

# Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits

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## Abstract

**Aim:** To investigate the community-level impacts of woody plant invasions using *Robinia pseudoacacia* as a model species, affecting organisms on different trophic levels: vascular plants, nocturnal Lepidoptera and birds.

**Location:** Czech Republic, central Europe.

**Methods:** Nineteen plots with strong dominance of the invader were compared to 20 plots with native deciduous trees on sites with similar conditions. Species richness was compared using marginal models, species composition and the distribution of species traits by ordination analyses. Functional relationships between the three groups of organisms were investigated using a path analysis.

**Results:** Only minor differences in species richness between invaded and uninvaded plots were detected for plants and birds, but the invaded stands hosted significantly fewer species of nocturnal Lepidoptera. On the contrary, all three groups differed in species composition and in the distribution of traits between the invaded and uninvaded stands. Nitrophilous plants, supported by human disturbances, were more represented in the invaded stands, while habitat specialist birds preferred uninvaded forest. Within nocturnal Lepidoptera, species of open habitats and fast life cycle preferred the invaded stands, and forest and canopy species and habitat generalists of larger sizes preferred the uninvaded stands. Path analysis showed a minor effect of *R. pseudoacacia* on the numbers of plants which were unrelated to species richness at higher trophic levels. However, *R. pseudoacacia* had a negative direct effect on nocturnal Lepidoptera, contributing to a weak negative indirect impact on birds.

**Main conclusions:** The impacts of *R. pseudoacacia* on species richness differed across the trophic levels, questioning the existence of simple cascading effects as a consequence of its invasion. Invasive plants do not always reduce the diversity of species per se, but cause shifts in species composition by replacing some of the pre-invasion biota by species with traits enabling tolerance to the invaded habitat.

## KEYWORDS

biodiversity, ecosystem-level approach, impact, invasive trees, native species, *Robinia pseudoacacia*

## 1 | INTRODUCTION

Impacts of invasive plants are considered as an important part of the global, human-induced environmental change, affecting the biodiversity worldwide (Gaertner et al., 2014; van Kleunen et al., 2015; Mack et al., 2000; Pyšek, Jarošík, et al., 2012). The impacts of invasive alien plants have been documented on both community and regional scale (e.g. Hejda, Pyšek, & Jarošík, 2009; Jäger, Tye, & Kowarik, 2007; McKinney & Lockwood, 1999; Pyšek, Jarošík, et al., 2012; Winter et al., 2009) and range from the depauperation of invaded communities, homogenization of regional floras (Hejda et al., 2009; Winter et al., 2009) to multiple effects on ecosystem functioning (Ehrenfeld, 2010; Levine et al., 2003; Rumlerová, Vilà, Pergl, Nentwig, & Pyšek, 2016; Vilà et al., 2011).

Several mechanisms of impacting the diversity of invaded communities have been suggested. A substantial reduction of the plant species richness and/or diversity at the community scale typically occurs if the invader is a lot stronger competitor than native dominants of that particular community (Hejda et al., 2009). Alternatively, the invasive aliens transform the site conditions in a way that eliminates some native species, but favours others; the latter are often species with a broad ecological tolerance, typically preferring eutrophic sites. This allows them to coexist with the invader or to be even promoted by its presence (Reif, Hanzelka, Kadlec, Štrobl, & Hejda, 2016). In general, the way how native species respond to the presence of a dominant invader depends on the species' ecological traits, as species that are easily eliminated differ systematically from those that are able to coexist with the invader (Hejda, 2013).

The impacts of invasive woody species, especially trees, are often massive. They form extensive areas of profoundly altered environment, often with conditions unsuitable for some native species (Jäger et al., 2007; Pyšek, Jarošík, et al., 2012; Richardson & Rejmánek, 2011). At the same time, data documenting the impacts of invasive trees on biological communities are surprisingly scarce and often confined to only one specific group of organisms (but see Proença, Pereira, Guilherme, & Vicente, 2010; López-Núñez, Heleno, Ribeiro, Marchante, & Marchante, 2017), which prevents from generalization about their impacts across different taxa and trophic levels of the ecosystems. Nevertheless, a recent meta-analysis of Schirmel, Bundschuh, Entling, Kowarik, and Buchholz (2016) demonstrates that the impacts of invasive trees on various groups of target organisms differ. For example, herbivorous insects are most affected, as many species specialize on particular native plants, which may be absent from the invaded community (van Hengstum, Hooftman, Oostermeijer, & van Tienderen, 2014; Litt, Cord, Fulbright, & Schuster, 2014; Schirmel et al., 2016). The invasive tree itself is often unpalatable to native herbivores that may not be adapted to cope with its phytochemicals (Bezemer, Harvey, & Cronin, 2014; Burghardt, Tallamy, Philips, & Shropshire, 2010). Further, the diversity of secondary consumers, such as birds, does not have to change following the decrease in herbivorous insect diversity, because they are often generalists, not depending on a particular insect species that may disappear from a community

following the invasion (Reif et al., 2016). Therefore, the cross-taxa approach is needed to provide a complex, ecosystem-level view of the real impacts of invasive plants, including trees.

