversity and descriptors of habitat structure. Moth diversity was the only variable significantly related to the species richness of habitat specialist birds, while the species richness of habitat generalist birds was related solely to the local habitat structure. Specialists were thus limited by a less diverse food supply in the invaded stands, most likely due to the absence of some arthropod species. In contrast, generalists were ecologically more flexible and exploited new breeding opportunities created by a shrub layer in the invaded stands. Our study thus provides evidence that impacts of an invasive tree scale up across trophic levels.

1. Introduction

Invasions of non-native species are widely recognized as an important aspect of the global impacts of human populations upon the biosphere (Gaertner et al., 2014; Pyšek et al., 2012; Tilman, 1999; Vitousek et al., 1996). In the case of non-native invasive plants (sensu Richardson et al., 2000), their influence includes the deterioration of native communities, expressed as reduction in the numbers of native species (Hejda et al., 2009; Pyšek et al., 2012; Vila et al., 2011). Invasions of woody species are particularly important from a conservation perspective because these species tend to be dominant and ecosystem engineers, which modify the conditions for most species living in the associated woodlands. Therefore, if a non-native woody plant becomes invasive (sensu Blackburn et al., 2011), it is likely to have a particularly massive impact on most species present in the community (Jäger et al., 2007; Moran et al., 2000; Rothstein et al., 2004; Weber, 2003).

Invasive plants can change the invaded community's composition in terms of niche breadth. A narrow niche breadth means that a species is adapted to a limited set of environmental conditions (Godet et al., 2015). Therefore, we can expect that a narrow niche breadth limits species' potential to resist the habitat change created by an invasion. At the same time, a wide niche breadth characterizes ecologically tolerant species with the potential to exploit novel habitats (Ducatez et al., 2015) and thus habitat generalists may even benefit from biological invasions. In practice, this process can result in biotic homogenization (Olden et al., 2004), when ecological communities become impoverished of specialized species and generalists become dominant at the same time (Olden and Rooney, 2006). Although the large-scale decline of ecological specialists had been well documented (Jiguet et al., 2007; Le Viol et al., 2012; Reif, 2013), the local mechanisms underlying this process remain poorly understood (Devictor et al., 2010a).

From a conservation perspective, the role of invasive plants as an important threat for biodiversity has recently become questioned due to the lack of evidence for an impoverishment of biodiversity at a regional scale, for instance in the case of British flora (Thomas and Palmer, 2015). However, modest large-scale effects may not imply that these species do not affect biodiversity at a local scale (Hulme et al., 2015). It is possible that small-scale impacts are indeed high (e.g. Pyšek et al., 2012) and that a limited regional distribution of invaders, which is most likely only temporary and will be more extensive in the future, precluded their upscaling to the regional level. It is therefore crucial to understand the cascading effects of invasive plants on different groups of organisms to assess their real threat potential. Given the strong

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relationship between habitat specialization and threat level across species (Koleček et al., 2014; Owens and Bennett, 2000), here we use specialized species as model organisms to elucidate the mechanisms of how invasive plants have the potential to threaten the consumer species that are potentially under higher extinction risk.

We studied the impacts of an invasive woody plant that is alien to Europe, *Robinia pseudacacia*, one of the most impacting and widely distributed invasive plant species in the world (Buchholz et al., 2015), on bird species of different levels of habitat specialization. We focused on birds as study organisms because they are on the top of food chain and encompass a broad range of specialization levels, from narrowly specialized species breeding in specific habitats to species with a wide geographic distribution (Gaston, 1994). Moreover, recent studies have provided information about bird traits related to habitat specialization including foraging habits (Ducatez et al., 2015; Godet et al., 2015; Reif et al., 2016) which is important for understanding the potential implications of the decline of specialists on ecosystem functioning (Devictor et al., 2010b). They may also serve as dispersers for some invasive plant species (Lenda et al., 2012). At the same time, only a handful of studies to date have focused on the impact of invasive alien plants on birds (Aslan and Rejmánek, 2010).

Invasive woody plants may affect secondary consumers such as birds either by altering habitat structure, or by changing their food supply (Chapman et al., 2004; Fleishman et al., 2003). Changes in habitat structure are due to the different architecture of the invasive plant compared to the native species, allelopathic effects on other plants, higher litter production and/or nitrogen fixation (Vila et al., 2011), all of which are the case for *R. pseudacacia* (Slavík, 1995). Consequently, birds adapted to the characteristics specific to the native habitat will no longer recognize the altered habitat as suitable (Holland-Clift et al., 2011). On the other hand, new habitats created by invasions can attract species formerly absent from native tree stands (Hajzlerová and Reif, 2014). With respect to the habitat niche breadth of bird species, we may assume that the negative impacts will concentrate on specialists, while positive effects will favour generalists that are more flexible in their habitat use. Differences in habitat structure between native and invaded stands may also be reflected in changes to the bird community composition relative to species' foraging techniques. For instance, fragmentation of the canopy and development of the lower vegetation layers in invaded stands should result in changes to bird communities according to species' foraging strata.

Changes in bird food supply due to woody plant invasions are often reflected in arthropod diversity, which is generally reduced in invaded stands (Cunningham et al., 2005; Degomez and Wagner, 2001; Hartley et al., 2010). Underlying drivers include an absence of host plants for insect herbivores, alteration of microclimatic conditions, and disturbed predator–prey relationships (Litt et al., 2014). Consequently, bird species depending on parts of their diet that are lacking in an invaded habitat will be absent in that habitat (Skórka et al., 2010). Specifically, species feeding exclusively on arthropods should be less represented in invaded stands, whereas species with a mixed diet should be less affected by the invasion. We may also assume that the limiting effect of food diversity will be stronger in species of narrower niche breadth than in species of broader niches.

Based on this framework, we tested the following predictions using data on bird occurrence, the food supply for birds and the habitat structure in native forest stands and in stands invaded by *R. pseudacacia* in the Czech Republic. (i) Habitat structure will differ between native stands and the stands dominated by the invasive *R. pseudacacia*. (ii) Food supply for birds will be more diverse in the native stands than in the stands of the invasive *R. pseudacacia*. (iii) The number of specialist bird species will be higher in the native stands, whereas the number of generalists will be higher in the stands of the invasive *R. pseudacacia*. (iv) Birds feeding on invertebrates and canopy foragers will have higher species richness in the native stands, whereas the species richness of birds with a mixed diet and shrub foragers will be higher in the *R. pseudacacia* stands. In addition, we can expect a tight relationship of bird species richness to habitat characteristics rather than to food supply if the altered habitat structure drives changes in bird community composition due to woody plant invasion. Taken together, these tests should help uncover the mechanisms of how invasive plant species, represented by *R. pseudacacia* in the Czech Republic, impact native bird communities.

2. Materials and methods

2.1. The invasive alien R. pseudacacia

R. pseudacacia (Fabaceae) is a woody species introduced into Europe from North America in the 16th century. Its native range covers the south-eastern United States. *R. pseudacacia* grows in forest clearings and disturbed forests, and declines in later successional stages (Slavík, 1995). In Europe, it was planted massively in the 19th century (Slavík, 1995). The introduced trees were able to grow on gravelly, unstable slopes, even on nutritionally poor bedrock, due to their nitrogen-fixing capacity (Slavík, 1995). While they tend to expand along dry forest edges, and sometimes overgrow steep slopes within dry forests, they are not particularly successful when reproducing in more mature, closed stands, partly due to its relatively short life cycle (Vítková et al., 2015). Within central Europe, stands of *R. pseudacacia* are generally floristically poor and dominated by a few nitrophilous plant species, but can also be floristically diverse, especially on xerothermic sites (Vítková and Kolbek, 2010). It has been previously documented that forest bird communities differ between native stands and stands of *R. pseudacacia* (Hanzelka and Reif, 2015; Plexida et al., 2012).

2.2. Study area and field surveys

The study was conducted in a forested area of ca 600 km^2 (50° 01′ N; 14° 21′ E) in central Bohemia, the Czech Republic, Europe, in the vicinity of the city of Prague. The forest cover is generally formed by native tree species: *Quercus petraea* and *Q. robur* as dominant trees, mixed with *Carpinus betulus* and *Tilia cordata*. Stands of native species were compared with dense stands of the invasive *R. pseudacacia*. For the purposes of this study, we established 20 study plots in stands of native trees and 19 study plots in pure stands of the invasive *R. pseudacacia*, following the protocol of Hanzelka and Reif (2015). Native forest stands were always formed by the tree species mentioned above, i.e. *Quercus* spp. dominated in all plots. Invaded stands were formed by a *R. pseudacacia* canopy, but lower vegetation layers contained various native shrub species such as *Sambucus nigra*, *Crataegus* sp. and *Rosa canina* together with young stems of *R. pseudacacia*. Square plots of 100 m × 100 m were located within large and continuous stands (i.e. native or invaded by *R. pseudacacia*). We avoided sites covered by a mixture of native and invasive trees. Study plots were at least 500 m apart to prevent the same bird individuals from being recorded at different plots. The plots were located at least 100 m away from the nearest forest edge.

The data on study plots were collected in 2014. Birds were monitored during three visits in the peak of their breeding season (April–June), to include both early and late breeders (Bibby et al., 2000). Each visit lasted 20 min. at each plot and was performed during the morning hours (05:00–10:00). During a visit, a researcher slowly walked across the study plot several times and recorded all bird individuals detected both visually and acoustically by indicating the position of each individual on a map (Hanzelka and Reif, 2015). Bird surveys were carried out under favourable weather conditions (no rain, no strong wind), and the order of plots surveyed on the same day changed between visits to factor out the possible effects of daytime. To express the bird species richness on a given study plot, we summed up the records from all three visits. As an estimate of the abundance of a given species on a study plot, we used its maximum count across the three visits (Jiguet et al., 2007).

Nocturnal Lepidoptera (species from superfamilies Hepialoidea, Cossoidea, Lasiocampoidea, Bombycoidea, Noctuoidea, Drepanoidea and Geometroidea; hereafter called "moths") were considered an indicator of the food supply for birds. Moths and especially their larvae are an essential part of the diet of almost all the bird species observed on the study plots during the breeding season (Cramp, 1977–1994; Krištín and Patočka, 1997). Even obligatory seed eaters supply their nestlings with some insect food, typically moth larvae, to provide essential proteins (Krištín and Patočka, 1997). Moths were surveyed using portable light traps (8 W UV light, powered by a 7.2 Ah/12 V lead battery). We focused on images with the assumption that their richness broadly mirrors the richness of the larval stages, which are mainly consumed by foraging birds (Ramaswamy et al., 1983; Jactel et al., 2006; Skórka et al., 2010). Moth surveys took place during a single night at the beginning of every month from April to November, i.e. eight samples in total. Such a sampling covered all major phenological aspects of the moths' diversity (see also Tropek et al., 2014) and included all relevant moth species that are part of potential food supply for birds. Each study plot was sampled using one light trap positioned in the middle of the plot, under suitable weather conditions (no strong winds or rain, no extreme temperatures; see Yela and Holyoak, 1997). All study plots were sampled on the same night in a given month to factor out biases due to weather changes or plant phenology. Light traps were activated at least one hour before dusk and were collected at dawn. Since the light sources of traps attract flying moths from only a few tens of metres around (Truxa and Fiedler, 2012; van Grunsven et al., 2014), our method avoided the unwanted sampling of moths from other forest stands and habitats in the vicinity of the study plots.

