




Impact of an invasive tree on arthropod assemblages in woodlots isolated within an intensive agricultural landscape

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Abstract

Aim: Landscape simplification and the spread of invasive species are considered beyond the main threats to global biodiversity. It is well recognized that non-crop habitats bring complexity to farmland and provide refuge for a wide range of organisms, including arthropods. However, knowledge about the effects of invasive trees on arthropods in non-crop habitats in intensive agricultural landscapes is still weak. Therefore, we examined differences in the arthropod assemblages between woodlots formed by the invasive black locust (*Robinia pseudoacacia* L.) and by native deciduous tree species in the intensive agricultural landscape.

Location: Czech Republic, Central Europe.

Methods: We used a multi-taxonomic approach to record arthropod assemblages using various sampling methods. The impacts of woodlot habitat structure were investigated across 13 arthropod taxa from different trophic levels.

Results: Total abundance and species richness of all arthropods and the majority of the herbivore taxa were lower in *R. pseudoacacia* woodlots, likely due to losses of the forest canopy specialists. The forest specialists were associated with the native woodlots with more developed canopy and shrub layers. The impoverished diversity of the forest specialists and canopy herbivores in the *R. pseudoacacia* woodlots was partly compensated by the higher presence of species exploiting a well developed herb layer and open-habitat specialists, including threatened species.

Main conclusions: Native woodlots and those formed by *R. pseudoacacia* differ in vegetation structure and host different assemblages of arthropods. Therefore, parallel presence of both types of woodlots supports arthropod diversity in otherwise simplified agricultural landscapes through creating more complex mosaic of habitats.

KEYWORDS

arthropods, biological invasion, forest fragments; habitat alternation, invasive plants, multi-taxonomic approach, non-crop habitats, *Robinia pseudoacacia*

1 | INTRODUCTION

Intensively farmed agricultural land dominates the current landscape in many regions of the world (Green, Cornell, Scharlemann, & Balmford, 2005; Stoate et al., 2009). In many countries, including the Czech Republic, finely structured traditional landscapes were altered into large blocks of intensive production fields (Benton, Vickery, & Wilson, 2003; Sklenicka, Janovska, Salek, Vlasak, & Molnarova, 2014), which led to the fragmentation of natural habitats and biodiversity loss (Konvicka, Benes, & Polakova, 2016; Kruess & Tschardtke, 1994; Tschardtke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Land use intensification in agricultural landscapes has caused rapid arthropod declines in recent years (Attwood, Maron, House, & Zammit, 2008; Hallmann et al., 2017). Many arthropod groups provide irreplaceable ecosystem services in agroecosystems as natural weed and pest control (Birkhofer et al., 2018; Bohan, Boursault, Brooks, & Petit, 2011; Holland, Smith, Birkett, & Southway, 2012) or pollination (Carvalho, Seymour, Nicolson, & Veldtman, 2012; Farwig et al., 2009). Along with their substantial diversity and biomass (Ødegaard, 2000), arthropods form the key elements of food webs (Mooney et al., 2010).

The overall biodiversity reflects the quality and composition of the landscape mosaic (González, Salvo, & Valladares, 2017; Öckinger et al., 2012; Steffan-Dewenter, 2002). Contemporary agroecosystems often contain only small remnants of semi-natural non-crop habitats (Attwood et al., 2008; Tschardtke, Steffan-Dewenter, Kruess, & Thies, 2002). More complex landscapes with a higher proportion of non-crop habitats mitigate the negative impacts of intensive farming activities on local biodiversity (Billeter et al., 2007; Duelli & Obrist, 2003; Schüepp, Herrmann, Herzog, & Schmidt-Entling, 2011). While interconnected linear non-crop habitats (hedgerows, field margin strips, grassy banks; Collins, Boatman, Wilcox, & Holland, 2003; Davies & Pullin, 2007; Dennis & Fry, 1992) are well-researched landscape elements, knowledge about the diversity and ecological function of permanent habitat islands, that is non-crop habitat patches completely isolated by cultivated arable fields, is limited (Cook, Lane, Foster, & Holt, 2002; Knapp & Řezáč, 2015; Moreno, Fernández, Molina, & Valladares, 2013). These islands largely vary in size (from a few m² up to several hectares) but even the smallest ones contribute to local biodiversity (Carvalho et al., 2012; Knapp & Řezáč, 2015). In many cases, they are left to spontaneous successional processes or are afforested (as a shelter for wild game) by fast-growing and durable tree species (Benayas, Bullock, & Newton, 2008; Lassoie, Buck, & Current, 2009). In general, biodiversity in forest habitats seems to strongly depend on vegetation structure, which is largely conditioned by the dominant tree species (Hanzelka & Reif, 2016; Highland, Miller, & Jones, 2013; Kadlec, Štrobl, Hanzelka, Hejda, & Reif, 2018; Tews et al., 2004). The dominant tree species has a strong effect on heterogeneity of habitat structure and canopy-openness, both of which are positively linked to arthropod diversity in large European lowland forests (Kadlec et al., 2018; Sebek et al., 2015). Similar effects can also be expected for the isolated woodlots in agricultural landscapes.

The non-crop habitats in agroecosystems are often afforested by invasive tree species (Richardson & Rejmánek, 2011; Van der Colff, Dreyer, Valentine, & Roets, 2015; Vítková, Müllerová, Sádlo, Pergl, & Pyšek, 2017). Plant invasions are among main biodiversity threats worldwide (Richardson & Rejmánek, 2011; Vitousek, D'Antonio, Loope, & Westbrooks, 1996). Woody invasive species significantly disrupt the trophic links within ecosystems (Heleno, Ceia, Ramos, & Memmott, 2008; Reif, Hanzelka, Kadlec, Štrobl, & Hejda, 2016; Tallamy, Ballard, & Amico, 2010) or alter the vegetation structure of habitats, both of which can lead to changes in arthropod communities (Harris, Toft, Dugdale, Williams, & Rees, 2004; van Hengstum, Hoofman, Oostermeijer, & van Tienderen, 2014; Kadlec et al., 2018; Van der Colff et al., 2015). The impacts of woody invasion on arthropods differ among taxa and trophic guilds. In general, herbivores have been found to be more negatively affected compared with predators or detritivores (Harris et al., 2004; van Hengstum et al., 2014; Litt, Cord, Fulbright, & Schuster, 2014). The vast majority of studies investigating impacts of invasive trees on arthropods focused on large forest stands (Buchholz, Tietze, Kowarik, & Schirmel, 2015; van Hengstum et al., 2014; Litt et al., 2014), while the effects in smaller woodlots within arable land have not been investigated as yet. It can be expected that small sizes and isolation may even exacerbate the alterations in trophic cascades.