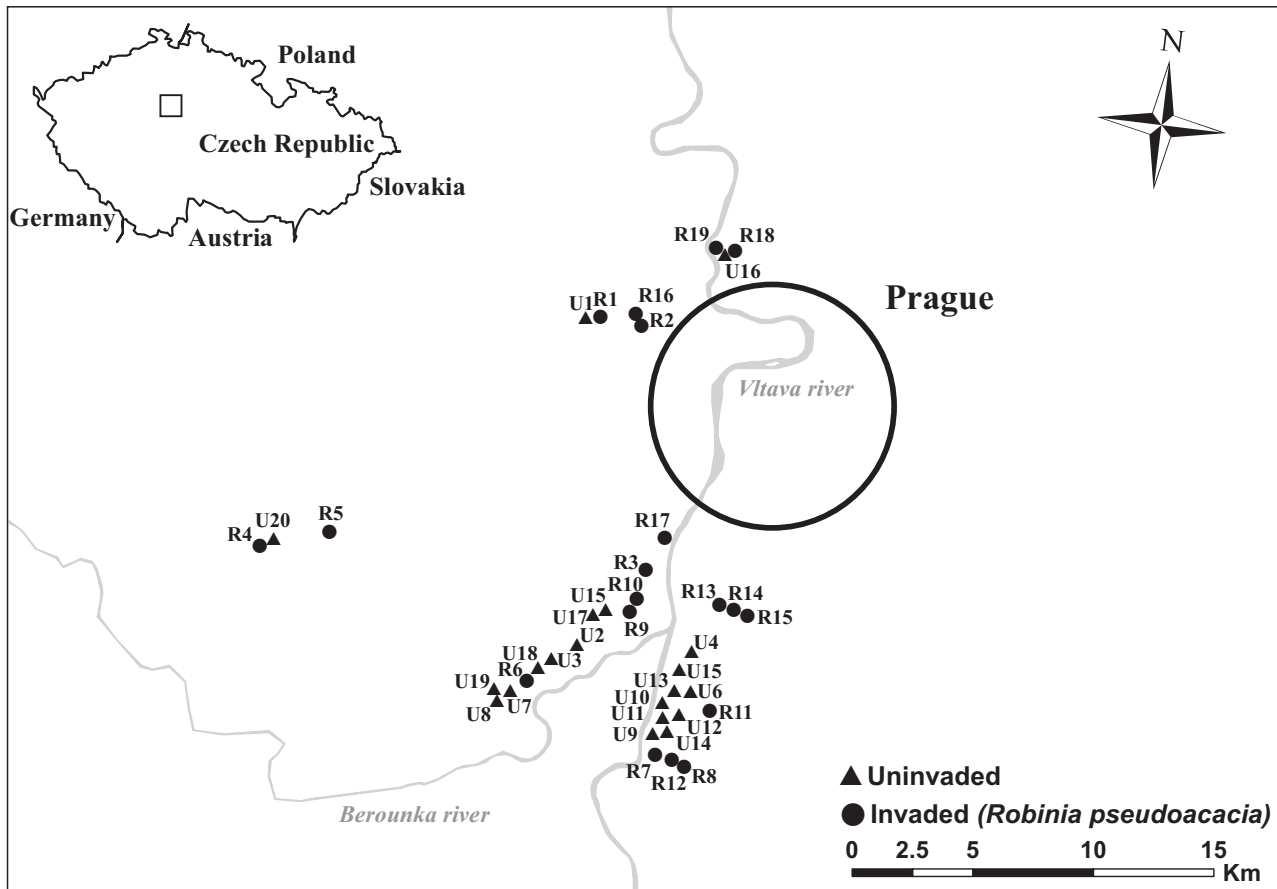
To bridge this knowledge gap, we focused on the impacts of a major tree invader, *Robinia pseudoacacia*, on three taxonomic groups at different trophic levels, functionally related by a food chain: vascular plants (further termed "plants") as producers, nocturnal Lepidoptera (further termed "moths") as primary consumers, and birds as secondary consumers. The vascular plants as primary consumers can be expected to be directly impacted by the invasive tree, as *Robinia pseudoacacia* creates novel habitats, with conditions different from those in the uninvaded community. One of the main mechanisms is the invader's ability to accumulate aerial nitrogen by the means of symbiotic bacteria, which results in nutrient-rich conditions, supporting nitrophilous and ruderal flora.

In deciduous forests, moths represent an important part of insect diversity (Merckx et al., 2012; Southwood, 1961; Summerville, Metzler, & Crist, 2001), which reflects the diversity of other insect groups as well (Hirao, Murakami, Kashizaki, & Tanabe, 2007). Moreover, Lepidoptera are generally used as an umbrella group of insects (New, 1997), mirroring the differences in biodiversity as well as in the forest condition and structure (Summerville, Ritter, & Crist, 2004). Further, larvae of moths make up an essential part of the food supply for the majority of birds, especially during the nesting period (Cholewa & Wesółowski, 2011; Cramp, 1977–1994; Krištín & Patočka, 1997). Therefore, the potential impact of *Robinia pseudoacacia* on the bird species diversity could manifest mainly through the lower diversity of moths.

We used *R. pseudoacacia* as a model example of an invasive tree because it forms extensive stands, especially in the warmer areas of central Europe, and is likely to expand further north and into higher altitudes with the changing climate (Kleinbauer, Dullinger, Peterseil, & Essl, 2010; Li, Xu, Guo, & Du, 2014). The invasion of *R. pseudoacacia* supports the spread of ruderal and nitrophilous plants (Dzwonko & Loster, 1997) and has important impacts on invertebrates (Buchholz, Tietze, Kowarik, & Schirmel, 2015) and birds (Hanzelka & Reif, 2015). Essl, Milasowszki, & Dirnböck (2011) suggest that it also facilitates the site for other alien plants, a phenomenon described as invasional meltdown (Simberloff & Von Holle, 1999).

