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Ekologie a diverzita členovců v porostech invazních dřevin

Ecology and diversity of arthropods in stands of invasive woody plants

Disertační práce

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ploštic ve spolupráci s Ondřejem Balvínem a Petrem Kmentem. Tiitovi Tederovi děkuji za konstruktivní komentáře a jazykovou korekturu mého prvoautorského článku.

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Abstrakt

Biologické invaze jsou považovány za jeden z hlavních faktorů recentně sledovaného globálního úbytku členovců. Z pohledu biologických invazí mají zásadní dopad na pokles členovců rostlinné invaze a zejména invazní dřeviny, které mají na původní společenstva členovců obecně větší dopad než invazní byliny. Dopady invazních dřevin na členovce se liší mezi jednotlivými skupinami členovců v závislosti na výběru studovaných taxonů. Rovněž není skoro vůbec prostudován jejich vliv na strukturu potravních řetězců a téměř úplně chybí informace o jejich významu pro biodiverzitu členovců v intenzivní zemědělské krajině.

Tato práce se prostřednictvím multi-taxonomického přístupu snaží na danou problematiku nahlížet komplexně, a sestává se z dílčích studií, ve kterých figuruje především invazní trnovník akát (*Robinia pseudoacacia* L.) jako modelový druh nepůvodní dřeviny. Trnovník akát je jednou z nejrozšířenějších invazních dřevin v Evropě i v ČR, a i když je poměrně detailně znám jeho vliv na původní rostlinná společenstva, jeho dopady na společenstva členovců nebyly dosud příliš studovány. Členovci byli odchytáváni prostřednictvím několika metod sběru – pomocí světelných lapačů, zemních pastí a smýkání vegetace. Rovněž byla studována vegetační struktura porostů trnovníku akátu a analyzován její vliv na společenstva členovců.

Prostřednictvím multi-taxonomického přístupu jsme zaznamenali jednak negativní vliv trnovníku akátu na celkovou abundanci i biomasu členovců v souvislých lesních celcích, tak jsme rovněž prokázali jeho negativní dopad na celkovou abundanci i celkový počet druhů členovců v izolovaných lesních fragmentech situovaných v intenzivní zemědělské krajině, v porovnání s porosty tvořenými původními druhy listnatých dřevin. Tyto výsledky souvisí zejména se zjištěným úbytkem druhové diverzity, abundance a biomasy herbivorního hmyzu v porostech trnovníku akátu. Většina druhů herbivorního hmyzu vázaných na korunové patro se totiž pravděpodobně nebyla schopna troficky adaptovat na nepůvodní trnovník akát, jelikož s ním během evoluce vlivem přirozených bariér nepřišly do styku. Rovněž jsme nezjistili průkazný rozdíl v celkové abundanci i biomasy členovců mezi porosty nepůvodní borovice černé (*Pinus nigra* Arnold) a kongenerické původní borovice lesní (*Pinus sylvestris* L.).

Vegetační struktura porostů trnovníku akátu se průkazně lišila v porovnání s porosty původních druhů listnatých dřevin. Trnovník akát vytváří světlé porosty s nezapojeným korunovým patrem a velmi dobře vyvinutým podrostem. Naopak porosty původních dřevin měly oproti akátovým porostům velmi dobře vyvinuté a zapojené korunové patro. Proto lesní specialisté napříč taxony s různou trofickou specializací převládali v porostech původních dřevin. Naopak druhy otevřených biotopů převládaly v akátových fragmentech s dobře

vyvinutým vyšším bylinným patrem. Tyto druhy zde dokázaly částečně nahradit ztrátu diverzity způsobenou úbytkem herbivorů korunového patra a lesních specialistů. Rovněž byla prokázána vyšší funkční diverzita nočních motýlů v souvislých lesních porostech trnovníku akátu v porovnání s porosty původních druhů dřevin. V neposlední řadě byl prokázán kaskádový efekt trnovníku akátu na diverzitu ptáků prostřednictvím úbytku diverzity nočních motýlů v souvislých lesních porostech. Ten souvisel zejména s poklesem diverzity habitatových specialistů v důsledku úbytku diverzity nočních motýlů vázaných na korunové patro.

Invazní trnovník akát obecně negativně působil převážně na hmyzí herbivory a lesní specialisty, což vedlo zejména v souvislých lesních porostech k poklesu celkové abundance, diverzity i biomasy členovců. Na druhou stranu prostřednictvím své vegetační struktury vytváří vhodné porosty pro druhy členovců vázaných na otevřené a lesostepní biotopy, které v porostech původních druhů listnatých dřevin chyběly nebo byly pouze minoritně zastoupeny. V zemědělské krajině sloužily fragmenty akátových porostů dokonce jako refugium diverzity mnoha ohrožených druhů členovců s vazbou na otevřené biotopy. Tato skutečnost poukazuje na palčivý problém v managementu nížinných lesů v České republice, a to zejména v chráněných územích. Většina původně rozvolněných a diverzifikovaných nížinných lesů v ČR se postupně transformovala v zapojené stinné lesní porosty, ve kterých nemohou společenstva členovců vázaná na otevřené lesní porosty prosperovat. Z tohoto důvodu doporučuji trnovník akát tolerovat jako součást izolovaných neprodukčních biotopů situovaných v intenzivně obhospodařované zemědělské krajině. V běžných hospodářských, a zejména biologicky cennějších lesích, by bylo vhodné trnovník akát postupně nahradit původními druhy dřevin a obecně zlepšit strukturu nížinných lesů v ČR.

Klíčová slova

Invazní rostliny, biodiverzita, ekologie společenstev, interakce rostlin a členovců, *Robinia pseudoacacia*, trofické interakce, Arthropoda.

Abstract

Biological invasions are considered as one of the main factors causing recent global decline of arthropods. It is generally perceived that invasive woody plants have greater effect on local native arthropod communities than invasive herbs. The observed impacts of woody invaders on arthropods differ among studies and depend on the choice of the taxon studied. Also, their effect on food webs has rarely been studied, and the knowledge about the impact of woody invaders for arthropod biodiversity in intensive agricultural landscapes is almost missing.

This thesis, adopting the multi-taxonomic approach, tries to look at this problem comprehensively. It consists of several studies, in which the invasive black locust (*Robinia pseudoacacia* L.) has been a model species of the non-native tree species. Black locust is one of the most widespread invasive tree species in Europe, including the Czech Republic, and although its effects on native plant communities are well known, its effects on arthropod communities have not been sufficiently studied. Arthropods were captured using multiple sampling methods – light trapping, pitfall trapping and sweep-netting. The vegetation structure of the black locust stands was also studied and its influence on arthropod communities was analysed.

Using the multi-taxonomic approach, we recorded a negative effect of black locust on the overall abundance and biomass of arthropods in continuous forests, and we also showed its negative impact on the total abundance and the total number of arthropod species in isolated woodlots situated in intensive agricultural landscape, in comparison with stands formed by native deciduous tree species. These results are mainly related to the observed loss of species diversity, abundance, and biomass of herbivorous insects in the black locust stands. Most species of insect herbivores bound to forest canopy were probably not able to adapt to feeding on black locust, because the natural barriers during the evolution of species prevented this adaptation. We neither found a significant difference in the total abundance and biomass of arthropods between the stands of non-native black pine (*Pinus nigra* Arnold) and congeneric native forest pine stands (*Pinus sylvestris* L.).

The vegetation structure of the black locust stands was significantly different in comparison with the stands of the native deciduous tree species. Black locust creates open stands with less developed and unclosed canopy and a very well-developed understorey. On the contrary, the stands of the native tree species form a very well developed and closed canopy in comparison with the black locust stands. Therefore, forest specialists across the taxa with different trophic specialization predominated in the stands of the native tree species, while open habitat

specialists predominated in the black locust stands with a well-developed higher herb layer. These species were able to partly compensate for the loss of diversity caused by the decline of herbivores specialized for canopy and forest specialists. Higher functional diversity of moths in continuous forests formed of the black locust was also detected in comparison with the stands of native tree species. Lastly, cascading effect of the black locust on bird diversity was demonstrated through the loss of moth diversity in continuous forest stands, which was mainly related to the decline in diversity of bird habitat specialists caused by the decrease in diversity of moths associated with canopy.

Invasive black locust generally had a negative effect on insect herbivores and forest specialists, which led to a decrease in the overall abundance, diversity, and biomass of arthropods, especially in continuous forest stands. On the other hand, through the vegetation structure, black locust creates suitable habitats for arthropod species associated with open and forest-steppe habitats, which were otherwise missing or only weakly represented in the stands of the native tree species. In the agricultural landscape, black locust woodlots were found to serve as a refuge for the diversity of many endangered arthropod species otherwise associated with open habitats. This fact points to the prickly problem in the management of lowland woodlands in the Czech Republic, especially in protected areas. Most of the originally open and diversified lowland forests in the Czech Republic have been gradually transformed into the continuous shady forests, where arthropod communities associated with open forests could not persist. Thus, I recommend tolerating black locust in isolated non-crop habitats situated in intensively managed agricultural landscapes. Otherwise, in commercial and especially in biologically valuable woodlands, black locust shall be gradually replaced by native tree species, and the structure of the native lowland forests should be generally improved in the Czech Republic.

Keywords

Obsah

1. Úvod

Členovci (Arthropoda) patří mezi nejpočetnější a druhově nejbohatší skupinu organismů na světě (Stork, 2018; Ødegaard, 2000) poskytující lidské společnosti řadu nenahraditelných ekosystémových služeb, jako je např. opylování (Dainese et al., 2019; Farwig et al., 2009; Klein et al., 2007), biologická regulace škůdců (Dainese et al., 2019; Landis et al., 2000) a plevelů (Bohan et al., 2011; Carbonne et al., 2020) či dekompozice organické hmoty (Culliney, 2013). V posledních letech bylo publikováno mnoho studií dokumentující masivní úbytek početnosti, druhové bohatosti, biomasy i funkční diverzity členovců napříč ekosystémy (např. Cardoso et al., 2020; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019). Právě členovci tvoří nepostradatelný prvek trofických interakcí v ekosystémech (Mooney et al., 2010; Wagner, 2020) a jejich úbytek se negativně promítá do početností i diverzity vyšších trofických úrovní, například hmyzožravých ptáků či netopýrů (Bowler et al., 2019; Wagner, 2020). Za hlavní důvody tzv. vymírání hmyzu jsou považovány zejména tyto antropogenní příčiny: ztráta a homogenizace přírodních habitatů, intenzifikace zemědělství, znečištění prostředí polutanty, klimatické změny, urbanizace a biologické invaze (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). Z pohledu biologických invazí mají zásadní dopad na pokles členovců rostlinné invaze (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Tallamy et al., 2020; Wagner, 2020).

Rostlinné invaze jsou všeobecně pokládány za jednu z hrozeb ohrožujících diverzitu organismů na Zemi (Mack et al., 2000; Pauchard & Shea, 2006; Pyšek, Jarošík, et al., 2012; Van Kleunen et al., 2015) s širokými ekologickými, ekonomickými i sociálními dopady v přírodních i člověkem pozměněných ekosystémech (Mack et al., 2000; Simberloff et al., 2013; Vilà et al., 2011). Dopady invazních rostlin (sensu Richardson et al., 2000) jsou recentně hojně studovány jednak na lokální, regionální, ale i globální úrovni, a jejich konsekvence pro původní biotu vždy závisí na konkrétním kontextu invadovaných společenstev (Pyšek et al., 2020; Pyšek, Jarošík, et al., 2012; van Hengstum et al., 2014; Vilà et al., 2011). Invazní rostliny svými invazními vlastnostmi zásadně mění stanovištní podmínky (Ehrenfeld, 2003; Hierro & Callaway, 2003; Vilà et al., 2011), čímž ovlivňují diverzitu, strukturu a produktivitu původních rostlinných společenstev (Chambers et al., 2007; Ehrenfeld, 2003; Hejda et al., 2009; Jäger et al., 2009; Vilà et al., 2011), i mají dopad na fitness původních druhů rostlin (Vilà et al., 2011). Vlivem výše uvedených vlivů invazní rostliny podstatně přeměňují strukturu vegetace

invadovaných habitatů (Crooks, 2002; Hanzelka & Reif, 2016; Harris et al., 2004; Šibíková et al., 2019). Zmíněné dopady invazních rostlin na rostlinná společenstva a vegetační strukturu habitatu se obecně negativně promítají do snížení diverzity, abundance a změn ve struktuře společenstvech členovců (Bezemer et al., 2014; Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014). V konečném důsledku mohou invazní rostliny významně narušovat trofickou strukturu v ekosystémech (Bezemer et al., 2014; Levin et al., 2006; Schirmel et al., 2016; Tallamy, Ballard, & Amico, 2010; Vilà et al., 2011).

Výsledky globálních studií (Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014) sice hovoří o převážně negativním impaktu invazních rostlin na společenstva členovců, avšak zároveň referují, že jejich dopady se často zásadně liší mezi jednotlivými taxony a trofickými gildami členovců. Herbivorní hmyz a opylovači koevolučně úzce spjatí s hostitelskými rostlinami jsou nejvíce negativně ovlivněnými gildami členovců (Bezemer et al., 2014; Litt et al., 2014; Moroń et al., 2009). Herbivoři se jednak v naprosté většině nejsou schopni troficky adaptovat nepůvodní invazní rostlině, jelikož s ní během evoluce vlivem přirozených bariér nepřišli do styku (Bezemer et al., 2014; Keane & Crawley, 2002; Liu & Stiling, 2006), a rovněž nepřímo přicházejí o hostitelské rostliny v důsledku poklesu rostlinné diverzity v invadovaných habitatech (Litt et al., 2014; Simao et al., 2010; van Hengstum et al., 2014). Invazní rostliny mají také obvykle negativní vliv na parazitoidy kvůli jejich sníženým možnostem najít svého hostitele v důsledku redukce početnosti herbivorů (Harvey & Fortuna, 2012; Simao et al., 2010). Naopak efekt invazních rostlin na ostatní karnivorní členovce není vždy jednoznačný. Predátoři obvykle negativně reagují na sníženou dostupnost kořisti zejména kvůli úbytku herbivorů (Litt et al., 2014; Simao et al., 2010), na druhou stranu mnohdy dokáží profitovat ze změny vegetační struktury habitatu způsobenou invazní rostlinou (Litt et al., 2014; Pearson, 2009, van Hengstum et al., 2014). Detritovorní členovci jsou obecně nejméně ovlivněnou gildou členovců, naopak invazní rostliny mají na jejich abundanci i diverzitu veskrze pozitivní efekt (Van der Colff et al., 2015; Harris et al., 2004; Litt et al., 2014; Schirmel et al., 2016; van Hengstum et al., 2014).

Mezi invazními rostlinami jsou obzvláště důležité dopady invazních dřevin na původní biotu. Jelikož jsou dřeviny silnými ekosystémovými inženýry, mají invazní dřeviny klíčový vliv na změnu environmentálních podmínek invadovaných habitatů, a vlivem silné interspecifické kompetice mají negativní dopad na původní rostlinná společenstva (Ehrenfeld, 2003; Hierro & Callaway, 2003; Richardson & Rejmánek, 2011). Řada invazních dřevin dokáže fixovat vzdušný dusík (Ehrenfeld, 2003; Vilà et al., 2011), některé také mohou využívat princip alelopatie (Hierro & Callaway, 2003), a v důsledku těchto konkurenčních výhod dochází

k homogenizaci rostlinných společenstev (Benesperi et al., 2012; Šibíková et al., 2019). Invazní dřeviny mají i v důsledku výše uvedených důvodů podstatně větší dopady na společenstva členovců než invazní byliny (Tallamy et al., 2020; van Hengstum et al., 2014), které jsou však rovněž mnohdy spojeny s pozměněnou vegetační strukturou invadovaného habitatu (Harris et al., 2004; Pawson et al., 2010; van Hengstum et al., 2014).

Trnovník akát (*Robinia pseudoacia* L.) je invazní dřevina původem ze severovýchodní části USA (Cierjacks et al., 2013; Huntley, 1990; Vítková et al., 2017), která patří mezi 40 celosvětově nejinvazivnějších druhů dřevin (Richardson & Rejmánek, 2011). V Evropě je trnovník akát jedna z nejpěstovanější invazních dřevin v Evropě s jedním z největších dopadů na původní společenstva (Campagnaro, Brundu et al., 2018; Cierjacks et al., 2013; Vítková et al., 2017). V České republice patří mezi hlavní invazní rostliny a zároveň je nejrozšířenější invazní dřevinou se zásadním dopadem na biotu v České republice s širokým areálem výskytu v nížinných a středních polohách České republiky (Pyšek, Chytrý, et al., 2012; Pyšek, Danihelka, 2012; Vítková et al., 2017). Přestože je dobře prozkoumán vliv trnovníku akátu na stanovištním podmínky (např. Cierjacks et al., 2013; Vítková et al., 2015) a rostlinná společenstva (např. Benesperi et al., 2012; Slabejová et al., 2019; Vítková & Kolbek, 2010), o jeho dopadech na společenstva členovců se toho doposud mnoho neví (Vítková et al., 2017). Recentně bylo publikováno jen několik málo studií (Buchholz et al., 2015; Degomez & Wagner, 2001; Della Rocca et al., 2016; Zhu et al., 2019), které ale dostatečně komplexní informace o vlivu invazního trnovníku akátu na společenstva členovců neposkytují. Proto se nabízí volit trnovník akát jako modelovou studijní dřevinu pro výzkum ekologie a diverzity společenstvech členovců v porostech invazních dřevin v prostředí České republiky.