All caught moths specimens were determined to the species level. We identified the time period of availability of every moth species as a prey for breeding birds from the literature (Macek et al., 2007, 2008, 2012) and excluded two species that were not available during the bird breeding season (*Eupithecia simplicata* and *E. absinthiata*) from our moth data. The dominant moth species differed markedly between invaded and native stands. While native stands were dominated by species associated with the canopy layer (*Drymonia dodonaea*, *Erannis defoliaria*, *Hypomecis roboraria*) or with the tree leaf litter (*Paracolax tristalis*), these ecological groups were missing or were underrepresented in *R. pseudacacia*. Among the moth species most closely associated with native stands were those most frequently reported as food resources for central European forest birds such as *E. defoliaria* and *Agriopis aurantiaria* (Krištín and Patočka, 1997). The majority of the moth diversity in the invaded stands was represented by species of the shrub layer (*Ligdia adustata*, *Macaria alternata*, *M. wauaria*) or by generalists without any closer habitat association (*Idaea aversata*, *Peribatodes rhomboidaria*).

In June, after collecting the bird data and at the peak of the growing season, we mapped the habitat structure in each study plot. We divided each plot into 4 subplots of 50 × 50 m and described the habitat structure in every subplot using 13 variables relevant for birds (see Honkanen et al., 2010; James and Wamer, 1982; Moning and Müller, 2008): coverage of the herb layer up to a height of 0.5 m (%), coverage of the herb layer above 0.5 m (%), coverage of the shrub layer from 1 to 5 m high (%), coverage of the tree layer from 5 to 10 m high (%), coverage of the tree layer above 10 m (%), the proportion of trees up to 0.2 m diameter at breast height (%), the proportion of trees of 0.2–0.5 m diameter at breast height (%), the proportion of trees above 0.5 m diameter at breast height (%), the presence of unbroken canopy (yes/no; canopy was defined as unbroken in case of absence of any gaps larger than 2 m), coverage of the canopy (%), coverage of clearings (%), the number of dead trees, and the number of fallen trees. Relative coverages were estimated by walking throughout the subplot and looking around without use of any specific measurements; numbers of trees were counted. Then we upscaled the data from subplots to the whole plot level. For variables with proportional data we calculated the mean value across subplots, while for variables with count data we summed the values across all subplots. The canopy was considered unbroken at the whole plot level when all subplots were classified as unbroken.

In addition, we assessed the composition of six main land cover types (water, rock, grassland, human settlement, broad-leaved forest, coniferous forest) within a circle of 500-m radius around each plot to obtain information about the possible influence of surrounding habitats. For this purpose, we analysed aerial photographs and calculated relative areas of the main land cover types in ArcGIS 10.2 (ESRI, 2011).

2.3. Bird community metrics

To describe bird communities by metrics relevant for assessing the impact of *R. pseudacacia* invasion, we focused on bird habitat specialization, diet and foraging techniques. With respect to these species' traits, we sorted the species into several groups and calculated (i) species richness and (ii) the Shannon diversity index of each group in each study plot. Species richness was expressed as the total number of species of a given group recorded in each study plot. The Shannon diversity index was calculated using the formula $-\Sigma p_i * \ln(p_i)$, where p is the proportion of individuals of a given species i in the total abundance of all species of the bird community on a given study plot.

2.3.1. Habitat specialization

For each bird species, we obtained its habitat specialization index from Reif et al. (2010). This index quantifies the degree of species' habitat specialization. It is a coefficient of variation of density of each species across several habitats (Julliard et al., 2006). The inference of this index is based on the assumption that the density of more specialized species varies more among habitats, having thus higher index values, whereas the density of generalist species is more uniform across habitats (Julliard et al., 2006). Testing this assumption against expert opinion showed a good agreement (Reif et al., 2010), so we can consider this index a reliable measure of species' habitat specialization (Ducatez et al., 2015). Using the data from a large-scale breeding bird monitoring scheme based on species' occurrence in eight main habitats throughout the country, Reif et al. (2010) calculated the habitat specialization index for the majority of species of the Czech bird fauna.

Based on their habitat specialization index, we ranked bird species in descending order, sorting them into a) two halves and b) four quartiles, respectively (see e.g. Jetz and Rahbek, 2002, for another example of this approach). We called the first half "specialist species" and the second half "generalists species". We then recognized "strong specialists", "moderate specialists", "moderate generalists" and "strong generalists", respectively, according to the quartiles (Table A.1). Although this sorting was based on the arbitrary definition of particular groups, all groups differed from each other in their habitat specialization indices, with strong specialists having the highest values and strong generalists the lowest values (Fig. A.1).

2.3.2. Diet and foraging techniques

We assessed the diet consumed during the breeding season by each bird species based on information in Cramp (1977–1994). We recognized two groups of species, "obligate invertebrate consumers" and "consumers of a mixed diet" (Table A.1), where a mixed diet means feeding on both animal and plant tissues. Since all species feed heavily on insect food during this part of the year (note, for example, that none of the species from our sample could be assessed as an obligate seed consumer) and descriptions of species' diets are not unified across species, we could not use a more detailed classification (e.g. recognizing different kinds of invertebrate food). Nevertheless, none of the species could be classified into both groups.

Concerning the foraging techniques, we used information in Cramp (1977–1994) to classify the species into groups recognizing (i) major foraging strata: canopy, shrub and ground; and (ii) parts of vegetation most often used for feeding: ground, foliage and bark (Table A.1). Note that we finally obtained five groups of species according to their feeding techniques because ground foragers appeared in both types of classification. Three species that mainly catch flying insects (*Ficedula albicollis*, *Muscicapa striata* and *Phoenicurus phoenicurus*) were not sorted according to the latter classification. They do not match any of the above categories, and a separate category of flying insect catchers would be too species poor for further analysis.

2.4. Characteristics of the study plots

For each study plot, we expressed the Shannon diversity index of moths in the same way as for birds (Table A.2).

Variables describing the habitat structure of plots were closely correlated among each other. For this reason, we performed a principal component analysis on data standardized to zero mean and unit variance in CANOCO for Windows 4.5 (Lepš and Šmilauer, 2003), obtaining ordination axes as uncorrelated variables (Table A.2). We used the first two most important ordination axes for further analyses. The first axis (explaining 40.6% of the variability in the habitat structure of study plots) was interpreted as a gradient from plots with tall trees and a well-developed canopy to plots with a dense scrub layer and a large amount of dead wood (Table 1a). The second axis (explaining 16.9% of the variability in the habitat structure of study plots) expressed a gradient of decreasing forest continuity and an increasing proportion of clearings (Table 1a).

The variables describing the land cover type composition around study plots suffered from the same problem of non-independence as the variables representing the habitat structure. We thus again performed principal component analysis, and used the first two ordination axes for further analyses (Table A.2). The first axis (explaining 65.3% of the variability in land cover composition) represented a gradient from a high proportion of broad-leaved forests to a high proportion of human settlements (Table 1b). The second axis (explaining 23.7% of the variability in land cover composition) was a gradient from all land cover types to coniferous forests (Table 1b).

2.5. Statistical analysis

In all analyses described below, the study plots were taken as statistical units and thus the sample size is always $n = 39$.

Table 1

Factor loadings of original variables along the first two most important principal components (PC1 and PC2), as revealed by principal component analysis performed separately for (a) the habitat structure on study plots and (b) the land cover composition in the 500-m surroundings of study plots. DBH — diameter at breast height. Variables with loadings of higher values than 0.70 are in bold.

Original variable	PC1	PC2
a)		
Herb layer coverage (<0.5 m)	−0.58	−0.56
Herb layer coverage (>0.5 m)	0.51	0.6
Shrub layer coverage (1–5 m)	**0.73**	0.2
Tree layer coverage (5–10 m)	**0.91**	−0.25
Tree layer coverage (>10 m)	**−0.91**	0.25
Trees proportion (<0.2 m DBH)	**0.75**	−0.45
Trees proportion (0.2–0.5 m DBH)	**−0.75**	0.46
Trees proportion (>0.5 m DBH)	0.03	−0.19
Continuous canopy (yes/no)	−0.58	−0.25
Canopy coverage	**−0.84**	−0.34
Clearings coverage	−0.04	0.56
Dead tree numbers	−0.22	0.45
Fallen tree numbers	0.46	0.36
b)		
Water	−0.05	−0.08
Rock	−0.44	−0.28
Grassland	−0.11	0.19
Human settlement	**0.98**	−0.16
Broad-leaved forest	**−0.88**	−0.42
Coniferous forest	−0.18	**0.96**

2.5.1. Gradients in the species composition of bird communities

To reveal which bird species are associated with native forest stands and which occur in *R. pseudacacia*, we performed multivariate redundancy analysis (RDA). RDA is a direct gradient analysis technique relating the abundance of particular species at study plots to explanatory variables, and obtaining independent gradients in bird community composition expressed as particular ordination axes ordered according to their declining explanatory power (Lepš and Šmilauer, 2003). The ordination axes are either canonical, i.e. represented by pre-defined explanatory variables (i.e. native stands vs. stands invaded by *R. pseudacacia* in the case of our data), or non-canonical, i.e. represented by unknown environmental gradients. We used RDA as implemented in CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002) to test whether forest stand type (i.e. native vs. invaded by *R. pseudacacia*) has a significant effect on the bird community composition. For this purpose, we used a Monte Carlo test within RDA with 999 permutations. We present results for the first four most important ordination axes: one canonical (represented by forest type) and three non-canonical. In RDA, we coded the native forest stands as 0 and the stands of *R. pseudacacia* as 1 as recommended by ter Braak and Šmilauer (2002) for the purposes of the analysis of categorical response variables.

2.5.2. Comparisons of invaded and native stands

We took forest stand type as a single explanatory two-level factor and used spatial autoregressive (SAR) models to compare the following response variables between native forest stands and the stands of *R. pseudacacia*: species richness and the Shannon diversity index of all bird species, species richness and the Shannon diversity index of particular groups of birds defined by habitat specialization, diet and foraging technique, the Shannon diversity index of moths, PC1 and PC2 describing the habitat structure of study plots, and PC1 and PC2 describing the land cover composition surrounding the plots. The SAR models controlled for the spatial non-independence of the data and were run in Spatial Analysis for Macroecology software, version 4.0 (Rangel et al., 2010). Similar to RDA, we coded the native forest stands as 0 and the stands of *R. pseudacacia* as 1 in the SAR models to reveal contrasts between the stand types for particular response variables.