This paper aims at answering the following research questions: (1) Does the invasive tree *R. pseudoacacia* reduce the species richness, change the community composition and affect the distribution of basic ecological traits, among the vascular plants, moths and birds? (2) Are these impacts consistent across the three different trophic levels, that is primary producers, primary consumers and secondary consumers as represented by plants, moths and birds, respectively?

Specifically, we expected a lower plant species richness in the invaded stands, as many plant species of the uninvaded stands are unlikely to be adapted to the novel habitat, created by the invasive tree. Subsequently, moth species richness may decrease due to the limited availability of host plants. Finally, birds would be negatively affected by the limited diversity of moths, which represent important source of their food.



**FIGURE 1** Map showing the location of study plots (19 invaded and 20 uninverted)

## 2 | METHODS

### 2.1 | Study species

*Robinia pseudoacacia* L. (Fabaceae) is a tree native to the eastern and south-eastern part of the USA (Burns & Honkala, 1990). In the native range, it mostly occurs on recently disturbed sites and is replaced by other trees in succession. At present, *R. pseudoacacia* occurs as naturalized in Europe, eastern Asia, northern and southern Africa, southern Australia, Tasmania and New Zealand (Akamatsu, Makishima, Taya, Nakanishi, & Miwa, 2014; Vítková & Kolbek, 2010). The first mention of planting in the current Czech Republic is from 1710, and of the first spontaneous occurrence outside cultivation from 1874 (Pyšek, Danihelka, et al., 2012). In the Czech Republic, it was massively planted in warm areas, especially on steep slopes with dry rocky soil, with the aim to stabilize it and to produce timber and honey in these otherwise unfavourable conditions (Vítková, Müllerová, Sádlo, Pergl, & Pyšek, 2017). *Robinia pseudoacacia* spreads by rhizomes and forms stands where it is a strong dominant, resulting in plant communities described as Chelidonio-Robinion and Balloto nigrae-Robinion, using the phytosociological terminology (Chytrý, 2014; Slavík, 1995). Being a nitrogen fixer, it is not limited by nutrient-poor soils, where it can also spread (Vítková & Kolbek, 2010). On the contrary, its reproduction output is rather limited in closed forests and some mature

stands are actually senescent plantations rather than stands of a spontaneous origin (Peloquin & Hiebert, 1999).

### 2.2 | Study area

The study area of  $\sim 20 \times 30$  km is located close to Prague, the capital of the Czech Republic, central Europe (coordinates of central point:  $50^{\circ}01'N$ ;  $14^{\circ}21'E$  – Figure 1), in a region with slightly dry, warm climate (mean annual precipitation of 500–600 mm and mean annual temperature 8–9°C; Quitt, 1971). This area harbours large stands of *R. pseudoacacia*, accompanied by the stands of native trees in a relatively natural state. The stands of native trees are represented by the oak-hornbeam mesophilous forests (*Carpinion betuli*), scree forests on slopes (*Tilio platyphylli-Acerion*) and thermophilous oak forests on rocky shallow soils (*Quercion pubescenti-petraeae*). Similarly to the stands of *R. pseudoacacia*, many of the uninverted stands are located on steep slopes in not easily accessible places, which has contributed to their relatively natural state (see the Appendix S1 for a more detailed information on the study plots).

### 2.3 | Sampling design

Based on tree species cover, we established 19 plots with a high dominance of the invasive *R. pseudoacacia* (cover 96%, range 80%–100%,

hereafter called “invaded plots”) and 20 plots with the dominance of native tree species (cover 97%, range 80%–100%, hereafter called “uninvaded plots”) on sites with similar soil conditions, topology and climate. The dominant native tree was oak, *Quercus petraea* Matt. (Liebl.), and the other native tree species were *Acer campestre* L., *A. platanoides* L., *A. pseudoplatanus* L., *Carpinus betulus* L., *Fraxinus excelsior* L., *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill., *T. platyphyllos* Scop. The plots were 100 × 100 m in size, located within closed stands of a given type to minimize the influence of edge effects, and at least 500 m apart from each other to minimize repeated counting of the same individuals on multiple plots during the bird surveys.

On each plot, we made an inventory of plants, moths and breeding birds. Plants were recorded in June and July 2015 and their abundances were estimated as a per cent cover (see Hejda et al., 2009). Moths were attracted to a light source (8W UV LEDs light, powered by lead battery 7.2 Ah/12 V), using portable light traps. At each plot, a single light trap was placed in the plot centre for one night each month (the same night for all plots, from dusk till dawn) from April to November 2014. Thus, the effects of different timing during the night (Nowinszky, Mészáros, & Puskás, 2007), moon phase (Nowinszky & Puskás, 2010) or weather (Jonason, Franzén, & Ranius, 2014) were eliminated or minimized. The lights used for sampling were of low wattage and luminosity; such light sources attract insects from a close distance of tens of metres at maximum (Truxa & Fiedler, 2012). Therefore, the samples contained only the moths actually occurring in the nearest surroundings of the trap, closely matching the area of our 100 × 100 m plots. The plots were located in inner parts of large forest blocks, which makes the random presence in samples of species from the different habitats in the surroundings unlikely. Birds were counted using a spot mapping technique during three early morning visits in April–June 2014. These months cover the breeding season of the species breeding in the temperate zone, during which the birds are territorial and thus closely associated with particular habitats (Wiens, 1989). The maximum count across all visits was used as an estimate of the abundance of a particular species on a given plot (see Reif et al., 2016 for more details on moths sampling and bird counts). We excluded one obligatory herbivorous bird species, *Columba palumbus* L., for which the moths are not a food source.