Obecným záměrem této práce je přispět k rozšíření poznatků o tom, jak se mohou invazní dřeviny podílet na celosvětovém úbytku členovců (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Tallamy et al., 2020; Wagner, 2020) prostřednictvích jejich dopadů na společenstva členovců na lokální úrovni. Konkrétním cílem této disertační práce je především přinést komplexní poznatky zejména o dopadech invazního trnovníku akátu, jakožto modelové nepůvodní dřeviny, na společenstva členovců a jejich konsekvencích pro další trofické úrovně, zejména ptáky. Dopady dřevinných invazí napříč různými taxonomickými skupinami členovců byly recentně hojně studovány (např. Buchholz et al., 2015; Van der Colff et al., 2015; Harris et al., 2004; Hartley et al., 2010; Pawson et al., 2010), avšak stále relativně malý počet studií (Buchholz et al., 2015; Harris et al., 2004; Pawson et al., 2010) se zabýval nepřímými dopady dřevinných invazí na členovce prostřednictvím změny vegetační struktury habitatu, a to i přestože je všeobecně známo, že struktura habitatu je pro členovce klíčovou determinantou pro

jejich výskyt v lesních porostech (Highland et al., 2013; Ober & Hayes, 2008; Sebek et al., 2015; Tews et al., 2004). Z tohoto důvodu byla vegetační struktura habitatu v našich jednotlivých studiích, které tvoří tuto práci, zahrnuta jako jeden ze základních faktorů určujících dopady invazní dřeviny na společenstva členovců. Jelikož se dopady invazních dřevin na různé taxonomické skupiny a trofické gildy členovců mohou velmi lišit (Litt et al., 2014; Schirmel et al., 2016; van Hengstum et al., 2014), bylo naší snahou v jednotlivých výzkumech co nejvíce využívat multi-taxonomický přístup (Seibold et al., 2018; **studie I, III, VI**) a posuzovat odezvu členovců prostřednictvím jejich funkčních vlastností (tzv. „species traits"; (Öckinger et al., 2010; Simons et al., 2020; Tilman et al., 1997; studie **II, V**), aby výsledky našich výzkumů co nejlépe odrážely vliv invazní dřeviny na společenstvo členovců jako celek. I když bylo publikováno několik lokálních studií s robustním multi-taxonomickým přístupem (např. Buchholz et al., 2015; Harris et al., 2014; Van der Colff et al., 2015), tak jejich autoři zkoumali pouze vliv jedné konkrétní invazní dřeviny na úbytek členovců v invadovaných lesních ekosystémech prostřednictvím srovnání s porosty jednoho z druhů původních dřevin. Parsons et al. (2020) zkoumali dopady více druhů nepůvodních dřevin, kongenerických k původním druhům dřevin, na biomasu pavouků a diverzitu přirozených nepřátel škůdců v okrasných zahradách. Rozdíly vlivu kongenerických i nekongenerických nepůvodních dřevin na členovce ve srovnání s původními druhy dřevin najednou byly studovány pouze u herbivorních skupin hmyzu (Burghardt et al., 2010; Zuefle et al., 2008). Komplexnější posouzení dopadů více druhů nepůvodních dřevin s různou fylogenetickou vzdáleností k původním druhům dřevin na abundanci a zejména biomasu členovců nebylo tedy dosud dostatečně studováno. Proto jsme prostřednictvím multi-taxonomického přístupu testovali (**studie I**), jaké mají invazní trnovník akát a naturalizovaná borovice černá (*Pinus nigra* Arnold) dopady na abundanci a biomasu členovců v souvislých lesních porostech v porovnání s původními druhy dřevin – borovicí lesní (*Pinus sylvestris* L.) a duby (*Quercus robur* L. a *Quercus petraea* (Matt.) Liebl.).

I přes nezpochybnitelný význam studia funkční diverzity v ekologických výzkumech nejen pro praktickou ochranu přírody (Öckinger et al., 2010; Simons et al., 2020; Tilman et al., 1997) bylo publikováno pouze minimum studií zabývající se dopady invazních dřevin na široce uchopenou funkční diverzitu členovců (Buchholz et al., 2015; Modiba et al., 2017). Modiba et al. (2017) studovali dopady invazních dřevin na funkční diverzitu vážek v lužních lesích v Jižní Africe a Buchholz et al. (2015) se zaměřili pouze na dopady invazního trnovníku akátu na úzkou skupinu funkčních vlastností pavouků a střevlíkovitých brouků. Posouzení vlivu invazních dřevin na široké spektrum funkčních vlastností členovců v temperátních lesích tedy chybí. Proto bylo naším cílem srovnat funkční diverzitu nočních motýlů (Lepidoptera), jakožto dobře

prozkoumanou skupinu členovců s detailními znalostmi o jejich ekologii (Summerville et al., 2004), v souvislých lesních porostech invazního trnovníku akátu s porosty původních druhů dřevin (**studie II**).

Recentně bylo publikováno mnoho prací (viz např. meta-analýza van Hengstum et al., 2014) referujících o dopadech invazních dřevin, včetně trnovníku akátu (Buchholz et al., 2015; Degomez & Wagner, 2001; Della Rocca et al., 2016), na společenstva členovců v souvislých lesních porostech. Avšak dosud chybí povědomí o významu porostů trnovníku akátu, a i invazních dřevin obecně (s výjimkou např. Van der Colff et al., 2015), pro biodiverzitu členovců v intenzivní zemědělské krajině. Invazní dřeviny rostoucí v neprodukčních biotopech situovaných v intenzivně zemědělské krajině mohou hrát pro biodiverzitu i pozitivní roli (Vítková et al., 2017). Proto jsme se rozhodli prostřednictvím multi-taxonomického přístupu porovnat společenstva členovců s různou habitatovou specializací v lesních fragmentech tvořených invazním trnovníkem akátem a původními dřevinami v intenzivně obhospodařované zemědělské krajině (**studie III**).

Invazní rostliny mohou významně narušovat trofické vztahy v invadovaných ekosystémech (Bezemer et al., 2014; Schirmel et al., 2016; Tallamy et al., 2010; Vilà et al., 2011), ale dosud nebyly přímo detailněji studovány funkční vztahy s cílem odhalení potenciálních kaskádových efektů mezi členovci reprezentující primární konzumenty, primárními producenty reprezentovanými cévnatými rostlinami a sekundárními konzumenty reprezentovanými ptáky v porostech invazních dřevin. Proto jsme v souvislých lesních porostech studovali dopady invazního trnovníku akátu na funkční vztahy mezi členovci zastoupenými nočními motýli a dalšími trofickými úrovněmi reprezentovanými cévnatými rostlinami, které využívá většina nočních motýlů jako hostitelské rostliny, a ptáky pro které jsou housenky nočních motýlů v lesních porostech esenciálním zdrojem potravy (**studie IV**, **studie V**). Úbytek diverzity ptáků v zemědělské krajině je úzce spojován s poklesem biomasy členovců (Bowler et al., 2019; Donald et al., 2001) v důsledku zejména intenzifikace zemědělství (Cardoso et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Wagner, 2020). Proto jsme stanovili celkovou biomasu členovců zachycených v lesních fragmentech a testovali jsme efekt biomasy členovců v lesních fragmentech invadovaných trnovníkem akátem na diverzitu ptačích společenstev (**studie VI**).

2. Cíle práce

Předkládaná disertační práce si klade za cíl lépe pochopit vliv nepůvodních dřevin na společenstva členovců. Disertační práce sestává z dílčích studií, ve kterých figuruje především invazní trnovník akát (*Robinia pseudoacacia* L.) jako modelový druh nepůvodní dřeviny. Záměrem jednotlivých studií bylo především přinést komplexní poznatky o dopadech invazního trnovníku akátu na společenstva členovců a jejich konsekvencích pro sekundární konzumenty, konkrétně ptáky. V dílčích studiích byly vytyčeny následující hlavní cíle:

1) Porovnat abundanci, biomasu a složení společenstev členovců s noční aktivitou v souvislých lesních porostech invazního trnovníku akátu, naturalizované borovice černé a původních druhů dřevin (**studie I**).

2) Srovnat společenstva nočních motýlů (Lepidoptera) v souvislých lesních porostech invazního trnovníku akátu a původních druhů dřevin (**studie II**).

3) Prostřednictvím multi-taxonomického přístupu srovnat společenstva členovců s různou habitatovou specializací v lesních fragmentech tvořených invazním trnovníkem akátem a původními dřevinami v intenzivně obhospodařované zemědělské krajině (**studie III**).

4) Analyzovat dopady invazního trnovníku akátu na funkční vztahy mezi členovci a dalšími trofickými úrovněmi reprezentovanými zejména ptáky (**studie IV**, **studie V**, **studie VI**).

Dílčí cíle a konkrétní hypotézy jednotlivých studiích zahrnutých do této disertační práce jsou uvedeny v přiložených manuskriptech (kap. 4.).

3. Literární rešerše

3.1 Vliv invazních rostlin na členovce

Dle výsledků globálních studií (Bezemer et al., 2014; Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014) mají invazní rostliny obecně převážně negativní dopad na původní společenstva členovců v invadovaných habitatech. Invazní rostliny mohou na členovce působit jednak přímými dopady – vlastní potravní nedostupností pro herbivorní členovce (Bezemer et al., 2014; Litt et al., 2014; Liu & Stiling, 2006; Schirmel et al., 2016; van Hengstum et al., 2014), tak dopady nepřímými – změnou vegetační struktury habitatu (Crooks, 2002; Hanzelka & Reif, 2016; Harris et al., 2004; Pearson, 2009; Šibíková et al., 2019), změnou spektra chemických látek na stanovišti využívaných členovci pro jejich interakce s rostlinami (Bezemer et al., 2014; Harvey & Fortuna, 2012; Schirmel et al., 2016) nebo obecným poklesem rostlinné diverzity (Litt et al., 2014; Simao et al., 2010; van Hengstum et al., 2014). Invazní rostliny mají tedy obecně negativní dopady na celkovou abundanci, diverzitu (Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014) a biomasu členovců i na jejich trofické interakce v invadovaných habitatech (Ballard et al., 2013; Heleno et al., 2008; Tallamy, 2004; Zuefle et al., 2008). Tyto dopady se často zásadně liší mezi jednotlivými taxony a trofickými gildami členovců (Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014). Obecně negativní trend dopadu invazních rostlin na členovce je spojen zejména s úbytkem hmyzích herbivorů, tvořících podstatnou část hmyzu (asi 50 % druhové bohatosti hmyzu; Grimaldi & Engel, 2005; Speight et al., 2008). Ti jsou koevolučně nejúžeji spjati s hostitelskými rostlinami, a jsou tedy potenciálně nejohroženější trofickou gildou členovců v důsledku rostlinných invazí (Bezemer et al., 2014; Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014).

Herbivorní hmyz a zejména herbivorní specialisté se v naprosté většině nejsou schopni troficky adaptovat nepůvodním invazním rostlinám, které mají často velice odlišné složení fytochemikálií ve svých pletivech (Bezemer et al., 2014; Cappuccino & Arnason, 2006) i rozdílné strukturální vlastnosti listů oproti původním druhům rostlin (Harvey & Fortuna, 2012; Schirmel et al., 2016), protože s nimi během evoluce nepřišli vlivem přirozených bariér do styku (Bezemer et al., 2014; Keane & Crawley, 2002; Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013). Tento princip je všeobecně přijímán jako součást tzv. hypotézy úniku

před nepřáteli („enemy release hypothesis"; Colautti et al., 2004; Keane & Crawley, 2002; Maron & Vilà, 2001), která hovoří o vysoké úspěšnosti invazních rostlin v důsledku absence herbivorních škůdců či patogenů v jejich sekundárním areálu. Herbivorní hmyz rovněž přichází o své hostitelské rostliny v důsledku poklesu rostlinné diverzity v invadovaných habitatech (Litt et al., 2014; Simao et al., 2010; van Hengstum et al., 2014). I když na výše uvedené změny v dostupnosti potravy nejvíce doplácejí herbivorní specialisté úzce spjatí s původní rostlinou (Bezemer et al., 2014; Burghardt et al., 2010; Liu & Stiling, 2006; Litt et al., 2014; Spafford et al., 2013), tak ani většina herbivorních generalistů se nedokáže rychle přizpůsobit nepůvodní rostlině a nedokáže tak kompenzovat ztráty herbivorních specialistů (Tallamy et al., 2010). Invazní rostliny také mohou fungovat jako evoluční past, pokud herbivory lákají k přijímání jejich rostlinných pletiv jako potravního zdroje a zároveň svojí nízkou nutriční kvalitou snižují jejich fitness (Bezemer et al., 2014; Harvey & Fortuna, 2012; Keeler & Chew, 2008). Invazní rostliny nicméně nemusejí mít ve všech případech na herbivorní hmyz pouze negativní dopady (Bezemer et al., 2014; Liu & Stiling, 2006; Schirmel et al., 2016). Vliv invazních rostlin na herbivorní hmyz totiž může záviset na míře fylogenetické vzdálenosti invazních rostlin vůči původním druhům rostlin (Agrawal & Kotanen, 2003; Agrawal et al., 2005; Bezemer et al., 2014; Spafford et al., 2013). V případě srovnání kongenerických původních a nepůvodních druhů rostlin nemusí docházet k úbytku herbivorního hmyzu v důsledku rostlinné invaze, dokonce kongenerické invazní druhy rostlin někdy hostí i více herbivorního hmyzu než původní druhy rostlin (Agrawal & Kotanen, 2003; Agrawal et al., 2005; Burghardt et al., 2010; Dostál et al., 2013; Zuefle et al., 2008). Tento trend naopak některé další studie (e. g. Liu and Stilling, 2006; van Hengstum et al., 2014) nepotvrdily, a například Bezemer et al. (2014) udávají, že rovněž záleží na míře invazivity nepůvodní rostliny. Šance původních druhů herbivorů troficky se přizpůsobit nepůvodním invazním rostlinám také stoupá s rostoucím časem od doby jejich zavlečení (Bezemer et al., 2014; Brändle et al., 2008; Siemann et al., 2006) a v některých případech i s rostoucí velikostí jejich oblasti rozšíření v sekundárním areálu (Brändle et al., 2008). Je ale rovněž prokázáno, že adaptace herbivorních generalistů na nepůvodní rostliny probíhá rychleji než u herbivorních specialistů (Brändle et al., 2008; Zuefle et al., 2008).

Invazní rostliny mají různé dopady na společenstva hmyzích opylovačů a interakce mezi původními druhy rostlin a opylovači (Bezemer et al., 2014; Litt et al., 2014). U specializovaných opylovačů, kteří jsou úzce koevolučně spjatí s původními druhy rostlin, jsou zaznamenány převážně negativní dopady rostlinných invazí na jejich diverzitu a abundanci (Bezemer et al., 2014; Litt et al., 2014; Moroń et al., 2009). Obecně dochází v důsledku ovlivnění opylovacích sítí invazními rostlinami zejména k negativnímu dopadům na frekvenci

návštěv opylovačů a následný reprodukční úspěch původních druhů rostlin (Aizen et al., 2008; Montero-Castaño & Vilà, 2012; Morales & Traveset, 2009). Negativní vliv invazních rostlin na frekvenci návštěv opylovačů a následný reprodukční úspěch původních druhů rostlin bývá výraznější, pokud mají květy invazních rostlin podobný tvar a barvu jako původní druhy rostlin nebo jsou vzájemně úzce fylogeneticky blízké (Morales & Traveset, 2009). Rovněž byly zaznamenány i pozitivní efekty invazních rostlin na abundanci i druhovou bohatost blanokřídlých opylovačů (Bezmer et al., 2014; Emery & Doran, 2013), které byly spojené s nárůstem generalistických opylovačů (Bezemer et al., 2014). Invazní rostliny lákají opylovače často vyšší produkcí nektaru než původní dřeviny (Chittka a Schurken 2001), také většinou kvetou delší dobu (Memmott a Waser 2002), a to může být důvodem zvýšení diverzity blanokřídlých v porostech kvetoucích invazních rostlin (Bezemer et al., 2014; Litt et al., 2014). Stejně jako u herbivorní hmyzu, schopnost hmyzích opylovačů se přizpůsobit nepůvodní invazní rostlině stoupá s časem od doby jejího zavlečení do sekundárního areálu (Pyšek et al., 2011). Invazní rostliny mohou díky svojí atraktivitě nalákat do invadovaného porostu velké množství hmyzích opylovačů, kteří mohou následně více navštěvovat i původní druhy rostlin, a v důsledku toho mohou i pozitivně působit na jejich opylení a reprodukční úspěch (Johnson et al., 2003). Z těchto důvodů mohou opylovači významně podpořit šíření invazních rostlin v jejich sekundárních areálech (Lopezaraiza-Mikel et al., 2007).

Invazní rostliny mají také obvykle negativní vliv na parazitoidy kvůli jejich sníženým možnostem najít svého hostitele v důsledku redukce početnosti a diverzity herbivorů (Harvey & Fortuna, 2012; Simao et al., 2010). Naopak efekt invazních rostlin na ostatní karnivorní členovce není vždy jednoznačný. Predátoři obvykle negativně reagují na sníženou dostupnost kořisti zejména kvůli úbytku herbivorů (Litt et al., 2014; Simao et al., 2010). Na druhou stranu výsledky jiných studií ukazují, že invazní rostliny nemají na predátory žádný průkazný efekt (Buchholz et al., 2015; Van Der Colff et al., 2015), naopak jsou dokumentovány i pozitivní dopady invazních rostlin na karnivorní členovce (Hartley et al., 2010; Pearson, 2009, Zhu et al., 2019). Predátoři mnohdy totiž dokáží profitovat ze změny vegetační struktury habitatu způsobenou invazní rostlinou (Litt et al., 2014; Pearson, 2009; van Hengstum et al., 2014). Jak predátoři, tak parazitoidi mohou být negativně ovlivněni horší nutriční kvalitou své kořisti i hostitelů (herbivorů). Zejména v důsledku požití sekundárních metabolitů obsažených v nepůvodních rostlinách původními druhy herbivorů může být přímo ovlivněna preference a hledání kořisti u predátorů či ovipozice u parazitoidů (Ode, 2006). Invazní rostliny ovlivňují strukturu chemických látek na stanovišti, které predátoři i parazitoidi využívají pro interakci s rostlinami, při disperzi, a zejména při trofických interakcích mezi predátory/parazitoidy a

jejich kořistí/hostiteli (Bezemer et al., 2014; Harvey & Fortuna, 2012; Schirmel et al., 2016). Konkrétně invazní rostliny obvykle produkují rozdílné volatilní látky oproti původním druhům rostlin, které predátoři a parazitoidi využívají pro jejich chemickou a vizuální orientaci, a mění se tak jejich schopnost vyhledat herbivory jako svou kořist / své vhodné hostitele (Harvey & Fortuna, 2012).