2.5.3. Relating bird community metrics to plot characteristics

To reveal possible mechanisms driving differences in bird community metrics between stand types, we took species richness and the Shannon diversity index of particular bird groups defined by habitat specialization, diet and foraging techniques as respective response variables and related them to the Shannon diversity index of moths, habitat structure of the study plots and to the land cover composition surrounding the study plots taken as explanatory variables. We used SAR models for this purpose and for each response variable we tested the main effects of all explanatory variables within a single model. Every model had thus six parameters.

In these models, we did not include forest stand type in the explanatory variables because the Shannon diversity index of moths, habitat structure of the study plots and land cover composition surrounding the study plots were significantly different between the native forests and the stands of *R. pseudacacia* (see Section 3.1). Therefore, the inclusion of forest type in the predictors would have resulted in a strong collinearity of explanatory variables and thus increase the risk of obtaining spurious results.

3. Results

We recorded 35 bird species in total, with native forests and stands of *R. pseudacacia* each hosting 31 species. At the level of individual study plots, bird species richness did not differ between stands of native trees (mean = 11.1 species, SD = 3.1) and stands of *R. pseudacacia* (mean = 11.8 species, SD = 2.7; SAR model: $F = 0.62$, $P = 0.437$). The same pattern applied for the Shannon diversity index of birds (native stands: mean = 2.26, SD = 0.25; stands of *R. pseudacacia*: mean = 2.33, SD = 0.25; SAR model: F = 0.71, P = 0.406).

3.1. Characteristics of the study plots

Native forests had higher moth diversity (SAR model: F = 14.77, P < 0.001; Fig. 1a) and tree canopy cover, but lower shrub layer cover and amount of dead wood, as indicated by the PC1 of habitat structure (SAR model: F = 81.49, P < 0.001; Fig. 1b). In their 500-m surroundings, native forests had a higher proportion of broad-leaved trees and a lower proportion of human settlements than the stands of *R. pseudacacia*, as indicated by PC1 of the land cover composition (SAR model: F = 16.78, P < 0.001; Fig. 1c). In contrast, both PC2 of the habitat structure on study plots (SAR model: F = 2.02, P = 0.163; Fig. 1b) and PC2 of the land cover composition within the 500-m wide surrounding of study plots (SAR model: F = 1.43, P = 0.240; Fig. 1c) did not differ between the native forest stands and *R. pseudacacia* stands.

3.2. Species composition of bird communities

The species composition of bird communities differed significantly between native forests and *R. pseudacacia* stands (RDA Monte Carlo test: F = 5.13, P = 0.001; Fig. 2). Species associated with *R. pseudacacia* (Fig. 2) were common birds of European forests (e.g. *Phylloscopus collybita*, *Aegithalos caudatus* and *Turdus philomelos*) typically preferring the shrub layer (*Sylvia atricapilla*, *Troglodytes troglodytes*) or discontinuous forest canopy (*Phoenicurs phoenicurus*). Native stands (Fig. 2) were occupied by species preferring a well-developed canopy (*Dendrocopos medius*, *Oriolus oriolus*) or forest interior (*Dryocopus martius*, *Phylloscopus sibilatrix*). According to the RDA, some species like *Parus major* and *Ficedula albicollis* did not discriminate among native forests and *R. pseudacacia* stands (Fig. 2).

RDA revealed that the stand type (i.e. native forest vs. *R. pseudacacia* stand) was among the most important predictors of bird community composition on the study plots accounting for 11.9% of its variability, whereas the other gradients in bird community composition (independent of stand type) explained 13.1%, 12.0% and 10.1% of its variability, respectively.

3.3. Habitat specialist and generalist birds

The species richness of bird groups defined by habitat specialization differed significantly between native forests and stands of *R. pseudacacia*. Specialists had more species in the native forests (SAR model: F = 6.48, P = 0.015; Fig. 3), whereas generalists had more species in *R. pseudacacia* stands (SAR model: F = 22.64, P < 0.001; Fig. 3). This pattern remained consistent even after considering strong and moderate specialists and generalists separately (Fig. 3). However the difference was significant only for the strong (SAR model: F = 4.25, P = 0.046) and moderate specialists (SAR model: F = 4.70, P = 0.037) and strong generalists (SAR model: F = 33.52, P < 0.001), but not for the moderate generalists (SAR model: F = 2.33, P = 0.136). If considering the Shannon diversity index of particular bird groups, the patterns were very similar (Appendix A.1), only the difference between native forests and stands of *R. pseudacacia* became insignificant for strong specialists (Appendix A.1).

The Shannon diversity index of moths was the only significant predictor of the number of specialist birds (Table 2a–c). A higher number of specialized birds was found on the plots with a higher diversity of moth species (Table 2a). The same relationship was found for moderate specialists (Table 2b). The relationship between moth diversity and species richness of strongly specialized bird species was also positive, but insignificant (Table 2c). Other variables, such as the habitat structure and land cover composition in the surroundings, were unrelated to the number of specialist bird species (Table 2a–c). The results remained qualitatively the same when we considered the Shannon diversity of birds instead of bird species richness (Appendix A.1).

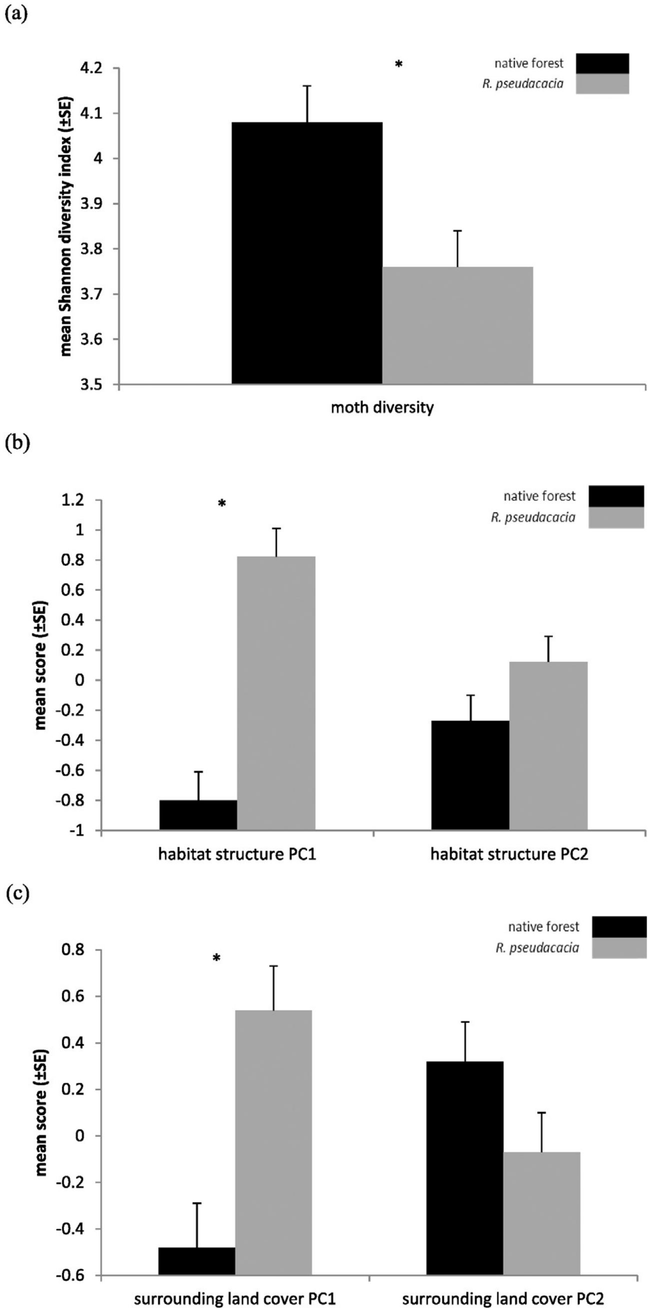

Fig. 1. Comparison of (a) the Shannon diversity index of moths, (b) habitat structure (PC1 and PC2 from principal component analysis on 13 variables describing habitat structure in the study plots) and (c) land cover composition in a 500-m radius surrounding the plots (PC1 and PC2 from principal component analysis on six variables describing the land cover) between the study plots located in native forest stands and in stands of invasive *Robinia pseudacacia*. The values are the least-square means estimated by simultaneous autoregressive models. A separate model was run for each variable. The asterisks mark significant differences between stands.

Habitat structure affected the species richness of generalist birds (Table 2d–f). The significant effect of PC1 (Table 2d) indicated that more habitat generalists were breeding in plots with a more developed shrub layer, a higher amount of dead wood, and trees of lower stature and lower canopy coverage. Strong and moderate generalists both showed the same significant pattern (Table 2e, f). The species richness

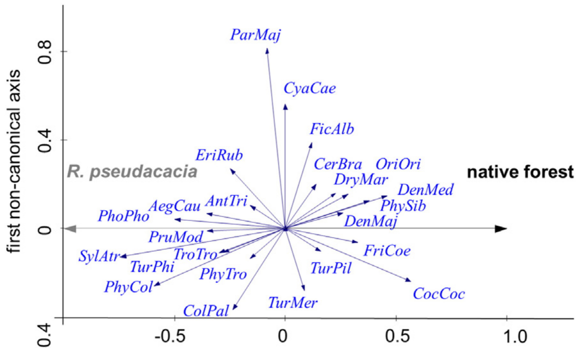

Fig. 2. Bird species' (blue arrows) associations with native forest stands (black arrow) and with stands of invasive *Robinia pseudacacia* (grey arrow) as revealed by redundancy analysis. The closer the position of a species' arrow to the extreme part of the x-axis, the higher the association of a given species with a given stand type. Species with unclear associations (i.e. those close to the centre of the plot) are not depicted. Birds are abbreviated by first three letters of their scientific names (see Table A.1 for full names). Note that positions of some species'identifiers were moved to improve readability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
The effects of habitat structure on study plots (PC1 and PC2 from principal component analysis on 13 variables describing the habitat structure), land cover composition in the 500-m surroundings of study plots (PC1 and PC2 from principal component analysis on six variables describing the land cover) and the Shannon diversity index of moths on species richness of bird groups defined by their habitat specialization. Separate simultaneous autoregressive models were run for: (a) all specialists, (b) strong specialists, (c) moderate specialists, (d) all generalists, (e) strong generalists and (f) moderate generalists. Significant results are in bold.