Considering environmental data, each plot was characterized by its geographic characteristics (geographic coordinates, altitude, exposition and steepness of the slope) and the percentage of surrounding habitats—urbanized area and spruce plantations—within the 500-m buffer zone around the plot. These two habitats were chosen as they host plants, insects and birds markedly distinctive from the assemblages typical of broad-leaved forests on the study plots (Oxbrough et al., 2012; Reif, Storch, & Šímová, 2008) and the proximity of such habitats could affect the species richness and composition, recorded on the study plots.

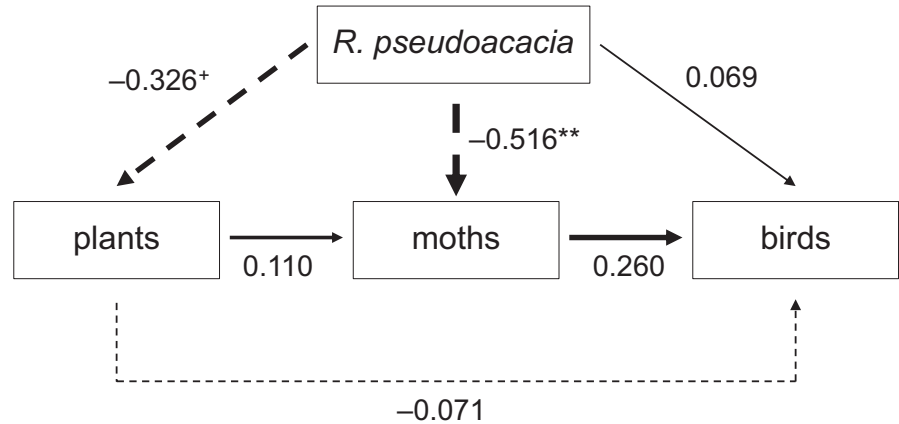
Finally, all species were assigned ecological traits, assumed to be relevant for their survival in the stands of the invasive *R. pseudoacacia*. Plant species were assigned Ellenberg indicator values for hemeroby (response to human impact), hemeroby—tolerance (a range of human impact, tolerated by a given species), nutrient demands, soil

moisture and soil reactivity requirements (the latter representing the species’ mineral requirements), light requirements and continentality (Ellenberg et al., 1991). These values characterize each plant species’ preferences of site conditions. Moreover, the differences in their distribution between the invaded and native stands indicate changes in site conditions, possibly attributable to the invasive tree’s impacts. The moth species were characterized by their life history (Pavlíková & Konvička, 2012): feeding specialization of larvae (feeding guilds: leaf eaters, other vegetative parts eaters (roots and stems), generative parts eaters (flowers, seeds), species feeding on moss or lichens, carnivorous moths, detritivorous moths on trees, detritivorous on herbs), affinity to basic vegetation types (open habitats, forest-steppe, forests, generalists), voltinism (one generation per year, two generations per year) and size of adults (small, medium, large), taken from Macek, Dvořák, Traxler, and Červenka (2007, 2008), Macek, Procházka, and Traxler (2012). Bird species were characterized by three traits: (1) life-history strategy, expressed as a position of each species along the gradient from slow to fast life cycles, as revealed by a principal component analysis based on six life-history traits (egg mass, clutch size, number of broods per year, laying date, length of incubation and body mass—Koleček & Reif, 2011), using the data from national bird handbooks (Hudec & Šťastný, 2005; Šťastný & Hudec, 2011); (2) vegetation type preference, expressed as a position of each species along the gradient from forest to open habitats, as revealed by a canonical correspondence analysis on species’ abundances in eight habitat classes, using the data from a nationwide breeding bird monitoring scheme (Reif, Jiguet, & Šťastný, 2010); and (3) habitat specialization, expressed as habitat specialization index, depicting a gradient from specialists to generalists, calculated as a coefficient of variation of species’ abundances across eight habitats, using the same dataset as for the vegetation type preference (Reif et al., 2010). We selected these traits because of their presumed relevance to the impact of plant invasions: concerning the life-history strategy, we can expect that species with faster strategies will be more resilient to invasive plants’ impacts; vegetation type preference can be linked to changes in vegetation structure due to *R. pseudoacacia* invasion (see Hanzelka & Reif, 2016); and habitat specialization was suggested as a major correlate of bird species’ sensitivity to plant invasions (Olden, Poff, Douglas, Douglas, & Fauch, 2004).