Detritovorní členovci jsou obecně nejméně negativně ovlivněnou gildou členovců, naopak invazní rostliny mají na jejich abundanci i druhovou diverzitu veskrze pozitivní efekt (Van der Colff et al., 2015; Harris et al., 2004; Litt et al., 2014; Schirmel et al., 2016; van Hengstum et al., 2014). Detritovoři totiž mohou profitovat z velké produkce biomasy v porostech invazních rostlin (Ehrenfeld, 2010; Vilà et al., 2011), následně většího množství rostlinného opadu s často větší rychlostí rozkladu (Standish et al., 2004), a na to navázanými vhodnějšími mikroklimatickými podmínkami (Spafford et al., 2013; Litt et al., 2014).

Invazní rostliny ovlivňují strukturu druhového složení společenstev (Bezemer et al., 2014; Burghardt et al., 2010; Litt et al., 2014; van Hengstum et al., 2014) i funkční diverzitu členovců (Buchholz et al., 2015; Modiba et al., 2017). Vliv invazních rostlin na funkční diverzitu byl studován zejména prostřednictvím trofické a habitatové specializace členovců (Bezemer et al., 2014; Buchholz et al., 2015; Burghardt et al., 2010; Litt et al., 2014; van Hengstum et al., 2014). Mimo hojně studované efekty invazních rostlin na různé gildy členovců, komplexní posouzení vlivu invazních rostlin na funkční diverzitu bylo recentně provedeno pouze v jedné případové studii u vážek (Modiba et al., 2017), a rovněž pouze několik málo studií se zabývalo změnami struktury složení společenstev vázaných na změnu vegetační struktury v porostech invazních rostlin (Buchholz et al., 2015; Harris et al., 2004; Pawson et al., 2010; Pearson, 2009; Platen & Kowarik, 1995). Dle Modiby et al. (2017), funkční diverzita vážek byla v porostech původních dřevin vyšší oproti porostům invazních dřevin. V porostech invazních dřevin se vyskytovali průkazně menší druhy vážek s menším rozpětím křídel (Modiba et al., 2017).

Invazní dřeviny mají podstatně větší vliv na společenstva členovců než invazní byliny (Tallamy et al., 2020; van Hengstum et al., 2014). To může být způsobeno znásobením přímého efektu nedostupnosti potravní nabídky pro herbivorní hmyz (Bezemer et al., 2014, Keane & Crawley, 2002; Litt et al., 2014; van Hengstum et al., 2014) a celkově menší alokací poživatelné biomasy do listů dostupné pro herbivory oproti bylinám (Haukioja & Koricheva, 2000). Dalším důvodem je, že invazní dřeviny jsou silní ekosystémovými inženýři (Ehrenfeld, 2003; Hierro & Callaway, 2003; Richardson & Rejmánek, 2011), kteří obvykle zásadně mění vegetační strukturu porostu (Crooks, 2002; Hanzelka & Reif, 2016; Šibíková et al., 2019) a vlivem silné interspecifické kompetice v jejich podrostu ovlivňují původní rostlinná

společenstva, což vede ke změně mikroklimatických podmínek v porostu a následně k zásadním změnám ve struktuře stanovištních i potravních nikách členovců (Harris et al., 2004; Pawson et al., 2010; van Hengstum et al., 2014).

3.2 Trnovník akát (*Robinia pseudoacacia* L.)

Primární areál trnovníku akátu

Trnovník akát je listnatá opadavá dřevina z čeledi bobovitých (*Fabaceae*) dorůstající do výšky až 20 m (ojediněle až 30 m) s primárním areálem výskytu v Apalačských horách v jihovýchodní části USA (Cierjacks et al., 2013; Huntley, 1990). Hlavním těžištěm primárního výskytu je území států Pensylvánie, Západní Virginie, Ohia, Kentucky, Alabamy, Arkansasu a Oklahomy (Huntley, 1990), kde se trnovník akát uplatňuje jako krátkověká světlomilná dřevina ranně sukcesních stádií v dubovo-ořechovcových lesích (Boring & Swank, 1984; Cierjacks et al., 2013). V těchto lesních porostech má zastoupení v řádu nízkých jednotek procent (Boring & Swank, 1984) a přibližně po 15 až 30 letech bývá nahrazován dřevinami pozdnějších sukcesních stádií (Boring & Swank, 1984, Cierjacks et al., 2013). Huntley (1990) uvádí, že maximální doba dožití akátu se v primárním areálu pohybuje většinou do 100 let.

Sekundární areál trnovníku akátu, historie jeho šíření a jeho využití

Sekundární areál výskytu trnovníku akátu leží kromě Antarktidy na všech světových kontinentech (Cierjacks et al., 2013; Weber, 2003). Trnovník akát patří mezi 40 celosvětově nejrozšířenějších invazivních druhů dřevin (Richardson & Rejmánek, 2011) a mimo Evropu je rozšířen v mírných podnebných pásmech Austrálie a Nového Zélandu, Jižní Ameriky, Afriky a Asie (Cierjacks et al., 2013; Weber, 2003). V Asii se nacházejí větší plochy akátu v Číně, v Rusku a zejména v Jižní Koreji, kam byl zavlečen v roce 1890 kvůli výrobě železničních pražců (Cierjacks et al., 2013; Lee et al., 2011). V Severní Americe byl rovněž introdukován na západní pobřeží USA (Degomez & Wagner, 2001; Weber, 2003).

První zmínky o introdukci trnovníku akátu do Evropy sahají do první poloviny 17. století. Dříve se spekulovalo, že ho jako první do Evropy zavlekl do Paříže zahradník Vespasian Robin, podle kterého byl akát následně pojmenován, ale pravděpodobně na území Evropy došlo k několika na sobě nezávislým introdukcím (Cierjacks et al., 2013, Vítková et al., 2017). I přestože je v Evropě považován za jednu z nejrozšířenějších a nejinvazivnějších nepůvodních druhů dřevin se zdokumentovanými výraznými dopady na původní biotu (Campagnaro, Brundu

et al., 2018; Nentwig et al., 2018; Vítková et al., 2017), nebyl trnovník akát doposud zařazen na seznam invazních druhu s významným dopadem na EU (prováděcí nařízení Komise (EU) 2016/1141 ze dne 13. června 2016, kterým se přijímá seznam invazních nepůvodních druhů s významným dopadem na Unii podle nařízení Evropského parlamentu a Rady EU č. 1143/2014). Stalo se tak nejspíše z důvodu silného hospodářského využití trnovníku akátu v některých členských státech EU, např. Maďarska, Polska či Slovenska (Sitzia et al., 2016). Trnovník akát je široce rozšířen prakticky ve všech evropských zemích, s výjimkou nejsevernějších oblastí (Cierjacks et al., 2013; Weber, 2003), s hlavním těžištěm výskytu v jižní (Vítková et al., 2020) a střední Evropě (Vítková et al., 2017). Vyskytuje se zejména v nížinných oblastech až pahorkatinách, kde vystupuje do nadmořské výšky 700 m n. m. Výjimku tvoří jižní úbočí Alp, kde akát roste až do výšky 1600 m n. m. (Cierjacks et al., 2013; Vítková et al., 2017). Dle Vítkové et al. (2017) se ve střední Evropě dají akátové porosty obecně rozlišit na akátiny pěstované v intenzivní zemědělské krajině nebo v urbánním prostředí, souvislé lesní porosty s dominantou akátu, smíšené akátové porosty a zakrslé akátiny na skalách. Ze všech zemí Evropy je trnovník akát nejvíce rozšířen v Maďarsku, kde v roce 2010 pokrýval plochu cca 410 000 ha, což tvoří přibližně čtvrtinu plochy maďarských lesních porostů (Rédei et al., 2010).

Na území České republiky byl zavlečen v roce 1710 (Nožička, 1957), první pokusy lesnického využívání trnovníku akátu na našem území započaly na počátku 60. let 18. století, avšak až na přelomu 19. a 20. století docházelo k jeho plošnému vysazování (Kolbek et al., 2004). První záznam o jeho spontánním šíření ve volné přírodě byl zdokumentován v roce 1874 (Pyšek, Chytrý, et al., 2012). V současnosti je akát nejrozšířenější invazní dřevinou v České republice (Pyšek, Chytrý, et al., 2012; Pyšek, Danihelka, et al., 2012) a je zařazený do kategorie BL2 (hojně rozšířené invazní neofyty, stromy a keře) černého seznamu nepůvodních druhů ČR (Pergl et al., 2016). Vyskytuje se téměř ve všech nížinných a střední polohách České republiky, zejména na Jižní Moravě, v Českém Středohoří a v údolích a nížinách okolo řek Vltavy, Berounky, Labe, Sázavy a Dyje (Kolbek et al., 2004; Pyšek, Chytrý, et al., 2012). Těžiště výskytu akátu se v ČR nalézá v nadmořských výškách 210–350 m n. m. a nejvíce se mu daří jižně exponovaných svazích se sklonem 30 až 40° (Vítková et al., 2015). Kolbek et al. (2004) udávají plochu cca 14 000 ha akátových porostů na našem území, v současnosti by to mělo být cca 0,5 % plochy lesních porostů v ČR (Vítková et al., 2017). V ČR jsou akátové porosty momentálně klasifikovány jako lesy ochranné s protierozní funkcí a nové výsadby trnovníku akátu na lesní půdě už nejsou zřizovány (Kolbek et al., 2004; Vítková et al., 2017). Současné akátové porosty v ČR tedy stárnou a postupně se dostávají do stadia rozpadu. Pouze minimální část z nich se obnovuje pařezením (Vítková et al., 2017).

Trnovník akát má velmi tvrdé a odolné dřevo o přibližné hustotě 690 kg/m^3 (Rédei et al., 2010), které se využívá pro venkovní stavby, vinohradnické kůly, sudy na víno, a především jako rychle obnovitelný zdroj vysoce výhřevného palivového dřeva (Cierjacks et al., 2013; Kolbek et al., 2004; Vítková et al., 2017). Nedostatek palivového dřeva byl jedním z hlavních důvodů jeho masivnějšího pěstování na území dnešní ČR (Kolbek et al., 2004). Jelikož má akát velmi rychlý růst a vysokou produkci biomasy, a zároveň regeneruje velmi dobře z pařezových výmladků (Rédei et al., 2010; Vítková et al., 2017), tak se v minulosti (Kolbek et al., 2004) akátové porosty pěstované pro produkci palivového dřeva obhospodařovaly, a i v současnosti obhospodařují, pařezinovým způsobem (Redei et al., 2010). Na území ČR byly akátové porosty obhospodařovány pařezinovým způsobem zejména v první polovině 20. století, kdy se doba jejich obmýtí pohybovala mezi 6–30 roky (Kolbek et al., 2004). V současnosti mají akátové porosty v ČR zejména ochrannou funkci a pařezinovým způsobem se zde obhospodařuje naprosté minimum akátin (Vítková et al., 2017). Naopak v Maďarsku se pařezinovým způsobem obhospodařují dvě třetiny zdejších akátových porostů (Rédei et al., 2010). Trnovník akát se rovněž hojně vysazoval pro stabilizaci erozních půd, zejména erozních svahů a v post-těžebních oblastech (Cierjacks et al., 2013; Kolbek et al., 2004; Vítková et al., 2017). Dle Kolbeka et al. (2004) se na našem území akát vysazoval z důvodu stabilizace strmých suťových svahů zejména v údolí řeky Vltavy a Berounky a v okolí železničních tratí.

V minulosti byl akát také hojně používán pro výrobu železničních pražců (Kolbek et al., 2004; Yong et al., 2011). Trnovník akát je velmi oceňován včelaři pro jeho vysokou produkci nektaru, z něhož jejich včely produkují velmi ceněný jednodruhový akátový med (Cierjacks et al., 2013; Farkas & Zajácz, 2007; Vítková et al., 2017). Hlavní doba kvetení trnovníku akátu v mírném pásmu jeho sekundárním areálu probíhá v květnu a v červnu (Cierjacks et al., 2013; Lee et al., 2011), kdy včelaři s jejich včelstvy do akátových porostů kočují (Farkas & Zajácz, 2007). Právě včelaři provedli podstatnou část výsadeb akátových porostů ve 20. století na území ČR (Kolbek et al., 2004). Akát a jeho kultivary jsou pro svůj dekorativní vzhled vysazovány v městských a parkových výsadbách (Cierjacks et al., 2013; Kolbek et al., 2004). Dobře totiž snáší tzv. urbanizační stres spojený se znečištěním ovzduší a zasolením půdy (Sjöman & Nielsen, 2010).

Ekologie akátu, jeho invazní strategie a vliv na rostlinná společenstva

Trnovník akát je teplomilná a silně světlomilná dřevina množící se jak generativním, tak klonálním způsobem, a je považován za jednu z nejrychleji rostoucích dřevin na světě

(Cierjacks et al., 2013; Niculescu et al., 2020; Vítková et al., 2017). V lesních porostech primárního areálu akát prosperuje po dobu 15–30 let a v následujících letech čelí velkému tlaku hmyzích herbivorů (Boring & Swank, 1984; Hargrove, 1986) i hub (Cierjacks et al., 2013), a je postupně nahrazen stínomilnými druhy dřevin, a to zejména liliovníkem tulipánokvětým (*Liriodendron tulipifera* L.), ořechovci (*Carya* spp.) a duby (*Quercus* spp.; Boring & Swank, 1984). Naopak v sekundárním areálu výskytu nejsou stínomilné druhy vůči akátu zejména v prvních desítkách let jeho růstu dostatečně konkurenceschopné a vyskytují se především v keřovém a bylinném patře (Sádlo et al., 2017). I když se v sekundárním areálu postupně šíří škůdci a patogeny akátu (Bakay & Kollár, 2014; Nicolescu et al., 2020), zatím nejsou schopni zásadněji snižovat věk dožití akátových porostů (Cierjacks et al., 2013). V sekundárním areálu výskytu se trnovník akát dožívá běžně více než 60 let (Cierjacks et al., 2013) a v České republice se dle Vítkové (2014) dožívá běžně až 100–120 let. Až v přestárlých rozpadajících se akátinách se postupně prosazují domácí druhy konkurenčně silných dřevin, jako je jasan ztepilý (*Fraxinus excelsior* L.), javor babyka (*Acer campestre* L.), javor mléč (*Acer platanoides* L.) nebo jilm horský (*Ulmus glabra* Huds.; Sádlo et al., 2017; Vítková, 2014). V případě výskytu těchto dřevin v okolních porostech, lze předpokládat, že jimi bude akát postupně vytlačován a nahrazován již ve staří přibližně 70 let (Vítková, 2014).

Trnovník akát je v sekundárním areálu schopen růst na rozmanitých půdách s extrémně různorodými fyzikálně-chemickými vlastnostmi a různou skeletovitostí půdy (Cierjacks et al., 2013; Vítková et al., 2015). Je schopen růst na stanovištích s širokou škálou matečných hornin, na extrémně kyselých až silně zásaditých půdách. V České republice nejčastěji roste na mělkých vývojově mladých půdách, jako jsou kambisoly, leptosoly, fluvisoly a písčité arenosoly (Vítková et al., 2015). Trnovník akát dokáže dobře růst na extrémně suchých, narušovaných a živinově chudých půdách, kterým je dokonale přizpůsoben svými vlastnostmi (Cierjack et al., 2013; Vítková et al., 2015).

Jako zástupce čeledi bobovitých rostlin, dokáže vázat atmosférický dusík (Boring & Swank, 1984; Cierjacks et al., 2013; Vítková et al., 2015) pomocí symbiózy s 37 kmeny hlízkových bakterií rodu *Rhizobium* na jeho kořenech (Vítková et al., 2015). V primárním areálu výskytu dokáže akát fixovat až 75 kg N ha/rok (Boring & Swank, 1984). V sekundární areálu dokáže akát fixovat dle Vítkové et al. (2015) cca 110 kg N ha/rok a Cierjacks et al. (2013) udávají, že takto akát dokáže fixovat až 300 kg N ha/rok. Fixace dusíku je inhibována vysokou hladinou spodní vody nebo v pravidelně zaplavovaných porostech (Vítková et al., 2015). Listový opad akátu obsahuje velké množství dusíku (až cca 43 kg N/ha/rok), který se jeho rozkladem dostává zpět do půdy (Tateno et al., 2007). V porostech akátu tedy dochází k intenzivní nitrifikaci i

mineralizaci a následně vyšší akumulaci minerálních forem dostupného dusíku v půdě (Lazzaro et al., 2018; Vítková et al., 2015), a v důsledku toho k homogenizaci rostlinných společenstev ve prospěch nitrofilních druhů rostlin (např. Benesperi et al., 2012; Lazzaro et al., 2018; Sitzia et al., 2018; Slabejová et al., 2019; Vítková & Kolbek, 2010). Naopak vyšší dostupnost dusíku zvyšuje diverzitu půdních bakterií v akátových porostech (Lazzaro et al., 2018). Vlivem intenzivní nitrifikace rovněž dochází k výrazné acidifikaci půdy (Lazzaro et al., 2018; Vítková et al., 2015). Hrabanka tvořená z opadu trnovníku akátu se rozkládá rychleji nežli hrabanka z opadu dubů (*Quercus* spp.), které velmi často zastupují původní druhy dřevin v komparativních studiích s trnovníkem akátem (Tateno et al., 2007; Lee et al., 2011). Rychlý rozklad akátové hrabanky z předchozího roku a odkvetlých květů způsobuje značné navýšení fosforečnanů v půdě. Fosfor je na začátku vegetačního období důležitým limitujícím prvkem, proto může být rychlý koloběh rozpadu akátového opadu jedním z prvků jeho strategie přežití na živinově chudých půdách (Lazzaro et al., 2018; Lee et al., 2011).