Explanatory variable	Coefficient	SE	T	P
a) All specialists				
Habitat structure PC1	−0.47	0.38	−1.26	0.217
Habitat structure PC2	0.19	0.34	0.56	0.588
Surrounding land cover PC1	−0.26	0.36	−0.73	0.472
Surrounding land cover PC2	−0.41	0.33	−1.24	0.224
Moth diversity	**2.97**	**1.19**	**2.49**	**0.018**
b) Strong specialists				
Habitat structure PC1	−0.26	0.25	−1.03	0.310
Habitat structure PC2	0.03	0.23	0.14	0.888
Surrounding land cover PC1	0.01	0.24	0.02	0.987
Surrounding land cover PC2	−0.24	0.22	−1.11	0.275
Moth diversity	1.41	0.79	1.77	0.086
c) Moderate specialists				
Habitat structure PC1	−0.20	0.22	−0.94	0.356
Habitat structure PC2	0.18	0.20	0.92	0.367
Surrounding land cover PC1	−0.27	0.21	−1.28	0.211
Surrounding land cover PC2	−0.17	0.19	−0.93	0.359
Moth diversity	**1.58**	**0.67**	**2.35**	**0.025**
d) All generalists				
Habitat structure PC1	**1.33**	**0.32**	**4.23**	**<0.001**
Habitat structure PC2	0.33	0.28	1.15	0.258
Surrounding land cover PC1	−0.15	0.30	−0.48	0.632
Surrounding land cover PC2	0.21	0.27	0.75	0.456
Moth diversity	0.87	0.99	0.88	0.387
e) Strong generalists				
Habitat structure PC1	**0.67**	**0.21**	**3.24**	**0.003**
Habitat structure PC2	0.15	0.19	0.78	0.440
Surrounding land cover PC1	−0.01	0.20	−0.01	0.992
Surrounding land cover PC2	0.05	0.18	0.27	0.788
Moth diversity	−0.29	0.67	−0.43	0.671
f) Moderate generalists				
Habitat structure PC1	**0.67**	**0.22**	**2.99**	**0.005**
Habitat structure PC2	0.16	0.20	0.77	0.446
Surrounding land cover PC1	−0.21	0.21	−0.98	0.335
Surrounding land cover PC2	0.14	0.19	0.72	0.477
Moth diversity	1.08	0.68	1.58	0.125

of generalist bird species was not related to either the Shannon diversity index of moth species or PC2 of habitat structure, or to either PC1 and PC2 of land cover composition within the 500-m surroundings (Table 2d–f). The results remained qualitatively the same when we considered the Shannon diversity of birds instead of bird species richness (Appendix A.1).

3.4. Diet and foraging techniques of birds

Neither birds feeding exclusively on invertebrates (SAR model: $F = 1.79$, $P = 0.189$; Fig. 4), nor birds with a mixed diet (SAR model: $F = 0.18$, $P = 0.682$; Fig. 4) showed any differences in species richness between the native forests and the stands of *R. pseudacacia*. The same pattern was observed, if the Shannon diversity index was applied instead of species richness (Appendix A.1). However, birds feeding exclusively on invertebrates had a higher species richness (Table 3a) and Shannon diversity index (Appendix A.1) at stands with a higher diversity of moths, whereas birds with a mixed diet had a higher species richness (Table 3b) and diversity (Appendix A.1) at stands with a higher proportion of coniferous trees in the 500-m surroundings. The opposite effect of the surrounding habitat composition was found in the case of the Shannon diversity index of bird species feeding exclusively on invertebrates (Appendix A.1).

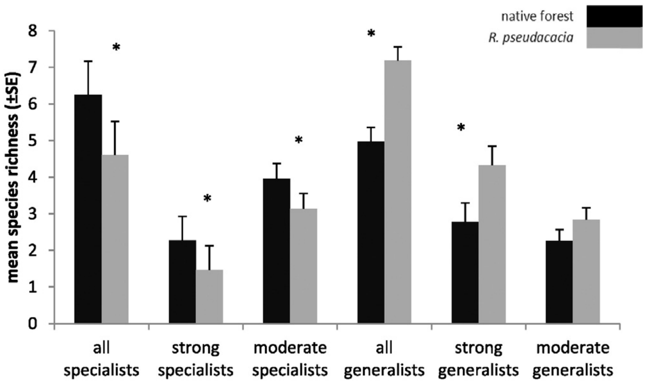

Fig. 3. Species richness of bird groups defined by habitat specialization in native forest stands and stands of invasive *Robinia pseudacacia*. The values are the least-square means estimated by simultaneous autoregressive models. A separate model was run for each species group. Asterisks indicate significant differences between stands.

Of the bird groups defined by foraging strata and the parts of vegetation used for feeding, the species richness of shrub foragers (SAR model: $F = 6.99$, $P = 0.012$; Fig. 4) and foliage gleaners (SAR model: $F = 8.92$, $P = 0.005$; Fig. 4) was significantly higher in *R. pseudacacia* stands than in native forest stands. The species richness of canopy foragers (SAR model: $F = 3.91$, $P = 0.056$; Fig. 4) and bark foragers (SAR model: $F = 3.35$, $P = 0.075$; Fig. 4) tended to be insignificantly richer in native forest stands. Ground foragers did not show any significant differences between forest types (SAR model: $F = 2.79$, $P = 0.103$; Fig. 4). Replacing species richness by the Shannon diversity index showed almost the same patterns (Appendix A.1); only the diversity of canopy foragers became significantly higher in native forest stands than in *R. pseudacacia* stands (Appendix A.1). Focusing on study plot characteristics (Table 3c–g) showed that the species richness of bark foragers significantly increased with moth diversity (Table 3g) and the richness of canopy foragers insignificantly (Table 3c). The species richness of birds foraging in the shrub layer, on the ground and in foliage significantly increased with PC1 (Table 3d–f), reflecting a less

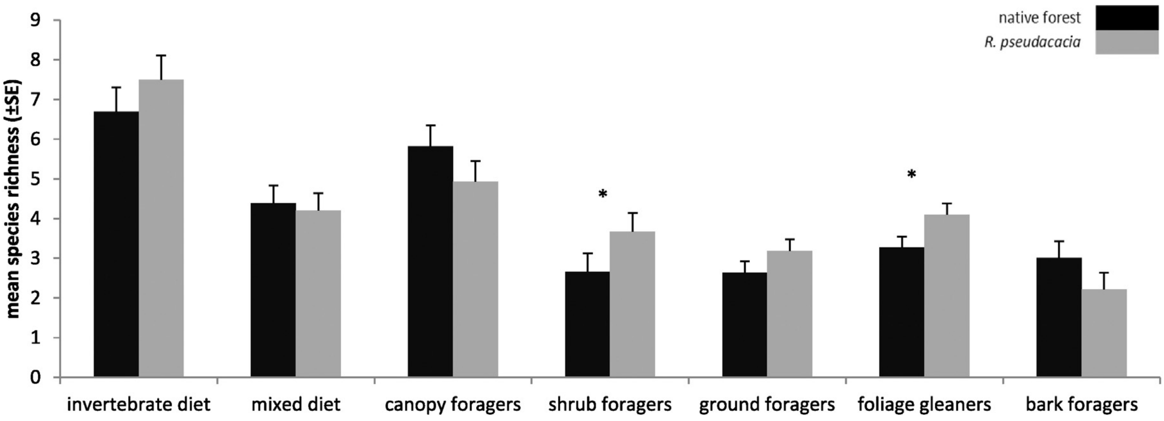

Fig. 4. Species richness of bird groups defined by diet and foraging techniques in native forest stands and stands of invasive *Robinia pseudacacia*. The values are the least-square means estimated by simultaneous autoregressive models. A separate model was run for each species group. Asterisks indicate significant differences between stands.

continuous canopy and more developed shrub and herb vegetation layers. These patterns remained mostly the same when we used Shannon diversity index instead of species richness for particular bird groups, with only the pattern for canopy foragers turning significant and for foliage gleaners insignificant (Appendix A.1).

4. Discussion

In accordance with the previous study of Hanzelka and Reif (2015), we found that the species richness of habitat specialist birds (represented by species like *D. medius*, *P. sibilatrix* and *O. oriolus*) was higher in the native stands, whereas habitat generalists (such as *S. atricapilla*, *P. collybita* and *A. caudatus*) were more species-rich in invaded stands. Here we develop those initial findings, showing that habitat specialists and habitat generalists differ in the sets of local environmental predictors, relating to their species-richness patterns across study plots. While the habitat specialists' species richness was only related to the diversity of moths, the species richness of habitat generalists was not affected by moths, but rather by the habitat structure of study plots, indicating that different mechanisms shape distribution and abundance of these groups.

In the case of habitat specialists, we suggest that their relationship to moth diversity is caused by a limited food supply for these species in the invaded stands. Indeed, a recent pan-European study on hundreds of bird species showed that habitat specialization can be used as a surrogate for several other species traits, including diet niche breadth (Reif et al., 2016).Therefore, the habitat specialists in our study are probably diet specialists at the same time. As a consequence, they likely lack some critical food resources in the stands of *R. pseudacacia*. This is indicated by the lower diversity of moths, probably caused by their limited ability to adapt to non-indigenous host plants forming the forest canopy (Litt et al., 2014).

Habitat generalists, on the other hand, are more likely tolerant to variability in the composition of the food supply and are not limited by the lower diversity of food in *R. pseudacacia* stands. Their species richness on our study plots is probably affected by other factors such as habitat structure. The stands of *R. pseudacacia* are characterized by a more developed shrub layer, which is probably caused by the ability of *R. pseudacacia* to fix nitrogen and thus to increase soil nutrients (Castro-Diez et al., 2014) and/or by the lower cover of the tree layer, enabling sunshine to reach the lower layers of vegetation. Of course, this increases the chances for the coexistence of more bird species (Hurlbert, 2004), probably leading to the higher number of generalist bird species. In addition, habitat generalists are capable of exploiting novel habitats created by *R. pseudacacia*. This corresponds to their ability to colonize new environments, such as urban areas (Evans et al., 2011), and benefit from new food types (Ducatez et al., 2015).

The higher species richness of habitat generalists in invaded stands may be a special case of woody plants like *R. pseudacacia* creating stands with well-developed shrub vegetation and might not be universal for plant invasions. If a plant invasion results in structurally homogenous stands, as is the case of *Salix* × *rubens* in Australia (Holland-Clift et al., 2011), we can expect a lower diversity of both specialist and generalist species.

It seems somewhat counterintuitive that habitat specialists are not affected by the structural components of habitat, unlike habitat generalists. However, we think this pattern is caused by the primary effect of lower food diversity in invaded stands, which precludes the occurrence of specialized birds. Note that in birds food limitation is generally stronger than limitation by habitat structure (Pigot and Tobias, 2013). In cases where such a food limitation is absent, we can speculate that habitat specialists may be equally or even more sensitive to changes in habitat structure than generalist species.