Black locust (*Robinia pseudoacacia* L.; Fabaceae; henceforth '*R. pseudoacacia*')—one of the most durable invasive tree species throughout the world influencing native communities in various habitat types (Campagnaro, Brundu, & Sitzia, 2018; Vítková et al., 2017)—has been frequently planted in woodlots in the intensive lowland landscape of Central Europe (Heroldová, 1994; Vítková et al., 2017). *Robinia pseudoacacia* occurs naturally in the south-eastern part of the United States as an early successional tree species (Boring & Swank, 1984), from where it was introduced to Europe at the beginning of the 17th century (Cierjacks et al., 2013; Vítková et al., 2017). This invasive species forms secondary forests with a spontaneously open-habitat structure and well developed understorey (Campagnaro, Nascimbene, Tasinazzo, Trentanovi, & Sitzia, 2018; Kadlec et al., 2018; Vítková et al., 2017). The influence of *R. pseudoacacia* on local biodiversity has been investigated in large forest stands (Campagnaro, Nascimbene, et al., 2018; Degomez & Wagner, 2001; Hejda, Hanzelka, et al., 2017; Kadlec et al., 2018; Reif et al., 2016), whereas its impact on biodiversity in isolated farmland woodlots remains unclear.

In this study, we compared the arthropod assemblages from woodlot islands dominated by invasive *R. pseudoacacia* with those formed by native tree species. The effects of *R. pseudoacacia* were investigated across several arthropod taxa from different trophic levels, including herbivores, carnivores and detritivores. We adopted this multi-trophic and multi-taxonomic approach to better understand the interactions within and between trophic levels (Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018). The following predictions were made:

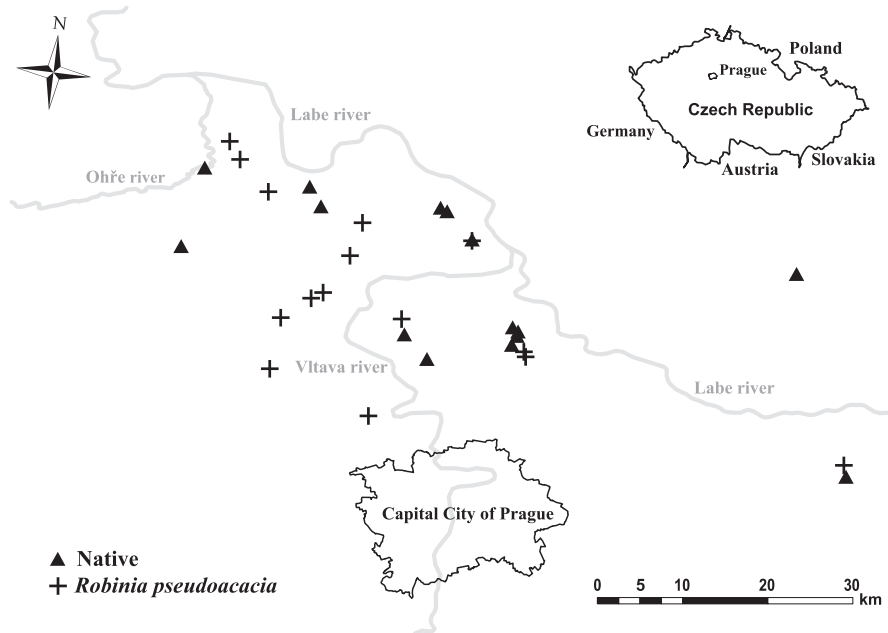


FIGURE 1 Map showing the location of the study plots (15 woodlots dominated by *Robinia pseudoacacia*, and 15 woodlots formed by native tree species)

1. Similar to large forest stands, *R. pseudoacacia* will create a more open-habitat structure of isolated woodlots in agricultural landscapes than native tree species.
2. The total arthropod species richness and abundance will be higher in woodlots dominated by native tree species and with a more open-habitat structure, but these effects could vary between taxa and trophic levels. We expect stronger effects in herbivorous taxa than in predators or detritivores.
3. Tree invasion and habitat structure will affect the composition of arthropod assemblages in woodlots. Forest specialists will be more dominant in native woodlots, whereas species of (semi) open habitats will be affiliated with *R. pseudoacacia* woodlots.

2 | METHODS

2.1 | Study area and sampling design

The study was conducted in a lowland agricultural landscape of the Czech Republic, Central Europe (Figure 1) in 2016. The study area (50.10°–50.46°N, 14.05°–14.83°E, ~1,300 km², 160–330 m a. s. l.) is located in a region with a moderately continental climate with an average annual precipitation of 500–600 mm and an average annual temperature of 8–9°C (Quitt, 1971). The landscape is dominated (>70%) by large, intensively managed arable fields, with scattered grasslands, cultivated lowland forests and human settlements making up most of the remaining area. The heavily fragmented forests are mainly formed by native broadleaved tree species or non-native trees, mostly by the invasive *R. pseudoacacia*.

Within the study area, we chose 30 small woodlots (<1.3 ha) that have been fully isolated for at least past 50 years (CENIA, 2018) within larger, intensively managed blocks of arable land (see Figure S1.1 in Appendix S1). Fifteen chosen woodlots were composed of native deciduous trees (dominated by oaks (*Quercus* spp.) and ash

(*Fraxinus excelsior* L.) mixed with maples (*Acer* spp.), limes (*Tilia* spp.), hornbeam (*Carpinus betulus* L.) and elms (*Ulmus* spp.); henceforth 'native woodlots') and 15 woodlots were dominated (>90% tree cover) by *R. pseudoacacia* (henceforth 'Robinia woodlots').

2.2 | Studied taxa and arthropod sampling

To describe the general arthropod assemblage patterns (Seibold et al., 2018), 13 arthropod groups from various trophic levels throughout different vegetation layers were sampled at the study sites: mostly herbivores—orthopteroids (Orthoptera), true bugs (Heteroptera), click beetles (Elateridae), weevils (Curculionoidea) and moths (nocturnal Lepidoptera); mostly carnivores—centipedes (Chilopoda), arachnids (Arachnida)—spiders (Araneae) and harvestmen (Opiliones), lace wings (Neuroptera), ground beetles (Carabidae) and rove beetles (Staphylinidae); mostly detritivores—millipedes (Diplopoda) and carrion beetles (Silphidae).