Trnovník akát produkuje různé alelopatické látky (např. robinetin, myricetin a quercetin), které jsou obsažené v jeho listech a mohou inhibovat klíčení a růst ostatních rostlin v akátovém podrostu (Nasir et al., 2005). Dle Vítkové & Kolbeka (2010) je ale vysoce pravděpodobné, že změny ve složení rostlinných společenstvech zapříčiněných akátem jsou způsobené změnou v dostupnosti živin v půdě než potencionální alelopatií akátu. Alelopatie akátu byla totiž doposud prokázána pouze v laboratoři a nebyla nikdy potvrzena v přírodních podmínkách (Nicolescu et al., 2020; Vítková et al., 2015; Vítková et al., 2017).

Trnovník akát má mohutný a rozvětvený kořenový systém, kterým zvýšeně čerpá půdní vlhkost (Rice et al., 2004; Cierjacks et al., 2013). Rovněž má velmi řídkou korunu, přes kterou propouští velké množství slunečního záření (Xu et al., 2009), a olisťuje se později než původní druhy dřevin (např. duby) až na přelomu dubna a května (Šibíková et al., 2019). Kombinací těchto faktorů dochází v podrostu akátin k značnému vysychání půdy a zejména v letních měsících k usychání vegetace v jejich podrostu (Vítková et al., 2017; Vítková & Kolbek, 2010). V akátových porostech je tedy obecně teplejší mikroklima než například v původních dubových porostech (Šibíková et al., 2019; Slabejová et al., 2019; Vítková et al., 2017). V případně velkého stresu vlivem nedostatky vody, mohou opadávat listy akátů již v průběhu srpna (Vítková et al., 2017). Trnovník akát tedy v Evropě vytváří světlé porosty s málo zapojeným korunovým patrem a dobře vyvinutým bylinným a keřovým patrem (Campagnaro et al., 2018; Hanzelka & Reif, 2016; Vítková et al., 2017).

Trnovník akát v důsledku svých vlastností výrazně mění složení invadovaných rostlinných společenstev a má obecně negativní dopad na diverzitu cévnatých rostlin (např. Benesperi et

al., 2012; Lazzaro et al., 2018; Sitzia et al., 2018; Slabejová et al., 2019; Vítková & Kolbek, 2010) i lišejníků (Nascimbene et al., 2012). Benesperi et al. (2012) udávají, že u věkově starších akátových porostů nedochází k průkaznému zvýšení diverzity cévnatých rostlin oproti mladším akátinám. V některých případech může mít trnovník akát na původní vegetaci i pozitivní dopad, jeho porosty jsou totiž často refugiem některých vzácných geofytů, například křivatců (*Gagea* spp.) nebo koniklece lučního (*Pulsatila pratensis* L.; Šibíková et al., 2019; Vítková et al., 2017; Vítková & Kolbek, 2010). Druhové složení a pokryvnost bylinného a keřového patra se v akátových porostech odvíjejí od jednotlivých fytocenologických typů akátin, které souvisejí s lokálními environmentálními a mikroklimatickými podmínkami (Campagnaro et al., 2018; Šibíková et al., 2019; Vítková et al., 2017; Vítková & Kolbek, 2010), přičemž jejich fytocenologická klasifikace není napříč Evropou úplně ustálená. Společných prvkem invaze trnovníku akátu v různých evropských zemích je vysoké zastoupení nitrofilních a ruderálních druhů cévnatých rostlin (Benesperi et al., 2012; Lazzaro et al., 2018; Sitzia et al., 2018; Slabejová et al., 2019; Vítková & Kolbek, 2010). Na území střední Evropy a ČR se akátové porosty rozdělují do čtyřech asociací (Vítková et al., 2017; Vítková & Kolbek, 2010). Nejrozšířenější jsou mezofilní akátiny asociace *Chelidonio majoris-Robinietum pseudoacaciae* Jurko 1963, ve kterých dominují nitrofilní byliny, jako např. vlaštovičník větší (Chelidonium majus L), svízel povázka (*Galium aparine* L.), kuklík městský (*Geum urbanum* L.) nebo kerblík lesní (*Anthriscus sylvestris* L.; Vítková & Kolbek, 2010). Do druhé asociace *Arrhenathero elatioris-Robinietum pseudoacaciae* Šimonovič et al. ex Vítková et Kolbek 2010 patří druhově chudé akátiny rostoucí na silně kyselých sedimentech, zejména na vátých a fluviálních píscích a štěrkových náplavách v rovinatém terénu. V jejich podrostu dominují vysoce konkurenčně schopné druhy trav, jako např. ovsík vyvýšený (*Arrhenatherum elatius* (L.) J. Presl et C. Presl), lipnice úzkolistá (*Poa angustifolia* L.) pnebo třtina křovištní (*Calamagrostis epigejos* (L.) Roth). V těchto akátinách je rovněž minimálně vyvinuté keřové patro (Vítková & Kolbek, 2010). Do třetí asociace *Poo nemoralis-Robinietum pseudoacaciae* Němec ex Vítková et Kolbek in Kolbek et al. 2003 spadají svahové akátiny s obvykle dominující lipnicí hajní (*Poa nemoralis* L.), kterou doplňují např. metlička křivolaká (*Avenella flexuosa* (L.) Drejer) či konopice pýřitá (*Galeopsis pubescens* Besser; Vítková & Kolbek, 2010). Zakrslé akátiny (o výšce 3–5 m) na skalnatých svazích tvoří asociaci *Melico transsilvanicae-Robinietum pseudoacaciae* Kolbek et Vítková in Kolbek et al. 2003, ve které rostou zejména stepní druhy a suchomilné keře, jako např. růže šípková (*Rosa canina* L.), strdivka sedmihradská (*Melica transsilvanica* Schur), pryšec chvojka (*Euphorbia cyparissias* L.) nebo tolita lékařská

(*Vincetoxicum hirundinaria* Medic). Jedná se o druhově nejbohatší akátiny na území ČR (Vítková & Kolbek, 2010).

Společenstva členovců v porostech trnovníku akátu

Callaway et al. (2011) uvádějí jako jeden z důvodů, který přispívá k velmi brzkému nahrazení trnovník akátu dřevinami pozdějších sukcesních stádií v lesích primárního areálu, vysokou druhovou diverzita hmyzích herbivorů živících se právě akátem (Hargrove, 1986). Jedná se především o motýly a brouky, jejichž herbivorní larvy se živí listy akátu, dále druhy sající mízu z jeho listových pletiv, a brouky živící se jeho lýkem a kůrou (Hargrove, 1986). Ze zmíněných skupin herbivorního hmyzu se v porostech primárního areálu například vyskytuje významný dvoukřídlý škůdce akátu bejlomorka akátová (*Obolodiplosis robiniae* (Haldeman, 1847)), z motýlů např. vzpřímenka akátová (*Parectopa robinella* (Clemens, 1863)) nebo klíněnka akátová (*Phyllonorycter robiniella* (Clemens, 1859); Hargrove, 1986). Jako nejvýznamnější herbivorní škůdce trnovníku akátu v jeho primárním areálu je považován tesařík *Megacyllene robiniae* (Forster, 1771), jehož larvy si vyžírají chodby v kmenu a větvích akátů, které jsou dále vstupní branou pro houbové infekce, a následně jsou napadené části náchylné na poškození větrem (Boring & Swank, 1984; Huntley, 1990). Dopady působení tohoto druhu tesaříka způsobují, že jsou akátové porosty v primárním areálu pro produkci dřeva prakticky nepoužitelné (Huntley, 1990).

Trnovník akát jako nepůvodní hostitelskou rostlinu využívají v sekundárním areálu kromě jeho zavlečených škůdců zejména polyfágní či oligofágní druhy motýlů (Kulfan, 2012) nebo saproxyličtí brouci (Della Rocca et al., 2016; Stejskal, 2018). Kulfan (2012) uvádí, že na Slovensku žije 35 druhů vesměs nočních motýlů využívajících trnovník akát jako hostitelskou rostlinu včetně jeho významných nepůvodních škůdců *Parectopa robiniella* a *Phyllonorycter robiniella*, kteří minují v listech akátu a způsobují zkroucení jeho listů, snížení jejich asimilační ploch až jejich předčasný opad (Bakay & Kollár, 2014). *Ph. robiniella* byla v Evropě objevena v roce 1984 ve Švýcarsku a *Pa. robiniella* byla prvně popsána v roce 1970 v Itálii a oba tyto druhy se postupně rozšířily ve zbytku Evropy (Csóka et al., 2009; Šefrová, 2002). V ČR byla *Pa. robiniella* prvně zaregistrována v roce 1989 (Marek et al., 1991) a *Ph. robiniella* poprvé roce 1992 (Šefrová, 2002). Oba tyto minující druhy jsou parazitovány širokým spektrem původních druhů parazitoidů, kteří primárně parazitovali na jiných původních druzích minujících motýlů s vazbou na duby a další původní druhy dřevin (Csóka et al., 2009). Proces schopnosti původních druhů parazitoidů se přeorientovat z původních druhů minujících motýlů

na nové hostitele proběhl velmi rychle, řádově v horizontu 10–20 let (Csóka et al., 2009). Jedním z druhů nočních motýlů přijímající akát jako hostitelskou rostlinu je bekyně velkohlavá (*Lymantria dispar* (Linnaeus, 1758); Kulfan, 2012; Lazarević et al., 2002). Lazarević et al. (2002) zjistili, že motýli z populace *Lymantria dispar* živící se primárně na trnovníku akátu více jak 40 let se od motýlů z populace živící se primárně na původním dubu zimním průkazně liší v délce trvání stádia kukly, relativní rychlosti spotřeby potravy, relativní rychlosti růstu a účinnosti asimilace. Z denních motýlů žijících ve střední Evropě se na trnovníku akátu dokáže vyvíjet např. bělopásek hrachorový (*Neptis sapho* (Pallas, 1771); Kulfan, 2012) nebo modrásek krušinový (*Celastrina argiolus* (Linnaeus, 1758); Beneš et al., 2002).

V posledních letech se do sekundárního areálu akátu šíří jeho významný škůdce bejlomorka akátová (*Obolodiplosis robiniae* (Haldeman, 1847)) s potvrzeným prvním výskytem v Evropě v roce 2003 (Duso & Skuhravá, 2003) a v roce 2004 v České republice v Praze (Skuhravá & Skuhravý, 2004). Tento druh dvoukřídlého hmyzu vytváří hálky na listech akátu a dle Bakaye a Kollára (2014) má poměrně vysoký potenciál v biologickém boji s trnovníkem akátem. Avšak Cierjacks et al. (2013) upozorňují, že tento potenciál je značně limitován faktem, že populace *Obolodiplosis robiniae* jsou i v Evropě velmi významně redukovány parazitoidy včetně zavlečeného druhu *Platygaster robiniae* Buhl & Duso 2008 (Buhl & Duso, 2008). Tesařík *Megacyllene robiniae*, který je nejzásadnějším škůdcem akátu v primárním areálu, nebyl doposud do Evropy zavlečen (Nicolescu et al., 2020).

Povědomí o dopadech invazního trnovníku akátu na původní společenstva členovců je velmi malé, protože bylo doposud publikováno pouze několik málo převážně úzce zaměřených komparativních studií řešících tuto problematiku. Nejvíce jsou probádány dopady trnovníku akátu na společenstva epigeických členovců, přičemž byly dosud publikovány dvě studie z Německa (Buchholz et al., 2015; Platen & Kowarik, 1995) a jedna z Číny (Zhu et al., 2019). Buchholz et al. (2015) neprokázali signifikantní rozdíl v diverzitě střevlíkovitých brouků a pavouků mezi porosty trnovníku akátu a porosty břízy bělokoré (*Betula pendula* Roth) v urbánním prostředí. Zhu et al. (2019) srovnávali společenstva epigeických členovců v různě starých porostech trnovníku akátu (16, 19, 31 let) vysázených na silně degradovaných erozních svazích s kontrolními plochami tvořenými nezalesněnými erozními svahy v Číně. Celková abundance epigeických členovců se nelišila mezi jednotlivými porosty a kontrolními plochami, avšak jejich celkový počet druhů byl prokazatelně vyšší v akátových porostech a zvyšoval se s jejich stářím (Zhu et al., 2019). Tyto trendy se ale výrazně lišili mezi karnivorními a herbivorními členovci. Abundance i diverzita predátorů se nelišila mezi různě starými akátovými porosty a kontrolami, naopak abundance a diverzity fytofágních epigeických

členovců byla signifikantně nejvyšší ve starších porostech trnovníku akátu (Zhu et al., 2019). Stejně jako v případě studie Buchholze et al. (2015), zde nebyl prokázán negativní dopad trnovníku na abundanci střevlíků a pavouků, naopak jejich četnosti byli signifikantně vyšší v jeho porostech oproti nezalesněným kontrolním plochám (Zhu et al., 2019). V případě druhového složení společenstev pavouků a střevlíků, byla zaznamenána průkazná afinita stínomilných druhů pavouků vázaných na lesní prostředí k akátovým porostům ve srovnání s porosty bříze bělokoré (Buchholz et al., 2015). K podobnému trendu došli již Platen & Kowarik (1995), kteří v akátových porostech po 35 letech od zalesnění zaznamenali dominanci lesních druhů pavouků i střevlíků oproti stejně starým porostům břízy bělokoré a topolu osiky (*Populus Tremula* L.), kde se jejich společenstva skládala zejména z druhů vázaných na otevřené habitaty. Ze všech epigeických taxonů členovců ve studii Buchholze et al. (2015) měl trnovník akát průkazný negativní vliv pouze na abundanci stonožek a mravenců, a rovněž Zhu et al. (2019) referují o negativním vlivu trnovníku akátu na abundanci mravenců. Naopak v kontrastu s dopady trnovníku akátu na abundanci a diverzitu epigeických skupin členovců, byl zjištěn jeho silně negativní vliv na abundanci i druhovou diverzitu půdní mesofauny členovců i druhovou diverzitu hlístic (Lazzaro et al., 2018).

Z dalších skupin členovců byl prokázán negativní dopad trnovníku akátu zejména na druhovou diverzitu i abundanci herbivorního hmyzu a jejich přirozených nepřátel (Degomez & Wagner, 2001). Degomez & Wagner (2001) zjistili celkově vyšší počet druhů členovců stromového patra v porostech původního trnovníku novomexického (*Robinia neomexicana* A. Gray) oproti porostům nepůvodního trnovníku akátu v Arizoně. I když se jedná o kongenerické druhy dřevin, tak jejich sdílená druhová diverzita členovců stromového patra se rovnala pouze dvanácti druhům po 100 letech od zavlečení trnovníku akátu do Arizony (Degomez & Wagner, 2001). V případě létajících členovců byly zjištěny nižší četnosti dvoukřídlých, blanokřídlých a ploštic v porostech trnovníku akátu v porovnání s porosty břízy bělokoré (Buchholz et al., 2015). Della Rocca et al. (2016) prokázali, že trnovník akát nemá prokazatelně negativní vliv na diverzitu saproxylických brouků v mrtvém dřevě padlých stromů a jejich druhová diverzita v padlých akátech se signifikatně nelišila v porovnání s padlými stromy původních druhů dřevin – dubem letním a topolem bílým (*Populus alba* L.). I druhové složení společenstev saproxylických brouků bylo velice podobné mezi akátovými stromy a stromy výše uvedených druhů původních dřevin. Tyto výsledky naznačují, že saproxyličtí brouci osidlují mrtvé dřevo bez rozlišení toho, zda se jedná o dřevo původních či nepůvodních druhů dřevin (Della Rocca et al., 2016).

Nepřímý vliv invaze trnovníku akátu na původní společenstva členovců spočívající ve změnách ve struktuře vegetace lesního porostu byl studován doposud marginálně (Buchholz et al., 2015; Lazzaro et al., 2018; Zhu et al., 2019). Proto byla vegetační struktura habitatu zahrnuta v jednotlivých výzkumech (**studie I**, **studie II**, **studie III**) této disertační práce jako jeden ze základních faktorů určující dopady invazní dřeviny na společenstva členovců. Zatím nejkomplexněji studovali vliv akátu na společenstva členovců Buchholz et al. (2015), v žádné studii ale nebyly studovány dopady trnovníku akátu na biomasu členovců, přičemž k doplnění těchto poznatků zásadně přispívají výsledky této disertační práce (**studie I**, **studie II**, **studie VI**). Komplexnější znalosti o vlivu invazního trnovníku akátu na široké spektrum funkčních vlastností členovců v temperátních lesích chybí. Z tohoto důvodu bylo naším cílem srovnat funkční diverzitu nočních motýlů prostřednictvím detailní analýzy jejich bionomických a ekologických funkčních vlastností v souvislých lesních porostech invazního trnovníku akátu s porosty původních druhů dřevin (**studie II**). Z recentních poznatků je zřejmé, že trnovník akát nemusí mít pouze negativní dopad na původní společenstva členovců, a to zejména v člověkem silně pozměněných (Buchholz et al., 2015) a degradovaných ekosystémech (Zhu et al., 2019). Vítková et al. (2017) poukazují i na potencionálně pozitivní roli trnovníku akátu jako refugia biodiverzity v intenzivně obhospodařované zemědělské krajině. V tomto kontextu nebyla nikdy společenstva členovců studována a výsledky této práce (**studie III**) tedy přinášejí detailní poznatky o roli fragmentovaných porostů trnovníku akátu pro společenstva členovců v intenzivně obhospodařované zemědělské krajině.