If the lower diversity of food resources in the *R. pseudacacia* stands limits some bird species, we would expect that this limitation will be stronger for those feeding on invertebrates than for species with a mixed diet. This expectation was partially confirmed because the species richness of birds feeding exclusively on invertebrates increased with moth diversity, and native stands host a more diverse moth community. However, stand type per se, if tested as a sole factor, did not predict the species richness of exclusive invertebrate feeders, suggesting that food limitation is probably not the only mechanism by which *R. pseudacacia* constrains the diversity of specialist birds. For instance, it was previously found that central European birds had lower breeding performance in *R. pseudacacia* than in native oak forests due to higher nest predation rates (Remeš, 2003). If specialists are more susceptible to nest predation, this mechanism may be an alternative explanation to the patterns observed in our data. However, this explanation is very speculative since we are not aware of any studies relating risk-taking behaviour to ecological specialization. Alternatively, our analysis of bird food niches suffered from the broad definition of diet categories, which was limited by the literature information on food consumed by particular bird species. Overcoming such problems would require studying the diet of particular bird species directly on study plots and matching it to the food supply revealed by light trapping. This would be a direct and decisive test of the mechanism of food limitation we propose above.

In contrast to exclusive invertebrate feeders, the species richness of birds with a mixed diet was positively related to the presence of coniferous trees in the surroundings of study plots, but not to moth diversity.

Table 3
The effects of habitat structure on study plots (PC1 and PC2 from principal component analysis on 13 variables describing the habitat structure), land cover composition in the 500-m surroundings of study plots (PC1 and PC2 from principal component analysis on six variables describing the land cover) and the Shannon diversity index of moths on the species richness of bird groups defined by their diet and foraging techniques. Separate simultaneous autoregressive models were run for: (a) species feeding exclusively on invertebrates, (b) species with a mixed diet, (c) canopy foragers, (d) shrub foragers, (e) ground foragers, (f) foliage gleaners and (g) bark foragers. Significant results are in bold.

Explanatory variable	Coefficient	SE	T	P
(a) Exclusive invertebrate feeders				
Habitat structure PC1	0.48	0.39	1.23	0.227
Habitat structure PC2	0.42	0.35	1.18	0.247
Surrounding land cover PC1	−0.23	0.38	−0.61	0.544
Surrounding land cover PC2	−0.65	0.34	−1.92	0.064
Moth diversity	**2.75**	**1.23**	**2.24**	**0.032**
(b) Mixed diet species				
Habitat structure PC1	0.42	0.26	1.61	0.117
Habitat structure PC2	0.04	0.24	0.17	0.865
Surrounding land cover PC1	−0.30	0.25	−1.23	0.228
Surrounding land cover PC2	**0.48**	**0.22**	**2.24**	**0.032**
Moth diversity	0.64	0.77	0.83	0.412
(c) Canopy foragers				
Habitat structure PC1	−0.38	0.3	−1.25	0.221
Habitat structure PC2	0.01	0.27	0.01	0.989
Surrounding land cover PC1	−0.17	0.29	−0.58	0.567
Surrounding land cover PC2	−0.25	0.26	−0.97	0.340
Moth diversity	1.82	0.94	1.94	0.061
(d) Shrub foragers				
Habitat structure PC1	**0.73**	**0.28**	**2.62**	**0.014**
Habitat structure PC2	0.35	0.25	1.4	0.171
Surrounding land cover PC1	−0.13	0.27	−0.50	0.623
Surrounding land cover PC2	−0.02	0.24	−0.10	0.921
Moth diversity	1.16	0.89	1.3	0.202
(e) Ground foragers				
Habitat structure PC1	**0.49**	**0.18**	**2.79**	**0.009**
Habitat structure PC2	0.11	0.16	0.69	0.497
Surrounding land cover PC1	−0.12	0.17	−0.70	0.492
Surrounding land cover PC2	0.11	0.15	0.78	0.444
Moth diversity	0.49	0.52	0.95	0.351
(f) Foliage gleaners				
Habitat structure PC1	**0.46**	**0.18**	**2.54**	**0.016**
Habitat structure PC2	0.06	0.16	0.35	0.727
Surrounding land cover PC1	−0.23	0.17	−1.33	0.194
Surrounding land cover PC2	0.01	0.16	0.08	0.937
Moth diversity	0.14	0.56	0.26	0.800
(g) Bark foragers				
Habitat structure PC1	−0.16	0.25	−0.64	0.528
Habitat structure PC2	0.12	0.23	0.51	0.612
Surrounding land cover PC1	−0.05	0.24	−0.22	0.826
Surrounding land cover PC2	−0.23	0.21	−1.08	0.288
Moth diversity	**1.88**	**0.77**	**2.45**	**0.020**

This is in accord with our predicted lower dependence of such species on insect food. They might also benefit from surrounding habitats different from the broad-leaved trees on the study plots enriching their food supply by seeds.

We also classified the birds according to their feeding strategies to gain further insight into species' sorting between invaded and native forest stands. Bark foragers and canopy foragers were more represented in native stands and their richness and diversity increased with the diversity of moths. On the other hand, species feeding in foliage were more species-rich in invaded stands. Because native oaks have a well-developed canopy and host many species of xylophagous insects (Vodka et al., 2009), bark foragers (such as *D. medius*, *D. martius* and *Certhia brachydactyla*) and canopy foragers (such as *O. oriolus* and *Coccothraustes coccothraustes*) find rich food resources in native stands, while *R. pseudacacia* lacks phytophagous insect species (Kuflan, 2012). The higher species richness and diversity of foliage gleaners in invaded stands might be surprising given the limited development of *R. pseudacacia* foliage and lack of phytophagous insects. However, this pattern is most likely driven by birds feeding in the shrub layer formed by native plants such as *S. nigra*, which is abundant in *R. pseudacacia* stands and rather scarce or even lacking in native forest stands. This also corresponds to the increasing diversity of birds foraging in the shrub layer, which are represented by species typical for *R. pseudacacia* stands like *S. atricapilla*, *P. collybita* and *A. caudatus*, with a higher shrub cover on study plots.

The observed response to the *R. pseudacacia* invasion was stronger in strong generalists than in moderate generalists, but the reverse was true for habitat specialists. We think that the weaker response of strong specialists is due to their overall rarity (Gaston et al., 1997) resulting in generally low sample sizes and thus less significant differences between stand types. This sampling effect does not apply to habitat generalists, which are generally common and well represented on study plots. In their case, the species' ecological characteristics most likely generate the observed pattern. For instance, moderate generalists may be less able to exploit new habitats than strong generalists, and therefore their species richness is less affected by the invasion of *R. pseudacacia*.

Total breeding bird species richness did not differ between the native forest and *R. pseudacacia* stands. This highlights the importance of considering species' traits such as habitat specialization instead of the analysis of sole total species richness, which can hide more complex patterns, as we observe in our results (see also Filippi-Codaccioni et al., 2010; Reif et al., 2013). However, the absence of a difference in total species richness between *R. pseudacacia* stands and native forest stands is also interesting per se, and corresponds to earlier studies focused on the effects of exotic plant species on bird diversity in shrublands invaded by *Tamarix* sp. in Nevada (Fleishman et al., 2003), woodlands invaded by *Eucalyptus* sp. in California (Sax, 2002) or savannah invaded by *Acacia* sp. thicket in South Africa (Rogers and Chown, 2014). In contrast, several other studies reported serious impoverishment of local bird communities due to plant invasions in rangelands invaded by exotic grasses in Texas (Flanders et al., 2006), meadows invaded by *Solidago* sp. in Poland (Skórka et al., 2010) or river banks invaded by *Reynoutria* sp. in the Czech Republic (Hajzlerová and Reif, 2014). In general, it seems that plant invasions into herbaceous vegetation such as grasslands have more pronounced impacts on bird species richness than invasions into forest stands. This may be caused by a higher sensitivity of less complex communities to plant invasions (Galiana et al., 2014): grassland communities are simpler relative to forest communities so the relative impact in grasslands is higher. Alternatively, woody plants, despite their exotic origin, create highly structured habitats, as was also the case for *R. pseudacacia* stands in our study, that can be occupied by various bird species resulting in species-rich communities (Schlaepfer et al., 2011; but see Holland-Clift et al., 2011).

Our results should be interpreted with caution because the data were collected over a single year and the study area covered only 600 km^2. It might be possible that repeating our survey in subsequent years and extending the study area would reveal different patterns. However, we consider this possibility quite improbable. Climatic conditions of the year of data collection were close to the long-term average: the mean temperature in May was only 0.4 °C warmer and the mean temperature in June was only −0.4 °C colder than mean temperatures between 1961 and 1990 (http://portal.chmi.cz/historicka-data/pocasi/uzemni-teploty#). Therefore, we think that adding more years would likely result in stronger conclusions, but not in reversed patterns. The observed effect of *R. pseudacacia* on specialist and generalist birds is in accord with ecological theory (Futuyma and Moreno, 1988) and the proposed mechanisms fit well the observed patterns. It would be very difficult to imagine a mechanism, for example, of how specialized bird species or exclusive invertebrate feeders would benefit from a limited food supply in invaded stands. Higher moth diversity in the native stands is also very intuitive and supported by ecological theory predicting a lack of insect species adapted to a novel host plant due to the short time since introduction (Liu and Stiling, 2006). Therefore, although a high level of detail in our study was compromised by limited spatial and temporal replication, we are convinced that our conclusions present real mechanisms of the impact of *R. pseudacacia* on birds.

5. Conservation implications

Our study revealed that habitat specialists and generalists respond differentially to a woody plant invasion and that different mechanisms were responsible for the observed patterns in species richness of these species groups. Specialists were limited by food supply in the invaded stands, probably due to the absence of some arthropod species they feed on. On the contrary, generalists were likely more flexible in their ecological demands and were able to exploit new breeding opportunities created by the development of the shrub layer in the invaded stands. Our results thus challenge the recent view that non-native plants do not have significant impacts on biodiversity (Thomas and Palmer, 2015; but see Hulme et al., 2015). Given the gradually increasing occupancies of invasive plants worldwide (Pyšek et al., 2012), we indeed suggest that they may be among the drivers of large-scale declines of habitat specialists recently observed across Europe (Le Viol et al., 2012) and of the increasing dominance of habitat generalists in local communities (Devictor et al., 2008; Reif et al., 2013). Further, if food limitation is among the mechanisms underlying the decline of specialists, then this can explain why such declines occur across habitats, regions and climatic zones (Davey et al., 2012; Jiguet et al., 2007; Shultz et al., 2005). Other studies reported the high importance of food resources to keep consumer populations stable (Hallmann et al., 2014; Hewson and Noble, 2009; Salido et al., 2012). Therefore, we suggest that for conservation of habitat specialists we should not only focus on preserving large areas of habitats, but we should also consider the quality of such habitats in terms of food supply.