The arthropods were sampled using pitfall traps, sweep-netting and light trapping. In each woodlot, a line of five pitfall traps (two nested plastic cups, 94 mm perimeter × 144 mm height, containing 4% formaldehyde; Spence & Niemelä, 1994) spaced every five metres was established and operated continuously from the beginning of April to the beginning of September (152 trap days, emptied at monthly intervals). The lines of traps were located at least 10 metres from the edge of the woodlot to minimize edge effects (Roume, Deconchat, Raison, Balent, & Ouin, 2011). The captured samples were frozen at –22°C. In parallel with trap emptying, all of the vegetation up to a height of 3 m in the 25 × 5 m strip area centred around the line of traps was swept when weather conditions were suitable (sunny, no strong wind) using a 35 cm diameter sweeping net. The captured arthropods were preserved in 95% ethanol. To sample nocturnal arthropods, portable light traps (Brehm & Axmacher, 2006) equipped with two 8 W UV LED strip lights (total luminous flux 400 lm, wavelength

range 400–420 nm, powered by 7.2 Ah/12 V lead batteries) were used, and collected specimen was euthanized by evaporating chloroform. A single portable trap was placed approximately in the middle of each woodlot and attracted arthropods within a radius of a few tens of metres (Truxa & Fiedler, 2012). To standardize for the weather and moon-phase (Yela & Holyoak, 1997) the light traps were exposed on the same night under suitable weather conditions (no strong wind, no rainfall and increased cloud cover), from dusk until dawn, at the beginning of each month from April to September. The samples from the light traps were frozen at -22°C .

All samples were sorted according to the target taxa, counted and identified to the species level (see Appendix S2). Data from all of the sampling methods and periods were pooled for the particular taxa and woodlots into a final data set. The conservation status of each species was classified according to the national red lists (Hejda, Farkač, & Chobot, 2017; Řezáč, Kůrka, Růžička, & Heneberg, 2015). All species were classified into four categories with respect to their known habitat use in Central Europe (see Appendix S2 for references): forest: forest specialists living mainly in closed continuous forest stands; semi-open: species bounded to scattered greenery (e.g. hedgerows, solitary trees and forest-steppes); open: open-habitat species (e.g. grasslands, arable lands and early successional stages); and habitat generalists: without a distinct habitat specialization (see Appendix S2).

2.3 | Environmental parameter sampling

According to the known effects of habitat structure (Highland et al., 2013; Kadlec et al., 2018; Tews et al., 2004), the land cover composition in the surroundings (Novotný, Zapletal, Kepka, Beneš, & Konvička, 2015) and the area of woodlots (Baz & Garcia-Boyero, 1995; Bender, Contreras, & Fahrig, 1998) on arthropod assemblages, we recorded variables describing these effects in all of the woodlots (according to Hanzelka & Reif, 2016). First, AGE of the forest stand was determined, and the numbers of fallen (FALLEN TREES) and dead (DEAD TREES) trees were counted. Percentage cover of herbs < 0.5 m in height (HERB1), herbs > 0.5 m (HERB2), shrubs 1–5 m (SHRUB), trees 5–10 m (TREE1), trees > 10 m (TREE2), the canopy (CANOPY) and clearings—gaps in the stands without full-grown trees integrated in the canopy cover (CLEARINGS)—was estimated by visual inspection on site. Hereafter, we estimated the proportion of trees with a diameter at breast height (dbh) < 0.2 m (TREES), with a dbh of 0.2–0.5 m (TREEM) and with a dbh > 0.5 m (TREET).

The proportions of the total area covered by the following land cover types were estimated within a circular buffer with a 500 m radius around each woodlot using ArcGIS 10.2 (ESRI, 2011): ARABLE: arable lands; WATER: water bodies; ROCK: rocks and quarries; GRASS: grasslands; URBAN: urban areas; BROAD: broadleaved forests; and CONIF: coniferous forests. Moreover, the forest proportion in the surrounding area could also mirror the degree of woodlot isolation (Baz & Garcia-Boyero, 1995; Torma, Gallé, & Bozsó, 2014). The area of each woodlot (AREA; in ha) was computed from aerial photographs using ArcGIS 10.2 software (ESRI, 2011).

2.4 | Statistical analysis

To reduce the complexity of habitat structure and landscape structure data without substantial loss of information and to describe the main gradients of habitat structure and land cover characteristics of the studied woodlots, two principal component analyses were conducted in CANOCO 5.0 (PCA; ter Braak & Šmilauer, 2012): one for the habitat structure and one for the land cover characteristics. We used the scree plot method (Jackson, 1993) to distinguish the principal components explaining most of the variability in the data. Based on this criterion, in both PCAs, the scores from the first two principal components (PC1 and PC2) of habitat structure (henceforth called 'HAB1' and 'HAB2') and land cover characteristics ('LAND1' and 'LAND2') were used as predictors in the following analyses.

To compare the habitat structure between the native and *Robinia* woodlots, linear models were fitted with the principal components of habitat structure (HAB1 or HAB2) as the respective response variables and the woodlot type (WOODLOT TYPE: native or *R. pseudoacacia*) as the predictor.

The two native woodlots were excluded from most of the analyses because the majority of the pitfall traps were destroyed by wild animals. Therefore, the data from 13 native and 15 *Robinia* woodlots were used in analyses, except for the models of Lepidoptera and Neuroptera, as these data were not based on pitfall traps.

As the first step, we examined the differences in the total abundance and total species richness (both summed across all taxa) between the two types of studied woodlots (WOODLOT TYPE: *R. pseudoacacia*/native) as the only explanatory variable. This approach is often used in studies on the effects of plant invasions (van Hengstum et al., 2014; Litt et al., 2014). Thus, we used generalized linear models (GLMs) with Poisson or negative binomial distributions (to reduce overdispersion) of the errors. In contrast, the simple effect of plot (WOODLOT TYPE in our study) may represent the combined effects of the origin of the dominant tree species (as a measure of food availability for herbivores) and woodlot habitat structure (as a measure of ecological niche diversity). Therefore, in the next GLMs, we examined the direct effects of dominant tree origin (predictor TREE TYPE: *R. pseudoacacia*/native) and the effects of habitat structure (predictors HAB1 and HAB2). The effects of the surrounding landscape composition (LAND1 and LAND2) and woodlot area (AREA) were also included in these models. Full GLMs with the total abundance or species richness per woodlot (for each taxon and summed for all taxa) as response variables with all the mentioned predictors were performed. Distributions of errors employed in models are mentioned in Table 1. Potential spatial autocorrelation of the residuals was checked by a Mantel test (integrated into R package 'ADE4'; Dray & Siberchicot, 2018), and geographic coordinates were added to these models to account for autocorrelation if needed (according to Carrié, Ekroos, & Smith, 2018).