Vliv trnovníku akátu na funkční vztahy jednotlivých trofických úrovní organismů ve smyslu rostlin (primárních producentů), členovců (primárních konzumentů) a ptáků (sekundárních konzumentů) nebyl doposud zásadněji studován. Členovci mohou být invazní dřevinou ovlivněny nepřímo ztrátou svých hostitelské rostlin v důsledku poklesu rostlinné diverzity v invadovaných habitatech (Litt et al., 2014; Simao et al., 2010; van Hengstum et al., 2014). V případě trnovníku akátu bylo doposud pouze prokázáno, že mezi druhovou diverzitou cévnatých rostlin v jeho porostech, druhovým složením epigeických členovců (Zhu et al., 2019) i diverzitou půdních členovců (Lazzaro et al., 2018) není žádný vztah. Výsledky této práce tyto poznatky rozšiřují o efekty trnovníku akátu na funkční vztah mezi cévnatými rostlinami a nočními motýly (**studie IV**). Hanzelka & Reif (2015) dedukují, že změny v zastoupení ptačích druhů – specialistů v akátových porostech mohou souviset se změnami ve společenstvech členovců způsobených invazí akátu. Z tohoto důvodu jsme studovali konsekvence vlivu trnovníku akátu na členovce pro sekundární konzumenty – ptáky s cílem odhalení potenciálních kaskádových efektů mezi ptáky a členovci v souvislých lesních porostech (**studie IV, V**) i

v lesních fragmentech situovaných v intenzivně obhospodařované zemědělské krajině (**studie VI**).

4. Výsledky disertační práce

Tato práce je sepsána jako komentovaný soubor šesti vědeckých prací – pěti publikovaných článků ve vědeckých časopisech s impakt faktorem (dále jen „IF") a jednoho rukopisu v rozpracované fázi s plánem odeslání do vědeckého časopisu s IF. Můj podíl na výzkumech prezentovaných v této práci je specifikován v rámci níže uvedeného seznamu výstupů a je rovněž vyjádřen mým pořadím v rámci autorského kolektivu předložených prací.

Studie I:
Štrobl M., Hanzelka J., Reif J., Hejda M., Kadlec T. Impacts of non-native trees *Robinia pseudoacacia* and *Pinus nigra* on arthropod communities. **in prep**.
Podíl autora: Pod vedením TK jsem navrhl koncept studie, významně se podílel na terénním sběru členovců a zásadně se podílel na jejich determinaci a laboratorním zpracování vzorků. Provedl jsem veškeré analýzy, interpretoval výsledky a rozpracoval manuskript pod vedením TK a s přispěním spoluautorů studie.

Studie II:
Kadlec, T., **Štrobl, M.,** Hanzelka, J., Hejda, M., & Reif, J. (2018). Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure. *Biodiversity and Conservation*, 27(10), 2661–2680. https://doi.org/10.1007/s10531-018-1560-8
Podíl autora: Podílel jsem se na terénním sběru nočních motýlů na jejich determinaci a laboratorním zpracování vzorků. Společně s TK jsme shromáždili data k funkčním vlastnostem druhů a provedl jsem veškeré analýzy dat a vytvořil grafické výstupy článku. Dále jsem se zásadně podílel na interpretaci výsledků, konceptu a psaní manuskriptu.

Studie III:
Štrobl, M., Saska, P., Seidl, M., Kocian, M., Tajovský, K., Řezáč, M., Skuhrovec, J., Marhoul, P., Zbuzek, B., Jakubec, P., Knapp, M., & Kadlec, T. (2019). Impact of an invasive tree on arthropod assemblages in woodlots isolated within an intensive agricultural landscape. *Diversity and Distributions*, 25(11), 1800–1813. https://doi.org/10.1111/ddi.12981
Podíl autora: Pod vedením TK a PS jsem navrhl koncept a design studie, studii koordinoval a z větší části zajistil její financování. Za přispění TK, MS a dalších kolegů mimo autorský

kolektiv jsem z větší části provedl terénní sběr členovců a laboratorní zpracování vzorků. Za přispění všech spoluautorů jsem shromáždil data a společně s TK jsme determinovali noční motýly. Rovněž jsem provedl sběr všech environmentálních dat, veškerá data analyzoval a vytvořil grafické výstupy článku. Pod vedením a ve spolupráci s TK, PS a MKA jsem interpretoval data a napsal manuskript článku.

Studie IV:

Reif, J., Hanzelka, J., Kadlec, T., **Štrobl, M.,** & Hejda, M. (2016). Conservation implications of cascading effects among groups of organisms: The alien tree *Robinia pseudacacia* in the Czech Republic as a case study. *Biological Conservation*, 198, 50–59. https://doi.org/10.1016/j.biocon.2016.04.003

Podíl autora: Podílel jsem se na terénním sběru nočních motýlů a na jejich determinaci. Provedl jsem analýzy v GIS a menší měrou jsem participoval na psaní manuskriptu.

Studie V:

Hejda, M., Hanzelka, J., Kadlec, T., **Štrobl, M.,** Pyšek, P., & Reif, J. (2017). Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. *Diversity and Distributions*, 23(9), 997–1007. https://doi.org/10.1111/ddi.12596

Podíl autora: Podílel jsem se na terénním sběru nočních motýlů a na jejich determinaci. Společně s TK jsme shromáždili data k funkčním vlastnostem nočních motýlů, provedl jsem analýzy mnohorozměrných dat a analýzy v GIS včetně grafických výstupů. Dále jsem participoval na psaní manuskriptu.

Studie VI

Rivas-Salvador, J., **Štrobl, M.,** Kadlec, T., Saska, P., & Reif, J. (2021). A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland. *Global Ecology and Conservation*, 26, e01458. https://doi.org/10.1016/j.gecco.2021.e01458

Podíl autora: Společně s TK, JR a PS jsem navrhl design studie, podílel se na jejím konceptu a z části zajistil její financování. Za přispění TK a dalších kolegů mimo autorský kolektiv jsem z větší části provedl terénní sběr členovců a laboratorní zpracování vzorků. Rovněž jsem provedl sběr veškerých environmentálních dat, analýzy v GIS, vytvořil mapu v článku a společně s TK a PS jsme s pomocí kolegů mimo autorský kolektiv shromáždili data o biomase členovců. Dále jsem se podílel na konceptu a tvorbě manuskriptu.

4.1 Studie I

Impacts of non-native trees *Robinia pseudoacacia* and *Pinus nigra* on arthropod communities.

Martin Štrobl, Jan Hanzelka, Jiří Reif, Martin Hejda, Tomáš Kadlec

<u>Abstrakt článku:</u>

The invasion of non-native tree species is among the main threats for arthropod communities in temperate forests. Invasive trees can rapidly change habitat structure of invaded habitats and have varying impacts on arthropod taxa and trophic guilds. One important aspect that modulates their impacts on arthropods is the degree of phylogenetical relatedness with native tree species. Therefore, using light traps together with the assessment of habitat structure, we studied the communities of nocturnal forest arthropods associated with exotic and native tree stands in lowland forests from the Czech Republic, Central Europe. Specifically, we compared the abundance, biomass, and community composition of nocturnal arthropods between forest stands of two non-congeneric tree species – the non-native tree species, black locust (*Robinia pseudoacacia* L.) and native oaks (*Quercus robur* (Matt.) Liebl and *Quercus petraea* L.) and two congeneric tree species – the exotic black pine (*Pinus nigra* Arnold) and native Scots pine (*Pinus sylvestris* L.).

 Invasive black locust created open stands with well-developed understory vegetation in contrast to oak stands, where the canopy was more developed. Non-native black pine stands had slightly more open habitat structure with more development of the shrub layer than stands of native Scots pine. Total arthropod abundance and biomass were significantly lower in black locust forests than in oak forest stands. This was mainly caused by the loss of mostly herbivorous taxa due to the replacement of their native host tree by unpalatable novel black locust. Arthropods linked to open habitat structure and well-developed understory vegetation in black locust stands did not replace the decline of arthropod abundance and biomass associated with oaks. Total arthropod abundance and biomass did not differ between forest stands of congeneric black pine and Scots pine. However, arthropod community composition was affected, probably due to changes in the shrub layer.

 Our results highlight that the negative effects of non-native tree species on native arthropods communities are stronger when phylogenetic and phylogeographic distance from native tree species increase. Therefore, the establishment of phylogenetically and phylogeographically

distant non-native trees in forest plantations should be avoided to prevent the loss of arthropod abundance and biomass.

Nepublikováno:

Nepublikovaný rukopis článku **in prep.** (plánováno odeslat do časopisu Forest Ecology and Management). Výsledky plynoucí z této studie budou diskutovány v kapitole 5., tedy v části obecné diskuse výsledků této disertační práce.

1 # Impacts of non-native trees *Robinia pseudoacacia* and *Pinus nigra*

2 # on forest arthropod communities

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11

12 # Abstract

13 The invasion of non-native tree species is among the main threats for arthropod communities

14 in temperate forests. Invasive trees can rapidly change habitat structure of invaded habitats and

15 have varying impacts on arthropod taxa and trophic guilds. One important aspect that modulates

16 their impacts on arthropods is the degree of phylogenetical relatedness with native tree species.

17 Therefore, using light traps together with the assessment of habitat structure, we studied the

18 communities of nocturnal forest arthropods associated with exotic and native tree stands in

19 lowland forests from the Czech Republic, Central Europe. Specifically, we compared the

20 abundance, biomass, and community composition of nocturnal arthropods between forest

21 stands of two non-congeneric tree species – the non-native tree species, black locust (*Robinia*

22 *pseudoacacia* L.) and native oaks (*Quercus robur* (Matt.) Liebl and *Quercus petraea* L.) and

23 two congeneric tree species – the exotic black pine (*Pinus nigra* Arnold) and native Scots pine

24 (*Pinus sylvestris* L.).

25 Invasive black locust created open stands with well-developed understory vegetation in

26 contrast to oak stands, where the canopy was more developed. Non-native black pine stands

27 had more open habitat structure with more development of the shrub layer than stands of native

28 Scots pine. Total arthropod abundance and biomass were significantly lower in black locust

29 forests than in oak forest stands. This was mainly caused by the loss of mostly herbivorous taxa

30 due to the replacement of their native host tree by unpalatable novel black locust. Arthropods

linked to open habitat structure and well-developed understory vegetation in black locust stands did not replace the decline of arthropod abundance and biomass associated with oaks. Total arthropod abundance and biomass did not differ between forest stands of congeneric black pine and Scots pine. However, arthropod community composition was affected, probably due to changes in the shrub layer.

Our results highlight that the negative effects of non-native tree species on native arthropods communities are stronger when phylogenetic and phylogeographic distance from native tree species increase. Therefore, the establishment of phylogenetically and phylogeographically distant non-native trees in forest plantations should be avoided to prevent the loss of arthropod abundance and biomass.

Keywords

Invasive plants, arthropods decline, black locust, black pine, arthropod-plant interactions, insect communities

Introduction

Arthropods are among the most diverse groups of animals (Ødegaard, 2000), provide important ecosystem services (Culliney, 2013; Dainese et al., 2019; Landis et al., 2000) and, due to their substantial biomass (Ødegaard, 2000), constitute an indispensable element of trophic interactions (Mooney et al., 2010; Wagner, 2020). The intensification of agriculture and forestry has caused dramatic alterations and homogenizations of the traditional cultural landscapes (Seibold et al., 2019; Sklenicka et al., 2014). These changes of land-use intensity resulted in global biodiversity decline in recent years (Dirzo et al., 2014), including arthropods (Cardoso et al., 2020; Hallmann et al., 2017; Seibold et al., 2019). Forest ecosystems, as environments with specific and stable microclimate/water regime, are highly sensitive to land-use change (Bengtsson et al., 2000).

Lowland temperate forests are one of the most threatened and economically exploited forest ecosystems across Europe (Bengtsson et al., 2000; Miklín & Čížek, 2014). These forests face pronounced changes in arthropod communities and ecosystem instability caused by intensification and changes of management practices (Bengtsson et al., 2000; Miklín & Čížek, 2014; Sebek et al., 2015). In general, arthropod diversity in lowland forests is strongly linked to the heterogeneity of vegetation structure and canopy-openness (Kadlec et al., 2018; Košulič

63 et al., 2016; Miklín & Čížek, 2014; Sebek et al., 2015), which is largely conditioned by the

64 dominant tree species (Hanzelka & Reif, 2016; Highland et al., 2013; Kadlec et al., 2018; Tews

65 et al., 2004), and management practices (Bengtsson et al., 2000; Miklín & Čížek, 2014; Sebek

66 et al., 2015).

67 One of the consequences of the forestry intensification is the plantation of non-native tree

68 species that often become invasive and alter the habitat structure of forests stands (Crooks,

69 2002; Hanzelka & Reif, 2016; Šibíková et al., 2019). In turn, this disrupts the trophic webs

70 within forest ecosystems (Ballard et al., 2013; Hejda et al., 2017; Reif et al., 2016; Richardson

71 & Rejmánek, 2011) and can lead to arthropod declines (van Hengstum et al., 2014; Litt et al.,

72 2014; Tallamy et al., 2020). However, the impacts of invasive trees on arthropods can vary

73 considerably between different arthropod taxa and trophic guilds (Litt et al., 2014; van

74 Hengstum et al., 2014; Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013). Herbivores,

75 in particular those inhabiting tree canopy, are generally the most affected arthropod guild due

76 to the replacement of their host tree species by unpalatable novel species (Bezemer et al., 2014;

77 Keane & Crawley, 2002; Litt et al., 2014; van Hengstum et al., 2014). Invasive trees also

78 negatively affect parasitoids mainly by decreasing their chances to find a suitable host (Harvey

79 & Fortuna, 2012; Simao et al., 2010). Predators and especially detritivores have been found to

80 be less influenced by tree invasion per se (Harris et al., 2004; Litt et al., 2014; Schirmel et al.,

81 2016; Štrobl et al., 2019), but respond to changes in habitat structure caused by tree invaders

82 (Litt et al., 2014; Štrobl et al., 2019; Van der Colff et al., 2015).

83 The effects of non-native tree species on arthropods can also depend on their phylogenetic

84 relatedness with native tree species (Agrawal & Kotanen, 2003; Agrawal et al., 2005; Zuefle et

85 al., 2008), invasiveness rate and the time of their introduction into novel areas (Bezemer et al.,

86 2014; Brändle et al., 2008). Non-native tree species that are closely phylogenetically related

87 with native tree species, especially their congeners, can host the same or even more individuals

88 and species of arthropod herbivores as native trees (Agrawal & Kotanen, 2003; Burghardt et

89 al., 2010; Zuefle et al., 2008). While the influence of specific non-native trees on habitat

90 structure and local arthropod communities has been well investigated in temperate forests (van

91 Hengstum et al., 2014; Kadlec et al., 2018; Štrobl et al., 2019), a detailed assessment of the

92 differential impacts of non-native congeners and non-congeners trees, by comparing them with

93 related native tree species on different arthropod taxa and guilds is missing.

94 In this study, we evaluated the impacts of two common non-native tree species – black locust

95 (*Robinia pseudoacacia* L.; Fabaceae) and black pine (*Pinus nigra* Arnold; Pinaceae) – on the

96 communities of nocturnal forest arthropods in lowland forests by comparing them with native

tree species with different degrees of phylogenetic relatedness. Specifically, we selected broad-leaved oaks (common oak (*Quercus robur* (Matt.) Liebl.) and sesille oak (*Quercus petraea* L); Fagaceae; henceforth 'oak stands'), and coniferous Scots pine (*Pinus sylvestris* L.; Pinacea) as non-congeneric and congeneric native trees, respectively. Nocturnal arthropods are represented by various groups and make up a substantial part of arthropod biomass in forest stands, which is an essential component of the diet of higher trophic levels (Bowler et al., 2019; Reif et al., 2016; Wagner, 2020). For this purpose, we adopted a multi-taxa approach (Seibold et al., 2018) and investigated the effects of focused non-native tree species across several arthropod groups from different trophic levels, including herbivores, parasitoids, predators and omnivores. Specifically, we asked the following questions:

1. Do forest stands of the non-native black locust and black pine differ in habitat structure compared to stands of native trees? We predicted bigger differences in habitat structure between black locust and oak stands than between black pine and Scots pines stands due to similar ecological strategy in these coniferous trees.

2. Are non-native tree species linked to differences on total arthropod abundance and biomass compared to native tree species? We predicted that black locust would host lower total arthropod abundance and biomass in comparison with oak stands due to its far phylogenetically relatedness to this native tree species. Moreover, we assumed that we would not find significant differences in total arthropod abundance and biomass between congeneric black pine and Scots pine stands because of their close relatedness. Finally, we expected that total arthropod abundance and biomass would be lower in stands of coniferous trees (black pine and Scots pine) than in oak stands due to the higher food quality for herbivores offered by broad-leaved species (Feeny, 1976; Mattson & Scriber, 1987).

3. Do these non-native tree species differently influence arthropod community composition in comparison to native tree species? We predicted changes in community composition caused by higher abundance and biomass of herbivorous and parasitoid arthropods associated with native tree species. At the same time, we assumed that these differences would be larger between black locust and oak stands in comparison with black pine and Scots pine stands. On the other hand, we did not expect strong differences in the abundance and biomass of predatory and omnivorous taxa between non-native and native tree stands.

Material and methods

Study area and sampling design

The study was carried out in central Bohemia, Czech Republic (Fig. 1) in 2014 and 2015. The study area (49.84°–50.16°N, 13.86°–14.46°E ~ 1200 km^2, 216–498 m a. s. l.) is located in a region with an average annual precipitation of 500–650 mm and an average annual temperature of 7–9 °C (Květoň & Voženílek, 2011). The landscape is characterized by cultivated forest stands surrounded by arable fields, grasslands, and human settlements. Forests are composed of native trees dominated by oaks (*Quercus* spp.), Scots pine (*Pinus sylvestris*), spruce (*Picea abies* (L.) Karsten), limes (*Tilia* spp.), maples (*Acer* spp.) and beech (*Fagus sylvatica* L.), which have been locally replaced by non-native species, mainly black locust (*Robinia pseudoacacia*) and black pine (*Pinus nigra*).