Concerning the specific case of our focal invasive woody plant species, *R. pseudacacia*, we provide evidence that its impacts scale up along food chain. Future studies should focus on better understanding its effects on functional relationships between trophic levels. For instance, it would be interesting to discriminate direct and indirect impacts of *R. pseudacacia* by studying changes of species richness simultaneously for plants, insects and birds, representing primary producers, primary consumers and secondary consumers, respectively. We found adverse impacts of *R. pseudacacia* on habitat specialists, which are usually of a higher conservation concern and undergo more rapid population decline than generalists (Koleček et al., 2014; Owens and Bennett, 2000; Skórka et al., 2006). This finding advocates for the eradication of *R. pseudacacia* from forests of high conservation value such as those in national parks (Reiterová and Škorpík, 2012). On the other hand, we may expect that more species of indigenous insects will be able to adapt to this novel environment with more residence time since the introduction of *R. pseudacacia* (Litt et al., 2014). Therefore, the adverse effect of *R. pseudacacia* on specialized birds may be reduced in the future.

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Paper IV

Hanzelka, J., Reif, J., 2015. Relativní míra predace umělých hnízd v invazních akátových a přírodě blízkých dubových porostech. Sylvia 51, 63–73.

Relativní míra predace umělých hnízd v invazních akátových a přírodě blízkých dubových porostech

Relative predation rate of artificial nests in the invasive black locust and semi-natural oak stands

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Hanzelka J. & Reif J. 2015: Relativní míra predace umělých hnízd v invazních akátových a přírodě blízkých dubových porostech. *Sylvia* 51: 63–73.

Hnízdní predace představuje jeden z hlavních faktorů ovlivňujících hnízdní úspěšnost ptáků. Míra predačního tlaku byla široce zkoumána v různých biotopech, přičemž se předpokládá, že v porostech invazních rostlin je predační tlak vyšší než v porostech původních. V naší studii jsme však z důvodu vyšší strukturní členitosti vybraných invazních porostů předpokládali nižší míru hnízdní predace. Porovnali jsme relativní míru hnízdní predace mezi invazními akátovými a přírodě blízkými dubovými porosty za pomoci umělých hnízd s jedním křepelčím a stejně velkým plastelínovým vejcem. Zohlednili jsme nejen typ porostu, ale i umístění hnízda (na zemi a ve větvích) a jeho míru zamaskování. Oproti předpokladům jsme zjistili, že míra predace křepelčích vajec se mezi oběma typy porostu neliší, a to ani při zohlednění umístění hnízda. Výsledky studie tedy naznačují obdobný predační tlak v invazním a přírodě blízkém porostu. Je však nutné připomenout, že míra predace umělých hnízd není plně srovnatelná s mírou predace skutečných hnízd.

Nest predation represents one of the main factors affecting nest success in birds. Nest predation rate has been widely studied in various habitats. Generally, higher predation pressure is assumed in invasive plant stands than in semi-natural stands. However, in our study we presumed lower nest predation rate in invasive stands due to their more complex vegetation structure. We analysed the relative nest predation rate in invasive black locust and semi-natural oak stands using artificial nests containing one quail and one plasticine egg. We took forest type, nest position (on the ground and on branches) and nest concealment into consideration. Despite our assumptions, we did not find differences in the level of nest predation between the two stand types, nor between nest positions. Results of this study thus indicate similar predation pressure in invasive and semi-natural stands. However, we should point out that the artificial nest predation is not fully comparable to real nest predation.

Keywords: habitat structure, invasive species, nest position, nest predation, quail and plasticine eggs

ÚVOD

Hnízdní predace představuje jeden z důležitých faktorů ovlivňujících hnízdní úspěšnost ptačích druhů (Newton 1998, Smith et al. 2010, White et al. 2014). Kromě druhu predátora ovlivňuje míru predace hnízdní biotop (Martin 1993, Hollander et al. 2011) včetně způsobu umístění samotného hnízda ve vegetaci (Seibold et al. 2013). Narušení či kompletní změna biotopu by se tak mohla projevit v jiné míře predačního tlaku ve srovnání s nenarušeným porostem. Jednou z příčin změny ptačích hnízdních biotopů je v poslední době stále více aktuální šíření invazních rostlin, které mají zásadní vliv na původní organismy (např. McGeoch et al. 2010, Vilà et al. 2011, Pyšek et al. 2012). Právě mezidruhové vztahy jsou rostlinnými invazemi výrazně ovlivněny a vliv na míru predace ptačích hnízd patří k fenoménům, o nichž se v rámci dopadů rostlinných invazí na ptáky nejčastěji mluví (např. Schmidt & Whelan 1999, Borgmann & Rodewald 2004, Schmidt et al. 2005, Schlossberg & King 2010, Gleditsch & Carlo 2014). Řada studií ukázala zvýšení míry predace, což může souviset se zjednodušenou vegetační strukturou typickou pro monokulturní porosty invazních rostlin (Borgmann & Rodewald 2004, Ortega et al. 2006, Rodewald et al. 2010) umožňující predátorům snadnější prohledávání porostu a následné nalezení hnízda (Schmidt & Whelan 1999, Seibold et al. 2013). Nicméně míra predace v nepůvodním porostu se v porovnání s původními porosty lišit nemusí (Kennedy et al. 2009, Schlossberg & King 2010).

V tomto kontextu jsme se v naší studii zaměřili na porovnání relativní míry hnízdní predace mezi porosty invazního trnovníku akátu (*Robinia pseudacacia*) a přirozeně se vyskytujícího dubu letního/zimního (*Quercus robur*, *Q. petraea*). Nepůvodní trnovník akát se na našem území pěstuje již od osmnáctého století (Slavík 1995) a v současnosti zaujímá rozlohu přibližně 12 000 ha (Vítková 2014). Přestože není mezi dřevinami nijak významně zastoupen, bylo zjištěno, že se může lokálně podílet na zvyšování míry hnízdní predace a jeho porosty mohou představovat ekologickou past (Remeš 2003). Akát také dokáže výrazně ovlivnit složení vegetace v rámci porostu, jednak možným potlačováním vegetace alelopatickými látkami (Nasir et al. 2005) a jednak zvýšením množství dusíku v půdě pomocí nitrifikačních bakterií (Castro-Díez et al. 2014). Akátové porosty tak mohou mít silně vyvinutý bylinný a keřový podrost s převahou nitrofilních druhů rostlin (Vítková & Kolbek 2010). To by se naopak mohlo projevit ve snížení predačního tlaku v těchto porostech, zejména v případě vizuálně se orientujících predátorů.

Ptačí druhy hnízdící v dutinách a norách mají hnízda více ukrytá před predátory oproti druhům s volně umístěným hnízdem na zemi, v keřích apod. Lze proto předpokládat, že pokud by se změna míry predace v invazních porostech měla projevit, bude to právě u druhů s otevřenými hnízdy. Proto jsme se zaměřili na predaci hnízd druhů z této skupiny. Konkrétně jsme pomocí umělých hnízd simulovali hnízda menších lesních pěvců (pěnicovití, budníčkovití) hnízdících na zemi a nízko nad zemí. Cílem práce bylo zjistit, zda se relativní míra hnízdní predace liší (i) mezi nepůvodními akátovými a přírodě blízkými dubovými porosty a (ii) v závislosti na umístění hnízda na zemi nebo ve větvích nízko nad zemí. Pakliže mají akátové porosty bohatší vegetační strukturu než dubové, lze v nich předpokládat nižší míru predace umělých hnízd. U hnízd umístěných ve větvích jsme v souladu s poznatky o hnízdní predaci v lesním prostředí (viz např. Martin 1993) předpokládali vyšší míru predace než u hnízd umístěných na zemi.

METODIKA

Výzkumné plochy

Studie byla provedena na 32 výzkumných plochách o velikosti 100 × 100 m ležících ve vzájemné vzdálenosti minimálně 500 m. Plochy se nacházely v souvislých lesních porostech v nadmořské výšce 250–350 m n. m., převážně jižně od Prahy na pravém břehu Vltavy (49°56'N, 14°24'E – 50°00'N, 14°27'E) a levém břehu Berounky (49°57'N, 14°19'E – 50°02'N, 14°24'E), čtyři plochy se nacházely v oblasti Šáreckého údolí (50°06'N, 14°19'E – 50°07'N, 14°22'E). Většina ploch byla situována na strmé svahy, na které byl akát v minulosti vysazován. Dubové porosty byly ekvivalentně vybírány ve svažitém terénu. Akátové a dubové porosty jsou v rámci studovaného území obvykle součástí větších lesních celků, v rámci nichž se rozmanitě prolínají, takže výzkumné plochy nikde netvořily skupiny navzájem blízko se nacházejících pouze dubových či pouze akátových ploch. Stáří porostu se na obou typech ploch pohybovalo kolem 60–80 let, avšak dubové porosty byly v porovnání s akátovými vyšší (podíl stromů nad 10 m výšky: dub 94 % ± 3 SE, akát 55 % ± 7 SE, Welchův t-test: $df = 19$, $t = 4{,}97$, $p < 0{,}001$), koruny měly větší pokryvnost (dub 72 % ± 1 SE, akát 41 % ± 4 SE, Welchův t-test: $df = 18$, $t = 7{,}26$, $p < 0{,}001$) a keřové (pokryvnost dub 11 % ± 5 SE, akát 57 % ± 7 SE, Welchův t-test: $df = 27$, $t = -5{,}10$, $p < 0{,}001$) i bylinné patro (pokryvnost dub 5 % ± 2 SE, akát 53 % ± 7 SE, Welchův t-test: $df = 18$, $t = -6{,}39$, $p < 0{,}001$) bylo méně rozvinuté. Naproti tomu akátové porosty byly více prosvětlené s výrazně vyvinutým bylinným a keřovým patrem. Výrazně dominantním keřem v akátových porostech byl bez černý (*Sambucus nigra*), z bylin převažovala kopřiva dvoudomá (*Urtica dioica*) a netýkavka malokvětá (*Impatiens parviflora*).