Furthermore, an information-theoretic approach (R package 'MuMIn', Bartoń, 2018; Burnham & Anderson, 2002) was used for model selection and multimodel inference. The candidate models containing all possible predictor combinations were compared

TABLE 1 Model-averaged estimates of the effects of particular predictors on the total number of individuals and the total number of species of the studied arthropod taxa between the native and *Robinia* woodlots

Taxa (no. individuals)	Model parameters ^a	Estimate	Confidence intervals		Taxa (no. species)	Model parameters ^a	Estimate	Confidence intervals	
			2.5%	97.5%				2.5%	97.5%
Total no. individuals ^{NB}	Intercept	7.884	7.712	8.056	Total no. species ^P	Intercept	5.447	5.402	5.492
	<i>Robinia</i>	-0.397	-0.631	-0.162		<i>Robinia</i>	-0.113	-0.186	-0.041
	Land1	-0.030	-0.194	0.0355		Hab1	0.072	0.037	0.106
						Land2	0.047	0.021	0.072
Arachnida ^{NB}	Intercept	6.006	5.751	6.267	Arachnida ^P	Intercept	3.803	3.697	3.908
	Area	0.580	0.082	1.135		Hab1	0.117	0.037	0.197
				<i>Robinia</i>		0.122	-0.038	0.281	
				Hab2		0.054	-0.038	0.112	
				Land1		-0.042	-0.105	0.021	
Carabidae ^{NB}	Intercept	6.907	6.587	7.225	Carabidae ^P	Intercept	3.544	3.469	3.619
	<i>Robinia</i>	-0.788	-1.225	-0.352		Hab2	-0.144	-0.112	0.023
	Land1	-0.194	-0.404	0.0152		Hab1	0.038	-0.004	0.127
				<i>Robinia</i>		0.009	-0.051	0.214	
				Land1		-0.005	-0.104	0.036	
Curculionoidea ^{NB}	Intercept	5.474	4.783	6.164	Curculionoidea ^P	Intercept	2.288	2.163	2.412
	<i>Robinia</i>	-1.236	-2.092	-0.381		Land2	0.093	-0.019	0.205
	Hab1	0.439	0.020	0.858		Hab1	0.085	-0.037	0.208
	Area	-0.659	-1.720	0.403					
Elateridae ^{NB}	Intercept	-150.130	-250.681	-51.197	Elateridae ^{NB}	Intercept	1.921	1.771	2.070
	Lat	3.040	1.076	5.037		Hab2	-0.058	-0.272	0.040
	<i>Robinia</i>	1.201	0.891	1.512		Land2	0.026	-0.052	0.223
	Area	0.677	0.181	1.193		Hab1	-0.015	-0.218	0.080
	Hab2	-0.231	-0.391	-0.697					
	Land1	0.209	0.058	0.364					
Diplopoda ^{NB}	Intercept	4.937	4.607	5.267	Diplopoda ^P	Intercept	1.543	1.259	1.828
	<i>Robinia</i>	0.264	-0.312	0.841		Land2	0.175	0.027	0.324
	Hab1	0.207	-0.072	0.487		Area	0.441	-0.123	1.004
						Hab2	-0.176	-0.367	0.015
				Land1		0.091	-0.875	0.269	
Heteroptera ^{NB}	Intercept	4.896	4.552	5.241	Heteroptera ^P	Intercept	3.071	2.836	3.306
	Hab1	0.347	0.041	0.652		<i>Robinia</i>	0.231	0.0597	0.403
	Area	-0.627	-1.596	0.342		Hab1	0.118	0.032	0.204
	Land2	0.264	-0.042	0.571		Hab2	0.116	0.032	0.201
	Hab2	0.258	-0.040	0.555		Area	-0.312	-0.627	0.004
	Land1	-0.207	-0.506	0.091					
Chilopoda ^{NB}	Intercept	-187.339	-346.188	-28.490	Chilopoda ^P	Intercept	1.350	1.116	1.584
	Lat	3.797	0.639	6.955		Area	0.045	-0.373	0.844
	Land2	0.146	-0.108	0.400		Land2	0.011	-0.122	0.244
	Hab2	-0.142	-0.398	0.113		Hab2	-0.011	-0.026	0.137
Lepidoptera ^{NB}	Intercept	3.348	5.728	6.058	Lepidoptera ^P	Intercept	4.256	4.136	4.376
	<i>Robinia</i>	-0.840	-1.078	-0.602		<i>Robinia</i>	-0.500	-0.654	-0.346
	Land2	0.114	-0.001	0.229		Hab1	0.123	0.047	0.199
						Land2	0.087	0.037	0.137
						Area	-0.137	-0.335	0.061
						Hab2	0.034	-0.016	0.084

(Continues)

TABLE 1 (Continued)

Taxa (no. individuals)	Model parameters ^a	Estimate	Confidence intervals		Taxa (no. species)	Model parameters ^a	Estimate	Confidence intervals				
			2.5%	97.5%				2.5%	97.5%			
Neuroptera ^{NB}	Intercept	3.165	2.828	3.502	Neuroptera ^P	Intercept	1.355	1.103	1.606			
	Hab1	-0.307	-0.503	-0.111		<i>Robinia</i>	-0.102	-0.664	0.121			
	Area	-0.565	-1.233	0.104		Hab1	-0.085	-0.284	0.113			
Orthoptera ^{LOGN}	Intercept	2.349	1.831	2.867	Orthoptera ^P	Intercept	0.558	0.075	1.041			
	<i>Robinia</i>	-0.456	-1.284	0.371		Area	-0.666	-1.902	0.570			
	Land1	-0.217	-0.631	0.196		<i>Robinia</i>	0.284	-0.324	0.891			
						Hab2	0.194	-0.088	0.476			
									Land2	0.131	-0.125	0.386
Silphidae ^{NB}	Intercept	2.103	1.476	2.730	Silphidae ^P	Intercept	0.715	0.305	1.125			
	Land1	-1.154	-1.766	-0.543		<i>Robinia</i>	-0.430	-1.215	0.355			
	Hab1	1.033	0.585	1.481		Hab1	0.405	0.091	0.718			
	Area	-1.179	-2.891	0.534		Land1	-0.274	-0.606	0.059			
									Land2	0.157	-0.119	0.432
Staphylinidae ^{NB}	Intercept	5.050	4.794	5.304	Staphylinidae ^P	Intercept	3.348	3.275	3.421			
	<i>Robinia</i>	-0.311	-0.646	0.023		Hab2	-0.075	-0.150	0.001			
	Land2	0.166	-0.007	0.338		Land2	0.042	-0.029	0.113			
	Land1	-0.100	-0.262	0.063								

Note: The estimates were obtained by averaging the best-performing candidate models assessed by the Akaike Information Criterion corrected for small sample sizes (AICc). Significant effects, indicated by confidence limits that do not overlap zero, are highlighted in bold. Model parameters are ordered by their significance and within groups of significant/insignificant terms by their effect size (estimate values).

^aModel parameters: *Robinia*: the effects of the dominant tree, *Robinia pseudoacacia*, on the response variables; Hab1 and Hab2: PC1 and PC2 scores of the habitat characteristics of the woodlots; Land1 and Land2: PC1 and PC2 scores of the land cover types in the surroundings of the woodlots and Area: area of the woodlots. The superscripts in each response variable indicate the distribution of errors used in the generalized linear models: P, Poisson; NB, negatively binomial; and LOGN, lognormal.

by AICc (Akaike, 1974; Burnham & Anderson, 2002). Models with $\Delta\text{AICc} < 2$ were considered superior. These models were used for inference employing model averaging using AIC weights (Bartoń, 2018; Burnham & Anderson, 2002). Univariate analyses were performed in R 3.5.1 (R Core Team, 2018).