Within the study area, we established 79 square plots (100 × 100 m): 19 plots in black locust forest stands, 25 in oak, 18 in black pine and 17 in Scots pine (Fig. 1). To minimize edge effect, all plots were placed within large forest areas and at a minimum distance of 100 m to most close edge. However, some plots in black pine were located closer to forest edges (distances of ca 50m) due to the fact that black pine was often planted on originally non-forested areas not directly adjacent to forest stands. Furthermore, plots were separated by at least 500 m (see Hanzelka & Reif, 2016 for details).

Focal non-native tree species

The invasive black locust occurs naturally in the Southeastern United States, where it grows as an early-successional tree in Quercus-Carya forests (Boring & Swank, 1984; Cierjacks et al., 2013). Black locust was introduced to Europe at the beginning of the 17th century (Cierjacks et al., 2013; Vítková et al., 2017) and is considered as one of the most widespread and long-lasting invasive tree species throughout Europe, including the Czech Republic (Campagnaro, Brundu et al., 2018; Nentwig et al., 2018; Vítková et al., 2017). Due to its nitrogen-fixing ability, this species enhances nitrogen and supports the spread of nitrophilous plant species (Benesperi et al., 2012; Šibíková et al., 2019; Vítková et al., 2017). Due to its ecology and physiognomy, black locust forests have an open structure and well developed understorey in novel areas (Campagnaro, Nascimbene et al., 2018; Hanzelka & Reif, 2016; Vítková et al., 2017). These changes in vegetation structure also influence local animal communities (Hanzelka & Reif, 2016; Reif et al., 2016; Vítková et al., 2017), including arthropods (Buchholz et al., 2015; Degomez & Wagner, 2001; Kadlec et al., 2018; Štrobl et al., 2019).

The alien black pine is native from southwestern Asia, North Africa to South Europe and the southern part of Central Europe (Gulezian & Nyberg, 2011). Black pine was introduced to Czech Republic at the beginning of the 19th century, and it was planted in warm regions in

163   extreme habitats (Křivánek, 2006). In the Czech Republic, black pine is considered as a

164   naturalized alien species with low invasive potential (Pyšek et al., 2012). Black pine forms open

165   stands with a well-developed shrub layer in novel areas of Central Europe (Hanzelka & Reif,

166   2016; Mikulová et al., 2019) and can change native plant communities (Mikulová et al., 2019).

167   In its novel European habitats, black pine is able to spread naturally into xeric forests and

168   scrublands (Křivánek, 2006), but its invasive potential is low in comparison with North

169   America or New Zealand (Weber, 2003). The effects of non-native black pine on native

170   arthropod communities remain poorly study, although Pawson et al. (2010) found that

171   increasing canopy cover of black pine had a negative influence on grassland arthropod

172   communities.

Environmental parameters sampling

174   To contemplate the responses of forest arthropods assemblages to habitat structure, age of the

175   forest stand, landscape composition and altitude (Highland et al., 2013; Kadlec et al., 2018;

176   Novotný et al., 2015; Štrobl et al., 2019), we recorded the following variables in all study plots.

177   Percentage cover of vegetation layers (herbs < 0.5 m in height (HERB1); herbs > 0.5 m

178   (HERB2); shrubs 1–5 m (SHRUBS); and canopy (CANOPY)) and clearings (gaps in the stands

179   without full-grown trees integrated in the canopy cover; CLEARINGS) were estimated by

180   visually according to Hanzelka & Reif (2016). We counted number of fallen (FALLEN TREES)

181   and dead trees (DEAD TREES) in the plot and determined age of the forest stand (AGE) as

182   well.

183   Furthermore, we determined the altitude of study plots (ALT) and the proportion of the forest

184   stands in the surroundings of study plots within a 500 m radius circular buffer around each plot

185   centre (FOREST) using ArcGis 10.2 (ESRI, 2011). This variable also mirrors the total size of

186   the forest stands and at the same time the proportion of non-forest habitats in the vicinity of

187   study plots.

Arthropod sampling and studied taxa

189   Arthropods were sampled using portable light traps (Brehm & Axmacher, 2006) equipped with

190   two 8W UV LED strip lights (total luminous flux 400 lm, wavelength range 400–420 nm) and

191   powered by 7.2 Ah/12 V lead batteries. The attraction of nocturnal arthropods to light sources

192   is a common and effective method for obtaining quantitative data on their abundance and

193   biomass (Fayle et al., 2007; Ober & Hayes, 2008). We sampled arthropods during two complete

194   seasons: 2014 (all black locust study plots, 20 oak study plots) and 2015 (all Scots pine and

195   black pine study plots, five oak study plots). At each plot, a single portable light trap was placed

196   approximately in the middle of plot, which attracts arthropods within a radius of a few tens of

197   metres (Truxa & Fiedler, 2012). Light traps were exposed on the same night under suitable

198   weather conditions (no strong wind, no rainfall), from dusk until dawn, at the beginning of each

199   month from April to November in both years. This sampling effort allowed us to cover all major

200   phenological phases of arthropod activity and standardized the effects of short-term climatic

201   conditions (Yela & Holyoak, 1997). All collected individuals were euthanized using chloroform

202   and subsequently frozen at −22°C.

203   All captured arthropods from the following taxonomic groups were counted and identified

204   to the suborder or order level: spiders (Araneae), harvestmen (Opillionida), orthopteroids

205   (Orthopthera), cockroaches (Blattodea), earwigs (Dermaptera), bark lice (Psocoptera),

206   "Homoptera" (Auchenorrhyncha and Sternorrhyncha, separately), true bugs (Heteroptera),

207   neuropterans (Neuroptera), beetles (Coleoptera: Adephaga, Polyphaga), mecopterans

208   (Mecoptera), true flies (Diptera: Brachycera and Nematocera), moths (nocturnal Lepidoptera),

209   and hymenopterans (suborder Apocrita excluding ants). These focal taxa widely represent

210   arthropods from different trophic levels – herbivores, parasitoids, predators and omnivores. The

211   arthropod taxa without affinity to forest ecosystems (i.e. water-depending groups as Trichoptera

212   or Ephemeroptera) were considered random migrants in forest habitats and excluded. To obtain

213   the dry biomass of each of the above-mentioned groups, all individuals from each plot and date

214   were dried in an oven for twelve hours at 80 °C and then weighed on the analytical scale with

215   an accuracy of 0.0001 g (van Langevelde et al., 2011).

216   **Data analysis**

217   **Habitat structure**

218   To reduce the complexity of habitat structure data without losing substantial information and

219   to describe the main gradients of habitat structure of the studied forest stands, three principal

220   component analyses (PCAs) were performed in Canoco 5.0 (ter Braak & Šmilauer, 2012): one

221   considering the four stand types combined and two for the comparing broad-leaved (black

222   locust vs. oak) and coniferous stand types (black pine vs. Scots pine) separately. We used the

223   scree plot method and Kaiser's rule (Jackson, 1993) to distinguish the principal components

224   explaining most of the variability in the data. Based on these criteria, the scores from the first

225   two principal components of habitat structure ('HAB1' and 'HAB2') were used as predictors

226   describing habitat structure of study plots in subsequent analyses. To compare the habitat

227   structure among stand types (STAND: black locust, oak, black pine, Scots pine), six linear

228 models (according to first two PC axes from all PCAs) were performed in R 3.6.3 (R Core
229 Team, 2020) with the principal components of habitat characteristics (HAB1 or HAB2) as
230 respective response variables and STAND as the predictor variable.

Arthropod abundance and biomass

232 We analysed the differences in the total abundance and the total biomass of arthropods (both
233 pooled across all taxa and samples) among the stand types using a linear models in R 3.6.3 (R
234 Core Team, 2020) with total abundance or total biomass as a response variable, both
235 transformed using natural logarithm. Due to potential spatial autocorrelation between study
236 plots, we employed generalized least squares (GLS) models (R package 'nlme'; Pinhiero, 2021)
237 in all the following univariate analyses. First, we fitted full models with all predictors: stand
238 type, HAB1 and HAB2, AGE, ALT and FOREST. Geographic coordinates of plot centres were
239 included in the full models to contemplate spatial effects and different autocorrelation structures
240 were fitted to the residuals (exponential, linear, rational quadratics, spherical and Gaussian) and
241 compared using the Akaike Information Criterion (AIC, Akaike, 1974). For both response
242 variables, the most parsimonious models (i.e., those with the lowest AIC value) were models
243 with a Gaussian autocorrelation structure. Second, an information-theoretic approach (R
244 package 'MuMin' Bartoń; 2018; Burnham & Anderson, 2002) was used for model selection
245 and multi-model inference. Candidate models containing all possible predictor combinations
246 were compared by their AICc values (Akaike, 1974; Burnham & Anderson, 2002) and models
247 within a ΔAICc < 2 were used for inference employing model averaging based on AIC weights
248 (r package 'MuMin'; Burnham & Anderson, 2002). To identify significant differences among
249 the stand types, Tukey's post hoc tests (package 'emmeans'; Length et al., 2020) were
250 performed.

Arthropod community composition

252 To compare arthropod community composition, analysed separately for the abundance and dry
253 biomass of each taxonomic group, we used multivariate ordination methods in Canoco 5.0 (ter
254 Braak and Šmilauer, 2012). Based on the gradient lengths (for all models a gradient was at
255 most 1.3 SD units long), redundancy analyses (RDAs) were used (Šmilauer & Lepš, 2014) for
256 comparing arthropod community composition among stand types (STAND: black locust, oak,
257 black pine, Scots pine). Before that, we tested possible correlations between the direct effects
258 of trees species (TREE: black locust, oak, black pine, Scots pine) and habitat structure of study
259 plots (HAB1 and HAB2) on the arthropod community composition (Kadlec et al., 2018; Štrobl

260 et al., 2019). For this purpose, we used the variation partitioning approach (Peres-Neto et al.,

261 2006) to distinguish between marginal (effects of a predictor without taking other predictors

262 into account) and conditional (effects of a predictor after controlling for the effects of the

263 remaining predictors) effects of TREE, HAB1 and HAB2 on arthropod community composition

264 (Šmilauer & Lepš, 2014).

265 Due to potential spatial autocorrelation among the study plots, the principal coordinates of

266 neighbour matrices framework (PCNM; Dray et al., 2006; Peres-Neto et al., 2006) were

267 implemented into the RDAs (Šmilauer & Lepš, 2014). Within PCNM, the principal coordinate

268 analysis (PCoA) was performed to obtain the spatial variables represented by the respective

269 PCo axes. Monte-Carlo permutation tests (999 permutations) were used to test the significance

270 of each PCo axis, and the scores of the most significant PCo axes were further used in the RDAs

271 as covariables, capturing the spatial autocorrelation in the models (Šmilauer & Lepš, 2014).

272 Furthermore, two sets (separately for arthropod abundance and biomass, both response

273 variables were log-transformed) of RDAs with Monte-Carlo significance testing (999

274 permutations) were performed: i) for all stand types together (black locust, oaks, black pine,

275 and Scots pine); ii) for broad-leaved tree species separately (black locust vs. oak); and iii) for

276 coniferous tree species separately (black pine vs. Scots pine). In these analyses, STAND, and

277 significant marginal and conditional effects of HAB1 and HAB2 on arthropod composition in

278 the variation partitioning method were the predictors, and the AGE, ALT, FOREST and the

279 PCo axes scores were included as covariables.

280

Results

Habitat structure

283 The PC1 axis of habitat characteristics considering all stand types (HAB1) explained 42.40 %

284 of the variation in habitat structure and described a gradient from open stands with well-

285 developed shrub and taller herb layers to stands with a continuous canopy and less developed

286 understory (Fig. 2a). Most stand types significantly differed in habitat structure along HAB1,

287 except for black pine – Scots pine and oak – Scots pine stands comparisons (Table S1). PC2

288 axis (HAB2) explained 28.28 % of the variation in habitat structure and reflected a gradient

289 from stands with a well-developed lower herb layer and continuous canopy to stands with a

290 higher number of fallen and dead trees (Fig. 2a). Most stand types did not differ along the HAB2

gradient, with the exception of the comparison between black pine and Scots pine stands (Table S1).

The PCA examining the differences in habitat structure between broad-leaved trees (black locust and oak) showed a gradient along a PC1 axis (HAB1, 58.74 % of the variation explained) from stands with well-developed shrub and taller herb layers and to stands with well-developed lower herb layer and continuous canopy (Fig. 2b). The black locust stands had significantly lower scores along the gradient of HAB1 than oak stands (t = −6.4, p < 0.001; Fig. 2b). PC2 axis (HAB2, 16.84 % of the variation in the habitat structure explained) described a gradient from stands with higher numbers of fallen and dead trees to stands without fallen and dead trees (Fig. 2b). Black locust and oak stands did not differ along the gradient of HAB2 (t = −0.6, p = 0.572).

The PCA comparing stands of coniferous tree species (black pine and Scots pine) showed a gradient along the PC1 axis (HAB1, 45.41 % of the variation in the habitat structure explained) from stands with well-developed shrub and herb layers to stands with higher numbers of fallen and dead trees (Fig. 2c). Black pine and Scots pine stands did not differ along the gradient of HAB1 (t = −0.2, p = 0.706; Fig. 2c). The PC2 axis of habitat characteristics (HAB2, 27.27 % of the variation in the habitat structure explained) slightly reflected a gradient from stands with a well-developed shrub layer and higher numbers of clearings and fallen and dead tress to stands with undeveloped understory and without clearings and fallen and dead trees (Fig. 2c). Black pine stands had significantly lower scores along the HAB2 axis than black pine stands (t = −3.4, p < 0.001; Fig. 2c).

Arthropod abundance and biomass

In total, 187 947 arthropod individuals were captured (see Table S2 for details). On average, we recorded lower abundances in non-native tree stands in comparison with native stands (Fig 2a). Concretely, 1203 (± 369 SD) individuals were captured in black locust stands and 1974 (± 985) in black pine stands, whereas 3164 (± 1921) were collected in oak stands and 2969 (± 1700) in Scots pine stands (Table S2). Altitude and stand type were only two predictors with significant impacts on arthropod total abundance (Table S3; Table 1). The total number of individuals was significantly higher in oak stands than in the remaining stand types (Table 2) and did not differ between forest stands dominated by black locust, black pine, and Scots pine (Table 2).

Altogether, 1,939.51 g of arthropod dry biomass were collected (see Table S4 for details). Following the same pattern that for total abundance, dry biomass was on average higher in

324   stands of native tree species – 32.94 g (± 12.44) of arthropods in oak forests and 25.89 g (±

325   10.37) in stands of Scots pine, than in non-native stands – 15.17 g (± 5.07) in stands dominated

326   by black locust and 21.53 g (± 9.64) in stands of black pine (Table S4). Stand type was included

327   in the two top models and had the strongest influence on total arthropod biomass (Table S3).

328   Final model of averaged coefficients included ALT and STAND and both of these predictors

329   had significant impacts on total arthropod biomass (Table 1). Total arthropod biomass was

330   significantly higher in oak stand in comparison with the remaining stand types (Table 2),

331   whereas no differences were detected between black pine, Scots pine and black locust stands

332   (Table 2).

Arthropod community composition

334   In all models, conditional effects of habitat structure on arthropod community composition were

335   not significant (see Table S5). Contrarily, the direct effect of dominant tree species (TREE) had

336   significant conditional effects on arthropod community composition, with the exception of

337   model comparing biomass of focal arthropod taxa between black pine and Scots pine stands

338   (Table S5).

339   Arthropod community composition significantly differed among stand types in all models

340   after the controlling for spatial (PCo scores from the PCNMs) and environmental effects (ALT,

341   FOREST, AGE; Table 3; Fig. 4; Fig. S1). The RDAs comparing the community composition

342   among all stand types (both for abundance and total dry biomass), showed a significant gradient

343   along the first axis from stands of native to non-native tree species (Fig. S1). Also, for the

344   analyses using arthropod abundance, a gradient along the second axis from stands of coniferous

345   to broad-leaved tree species was detected (Fig. S1a).

346   Arthropod community composition, both for abundance and dry biomass, significantly

347   differed between black locust and oak stands (Table 3; Fig. 3a–b). Abundance of most studied

348   taxa (Polyphaga, Apocrita, Nematocera, Brachycera, Auchenorrhyncha, Adephaga and

349   Opilionida) were associated with oak stands and other taxa did not differ between these stand

350   types (Fig. 3a). Higher biomass of Lepidoptera and Polyphaga (mostly herbivorous) was

351   recorded in oak than in black locust stands (Fig. 3b). Moreover, Diptera, Apocrita, Opilionida

352   and Adephaga also had higher biomass in oak stands in comparison with black locust stands

353   (Fig. 3b). In contrast, only biomass of mostly omnivorous Dermaptera was higher in black

354   locust stands (Fig. 4b).

355   Arthropod community composition, analysed with both abundance and dry biomass, was

356   significantly different between black pine and Scots pine stands (Table 3; Fig. 3c–d).

357 Abundance and biomass of mostly omnivorous Orthoptera was higher in black pine than in
358 Scots pine stands. Also, carnivorous Aranea and Adephaga, and biomass of Neuroptera, were
359 slightly associated with black pine stands (Fig. 3c–d). On the contrary, higher abundance and
360 biomass of mostly herbivorous Heteroptera and Sternorhyncha occurred in stands of Scots pine
361 (Fig. 3c–d). Abundance and biomass of other taxa was not linked to either of these stand types
362 (Fig. 3c–d).
363

364 **Discussion**

365 **Conclusions and conservation implications**

366 **Acknowledgements**

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631 **Table 1.** Effects of altitude and stand types on total abundance and total dry biomass of arthropods. For each estimate, the standard error (SE), t-
632 and p-values are shown.