Predační experiment

Na výzkumných plochách jsme v hnízdní sezóně 2014 provedli jednorázový predační experiment s umělými hnízdy. Použili jsme umělá hnízda s jedním křepelčím a jedním plastelínovým vejcem. Základ hnízda – košíček o šířce 10 cm a výšce 5 cm – jsme vyrobili z černé netkané mulčovací textilie. Do něj jsme pomocí voděodolného disperzního lepidla na dřevo vlepili seno, abychom simulovali výstelku hnízda. Takto připravené hnízdo napodobovalo hnízda ptáků velikosti červenky obecné (*Erithacus rubecula*) či pěnic (*Sylvia* sp.). Celkem jsme umístili 128 hnízd na 16 akátových a 16 dubových výzkumných ploch, tedy 64 hnízd do každého typu plochy. Na každé ploše byla umístěna čtyři hnízda, vždy dvě na zemi a dvě ve větvích (výška nad zemí cca 1,5 m), cca 50 m od sebe. Umístění v takové vzdálenosti mělo omezit motivaci predátora pro hledání dalších hnízd v rámci plochy po úspěšné predaci některého z nich. Hnízda na zemi byla umístěna k patě stromu (max. vzdálenost 0,5 m od stromu), hnízda na větvích byla umístěna na obvod keře (v akátových porostech) či konec větve stromu (většinou v dubových porostech obsahujících málo keřů) a připevněna drátem. Hnízda ve větvích v dubových porostech tak byla často umisťována na silnější větve než v akátových porostech. Do každého hnízda jsme vložili (bez jakéhokoli připevnění) jedno křepelčí vejce (délka cca 30 mm, šířka cca 25 mm) a jedno vejce z šedé modelovací hmoty Koh-i-noor Mass (velikost vejce podobná křepelčímu). Po umístění hnízda jsme zaznamenali míru jeho zamaskování na následující stupnici: 1 – hnízdo je dobře vidět, slabě maskováno; 2 – hnízdo není na první pohled viditelné, částečně zakryto vegetací; 3 – hnízdo velmi dobře maskováno, významně zakryto vegetací. Hnízda jsme umístili na plochy v polovině května 2014 a zkontrolovali jsme je po 13 dnech, což zhruba odpovídá době sezení na vejcích u našich menších lesních pěvců (Šťastný & Hudec 2011). Hnízda s poškozeným či chybějícím křepelčím vejcem jsme považovali za predovaná. Plastelínová vejce jsme využili pouze k odhadu typu predátora, protože predátor mohl reagovat jinak na plastelínová než na křepelčí vejce (např. Purger et al. 2012). Z hlediska struktury a typu lesa jsme předpokládali, že predátory by mohli být malí i větší hlodavci, malé šelmy, velcí savci a ptáci. Ve studii dále pracujeme pouze s následujícími předpokládanými skupinami predátorů: drobní hlodavci, šelmy a ptáci. Typ predátora jsme určovali podle otisků na vejcích. Drobné hlodavce jsme identifikovali z jemných otisků drápků a zubů, šelmy podle otisků zubů (výrazné vpichy) a ptáky podle otisků zobáku. Pokud vejce v hnízdě nalezeno nebylo, jednalo se o kategorii neznámý predátor. V akátových porostech bylo zkontrolováno 32 hnízd na zemi a 31 hnízd na větvích (jedno hnízdo nedohledáno), v dubových porostech bylo zkontrolováno 31 hnízd na zemi (jedno hnízdo nedohledáno) a 32 hnízd na větvích. V analýzách jsme vyhodnocovali celkem 126 křepelčích a 126 plastelínových vajec.

Statistické analýzy

Do statistické analýzy míry hnízdní predace vstupovala pouze křepelčí vejce, kdy pro každé hnízdo bylo zjištěno, zda bylo vejce predováno (hodnota 1), či nepredováno (hodnota 0). Pro zjištění míry hnízdní predace v závislosti na typu porostu a umístění hnízda jsme použili zobecněné lineární modely se smíšenými efekty (GLMM) s logit-link funkcí a binomickou strukturou vysvětlované proměnné (tj. predované vs. nepredované vejce), přičemž vysvětlující proměnnou s náhodným efektem byla výzkumná plocha. Vysvětlující proměnné s pevnými efekty byly sestaveny do dvou modelů následujícím způsobem. První model testoval, zda se liší míra predace mezi akátovými a dubovými porosty se zohledněním vlivu umístění hnízda a jeho maskování. Zahrnoval tedy hlavní efekty proměnných: typ porostu (kategoriální proměnná s hladinami „dub“ a „akát“), umístění hnízda (kategoriální proměnná s hladinami „na zemi“ a „ve větvích“) a míra maskování hnízda jako spojitá proměnná. Druhý model testoval, zda se liší míra predace mezi akátovými a dubovými porosty v závislosti na tom, jestli je hnízdo umístěno na zemi, nebo ve větvích se zohledněním vlivu maskování. Zahrnoval tedy kromě hlavních efektů všech proměnných z prvního modelu ještě interakci typ porostu × umístění hnízda.

Míru maskování hnízd jsme porovnali mezi akátovými a dubovými porosty a mezi typy hnízd pomocí Kruskal-Wallisova testu. Všechny statistické analýzy byly provedeny v programu R verze 3.2.1 (R Core Team 2015).

VÝSLEDKY

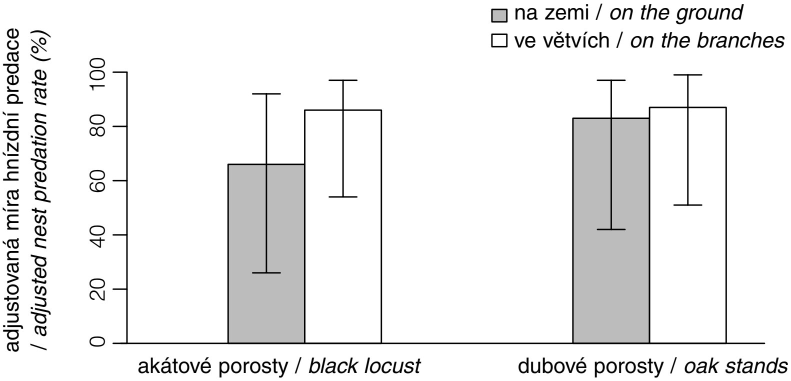
Míra predace křepelčích vajec v akátových porostech dosáhla 57 % a v dubových porostech 70 %. Rozdíl v míře predace mezi porosty ale nebyl statisticky průkazný (tab. 1). Míra predace křepelčích vajec ve větvích dosáhla 67 % a na zemi 60 %. Rozdíl v míře predace v závislosti na umístění hnízda však také nebyl statisticky průkazný (tab. 1).

V akátových porostech bylo predováno 65 % hnízd ve větvích a 50 % hnízd na zemi. V dubových porostech bylo predováno 69 % hnízd ve větvích a 71 % hnízd

Tab. 1. Odhady vlivů typu porostu (akát vs. dub), umístění hnízda (na zemi vs. větve) a maskování hnízda na míru predace umělých hnízd s křepelčími vejci spočítané pomocí zobecněného lineárního modelu se smíšenými efekty a logit-link funkcí. Intercept zahrnuje referenční hladinu „akát“ pro proměnnou typ porostu a referenční hladinu „na zemi“ pro proměnnou umístění hnízda. Řádek „typ porostu (dub)“ ukazuje, o kolik se liší predace v tomto typu porostu vůči interceptu, tj. hnízdům v akátu. Řádek „umístění hnízda (větve)“ ukazuje, o kolik se liší predace u tohoto typu umístění hnízda vůči interceptu, tj. hnízdům umístěným na zemi. Řádek „maskování hnízda“ ukazuje, jak se míra predace hnízd mění s jejich rostoucím zamaskováním. Vliv proměnné s náhodnými efekty zde není prezentován.

Table 1. *Estimates of the effects of stand type (black locust vs. oak), nest position (on the ground vs. branches) and nest concealment on the quail egg predation rate as revealed by the generalized linear mixed-effects model. Intercept includes the reference level "black locust" for the explanatory variable stand type and the reference level "on the ground" for the explanatory variable nest position. Line "stand type (oak)" shows difference in predation rate between nests in oak and the intercept, i.e. nests in black locust. Line "nest position (branches)" shows difference in predation rate between nests on branches and the intercept, i.e. nests placed on the ground. Line "nest concealment" shows the change in predation rate with increasing nest concealment. The variable with random effects is not presented.*

proměnná / *variable*	odhad / *estimate*	SE	z	p
intercept	0,89	0,83	1,07	0,285
typ porostu (dub) / *stand type (oak)*	0,73	0,77	0,95	0,345
umístění hnízda (větve) / *nest position (branches)*	0,59	0,49	1,21	0,226
maskování hnízda / *nest concealment*	−0,53	0,45	−1,19	0,233



Obr. 1. Adjustovaná míra predace (%) umělých hnízd s křepelčími vejci umístěných v akátových porostech na zemi (n = 32) a ve větvích (n = 31) a v dubových porostech na zemi (n = 31) a ve větvích (n = 32) spočítaná pomocí zobecněného lineárního modelu se smíšenými efekty a logit-link funkcí. Do modelu vstupovaly stejné proměnné jako v tab. 1 a navíc interakce typ porostu × umístění hnízda. Chybové úsečky zobrazují 95% intervaly spolehlivosti. Interakce typ porostu × umístění hnízda nebyla průkazná ($F_{1,122}$ = 0,72, p = 0,398).

Fig. 1. *Adjusted predation rate (%) of artificial nests with quail eggs placed in black locust stands on the ground (n = 32) and on the branches (n = 31) and in oak stands on the ground (n = 31) and on the branches (n = 32) as revealed by the generalized linear mixed-effects model. The same variables as in Table 1 together with the interaction stand type × nest position entered the model. Error bars denote 95% CI. The interaction stand type × nest position was non-significant ($F_{1,122}$ = 0.72, p = 0.398).*

Tab. 2. Počet predačních událostí plastelínových vajec (n = 126) umístěných v hnízdech na zemi a ve větvích v akátových a dubových porostech způsobených predátory v jednotlivých skupinách. Neznámý predátor znamená nepřítomnost vejce v hnízdě v době kontroly. Kategorie „nepredováno" ukazuje počet netknutých plastelínových vajec. Pět plastelínových vajec bylo predováno současně dvěma skupinami predátorů.
Table 2. *Number of predation events in plasticine eggs (n = 126) placed in ground nests and branch nests in black locust and oak stands caused by predators in particular categories. Unknown predator denotes the absence of a plasticine egg during the nest check. Category "non-predated" denotes the number of intact plasticine eggs. Five plasticine eggs were simultaneously predated by two groups of predators.*

predátor / *predator*	akát / *black locust*		dub / *oak*	
	zem / *ground*	větve / *branches*	zem / *ground*	větve / *branches*
drobní hlodavci / *small rodents*	14	6	15	2
šelmy / *carnivores*	1	1	2	0
ptáci / *birds*	3	4	3	6
neznámý / *unknown*	12	16	13	16
nepredováno / *non-predated*	0	3	1	9

na zemi. Umístění hnízda však nemělo vliv na míru predace v rámci porostu ani při porovnání mezi porosty (obr. 1).