Differences in species composition between the woodlot types were analysed by multivariate ordination methods. Based on the gradient lengths (for all models a gradient was at least 1.9 SD units long), canonical correspondence analyses (CCAs) were used (Šmilauer & Lepš, 2014). In the first step, CCA with the species data pooled across all taxa was performed to investigate differences in the total species composition between the woodlot types. The species compositions of particular taxa were compared between the native and *Robinia* woodlots using separate CCAs. Prior to this, we checked for possible correlations between the effects of TREE TYPE (*R. pseudoacacia*/native) and habitat structure (HAB1 and HAB2) in the woodlots on the arthropod species compositions (Kadlec et al., 2018). We used the variation partitioning approach (Peres-Neto, Legendre, Dray, & Borcard, 2006) to distinguish between the marginal (the effects of a predictor without taking the other predictors into account) and the conditional (to quantify the effects of a predictor after controlling for the effects of the other predictors) effects of TREE TYPE, HAB1 and HAB2 on the species

composition (Šmilauer & Lepš, 2014). Due to potential spatial autocorrelation among the study plots, the principal coordinates of neighbour matrices framework (PCNM; Dray, Legendre, & Peres-Neto, 2006; Peres-Neto et al., 2006) were implemented into the CCAs (Šmilauer & Lepš, 2014). Within PCNM, the principal coordinate analysis (PCoA) was run to obtain the spatial variables represented by the respective PCo axes. Monte-Carlo permutation tests (999 permutations) were used to test the significance of each PCo axis, and the scores of the most significant PCo axes were further used in the CCA as covariables, capturing the spatial information in the data (Šmilauer & Lepš, 2014). In the following step, a separate CCA with Monte-Carlo significance testing (999 permutations) for each studied taxa was performed, and TREE TYPE and the significant marginal and conditional effects of HAB1 and HAB2 on the species composition in the variation partitioning method were the predictors. The land cover characteristics (LAND1 and LAND2), the area of the woodlots (AREA) and the PCo axes scores were used in the CCAs as covariables. The response variables were log-transformed, and the rare species were downweighted in all of the CCAs. To show species affinity to the main type of habitat structure, four categories were visualized in the ordination diagrams (for details, see section 2.2.). All of the multivariate analyses were performed in CANOCO 5.0 (ter Braak & Šmilauer, 2012).

3 | RESULTS

3.1 | Vegetation and land cover characteristics of the native and *Robinia* woodlots

PC1 axis of the habitat characteristics (HAB1, 33.16% of the variation in the habitat structure explained) described the gradient from woodlots with larger trees, a more developed shrub layer and a continuous canopy to more open woodlots with smaller and thinner trees, a more developed taller herb layer and a higher number of dead trees (see Figure S1.2 in Appendix S1 and Figure 2a). The *Robinia* woodlots had significantly higher scores along the gradient of HAB1 than the native woodlots ($t = 4.814, p < .001$; Figure 2a). PC2 axis of the habitat characteristics (HAB2, 14.39% of the variation in the habitat structure explained) reflected the gradient from woodlots with larger clearing areas, younger trees and a more developed lower herb layer to woodlots with older and taller trees (Figure 2a). The native and *Robinia* woodlots did not differ along the gradient of HAB2 ($t = 0.086, p = .932$).

Regarding the surrounding land cover characteristics, PC1 axis (LAND1, 45.86% of the variation in the land cover structure explained) reflected the gradient from landscapes with a larger proportion of arable fields to landscapes with a higher proportion of non-crop habitats, such as coniferous woodlands, urban areas and grasslands (Figure 2b). PC2 axis of the surrounding land cover characteristics (LAND2, 20.64% of the variation in the land cover structure explained) mainly described the gradient from landscapes with a larger proportion of wetlands, exposed rocks and broadleaved forests to landscapes without these habitats (Figure 2b). The native and *Robinia* woodlots did not differ along their land cover gradients (Figure 2b).

3.2 | Arthropod abundance and species richness

Altogether, 62,133 individuals (see Table S1.1 in Appendix S1) of 989 arthropod species (742 species in native/767 in *Robinia*/523 shared by both woodlot types) were recorded (see Appendix S2 and Table S1.2 in Appendix S1). As indicated by the GLMs with WOODLOT

TYPE as the only predictor, the total abundance of arthropods in the *Robinia* woodlots (mean \pm SD = 1,782 \pm 479) was lower than that in the native woodlots (2,665 \pm 887; $z = -3.497, p < .001$), while the total species richness did not differ between the *Robinia* (mean \pm SD = 217 \pm 22) and native woodlots (220 \pm 28; $z = 0.542, p = .588$). Overall, 89 of the species recorded (ca. 10% of all species; 28 in native/38 in *Robinia*/28 in both) are included in the national red lists.

The more detailed analyses considering habitat characteristics showed a significant negative relationship between the presence of *R. pseudoacacia* and both the total abundance and the total species richness of arthropods (Table 1). The total species richness also increased along the gradients of HAB1 (towards a more developed taller herb layer, a more open canopy and a higher number of dead trees) and LAND2 (towards a higher proportion of broadleaved forests and water habitats in the vicinity of the woodlots) (Table 1). Based on the GLMs for the particular taxa, *R. pseudoacacia* was negatively related to the abundances of Carabidae, Curculionoidea and Lepidoptera and the species richness of Lepidoptera. Inversely, the abundance of Elateridae and the species richness of Heteroptera were positively linked to the presence of *R. pseudoacacia*. For the remaining arthropod taxa, no relationship between TREE TYPE and the abundances or species richness was found (Table 1).

Habitat structure had significant effects on the arthropod communities. Specifically, the abundances of Curculionoidea, Heteroptera and Silphidae and the species richness of Arachnida, Heteroptera and Lepidoptera significantly increased along the gradient of HAB1 (higher with a more developed taller herb layer, a more open canopy and a higher number of dead trees) (Table 1). In the woodlots with more developed shrub and canopy layers and larger trees, the abundance of Neuroptera increased (Table 1). Furthermore, the abundance of Elateridae significantly decreased along the gradient of HAB2 (younger woodlots with a high proportion of clearings in the canopy and lower trees) (Table 1). By contrast, the species richness of Heteroptera increased along the gradient of HAB 2 (Table 1).