Best fitting model (total arthropod abundance)					Model with averaged coefficients (total arthropod biomass)				
Model parameters	Estimate	SE	t-value	p-value	Model parameters	Estimate	SE	z-value	p-value
Intercept	**5.633**	**0.377**	**14.96**	**<0.001**	**Intercept**	**2.199**	**0.624**	**3.514**	**<0.001**
ALT[a]	**0.005**	**0.001**	**4.40**	**<0.001**	**ALT[a]**	**0.004**	**0.001**	**3.98**	**<0.001**
STAND[b] (black pine)	−0.071	0.185	−0.38	0.703	STAND[b] (black pine)	−0.006	0.201	0.03	0.976
STAND[b] (oak)	**0.658**	**0.135**	**4.89**	**<0.001**	**STAND[b] (oak)**	**0.6296**	**0.136**	**4.58**	**<0.001**
STAND[b] (Scots pine)	0.256	0.180	1.42	0.160	STAND[b] (Scots pine)	0.157	0.197	0.79	0.430

633 [a] ALT – altitude of the study plots; [b] STAND – stand type of the study plots (black locust, oak, black pine and Scots pine stands).

634

635 **Table 2.** Results of Tukey's HSD tests comparing total abundance and total dry biomass of arthropods among forest stand types. For each pair of
636 stand types, the estimate and its standard error, t-ratio and p-value are shown.

Total abundance					Total dry biomass				
Compared stands	Estimate	SE	t-ratio	p-value	Compared stands	Estimate	SE	z-ratio	p-value
black locust – black pine	0.071	0.185	0.38	0.981	black locust – black pine	0.006	0.201	0.03	1.000
black locust – oak	**−0.658**	**0.134**	**−4.89**	**<0.001**	**black locust – oak**	**−0.630**	**0.136**	**−4.64**	**<0.001**
black locust – Scots pine	−0.255	0.180	−1.42	0.492	black locust – Scots pine	−0.157	0.197	−0.80	0.856
black pine – oak	**−0.728**	**0.148**	**−4.92**	**<0.001**	**black pine – oak**	**−0.636**	**0.138**	**−4.61**	**<0.001**
black pine – Scots pine	−0.326	0.164	−1.99	0.205	black pine – Scots pine	−0.163	0.140	−1.16	0.649
oak – Scots pine	**0.402**	**0.146**	**2.76**	**0.036**	**oak – Scots pine**	**0.472**	**0.136**	**3.49**	**0.003**

637

638 **Table 3.** Results of the redundancy analyses (RDAs) evaluating the differences in community composition of arthropod taxa among stand types

639 using **a)** abundance and **b)** total dry biomass. All RDAs controlled for the effects of environmental (ALT, FOREST, AGE) and spatial variables

640 (PCo scores from PCNMs).

Model	Eigenvalues				Test of all canonical axes			
a) Arthropod abundance	Axis 1	Axis 2	Axis 3	Axis 4	Trace	pseudo-F	p	Adj. VAR[a] %
all stand types[b]	0.069	0.038	0.017	0.206	0.124	4.8	0.001	13.3
black locust – oak	0.056	0.114	0.074	0.054	0.056	4.4	0.001	8.3
black pine – Scots pine	0.081	0.237	0.110	0.081	0.081	3.5	0.008	7.6
b) Arthropod dry biomass	Axis 1	Axis 2	Axis 3	Axis 4	Trace	pseudo-F	p	Adj. VAR[a] %
all stand types[b]	0.149	0.021	0.004	0.249	0.174	6.6	0.001	18.64
black locust – oak	0.079	0.158	0.094	0.076	0.079	6.4	0.001	12.4
black pine – Scots pine	0.080	0.258	0.155	0.086	0.080	3.5	0.008	7.8

641 [a] Adj. VAR (%): adjusted percent variance explained by the predictors; [b] all stand types – analysis investigating the effects of all forest stand types

642 (black locust, oak, black pine, and Scots pine) together.

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Figure captions

648   **Fig. 1.** Map showing the location of the study plots (19 plots dominated by black locust, 25 by

649   oak, 18 by black pine and 17 by Scots pine) in the Czech Republic.

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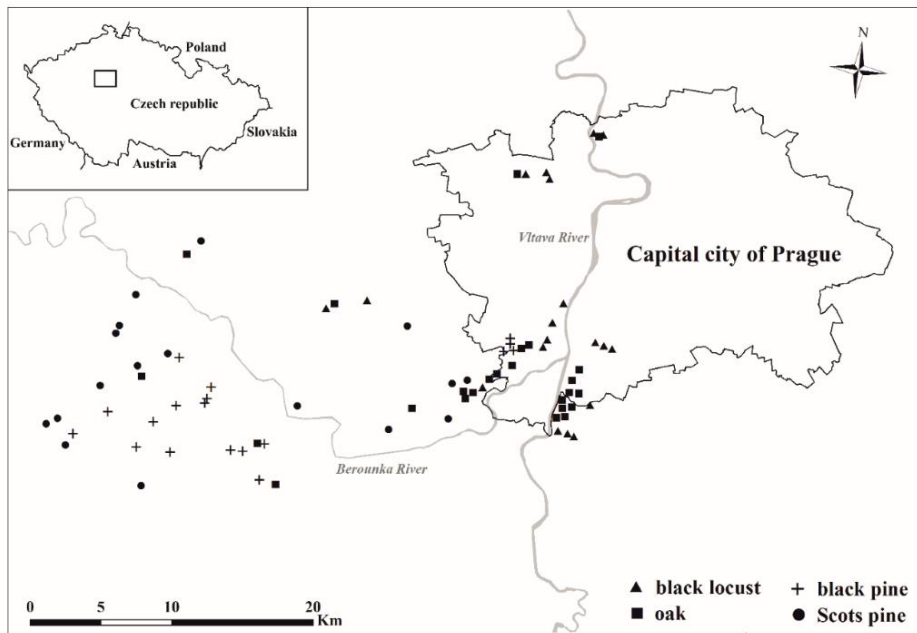
Fig. 2. Principal components analyses (PCAs) of habitat structure among **a)** all stand types; **b)** black locust and oak stands; **c)** black pine and Scots pine stands. Polygons indicate convex hulls bounding the black locust (yellow circles), oak (blue squares), black pine (brown stars) and Scots pine (green triangles) plots.
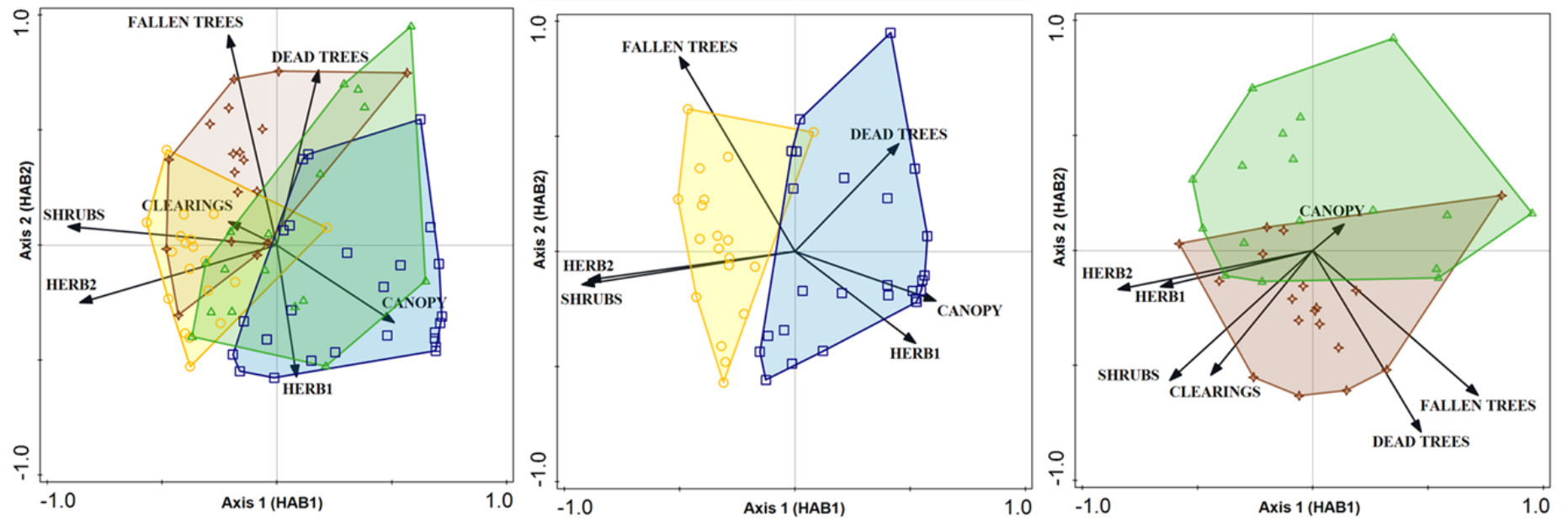
657 **Fig. 3.** Ordination diagrams of redundancy analyses (RDAs) evaluating the differences in the
658 community composition of arthropod taxa among forest stand types, using abundance and total
659 dry biomass. (**a**, **b**) Differences between black locust and oak stands, (**c**, **d**) differences between
660 black pine and Scots pine forest stands.

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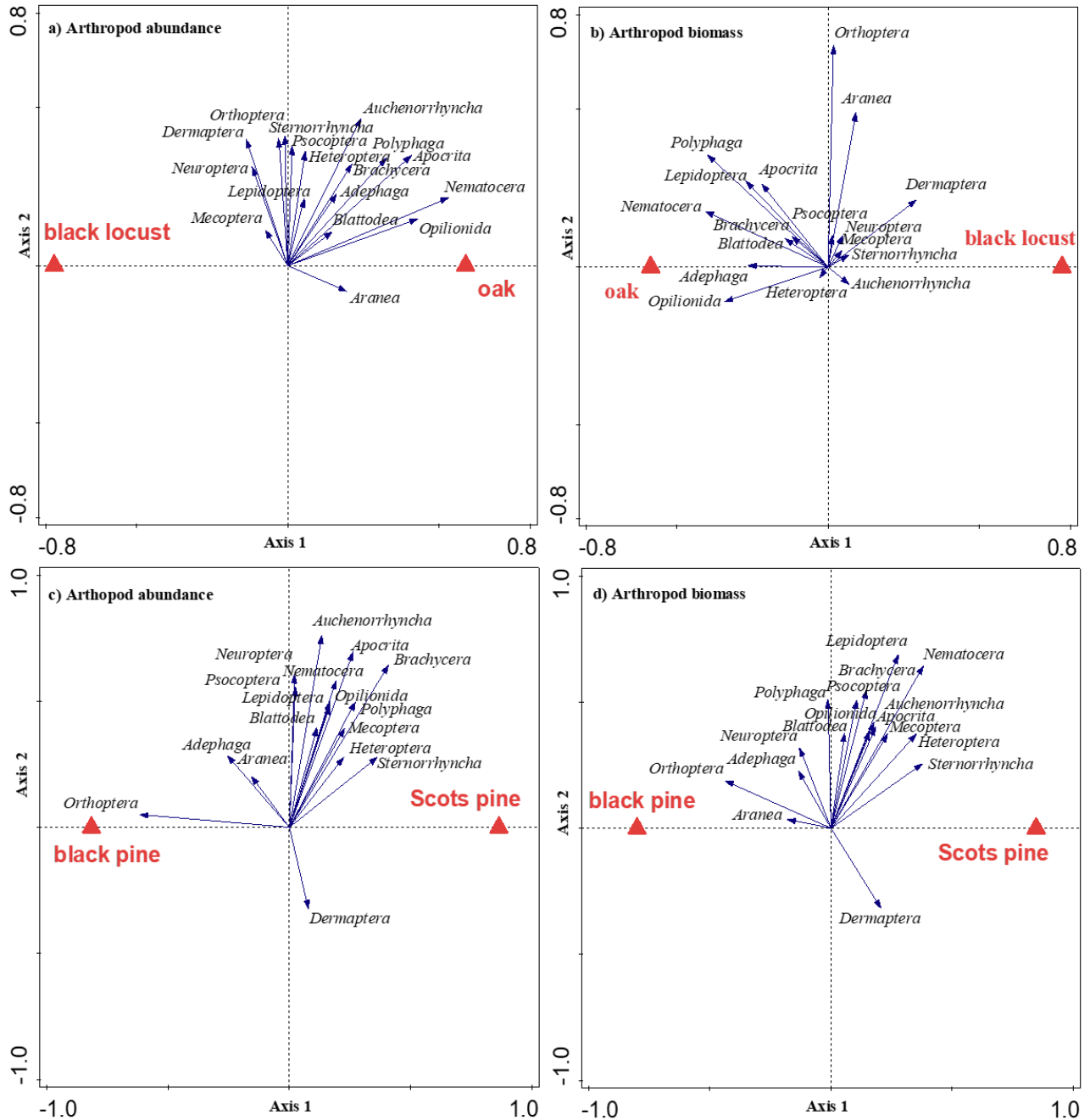
Appendices

Table S1. Results of Tukey's HSD post hoc tests analysing the differences in habitat structure between stand types. Significant differences (p < 0.05) are highlighted in bold, and marginally significant effects (p < 0.1) are shown in italic.

Tukey's HSD post hoc test (HAB1[a])		Tukey's HSD post hoc test (HAB2[b])	
Compared stands	p-value	Compared stands	p-value
black locust – black pine	**0.013**	*black locust – black pine*	*0.083*
black locust – oak	**<0.001**	black locust – oak	0.922
black locust – Scots pine	**0.003**	black locust – Scots pine	0.260
black pine – oak	**0.020**	black pine – oak	0.217
black pine – Scots pine	0.964	**black pine – Scots pine**	**<0.001**
oak – Scots pine	*0.082*	*oak – Scots pine*	*0.058*

[a] HAB1 – scores from PCA describing habitat structure of woodlots along the first PC axes; [b] HAB2 – scores from PCA describing habitat structure of woodlots along the second PC axes.

Table S2. Average (± standard deviation) and total numbers of arthropod individuals recorded in stands of black locust, oak, black pine, and Scots pine.

Taxa	Number of individuals mean ± SD				Total number of individuals				
	black locust mean ± SD	oak mean ± SD	black pine mean ± SD	Scots pine mean ± SD	black locust sum	oak sum	black pine sum	Scots pine sum	Total
Aranea	31 (± 46)	41 (± 19)	58 (± 56)	42 (± 47)	597	1015	1045	714	3371
Opilionida	2 (± 3)	9 (± 18)	2 (± 3)	4 (± 7)	32	219	32	76	359
Orthoptera	5 (± 6)	7 (± 7)	10 (± 8)	2 (± 3)	92	165	186	39	482
Blattodea	1 (± 1)	11 (± 10)	6 (± 7)	10 (± 9)	24	270	115	173	582
Dermaptera	5 (± 9)	3 (± 8)	1 (± 2)	2 (± 3)	101	87	26	31	245
Psocoptera	2 (± 2)	11 (± 21)	10 (± 8)	13 (± 17)	29	269	173	218	689
Auchenorrhyncha	7 (± 8)	133 (± 295)	47 (± 44)	80 (± 70)	142	3332	843	1357	5674
Sternorrhyncha	1 (± 1)	18 (± 49)	8 (± 7)	25 (± 23)	15	462	152	424	1053
Heteroptera	5 (± 7)	16 (± 21)	20 (± 20)	58 (± 99)	91	401	362	990	1844
Neuroptera	7 (± 5)	13 (± 19)	25 (± 28)	18 (± 13)	138	330	449	312	1229
Adephaga	1 (± 1)	4 (± 5)	7 (± 6)	2 (± 3)	23	94	117	41	275
Polyphaga	92 (± 43)	236 (± 121)	144 (± 79)	244 (± 150)	1745	5912	2584	4148	14389
Mecoptera	1 (± 1)	1 (± 1)	1 (± 1)	2 (± 3)	15	19	10	27	71
Brachycera	44 (± 29)	165 (± 168)	64 (± 53)	279 (± 337)	837	4135	1153	4741	10866
Nematocera	297 (± 190)	1245 (± 885)	377 (± 331)	843 (± 936)	5637	31135	6778	14323	57873
Lepidoptera	666 (± 225)	1140 (± 813)	1155 (± 612)	1277 (± 529)	12653	28501	20797	21712	83663
Apocrita	36 (± 16)	110 (± 97)	39 (± 22)	67 (± 45)	690	2749	702	1141	5282
All arthropods	1203 (± 369)	3164 (± 1921)	2969 (± 1700)	1974 (± 985)	22861	79095	35524	50467	187947

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671 **Table S3.** Characteristics of the best models (ΔAICc < 2) analysing the responses of **a)** total

672 abundance and **b)** total dry biomass of arthropods to stand type and environmental variables.

Model / Predictors	Intercept	ALT[a]	STAND[b]	K[c]	AICc[d]	ΔAICc	AICc weight
a) Total abundance							
m7	+	+	+	8	−14.100	0.270	0.466
b) Total dry biomass							
m7	+	+	+	8	39.300	0.000	0.315
m5	+	−	+	7	40.600	1.210	0.172

673 [a] ALT – altitude of the study plots; [b] STAND – stand type of the study plots (black locust, oak,

674 black pine and Scots pine stands); [c] K – number of estimated model parameters; [d] AICc –

675 Akaike information criterion corrected for small sample sizes. The +/− symbols indicate if the

676 predictor was included (+) or not (−) in the model.

