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Management implications of bird responses to variation in non-native/native tree ratios within central European forest stands

Magdalena Kroftová, Jiří Reif *

Institute for Environmental Studies, Faculty of Science, Charles University, Prague, Benátská 2, 128 01 Praha 2, Czech Republic

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ABSTRACT

Plant invasions are a serious threat for global biodiversity and various studies have reported their impacts on forest bird populations. However, a majority of these studies involved comparisons of sites covered solely by invaded or native forest habitats, whereas the real world is dominated by habitat gradients. To address this issue, we counted birds in central European forest stands differing in the coverage of an invasive woody plant, *Robinia pseudoacacia* L., a major global tree invader. This species significantly affects the vegetation composition in invaded habitats, resulting in shifts in bird community compositions toward a dominance of generalist species at the expense of specialists. Here we ask: (i) how the bird species richness changes with the increasing relative coverage of *R. pseudoacacia*, recognizing several bird groups represented by all species, habitat specialists, habitat generalists and forest specialists, (ii) to what extent the alteration of vegetation composition accounts for these changes. By employing conditional autoregressive models, and by taking forest stand area and distance to the forest edge into account, we found that the numbers of all bird species, habitat specialists and forest specialists were highest in stands with intermediate coverage of *R. pseudoacacia*. This result indicates that the non-native tree was not detrimental for bird biodiversity, and that birds indeed benefited from its presence in focal forest stands, but only if native and non-native trees were present in approximately equal proportions, which was particularly true for forest specialists. The effect of *R. pseudoacacia* on bird species richness was significant even after taking changes in vegetation composition into account, suggesting that this invasive species affects birds not only by altering structural components of the habitat, but also by some other factors that might include food supply for birds or nest-holes. Our sampling was quite limited, particularly with respect to the range of structures and management types typically encountered in native trees, and results must be treated accordingly. However, our results appear to suggest that eradication of *R. pseudoacacia* from forest within our study area may not be necessary for achieving bird conservation aims, because this species does not markedly depress bird species richness, including specialists. However, the generality of our findings require further testing across other forests affected by *R. pseuadoacacia* invasion, to examine whether retention of this non-native tree is more widely justified.

1. Introduction

Plant invasions rank among the top threats for biodiversity worldwide (Butchart et al., 2010) and numerous studies have reported their impacts on native communities of various organisms including vascular plants, lichens, various invertebrate taxa and vertebrates such as birds and mammals (see Vilà et al., 2011; Pyšek et al., 2012a; Schirmel et al., 2016 for reviews). These studies have generally been based on comparisons between native and invaded habitats, and in majority of these studies the habitats were selected as "entirely invaded" or "entirely native", i.e. neglecting any transitional stages. Such an approach is reasonable in terms of achieving the greatest contrast between the focal habitats and maximizing the chance of detecting significant differences between local communities occupying these habitats. However, such "pure" habitats represent only the extremes of a gradient, and in the real world many transitional stages exist and indeed account for a substantial proportion of areas affected by invasions (Pyšek et al., 2012b).

To fill this knowledge gap, we counted birds in stands differing in proportional coverage of *Robinia pseudoacacia* L., a major tree invader in European forests (Buchholz et al., 2015; Vítková et al., 2015). This tree is the most widespread invasive woody plant in central Europe (Pyšek et al., 2012b), with significant socioeconomic and environmental impacts on various organisms including birds

* Corresponding author.
E-mail address: jirireif@natur.cuni.cz (J. Reif).

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(Dzwonko and Loster, 1997; Hanzelka and Reif, 2015; Plexida et al., 2012). Compared to other alien tree species introduced to central European forests, it has been the cause of the greatest conservation concern due to its spread in protected areas (Vítková et al., 2017). Previous studies found that this invasive tree has considerable impacts on central European forest birds: bird communities occupying invaded stands were significantly different from bird communities in control native stands, while total bird species richness did not differ between these stands (Hanzelka and Reif, 2015, 2016). For example, stands of *R. pseudoacacia* were dominated by shrub species, while native stands by canopy species (Reif et al., 2016a). However, these results were obtained from data collected in stands fully covered by either *R. pseudoacacia* or native tree species, and it remains unclear to what extent the number of bird species changes along a gradient of increasing proportion of *R. pseudoacacia* coverage.

In respect to species' ecological traits related to the impact of an invasive plant, habitat specialization has been established as a key trait responsible for the sensitivity of species to be affected by the invasion (Olden et al., 2004; Devictor et al., 2008; Vilà et al., 2011; Reif et al., 2016a). This observation was also supported by data about bird communities in *R. pseudoacacia*: whereas specialists were negatively affected by the invasive tree, habitat generalists indeed benefited from its widespread occurrence (Hanzelka and Reif, 2015; 2016). Considering a variable proportion of *R. pseudoacacia* within forest stands, we can hypothesize that habitat specialists and generalists will show divergent responses: habitat specialists will be most species-rich in the pure native habitat and their number will gradually decline with the increasing proportion of *R. pseudoacacia*. This pattern should be particularly strong for forest-interior species. In contrast, habitat generalists should be less sensitive to the variability in the invasive tree coverage because these species do not discriminate among habitat types as precisely as habitat specialists (Julliard et al., 2006; Clavel et al., 2011). Therefore, we expect that their species richness will show weaker relationship to the increasing proportion of *R. pseudoacacia* than the species richness of specialists. When considering all bird species containing both specialists and generalists together, we can predict that the relationship of their species richness to the increasing proportion of *R. pseudoacacia* will be weaker than that for specialists, but stronger than that for generalists.