The land cover in the surrounding landscape also contributed to the variation in the arthropod communities. Along the gradient of

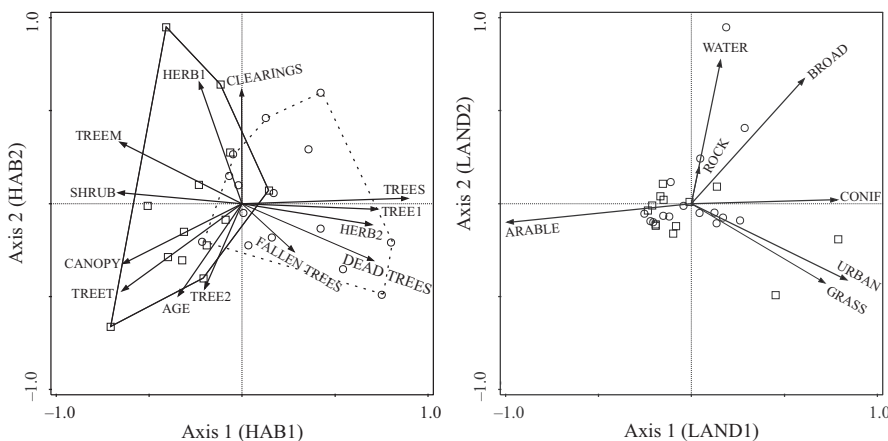


FIGURE 2 Principal components analysis (PCA) of (a) habitat structure and (b) land cover characteristics between the native and *Robinia* woodlots. Polygons indicate convex hulls bounding the native and *Robinia* plots

LAND1, the abundances of Elateridae were higher in the woodlots surrounded by a higher proportion of non-crop habitats (Table 1), while a higher proportion of arable land favoured the abundance of Silphidae (Table 1). Along the gradient of LAND2, a higher proportion of broadleaved forests and water habitats around the woodlots was positively related to the species richness of Diplopoda and Lepidoptera. AREA was positively correlated with the abundance of Arachnida and Elateridae (Table 1). No significant relationship between any of the predictors and the abundance and species richness of Staphylinidae and Orthoptera, the abundance of Diplopoda and the species richness of Carabidae, Curculionoidea, Elateridae, Chilopoda and Silphidae were detected (Table 1).

3.3 | Arthropod species composition

The *Robinia* woodlots were more heterogeneous in their overall arthropod species composition and differed from the native woodlots (pseudo- $F = 2.8$, $p < .001$; see Figure S1.3 in Appendix S1). For most of the taxa, significant marginal effects of habitat structure on the species compositions were found (see Table S1.3 in Appendix S1). For the majority of these taxa, conditional effects of the dominant tree species and habitat structure were still significant (except for Diplopoda), but the percentage of explained variance was rather low compared to that of the marginal effects (see Table S1.3 in Appendix S1). Moreover, the species compositions of particular taxa (except for Neuroptera, Orthoptera and Silphidae) were significantly different between the native and *Robinia* woodlots (Table 2) after controlling for spatial (PCo scores from the PCNMs) and environmental variables (LAND1, LAND2 and AREA). Forest specialists occurred primarily in the native woodlots and were more frequent in the woodlots characterized by a more developed canopy and shrub

layer (decreasing HAB1; Figure 3). In contrast, open-habitat species were more frequent in the *Robinia* woodlots, with the exception of Carabidae (Figure 3), and preferred woodlots with more developed taller herb layers, more open canopies and a higher number of dead trees (increasing HAB1). These trends were also evident in the majority of the threatened species with an affinity for a given habitat structure type. The majority of the predominantly herbivorous taxa (Curculionoidea, Heteroptera and Lepidoptera), which are typical of scattered greenery, were more abundant in the native woodlots (Figure 3).

4 | DISCUSSION

This study shows conservation value of woodlots scattered throughout agricultural fields. Woodlots formed by the native tree species hosted different arthropod communities compared with the woodlots formed by the invasive *R. pseudoacacia*. It was found that both woodlot types hosted red-listed species, and form an important reservoir of arthropod biodiversity in intensively managed agricultural landscapes. In contrast to existing studies, this study analysed not only identity of dominant trees (woodlots dominated by invasive vs. native trees; Litt et al., 2014; van Hengstum et al., 2014), but included also woodlot habitat structure and other environmental characteristics in the analyses. Interestingly, more complicated models were able to reveal negative relationship between the presence of *R. pseudoacacia* and the overall arthropod species richness after correcting for differences in habitat structure. Such difference was undetectable when simple models were applied.

The negative relationship between the presence of *R. pseudoacacia* and the total arthropod abundance and species richness

TABLE 2 Results of the canonical correspondence analyses (CCAs) showing differences in the species composition of the studied taxa between the native and *Robinia* woodlots

Taxa	Adj. VAR ^a %	Pseudo-F	Axis 1	Axis 2	Axis 3	Axis 4	Trace	<i>p</i>
Arachnida ^b	11.6	2.0	0.206	0.064	0.057	0.116	0.327	.001
Carabidae ^b	10.0	1.9	0.137	0.064	0.050	0.107	0.251	.001
Curculionoidea ^b	10.5	1.9	0.317	0.123	0.063	0.342	0.503	.001
Diplopoda ^b	3.9	1.9	0.103	0.264	0.207	0.157	0.103	.029
Elateridae ^b	21.3	3.1	0.228	0.037	0.017	0.131	0.282	.001
Heteroptera ^b	10.7	1.9	0.289	0.116	0.091	0.196	0.496	.001
Chilopoda	5.0	2.3	0.078	0.168	0.092	0.083	0.078	.040
Lepidoptera ^b	6.4	1.6	0.132	0.059	0.038	0.101	0.229	.001
Neuroptera	0.0	0.5	0.025	0.233	0.177	0.140	0.025	.896
Orthoptera	0.0	0.5	0.032	0.493	0.296	0.204	0.032	.813
Silphidae	2.3	1.5	0.209	0.685	0.535	0.439	0.209	.149
Staphylinidae ^b	5.3	1.4	0.147	0.103	0.060	0.160	0.310	.002

Note: The effects of habitat structure (HAB1 and HAB2) were included in case of their significance for particular taxa. All of the CCAs were controlled for the environmental (LAND1, LAND2 and AREA) and spatial effects (PCo scores from PCNMs). The significant effects ($p < .05$) are highlighted in bold.

^aAdj. VAR (%): adjusted percent variance explained by the predictors.

^bHabitat structure (HAB1, HAB2) was included in the analyses.