## 2.4 | Statistical analysis

We first investigated the effect of *R. pseudoacacia* invasion on species richness of particular groups of organisms and performed separate analyses for plants, moths and birds. The data on species richness were analysed by the marginal analyses of variance, using the generalized least square regression (“gls” function from the package “nlme”—Pinheiro, Bates, DebRoy, & Sarkar, 2016), available in the R freeware (R Development Core Team, 2011). Marginal models based on the generalized least square method represent an extension of ordinary least squares models, which (1) account for autocorrelated data in a robust yet efficient way; and (2) are robust towards deviations from normality within the data. Species richness (numbers of

**FIGURE 2** Path analysis diagram for the influence of *Robinia pseudoacacia* on plant, moth and bird species richness. The arrows denote how the focal variables affect each other. The significance of the regression coefficients is indicated:  $^+p < .1$ ,  $^{**}p < .01$ , and the thickness of the lines denotes the strength of the relationship. Solid lines indicate positive relationships, and dashed lines indicate negative relationships



species excluding neophytes for plants—see Pyšek, Danihelka, et al., 2012) was the response variable and the stand type (invaded vs. uninvaded) was the predictor variable. The geographic coordinates were used to model the possible inter-plot similarity, given by their spatial arrangement. This was included into the models on species richness as a residual covariance structure. Various models of residual covariance (no residual covariance, Gaussian covariance, exponential covariance) were compared using the Akaike information criterion, which evaluates the explanatory power of the models vs. their complexity (see for example Lukacs et al., 2007). The accuracy of the models was checked based on the distribution of standardized residuals (Crawley, 2007). Two sets of marginal models were created: one with the stand type as the only explanatory variable and the second one with the stand type and geographic and surrounding habitat characteristics as explanatory variables (see section “Sampling design”).

Path analysis was used to explore the functional relationships between the taxonomic groups of organisms (plants, moths and birds), to reveal the potential cascading effects of the impact of *R. pseudoacacia*. A comprehensive investigation of hypothesized causal relationships between the taxonomic groups is the main strength of this approach (Shipley, 2000). The analysis consists of a set of multiple regressions between particular variables in the direction of hypothesized cascading effects (see Figure 2). At the same time, the effects of dependent variables on one another are considered and the relationships are assessed by their direct and indirect effects (Shipley, 2000). The direct effects were calculated as standardized partial regression coefficients between the response and predictor variable. Indirect effects were calculated as the products of all standardized partial regression coefficients in the indirect path, that is regression coefficients in all other paths between the response and predictor variable. The standard errors of the indirect effects required for significance tests were calculated using multivariate delta method, as described in Cheung (2009, see the equation 11).

First, we created a scheme of the hypothesized relationships between the taxonomic groups (Figure 2). Then we calculated the standardized regression coefficients between particular variables employing generalized least squares (GLS) models with a spherical covariance structure of residuals using the R package “NLME”, instead of the ordinary least squares regressions (OLS), to account for possible

spatial autocorrelation. To describe all the paths in the scheme, the models were set as follows: (1) bird species richness as a response variable, and moth species richness, plant species richness and stand type (coded as 0 = uninvaded stands, 1 = invaded stands) as the explanatory variables; (2) moth species richness as a response variable, and plant species richness and stand type as the explanatory variables; and (3) plant species richness as a response variable, and stand type as an explanatory variable. In all models, the variables were centred to zero mean, and standardized to unit variance.

To test for the differences in species composition between the invaded and uninvaded stands, we used direct gradient analyses of the multivariate ordination models (CANOCO 5; ter Braak & Šmilauer, 2012; Šmilauer & Lepš, 2014), separately for each group of the focal taxa, that is plants, moths and birds. Species’ covers (in case of plants) and abundances (in case of moths and birds) were the response variables, the type of stand (invaded vs. uninvaded) was the predictor variable and the Monte Carlo permutation tests (499 runs) were used to express the significance of the ordination models. However, as data may be spatially autocorrelated, we used the method of variation partitioning (Peres-Neto, Legendre, Dray, & Borcard, 2006), using the principal coordinates of neighbour matrices (PCNM—Dray, Legendre, & Peres-Neto, 2006; Šmilauer & Lepš, 2014). This method uses the most significant eigenvectors, obtained by the principal coordinate analysis (PCoA) in the form of PCO scores of a truncated matrix of geographic distances as predictors, that we used in all ordination models as covariables (Šmilauer & Lepš, 2014). The cut-off threshold value for truncation of the distance matrix was set to 1, i. e. to the nearest neighbour. Same as with the unidimensional marginal models on species richness (see above), two sets of direct gradient ordination models were created: one with the stand type as the only predictor variable and the most significant PCO scores as covariables, and the second, where the other characteristics of the study plots (see section “Sampling design”) were included as covariables.

Finally, we used direct gradient ordination analyses to test whether the distribution of basic ecological traits of recorded species of plants, moths and birds, respectively, (see section “Sampling design”) differed between the invaded and uninvaded stands. The values of individual traits were weighted by the relative abundance of each species present within a sample (plot), and mean values of each trait for each

**TABLE 1** Standardized partial regression coefficients of the hypothesized relationships within the path analysis (see Figure 2), expressed as direct effects (DE) and indirect effects (IE) with respective *p*-values revealed by GLS models. Indirect effects are regression coefficients in all other (indirect) paths between the variables in these relationships. Significant relationships are in bold

Variable	Plants		IE	Moths		IE	<i>p</i> -value	Birds		IE	<i>p</i> -value
	DE	<i>p</i> -value		DE	<i>p</i> -value			DE	<i>p</i> -value		
<i>R. pseudoacacia</i>	-0.326	.050	-	<b>-0.516</b>	<b>&lt;.001</b>	<b>-0.036</b>	<b>&lt;.001</b>	0.069	.730	<b>-0.120</b>	<b>&lt;.001</b>
Plants	-	-	-	0.110	.348	-	-	-0.071	.665	0.029	.731
Moths	-	-	-	-	-	-	-	0.260	.236	-	-

sample were then used as response variables in these ordination analyses (see Hejda, 2013 for details on this approach).