Invasive plants affect native species by various means including competition, predation or alteration of trophic cascades (Litt et al., 2014; Vilà et al., 2015). In the case of birds and invasive trees, a change of habitat is among the most important mechanisms of impact (Hanzelka and Reif, 2016), together with changes of food supply for birds (Reif et al., 2016a) and nest predation (Remeš, 2003). However, compositional changes in vegetation (i.e. changes in relative coverage of particular vegetation layers) are an important general driver of gradients in bird community composition even within native habitats (James and Wamer, 1982; Laiolo, 2002; Díaz, 2006; Reif et al., 2008; Nájera and Simonetti, 2010; Birčák and Reif, 2015). It is thus interesting to discriminate to what extent the invasive tree affects bird communities by the alteration of vegetation characteristics and what is the role of the tree invader *per se* when the vegetation composition effect is factored out (and thus suggesting the effects of other mechanisms). Since habitat specialists are, by definition, sensitive to changes in habitats (Julliard et al., 2006; Devictor et al., 2010), we expect that their species richness will mainly be affected by vegetation composition and the no effect of *R. pseudoacacia* will be observed after taking the vegetation composition into account. In contrast, habitat generalists should be less susceptible to changes in habitat and we thus expect a significant effect of *R. pseudoacacia* even after controlling for the influence of vegetation composition.

In this study, we aim to investigate how bird species richness changes along a gradient of an increasing proportion of *R. pseudoacacia*, taking vegetation composition and other local habitat characteristics into account and focusing on particular groups of species defined by habitat specialization to test the predictions formulated above.

2. Material and methods

2.1. Study area

The study was conducted in a 600 km^2 area in central Bohemia, the Czech Republic, Europe, located in the south-western and northern vicinities of the city of Prague. The area is situated at a low-intermediate altitude (range 200–400 m asl) and covered mostly by agricultural land disrupted by extensive forest blocks and human settlements (Hanzelka and Reif, 2015). Forests are mostly commercially planted for timber harvest, but some areas are protected and left to spontaneous development or managed for conservation purposes (Hanzelka and Reif, 2015), including the gradual replacement of non-native tree species by native ones (Anon., 2009, 2012; Karlík, 2011; Kohlík, 2008). In forests, the dominant tree species are oak (*Quercus robur* L. and *Q. petraea* Matt.), hornbeam (*Carpinus betulus* L.) and *R. pseudoacacia* with minor proportions of lime (*Tilia cordata* Mill., *T. platyphyllos* Scop.) and ash (*Fraxinus excelsior* L.). The potential natural vegetation is represented by a broad-leaved forest with a dominance of oak and hornbeam (Chytry, 2012).

Black locust was deliberately introduced into the study area in 19th century and was planted on sites difficult to afforest such as steep slopes and rocky outcrops (Slavík, 1995). It has spontaneously spread into the surrounding broad-leaved forests and now forms large tracks with a variable proportion of native *Quercus* sp. div. and *R. pseudacacia* trees (Vítková and Kolbek, 2010; Hanzelka and Reif, 2016).

For the purposes of our study, we selected broad-leaved forest stands within the study area where the proportion of *R. pseudoacacia* trees ranged from 0 to 100% (Supplementary Table 1). In these forest stands, we established study plots 100 × 100 m in size to be used for data collection. Such square plots have already been used in our previous studies on invaded forest stands within the study area, and were found suitable for the characterization of local bird communities (Hanzelka and Reif, 2015, 2016; Reif et al., 2016a). We had 18 study plots in total: four plots were in almost pure *R. pseudoacacia* stands, three plots were in almost pure *Quercus* sp. div. stands and 11 plots were in stands where both species trees had significant coverage (Supplementary Table 1). Six of our 18 study plots were located in protected areas where eradication of *R. pseudoacicia* ranks among the top priorities of forest management (Anon., 2009, 2012; Karlík, 2011; Kohlík, 2008), though no signs of such management were visible on these study plots. Following Hanzelka and Reif (2015), the plot borders were marked in the field with visible tape to give the field workers adequate orientation.

In addition, we located our study plots within large continuous forest stands and aimed to establish them at least 100-m from forest edges to avoid the area effects and edge effects that could potentially confound the bird community composition. However, it was not always possible to meet these rules and thus the surrounding forest stand area and distance to the forest edge varied among study plots. Therefore, we measured forest stand area (in hectares) and distance to the forest edge (in metres) for each study plot in UTHSCSA ImageTool version 3.0 (Dove, 2002) and controlled for their potential effects on birds in the statistical analyses (see below). Another issue is the potential effects of the isolation of habitat patches within study plots. For example, a small patch of