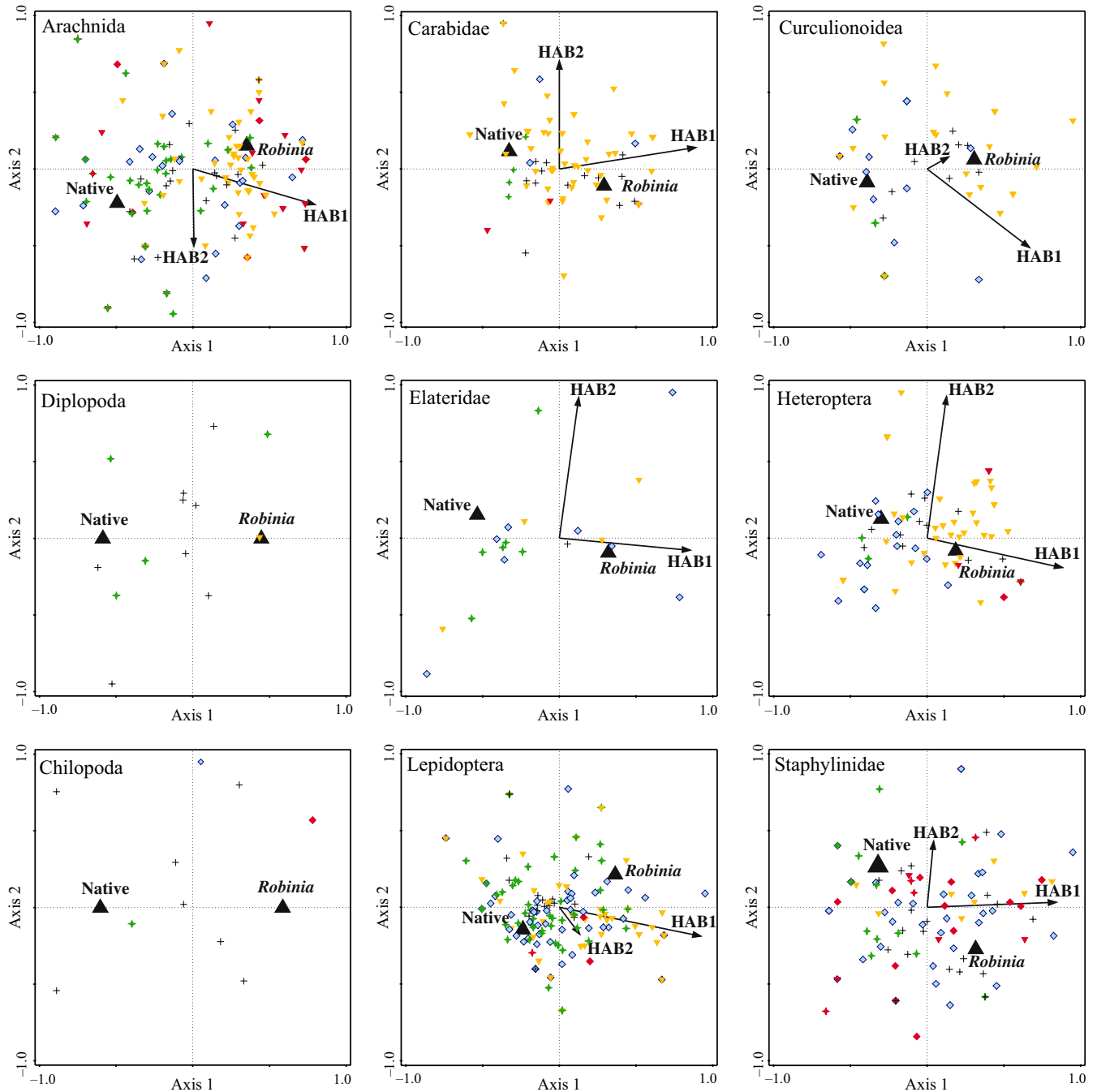


FIGURE 3 Canonical correspondence diagrams showing the species distribution of the studied taxa between the native and *Robinia* woodlots. The effects of habitat structure (HAB1 and HAB2) were included in case of their significance for particular taxa. Only the best fitting species (>5%) in the ordination models are displayed. The symbols refer to forest specialists: green stars; species bounded to scattered greenery: blue diamonds; open-habitat species: yellow down triangles; and habitat generalists: black crosses. Red-listed species are displayed by red-coloured symbols. See Table 2 for model details

is in accordance with the recent findings of the general impacts of invasive plants on arthropods (Degomez & Wagner, 2001; van Hengstum et al., 2014; Litt et al., 2014). These relationships could be mainly attributed to the lower frequency of herbivores (mainly Curculionoidea and Lepidoptera) in the total samples. Indeed, herbivores are generally the most negatively influenced arthropod guild by plant invasions due to the replacement of their host plants by

unpalatable novel species (van Hengstum et al., 2014; Litt et al., 2014; Liu & Stiling, 2006).

Robinia and native woodlots differed significantly in their habitat structure, which may be another key driver for the observed differences in the arthropod communities. A higher total arthropod species richness was found in the woodlots with a more open canopy, a higher coverage of taller herbs and a higher number of

dead trees (represented by increasing HAB1). Such habitat structure (more common in the *Robinia* woodlots) offers a more irradiated and warmer understorey due to higher amounts of solar radiation penetrating through the canopy layer (Cierjacks et al., 2013; Vítková et al., 2017; Xu et al., 2009). Contrary to the recent findings from larger *R. pseudoacacia* forests (Buchholz et al., 2015; Kadlec et al., 2018), the shrub layer was better developed in the native woodlots. The majority of the *Robinia* woodlots in this study could be included in phytocoenological units dominated by well-competitive grasses (e.g. false oat-grass, *Arrhenatherum elatius* (L.) J. Presl et C. Presl) in their understories, which could effectively suppress shrub seedlings (Campagnaro, Nascimbene, et al., 2018; Vítková & Kolbek, 2010; Vítková et al., 2017). This effect could be enhanced by heat and water stress in the understorey caused by *R. pseudoacacia* (Xu et al., 2009). Arthropods linked to such insolated understorey vegetation in the *Robinia* woodlots could partly compensate for loss of forest canopy herbivores due to plant invasion (Kulfan, 2012; Litt et al., 2014; Liu & Stiling, 2006) by filling new available niches (e.g. insolated herbs, rotten wood; Highland et al., 2013; Tews et al., 2004). Nevertheless, the above-mentioned direct negative relationship between the presence of *R. pseudoacacia* and herbivorous Lepidoptera and Curculionoidea was stronger than the effect of changes in vegetation structure. This was probably caused by a higher contribution of herbivorous canopy specialists within the moth assemblages (Kadlec et al., 2018) and high abundances of Curculionoidea exploiting broad-leaved trees in the native woodlots (Koch, 1992), but not able to feed on exotic *Robinia* (Kulfan, 2012; Litt et al., 2014; Liu & Stiling, 2006). By contrast, higher abundance of Elateridae and abundance and species richness of Heteroptera is probably linked to the habitat structure as many open-habitat specialists were present mainly in the *Robinia* woodlots. Similarly, Buchholz et al. (2015) found an increased abundance of Heteroptera within stands with a more open canopy. Simultaneously, Elateridae had higher abundances in the woodlots with older and larger trees (represented by negative HAB2 scores), probably due to the higher occurrence of xylophagous species in such conditions (Irmeler, Heller, & Warning, 1996).