Maskování hnízda nemělo vliv na míru predace křepelčích vajec, ačkoliv v modelu je naznačen trend směrem k nižší míře predace u více zamaskovaných hnízd (tab. 1). Hnízda na zemi byla méně maskována než hnízda ve větvích (Kruskal-Wallisův test: df = 1, χ^2 = 13,55, p < 0,001). Zároveň hnízda v akátových porostech byla více maskována než hnízda v dubových porostech (Kruskal-Wallisův test: df = 1, χ^2 = 6,47, p = 0,011). Z otisků na plastelínových vejcích jsme určili tři skupiny pravděpodobných hnízdních predátorů (v závorce je uveden podíl z celkového počtu predačních událostí): drobní hlodavci (36 %), šelmy (4 %) a ptáci (14 %). Otisky byly vždy rozpoznány a přiřazeny k příslušné skupině predátorů. Pět vajec bylo predováno současně dvěma skupinami predátorů. Počty predačních událostí plastelínových vajec v jednotlivých skupinách predátorů v akátových porostech byly velmi podobné počtům v dubových porostech a to i při porovnání počtu predačních událostí hnízd na zemi a ve větvích (tab. 2). Výjimkou jsou otisky drobných hlodavců, jichž jsme zaznamenali mírně vyšší počet v akátových porostech. Polovina plastelínových vajec (50 %) chyběla úplně. U nich nebylo možné určit predátora. Z celkového počtu 126 plastelínových vajec zůstalo netknutých pouze 13 vajec.

DISKUSE

V této studii jsme porovnávali míru hnízdní predace mezi akátovými a dubovými porosty se zohledněním umístění hnízda na zemi a ve větvích a míry jeho zamaskování. Oproti očekávání jsme nezjistili nižší míru hnízdní predace v akátových porostech, ačkoliv se tyto porosty vyznačovaly bohatším bylinným i keřovým patrem a umělá hnízda zde byla lépe maskována. Ani hnízda ve větvích nebyla častěji predována než hnízda na zemi jak v rámci porostu, tak mezi porosty.

Absence rozdílu v míře predace hnízd mezi akátovými a dubovými porosty i přes jejich značně rozdílnou vegetační strukturu na našich výzkumných plochách může souviset s obecně malým vlivem struktury vegetace na hnízdní predaci (Hanski et al. 1996, Díaz & Carrascal 2006). Je možné, že více rozvinuté keřové patro v akátových porostech sice více maskovalo hnízda, ale menší míra predace v porovnání s dubovými porosty nemusela být zaznamenána z důvodu projevu ekologické pasti, jak ji v akátových porostech popsal Remeš (2003). Ten ve své studii zaznamenal vyšší populační hustotu, avšak nižší hnízdní úspěšnost pěnic černohlavých (*Sylvia atricapilla*) v akátových porostech z důvodu časnějšího olistění keřů v podrostu akátin v porovnání s blízkými lužními lesy. Tyto keře tak lákaly ptáky v rané fázi hnízdní sezóny do méně vhodného prostředí s vyšší mírou hnízdní predace. Podobně mohla být i na našich výzkumných plochách hnízdní predace v akátových porostech zvýšena na úroveň predace v dubových porostech.

Další vliv na míru hnízdní predace by mohla mít míra maskování hnízda, která byla v našem případě nižší u hnízd umístěných na zemi než u hnízd ve větvích. Jelikož hůře maskovaná hnízda mívají vyšší míru predace (Sloan et al. 1998, Zieliński 2011), dalo by se předpokládat, že vyšší míra predace bude právě u hnízd umístěných na zemi. Lépe viditelná hnízda by pravděpodobně častěji predovali ptáci, kteří se řídí při hledání potravy vizuálně, na rozdíl od menších savců využívajících především čich. Avšak toto se nepotvrdilo. Hnízda na zemi nebyla predována více než hnízda ve větvích. Kromě toho ptáci predovali hnízda velmi málo a navíc častěji ve větvích než na zemi, na rozdíl od drobných hlodavců, kteří predovali častěji hnízda na zemi než hnízda ve větvích. Nicméně drobní hlodavci se na predaci reálných hnízd téměř nepodílejí (např. Weidinger 2009, Mallord et al. 2012). Velké množství jejich otisků na plastelínových vejcích lze vysvětlit tak, že plastelínová vejce mohou drobné hlodavce přitahovat svým pachem (Rangen et al. 2000, Maier & DeGraaf 2001). To by pravděpodobně vyústilo ve vyšší míru predace hnízd umístěných na zemi, což je v souladu s našimi výsledky. Mnoho neznámých predátorů plastelínových vajec v hnízdech na zemi i ve větvích by však mohlo poměry v predaci úplně změnit, zvláště pokud by mezi těmito neznámými predátory byli ve velké většině skuteční hnízdní predátoři, tj. ptáci a/nebo šelmy. Případné využití fotopastí k identifikaci predátorů by přesněji ukázalo jejich skutečný poměr.

Prezentované výsledky je třeba brát s ohledem na design studie využívající umělá hnízda. Umělá hnízda často neposkytují údaje o predaci srovnatelné s predací pravých hnízd (Weidinger 2001, Zanette 2002, Moore & Robinson 2004). Míra predace je většinou vyšší u umělých hnízd (Wilson & Brittingham 1998, King et al. 1999, Burke et al. 2004). Umělá hnízda mohou být dobře využita pro zjišťování relativní míry predace mezi biotopy (Roos 2002), avšak pouze pokud jsou pravá i umělá hnízda predována stejnými predátory (Pärt & Wretenberg 2002). V našem případě však byla umělá hnízda velmi často predována drobnými hlodavci, kteří ovšem nepředstavují predátora pravých hnízd (viz výše).

Kvůli povaze experimentu představující jednoletý výzkum hnízdní predace jsme také zanedbali vliv možné fluktuace populace predátorů. Pokud by došlo ke zvýšení/snížení početnosti predátorů, pravděpodobně by se tak stalo v podobné míře na všech plochách, které se nacházejí poměrně blízko sobě navzájem. Avšak v případě nárůstu početnosti predátorů pouze v prostředí s vyšší/nižší pokryvností vegetace by mohl být rozdíl v hnízdní predaci mezi akátovými a dubovými porosty průkazný z důvodu významného rozdílu ve struktuře vegetace srovnávaných porostů. Jasnou odpověď by mohlo přinést pouze opakování experimentu několik let po sobě a podrobný výzkum populací potenciálních predátorů.

Výzkum míry hnízdní predace doplnil naše předchozí poznatky zaměřené na výzkum druhové bohatosti a habitatové specializace ptáků, kterou jsme provedli na stejných výzkumných plochách (Hanzelka & Reif 2015). Podle výsledků této studie o hnízdní predaci lze předpokládat, že míra predačního tlaku nemusí poukazovat na riziko hnízdění ptáků v porostech invazních dřevin v porovnání s přirozenými porosty. Jsme si však vědomi nejisté vypovídací hodnoty pokusů s umělými hnízdy v porovnání s výzkumem skutečných hnízd. Zjištění míry predačního tlaku na reálných hnízdech v akátových porostech by vneslo více světla do poznání vztahu ptáků k invazním rostlinám na našem území.

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SUMMARY

Nest predation ranks among the most important factors affecting bird breeding success. Alteration of the breeding habitat could be reflected in the nest predation rate. Recently, habitats are increasingly altered by plant invasions. Modified vegetation structure of invasive plant stands may facilitate detection of the nests by predators and thus increase predation pressure. Here we investigate the relative nest predation rate in stands of the invasive black locust (Robinia pseudacacia) *and in semi-natural oak* (Quercus robur, Q. petraea) *woods using artificial nests.*

Altogether thirty two 100 × 100 m study plots were established in continuous forest stands in the vicinity of the city of Prague, mainly southward from the city on the right bank of the Vltava river (49°56'N, 14°24'E – 50°00'N, 14°27'E) and on the left bank of the Berounka river (49°57'N, 14°19'E – 50°02'N, 14°24'E), at the altitude between 250 and 350 m a.s.l. Four of the study plots were located in the Divoká Šárka valley (50°06'N, 14°19'E – 50°07'N, 14°22'E). The minimum distance between two adjacent plots was 500 m. Black locust stands had a lower tree canopy cover (black locust: 41% ± 4 SE, oak 72% ± 1 SE, Welch's t-test: $df = 18$, $t = -7.26$, $p < 0.001$) but strongly developed shrub (black locust: 57% ± 7 SE, oak 11% ± 5 SE, Welch's t-test: $df = 27$, $t = 5.10$, $p < 0.001$) and herb layers (black locust: 53% ± 7 SE, oak 5% ± 2 SE, Welch's t-test: $df = 18$, $t = 6.39$, $p < 0.001$) compared to oak stands. To examine the difference in the rate of nest predation between invasive and semi-natural tree stands, we used artificial nests containing one quail and one similar-sized plasticine egg. We placed 64 nests in oak stands and 64 nests in black locust stands (four nests per plot) in mid May 2014. In each stand type, a half of the nests were placed on the ground and the other half on branches ca 1.5 m above ground. We also estimated the level of nest concealment (scale 1–3). The nests were checked after 13 days. Nest predators were identified upon imprints on plasticine eggs and sorted into three groups of small rodents, carnivores and birds. An absent egg was interpreted as being removed by an unknown predator.

Data on nest predation were analysed using generalized linear mixed-effects models (GLMM) with logit link function and binomial structure of response variable (i.e. quail egg predation rate). We used plot identity as a random factor. We employed the model containing main effects of explanatory variables (stand type, nest position and nest concealment) to identify the effect of stand type on nest predation factoring out the effect of nest position, and to identify the effect of nest concealment on nest predation. To find out the effect of nest position taking the stand type into account, we included the stand type × nest position interaction in the second model. Further, the nest concealment was compared between stand types and between nest positions using the Kruskal-Wallis rank sum test.

The difference in nest predation rate of quail eggs was not significant, neither between stand types ($p = 0.345$; Table 1) nor between nest positions ($p = 0.226$; Table 1). Moreover, nest position did not affect the nest predation rate both within and between stands (Fig. 1). Higher nest concealment was not associated with a lower quail egg predation rate (Table 1). However, ground nests were less concealed than branch nests (Kruskal-Wallis rank sum test: $df = 1$, $\chi^2 = 13.55$, $p < 0.001$) and nests in black locust stands were more concealed than those in oak stands (Kruskal-Wallis rank sum test: $df = 1$, $\chi^2 = 6.47$, $p = 0.001$). Imprints on plasticine eggs showed that the number of predation events in black locust stands was similar to that in oak stands (Table 2). Small rodents left the most of all imprints (Table 2), slightly prevailing in black locust stands. However, recent studies have shown that small rodents only marginally participate in the predation of real nests and thus are unimportant as nest predators in our study.

Contrary to our predictions we did not find a lower nest predation rate in invasive stands compared to semi-natural tree stands. More developed herb and shrub layer in invasive stands thus apparently did not result in the decrease of the predation rate there. This pattern might be related to the ecological trap phenomenon, already described in the invasive black locust stands by a previous study using real nests. We should note that our experiment was conducted using artificial nests during a single breeding season without extensive sampling of abundance of potential predators. It would be relevant for future studies to confirm our results using real nests, to extend the sampling over time and to focus more closely on populations of potential predators.

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