### 3 | RESULTS

#### 3.1 | Species richness

Plant species richness was slightly higher in uninvaded than in invaded stands ( $18.8 \pm 7.0$  and  $15.3 \pm 4.2$ , respectively), but the difference was only marginally significant in the model without the geographic characteristics and surrounding habitats ( $p = .091$ ; see Appendix S2 for more details on marginal models) and this significance disappeared after including these variables ( $p = .482$ ). However, the invaded stands hosted fewer moth species than uninvaded stands ( $88.7 \pm 17.4$  and  $121.7 \pm 26.0$ , respectively) and the difference was significant regardless of whether or not the geographic and surrounding habitat characteristics were included ( $p < .001$  and  $p = .001$ , respectively). There was no difference in bird species richness between the invaded and uninvaded plots ( $11.5 \pm 2.6$  and  $10.9 \pm 2.8$ , respectively;  $p = .557$ ) and including the geographic and surrounding habitat characteristics did not change the result ( $p = .938$ ).

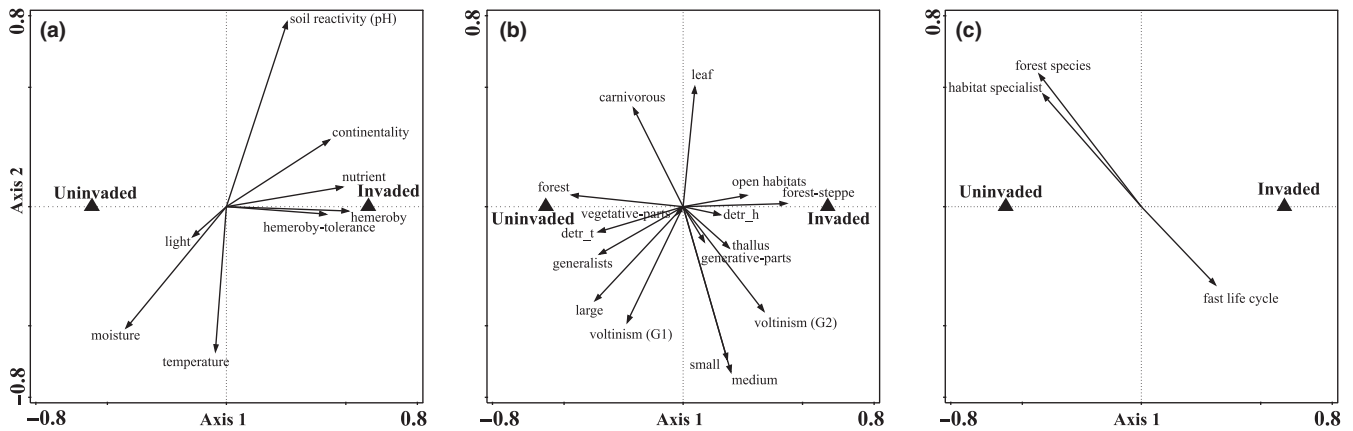
Path analysis confirmed a minor direct negative impact of *R. pseudoacacia* on the species richness of plants (standardized partial regression coefficient of  $-0.326$ ) and a major direct negative impact on moths ( $-0.516$ ; Table 1). *Robinia pseudoacacia* reduced the species richness of moths also indirectly, even though the significant effect was small ( $-0.036$ ). Similarly to the marginal models, path analysis revealed no detectable direct impact of *R. pseudoacacia* on the species richness of birds, but there was an indirect significant effect on birds ( $-0.120$ ). The relations between the species richness of the three taxonomic groups of recorded organisms (effects of plants on birds, plants on moths and moths on birds) were not significant (Table 1).

#### 3.2 | Species composition

The species composition and the distribution of their ecological traits differed between the invaded and uninvaded stands for all three taxonomic groups studied (Table 2). The differences were significant, irrespective of whether the geographic and surrounding habitat variables were included among the covariables or not. The invaded stands harboured a higher proportion of plants with a high nitrogen demand

Organisms	Response variables	Covariables	<i>p</i> -value	Trace
Plants	Species composition	Spatial effects	.004	0.385
Moths	Species composition	Spatial effects	.002	0.049
Birds	Species composition	Spatial effects	.002	0.051
Plants	Species' functional traits	Spatial effects	.002	0.036
Moths	Species' functional traits	Spatial effects	.002	0.172
Birds	Species' functional traits	Spatial effects	.002	0.163
Plants	Species composition	Spatial effects, geographic traits, surrounding habitats	.028	0.192
Moths	Species composition	Spatial effects, geographic traits, surrounding habitats	.002	0.041
Birds	Species composition	Spatial effects, geographic traits, surrounding habitats	.028	0.040
Plants	Species' functional traits	Spatial effects, geographic traits, surrounding habitats	.002	0.140
Moths	Species' functional traits	Spatial effects, geographic traits, surrounding habitats	.002	0.077
Birds	Species' functional traits	Spatial effects, geographic traits, surrounding habitats	.002	0.150

**TABLE 2** Results of multivariate (direct gradient) ordination analyses testing the differences in (i) species composition and (ii) distribution of species ecological traits between the invaded and uninvaded stands. The table presents both the models with and without the geographic and surrounding habitat characteristics included as covariables. The permutation tests were set to 499 runs



