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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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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.

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## 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).

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