No direct relationship between the presence of *R. pseudoacacia* and the abundance and species richness of carnivorous taxa was found, except for Carabidae. This is in accordance with the weak impact of woody invaders on carnivorous arthropods that have been found elsewhere (Buchholz et al., 2015; Litt et al., 2014; Van der Colff et al., 2015). The lower abundance of carabids in the *Robinia* woodlots is surprising, as it contradicts the earlier findings from *R. pseudoacacia* forests (Buchholz et al., 2015). We suppose that carabids benefit from the more favourable microclimate in the native woodlots, in which relatively greater humidity may support more ample food resources, such as springtails, earthworms and gastropods. Similar to our results, Knapp and Řezáč (2015) found a higher species richness of Arachnida in more open woodlots with increased herb cover. Conversely, Buchholz et al. (2015) did not find a similar trend in *R. pseudoacacia* forests. The abundance of

Neuroptera increased with increasing canopy and shrub coverage (represented by decreasing HAB1). This can be explained by the availability of their main prey, aphids, which are more abundant and species rich in woodlots with more diverse ranges of native tree species and more developed shrub layers. According to Holman (2009), *R. pseudoacacia* hosts only 16 species of aphids, a much lower number of species compared with native tree species frequently grown in woodlots (e.g. 39 species on common oak (*Quercus robur* L.) or 25 species on sessile oak (*Quercus petraea* Matusch)).

The abundance and species richness of detritivorous Diplopoda did not differ between the two woodlot types. A high amount of nitrogen in the *R. pseudoacacia* litter (Tateno et al., 2007) and more decaying vegetation in its understorey (Vítková et al., 2017) could compensate for the lack of leaf litter from the native tree species. Detritivorous arthropods are often even positively influenced by plant invasions (Harris et al., 2004; Litt et al., 2014), but it has not been shown in the case of *Robinia* woodlots or in large *R. pseudoacacia* forests (Buchholz et al., 2015).

The surrounding land cover composition was also significantly linked to the woodlot arthropod assemblages. Increasing proportions of broadleaved forest (decreasing rates of woodlot isolation; Baz & Garcia-Boyer, 1995; Torma et al., 2014) and wetlands (represented by LAND2) in the vicinity of the woodlots were positively related to the total arthropod species richness. In contrast to generally positive species–area relationship (Mac Arthur & Wilson, 1967) as well as the previous examinations of species–area relationships for woodlot arthropods (Baz & Garcia-Boyer, 1995; Knapp & Řezáč, 2015), the woodlot area was not linked to the species richness and abundance of almost any of the investigated arthropod taxa in our study. This could be caused by a limited variation in sizes of our woodlots (0.11–1.31 ha). Nevertheless, within a limited range of areas, the effects of vegetation cover and habitat structure may outweigh the importance of area (see also Knapp & Řezáč, 2015; Torma et al., 2014).

Similar to the species richness and the abundance of the target groups, the differences in habitat structure between the native and *Robinia* woodlots were also reflected in the species composition of the arthropods. Across all trophic levels and specialized threatened species, the forest specialists were linked to the native woodlots, while the majority of the open-habitat species were predominantly restricted to the *Robinia* woodlots. Similar to large forests (Kadlec et al., 2018), forest specialists could find more favourable nutritional or microclimatic conditions in the stands formed by native tree species. On the other hand, a more open-habitat structure with a well developed herb layer in the *Robinia* woodlots provides higher niche diversity for the species that require different types of grasslands, early succession stages and arable land, including the red-listed species. A portion of these species were steppe specialists, which could benefit from a warmer and drier microclimate in the herb layer of the *Robinia* woodlots in summer conditions (Kadlec et al., 2018; Vítková et al., 2017; Xu et al., 2009).

5 | CONCLUSIONS

The results of this multi-taxonomic study covering various trophic levels highlight the importance of habitat structure in assessments of the impacts of tree invasion on native arthropod communities. Despite their small size, the forest islands isolated within the intensively managed agricultural landscapes of Central Europe host diverse arthropod assemblages and are enriched by a considerable number of threatened species. Although *R. pseudoacacia* is considered one of the most harmful invasive trees for native ecosystems (Campagnaro, Brundu, et al., 2018; Vítková et al., 2017), our study on the arthropod assemblages in woodlots does not fully support this view. Due to their more open-habitat structure, the *Robinia* woodlots support open-habitat arthropod species, including endangered specialists. These specialists could also use woodlots as short-term refuges or shelters during agricultural disturbances in the arable fields. Nevertheless, the majority of forest specialists, including canopy herbivores, were negatively influenced by *R. pseudoacacia* and were more common in the native woodlots. Thus, presence of *Robinia* and native woodlots scattered across intensively managed arable fields deliver substantial support for arthropod biodiversity and provide refuges for arthropods with different ecological and trophic requirements. Moreover, forest management of small woodlots supporting biodiversity is limited due to their isolation by arable land. The habitat structure of the native woodlots could turn to shaded dense stands in later successional stages, whereas similarly old *Robinia* woodlots form spontaneously more open stands (Vítková et al., 2017) inhabited by different arthropod assemblages. Moreover, due to the limited spreading of *R. pseudoacacia* (Cierjacks et al., 2013; Vítková et al., 2017) from isolated woodlots, its negative impact on more valuable native habitats in the surroundings is minimized. For these reasons, we conclude there is no need for eradicating *R. pseudoacacia* from existing woodlots within agricultural landscapes, as has been recommended for valuable native habitats (Campagnaro, Brundu, et al., 2018; Cierjacks et al., 2013; Vítková et al., 2017).

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DATA AVAILABILITY STATEMENT

The data are provided in the Supporting Information.

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SUPPORTING INFORMATION

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BIOSKETCH

The authors' research interests include the ecology of arthropods, invasion ecology, community ecology, biodiversity conservation and agroecology. Various members of the research team focus on the ecology of target arthropod groups in this study: M.Š. and T.K. focus on Lepidoptera; P.S., M.S. and M.K.A. focus on Carabidae; M.K.O. focuses on Staphylinidae; K.T. focuses on Chilopoda and Diplopoda; M.Ř. focuses on Arachnida; J.S. focuses on Curculionidae; P.M. focuses on Orthoptera and Neuroptera; B.Z. focuses on Elateridae and P.J. focuses on Silphidae.

Author contributions: M.Š., T.K. and P.S. conceived basic idea and designed the study; M.Š., T.K. and M.S. collected the samples; all the authors determined the arthropods; M.Š. analysed the data; M.Š., T.K., P.S. and M.K.A. drafted the manuscript. All authors have been involved in an interpreting the data and contributed to early drafts.