**FIGURE 3** Ordination plots presenting the analyses on the differences in the distribution of species' ecological traits between the invaded and uninvaded stands for plants (3a – RDA,  $p = .002$ ), moths (3b – RDA,  $p = .002$ ) and birds (3c – RDA,  $p = .012$ ). Geographic and surrounding habitat characteristics are included among the covariables in all these models. Plant species preferring continental climate, hemerophilic and hemeroby-tolerant plants and plant species of eutrophic sites were detected to favour the invaded stands, while species with higher moisture demands, hemerophobic species, species of oligotrophic sites and species preferring the oceanic climate favour the uninvaded stands (Figure 3a). Concerning moths, herbal detritivores (det\_h), forest-steppe species and moss/lichen feeders (thallus) favour the invaded stands, while habitat generalists, tree detritivores (det\_t) and large forest species favour the uninvaded stands (Figure 3b). Birds with fast life cycle reveal some preference for the invaded stands, while forest bird species and habitat specialists reveal weak preference for the uninvaded stands (Figure 3c)

and tolerant of drought and human impact, and with a preference for continental climate (Figure 3a). Concerning moths, the invaded stands hosted more specialized feeding guilds (detritivorous on herb and shrub litter; moss and lichen feeders; and feeders on generative part of plants), forest-steppe moths and species associated with open habitats and with faster life cycle (Figure 3b). For birds, the invaded stands were mostly occupied by species with fast life history, habitat generalists and species more associated with open habitats (Figure 3c). Complementarily, the stands of native trees had a greater proportion of (1) moisture-demanding plants with a preference for oceanic climate, hemerophobic plants and plants preferring oligotrophic sites; (2) forest moths confined to the canopy, habitat generalist moths, moths feeding on tree detritus and large moths; and (3) forest bird species, habitat specialists and bird species with slow-life-history strategies (Figure 3a–c).

## 4 | DISCUSSION

Our results showed that the impact of *R. pseudoacacia* on the species richness of target groups of organisms was generally weak. While the species richness of primary consumers, moths, was significantly reduced in the invaded stands, no significant differences were detected for primary producers, plants, and secondary consumers, birds. Thus, the evidence for cascading effects across trophic levels was modest, at least in terms of species richness. However, the community composition and species traits within those three taxonomic groups significantly differed between the uninvaded stands and the stands of the invasive *R. pseudoacacia*. Invasion promoted species possessing traits associated with the tolerance of human disturbances such as increased nutrient demands in plants or habitat generalism in birds.

### 4.1 | Effect of the invasive tree on species richness: differences among taxonomic groups

The lack of significant effects of *R. pseudoacacia* on the species richness of plants and birds is somewhat surprising, given its high ranking among European invaders by impact (Rumlerová et al., 2016). In case of birds, the potential negative effects of *R. pseudoacacia* could be compensated by the higher structural heterogeneity of the invader's stands compared to the stands of native tree species (Dzwonko & Loster, 1997), creating suitable environment for birds (Hanzelka & Reif, 2016).

Concerning plants, the impact of *R. pseudoacacia* is not manifested by changes in the species richness of their communities, as reported for other invasive woody plants such as *Cinchona pubescens* (Jäger et al., 2007) or *Acacia longifolia* (Marchante, Marchante, Freitas, & Hoffmann, 2015). However, it needs to be borne in mind that the impacts of *R. pseudoacacia* on the richness of understory plants are context-dependent (Vítková & Kolbek, 2010). If the productivity is stress-limited (usually by drought), understory of invaded forest can be species rich and even host species of conservation concern, while the herbal layer of more productive (wet) stands of *R. pseudoacacia* tends to be overgrown by a few dominant ruderal species, with relatively low diversity of herbs. Our study included a broad selection of both uninvaded and invaded stands, ranging from dry to mesic, which probably resulted in a high residual variability when comparing the invaded vs. uninvaded stands.

Patterns found for plants and birds were in sharp contrast with the results for moths, where significant differences in species richness between the invaded and uninvaded stands were detected. We suggest that the direct utilization of plant tissues is the key characteristic, making the moths sensitive to invasion, as the pattern was caused mostly by herbivorous moth species. Consistent with the enemy release

hypothesis (e.g. Blumenthal, 2006; Colautti, Ricciardi, Grigorovich, & MacIsaac, 2004; Keane & Crawley, 2002), the majority of native canopy moths are not adapted to phytochemicals produced by *R. pseudoacacia* (Liu & Stiling, 2006). These results are in accord with other studies that have studied the impact of woody invasions on the diversity of herbivorous arthropods (Burghardt et al., 2010; Degomez & Wagner, 2001; Gerber et al., 2008; van Hengstum et al., 2014; Litt et al., 2014; Liu & Stiling, 2006; Schirmel et al., 2016).

#### 4.2 | Cascading effects across trophic levels?

One signal revealed by the path analysis is the cascading effects of the invasive *R. pseudoacacia* across the three trophic levels—plants as producers, moths as herbivores and birds as predators. These effects were mostly indirect, suggesting that at least within our study system, the factors limiting species richness at these trophic levels act independently and that the functional relations among these taxonomic groups are not the key determinants of their species richness. This result is not particularly surprising, given the variability in responses to plant invasions across different organisms (Schirmel et al., 2016). To explain the absence of a direct relationship between primary producers and primary consumers, it needs to be kept in mind that the majority of plant species recorded on study plots do not host many species of moths, which mostly develop in the canopy or shrub layer. As a consequence, the functional relationship between these two groups of taxa is unlikely to be a tight one; therefore, the impact of *R. pseudoacacia* on moths is via food limitation for leaf-eating herbivores rather than via total plant richness (but note that even the indirect effect of *R. pseudoacacia* on moths was significant, but close to zero).

The situation is more complex in birds that were not significantly related to moth species richness in the path analysis, but their species richness was indirectly and negatively affected by the invader. This can be interpreted by different levels of food specialization between moths and birds, and, therefore, different sensitivity to changes in food supply (Krištín & Patočka, 1997). While the specialists are particularly sensitive to *R. pseudoacacia* invasion and most likely suffer from a limited food supply in its stands (Reif et al., 2016), generalists benefit from its more heterogeneous habitat structure (Hanzelka & Reif, 2015, 2016) and, at the same time, are not limited by the lower richness of moth species (Reif et al., 2016). These opposing forces probably made the direct effect of moth species richness on birds nonsignificant, but the composition of the moth community could probably facilitate a significant indirect effect of *R. pseudoacacia* on bird species richness.

#### 4.3 | Effects on the species composition of communities across trophic levels

Contrary to generally weak differences in species richness, the species composition of communities of all groups of organisms included in the study highly significantly differed between the invaded and uninvaded stands, and so did the distribution of traits within their communities. These results remained significant after accounting for the geographic characteristics of the plots and their surrounding habitats. For plants,

species tolerating increased levels of human-induced disturbances and confined to nutrient-rich soils (*Galeopsis pubescens* Besser, *Chelidonium majus* L., *Urtica dioica* L.) prevailed in stands of the invasive *R. pseudoacacia* (see also Dzwonko & Loster, 1997). Interestingly, the invaded stands also host more species with a preference for the continental character of climate (*Allium schoenoprasum* L., *Calamagrostis epigejos* (L.) Roth., *Rubus saxatilis* L.), possibly due to the fact that the stands of *R. pseudoacacia* are more prone to summer droughts, compared to the stands of native trees. This can be caused by the fact that the leaves of *R. pseudoacacia* rotate during strong summer heats to capture less radiation and, in concordance with the more open structure of *R. pseudoacacia* stands, more light reaches lower layers (Xu et al., 2009). This explanation is also supported by the fact that plants with higher moisture demands (*Campanula trachelium* L., *Corydalis cava* (L.) Schweigg. et Koerte) prefer the uninvaded stands.

For moths, the uninvaded stands host more canopy leaf-feeders, detritivorous feeders on trees and moths of larger sizes and with slower life cycle. The stands of *R. pseudoacacia* had higher proportion of more specialized feeding guilds (e.g. *Idaea deversaria* H.-S., *Laspeyria flexula* D. & Schiff.) and moths with faster life cycle (e.g. *Macaria alternata* D. & Schiff., *Peribatodes rhomboidaria* D. & Schiff.). This may be explained by the same mechanism responsible for the occurrence of plants preferring continental climate: by warmer and drier conditions in *R. pseudoacacia* stands compared to the stands of native trees. The invasion resulted in more open and heterogeneous habitat structure with well-developed shrub and herb layers, offering a variety of food niches for moths. Many of such moths belong to non-specialized species (Slade et al., 2013), which may be the explanation for the high proportion of generalist moths in the uninvaded stands.

Habitat generalist birds showed the opposite and predictable pattern, that is an increased proportion of these species in *R. pseudoacacia* stands (e.g. *Sylvia atricapilla* L., *Phylloscopus collybita* Viellot). This shows that the invaded stands represent more disturbed habitats with poorly predictable food sources, compared to the uninvaded stands, which host more habitat specialists (e.g. *Dendrocopos medius* L., *Ficedula albicollis* Temminck) and species with slow-life strategy (e.g. *Dryocopus martius* L., *Garrulus glandarius* L.), that is traits rather associated with undisturbed environment (Büchi & Vuilleumier, 2014; Devictor et al., 2008; Koleček, Albrecht, & Reif, 2014). Moreover, a lower proportion of forest-interior birds (e.g. *Phylloscopus sibilatrix* Bechstein, *Turdus viscivorus* L.) in the invaded forests suggests that these stands may resemble open woodlands (preferred by e.g. *Turdus pilaris* L., *Sturnus vulgaris* L.) rather than closed-canopy forests. This is also supported by the presence of moths preferring steppe habitats in the samples from *R. pseudoacacia* stands.

In summary, our study shows that even though an invasive tree does not depauperate the invaded communities in terms of the number of present species, it eliminates some native species and favours others. This observation is important, as it challenges the use of the simple numbers of species in the analyses of invasive plants' impacts, as is the case for many studies, particularly large-scale meta-analyses. We argue that such approach may mask patterns at the species level, potentially important for ecosystem functioning. This results in overly optimistic



conclusions about low impacts of invasive plants and in incomplete understanding of their mechanisms. We opt for focusing on the distribution of traits of the species recorded in invaded communities as a more informative currency for measuring the impacts of invasion.

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## BIOSKETCH

Various members of the research team focus on the ecology of different groups of target organisms: MH and PP focus on plants, MS

and TK focus on insects, and JR and JH focus on birds. Such diversity of expertise was needed to look at the impacts of the selected invasive tree, *Robinia pseudoacacia*, in a complex way. Further, MH and JR conceived the basic idea of the manuscript; MH, JH, MS, TK and JR all contributed to the sampling effort. MH, JH and MS performed the analyses, and all members of the author team contributed to the preparation of the manuscript. PP supervised the manuscript's preparation and made sure the text is concise and clear.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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