677 **Table S4.** Average (± standard deviation) and total arthropod dry biomass (in grams) recorded in stands of black locust, oak, black pine, and Scots pine.

| Taxa	Number of individuals mean ± SD				Total number of individuals				
	black locust mean ± SD	oak mean ± SD	black pine mean ± SD	Scots pine mean ± SD	black locust sum	oak sum	black pine sum	Scots pine sum	Total
Aranea	0.4320 (± 0.8691)	0.4040 (± 0.2856)	0.4472 (± 0.6924)	0.2755 (± 0.3924)	8.2074	10.1003	8.0501	4.6833	31.0411
Opilionida	0.0093 (± 0.0150)	0.0714 (± 0.1345)	0.0170 (± 0.0277)	0.0327 (± 0.0489)	0.1765	1.7856	0.3065	0.5562	2.8248
Orthoptera	0.4962 (± 0.8374)	0.7198 (± 0.8537)	1.0655 (± 0.9490)	0.2962 (±0.3888)	9.4271	17.9938	19.1787	5.0361	51.6357
Blattodea	0.0073 (± 0.0088)	0.0750 (± 0.0631)	0.0509 (± 0.0545)	0.0814 (± 0.0771)	0.1390	1.8760	0.9161	1.3845	4.3156
Dermaptera	0.0874 (± 0.1379)	0.0256 (± 0.0534)	0.0210 (± 0.0272)	0.0290 (± 0.0435)	1.6601	0.6390	0.3779	0.4934	3.1704
Psocoptera	0.0008 (± 0.019)	0.0036 (± 0.0067)	0.0032 (± 0.0036)	0.0047 (± 0.0084)	0.0151	0.0896	0.0583	0.0800	0.2430
Auchenorrhyncha	0.0042 (± 0.0041)	0.1629 (± 0.5533)	0.0310 (± 0.0275)	0.0440 (± 0.0269)	0.0800	4.0731	0.5584	0.7473	5.4588
Sternorrhyncha	0.0001 (± 0.0001)	0.0017 (± 0.0039)	0.0019 (± 0.0018)	0.0054 (± 0.0072)	0.0016	0.0414	0.0349	0.0911	0.1689
Heteroptera	0.0134 (± 0.0165)	0.0687 (± 0.1000)	0.0455 (± 0.0328)	0.1108 (± 0.1250)	0.2548	1.7184	0.8198	1.8844	4.6773
Neuroptera	0.0249 (± 0.0193)	0.0273 (± 0.0275)	0.0519 (± 0.0445)	0.0341 (± 0.0206)	0.4726	0.6822	0.9333	0.5803	2.6684
Adephaga	0.0117 (± 0.0175)	0.0480 (± 0.0611)	0.0678 (± 0.0769)	0.0321 (± 0.0435)	0.2222	1.2004	1.2210	0.5457	3.1893
Polyphaga	1.1921 (± 0.4159)	2.8852 (± 1.3571)	1.4995 (± 0.5123)	1.8023 (± 0.8960)	22.6491	72.1302	26.9909	30.6398	152.4100
Mecoptera	0.0062 (± 0.0088)	0.0057 (± 0.0103)	0.0045 (± 0.0099)	0.0168 (± 0.0339)	0.1178	0.1435	0.0810	0.2854	0.6277
Brachycera	0.0673 (± 0.0480)	0.3064 (± 0.2842)	0.1138 (± 0.0892)	0.4593 (± 0.5325)	1.2782	7.6600	2.0477	7.8089	18.7948
Nematocera	0.4750 (± 0.3480)	1.7667 (± 1.2582)	0.5680 (± 0.7597)	1.0073 (± 1.1085)	9.0245	44.1672	10.2247	17.1243	80.5407
Lepidoptera	12.2180 (± 4.3576)	26.0440 (± 10.1231)	17.4189 (± 8.9709)	21.5025 (± 8.9249)	232.1414	651.0999	313.5406	365.5433	1562.3251
Apocrita	0.1236 (± 0.0767)	0.3251 (± 0.2305)	0.1262 (± 0.1037)	0.1574 (± 0.0887)	2.3492	8.1269	2.2711	2.6753	15.4225
All arthropods	15.1693 (± 5.0693)	32.9411 (± 12.4387)	21.5339 (± 9.6399)	25.8917 (± 10.3714)	288.2166	823.5274	387.6109	440.1593	1939.5142

678

Table S5. Results of variation partitioning analysing marginal and conditional effects of dominant tree species and habitat structure on arthropod community composition. Significant effects ($p < 0.05$) are highlighted in bold.

Arthropod abundance	Factor groups	Marginal effects			Conditional effects		
		pseudo-F	p	adj. VAR[a]	pseudo-F	p	adj. VAR[a]
all stand types[b]	TREE[c]	**9.1**	**0.001**	**23.65**	**6.2**	**0.001**	**17.15**
	HABITAT[d]	**4.8**	**0.001**	**8.84**	1.4	0.135	1.07
black locust – oak	TREE[c]	**11.7**	**0.001**	**19.94**	**4.3**	**0.008**	**7.35**
	HABITAT[d]	**4.5**	**0.002**	**14.01**	1.1	0.315	0.48
black pine – Scots pine	TREE[c]	**5**	**0.001**	**10.48**	**2**	**0.048**	**3.05**
	HABITAT[d]	**2.8**	**0.004**	**9.35**	1.3	0.194	1.83
Arthropod dry biomass	**Factor groups**	**Marginal effects**			**Conditional effects**		
		pseudo-F	p	adj. VAR[a]	pseudo-F	p	adj. VAR[a]
all stand types[b]	TREE[c]	**8.7**	**0.001**	**22.82**	**4.1**	**0.001**	**10.86**
	HABITAT[d]	**7.1**	**0.001**	**13.58**	1.1	0.353	0.19
black locust – oak	TREE[c]	**19.2**	**0.001**	**29.76**	**6.9**	**0.003**	**12.49**
	HABITAT[d]	**6.7**	**0.001**	**21.07**	1.4	0.206	1.67
black pine – Scots pine	TREE[c]	**4.5**	**0.004**	**9.43**	1.6	0.133	1.92
	HABITAT[d]	**2.4**	**0.028**	**7.6**	1.0	0.432	0

[a] Adj. VAR (%) – adjusted percent variance explained by the predictors; [b] all stand types – analysis investigating the effects of all forest stand types (black locust, oak, black pine, and Scots pine) together; [c] TREE – dominant tree species (black locust, oak, black pine, Scots pine) in the forest stands; [d] HABITAT – HAB1 and HAB2 scores from PCA describing habitat structure of study plots.

Fig. S1. Ordination diagrams of redundancy analyses (RDAs) evaluating the differences in the community composition of arthropod taxa among stand types using **a)** abundance and **b)** total dry biomass.
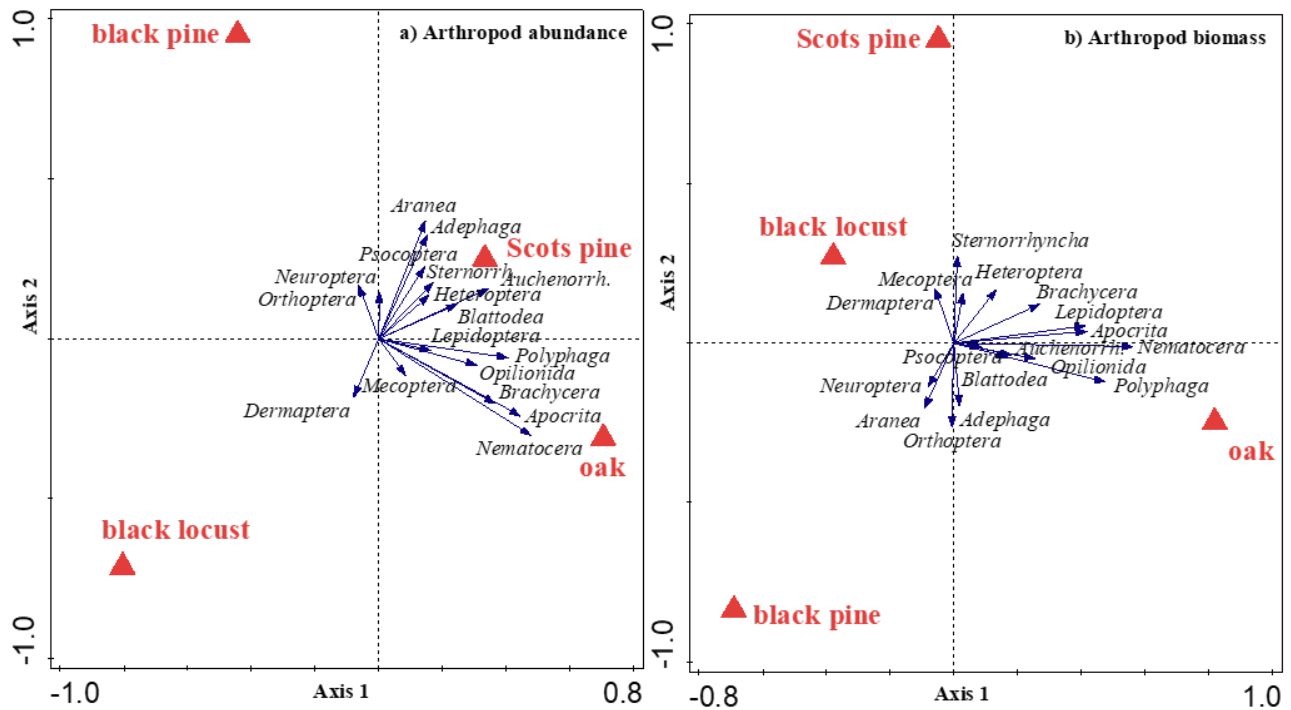
4.2 Studie II

Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure.

Tomáš Kadlec, **Martin Štrobl**, Jan Hanzelka, Martin Hejda, Jiří Reif

Abstrakt článku:

Non-native invasive plants are among the main threats to global biodiversity, including insects, and it is thus important to understand the mechanisms of how invasive plants impact native species. The community composition of nocturnal Lepidoptera was studied in the Czech Republic (Central Europe) in stands of native deciduous trees and in stands dominated by the invasive tree *Robinia pseudoacacia*, using automatic portable light traps together with an assessment of habitat characteristics. Native stands had more closed canopies and poorly developed understories. Conversely, *R. pseudoacacia* stands were more open and heterogeneous, with sparse canopies, well-developed shrub layers and a higher cover of taller herbs. Moth species richness, abundance and biomass were lower in *R. pseudoacacia*, likely due to the low richness of canopy herbivores not adapted to feed on the exotic host. However, feeding guilds associated with the understorey were more represented in stands of *R. pseudoacacia*, likely due to the more heterogeneous habitat structure. The Lepidopteran communities observed in stands of *R. pseudoacacia* resembled communities of open-forests or forest-steppe habitats. In contrast, native stands were dominated by Lepidoptera associated with trees, including forest specialists but also habitat generalists. From a conservation perspective, it appears that the invasive *R. pseudoacacia* created structurally more heterogeneous environment and more Lepidopteran open-forest guilds were associated with this habitat. However, further spread of *R. pseudoacacia* should be prevented because it reduces the species richness of Lepidoptera. Simultaneously, we recommend increasing the habitat heterogeneity of native forests to support functionally more diverse Lepidopteran communities.

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CrossMark

ORIGINAL PAPER

Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure

Tomáš Kadlec[1] · Martin Štrobl[1] · Jan Hanzelka[2] · Martin Hejda[3] · Jiří Reif[2]

Abstract Non-native invasive plants are among the main threats to global biodiversity, including insects, and it is thus important to understand the mechanisms of how invasive plants impact native species. The community composition of nocturnal Lepidoptera was studied in the Czech Republic (Central Europe) in stands of native deciduous trees and in stands dominated by the invasive tree *Robinia pseudoacacia*, using automatic portable light traps together with an assessment of habitat characteristics. Native stands had more closed canopies and poorly developed understories. Conversely, *R. pseudoacacia* stands were more open and heterogeneous, with sparse canopies, well-developed shrub layers and a higher cover of taller herbs. Moth species richness, abundance and biomass were lower in *R. pseudoacacia*, likely due to the low richness of canopy herbivores not adapted to feed on the exotic host. However, feeding guilds associated with the understorey were more represented in stands of *R. pseudoacacia*, likely due to the more heterogeneous habitat structure. The Lepidopteran communities observed in stands of *R. pseudoacacia* resembled communities of open-forests or forest-steppe habitats. In contrast, native stands were dominated by Lepidoptera associated with trees, including forest specialists but also habitat generalists. From a conservation perspective, it appears that the invasive *R. pseudoacacia* created

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structurally more heterogeneous environment and more Lepidopteran open-forest guilds were associated with this habitat. However, further spread of *R. pseudoacacia* should be prevented because it reduces the species richness of Lepidoptera. Simultaneously, we recommend increasing the habitat heterogeneity of native forests to support functionally more diverse Lepidopteran communities.

Keywords Moths · Exotic species · Species traits · Light trapping · *Robinia pseudoacacia* · Forest management

Introduction

Invasive plant species have broad ecological and economic impacts in both natural and human-altered environments (Higgins et al. 1997; Leung et al. 2002; Vilà et al. 2011), and are among the main global threats to biodiversity (Vitousek et al. 1996; Pauchard and Shea 2006; van Kleunen et al. 2015). In particular, they alter the structure and diversity of native plant communities (Vitousek et al. 1996; Vilà et al. 2011; Benesperi et al. 2012), affect the productivity of native plant species (Chambers et al. 2007) and significantly disrupt the trophic structure of ecosystems (Levin et al. 2006; Heleno et al. 2008; Tallamy et al. 2010; Schirmel et al. 2016), with prolonged impacts on diversity at higher trophic levels (Spafford et al. 2013; Bezemer et al. 2014; Litt et al. 2014; van Hengstum et al. 2014).

The impacts of plant invasions on arthropod assemblages strongly vary among different taxa (Spafford et al. 2013; Bezemer et al. 2014; Litt et al. 2014; van Hengstum et al. 2014; Buchholz et al. 2015). Specialized herbivores or pollinators, evolutionarily bound to a small number of plant species (Traveset and Richardson 2006; Aizen et al. 2008; Moroń et al. 2009; Burghardt et al. 2010) or parasitoids (Simao et al. 2010), usually respond to plant invasions negatively, by decreasing in diversity or abundance (Degomez and Wagner 2001; Spafford et al. 2013; Litt et al. 2014). On the other hand, non-specialized pollinators (Bezemer et al. 2014), predators (Pearson 2009; Hartley et al. 2010) and detritivores (Standish 2004; Litt et al. 2014) are often unaffected by invasions, or their diversity and abundance may even increase in novel habitats.

Among invasive plants, the ecological consequences of woody invaders are particularly profound, due to their strong effects on native habitats (Richardson 1998; Hierro and Callaway 2003). Alien woody plants, by eliminating native species as a consequence of interspecific competition (Vilà et al. 2011; Benesperi et al. 2012), can decrease the food supply in the forest canopy (Litt et al. 2014; Reif et al. 2016; Hejda et al. 2017), or change the habitat structure and therefore affect the composition of the whole community (Harris et al. 2004; Pawson et al. 2010; Litt et al. 2014; van Hengstum et al. 2014; Buchholz et al. 2015).

Arthropods are among the most diverse groups of animals (Ødegaard 2000) and significantly contribute to trophic interactions (Mooney et al. 2010). Therefore, a deeper understanding of the impact of woody invaders on arthropods is important, as the impacts of invasive plants on organisms at lower trophic levels may have consequences for the functioning of the whole ecosystem (Heleno et al. 2008; Tallamy et al. 2010; Bezemer et al. 2014; Litt et al. 2014; Reif et al. 2016; Schirmel et al. 2016; Hejda et al. 2017). Even though there are some studies that focus on the effects of woody invaders on arthropods (e.g. Bezemer et al. 2014; Litt et al. 2014; van Hengstum et al. 2014; Buchholz et al. 2015, Schirmel et al. 2016), our knowledge is still incomplete, given the enormous diversity of arthropods, and their ecological traits and life history strategies. For example, we

can predict that herbivores bound to different layers of vegetation may vary in response to changes in light conditions or stand structure (Harris et al. 2004; Pawson et al. 2010), but the studies available have mostly used coarse groups of arthropod communities, and more detailed relationships remain unclear. In fact, woodland arthropod diversity may be more affected by habitat structure than by variability in plant diversity (Gardner et al. 1995; Highland et al. 2013).

The main objective of this study was to compare the assemblages of nocturnal Lepidoptera between stands invaded by a widespread invasive tree, the black locust (*Robinia pseudoacacia*) and forest stands formed by native tree species. Impacts of invasive *Robinia pseudoacacia* have been documented for various kinds of organisms (Degomez and Wagner 2001; Cierjacks et al. 2013; Buchholz et al. 2015; Rocca et al. 2016; Vítková et al. 2017). Nocturnal Lepidoptera (further called "moths") are a well-studied group of arthropods in Central Europe, with detailed knowledge of their ecology (Summerville et al. 2004; Pavlikova and Konvicka 2012), known direct links to vegetation structure (Highland et al. 2013) as well as with a high diversity of larval feeding strategies, life-histories and other ecological traits (Strong et al. 1984; Pierce 1995). These moths therefore represent excellent study organisms for testing the effects of plant invasions on groups of species defined by their (ecological) traits. In particular, we asked: (i) Do stands of the invasive *R. pseudoacacia* differ in habitat structure compared to stands of native trees? (ii) Do these stand types differ in the species richness, abundance and biomass of moths? (iii) Do the moth assemblages associated with these stand types differ in their ecological traits and could the alteration of habitat structure explain these potential differences?

Materials and methods

Focal invasive tree

Invasive black locust (*Robinia pseudoacacia*) occurs naturally in the southeast of the USA, where it represents an important part of early-successional forests, being eventually replaced by climax species (Boring and Swank 1984; Cierjacks et al. 2013). It was introduced to Europe at the beginning of the Seventeeth Century and has further spread worldwide (Cierjacks et al. 2013). At present, it is considered as one of the most widespread invasive species in Europe (Vítková et al. 2017). It was introduced to the Czech Republic at the beginning of Eighteenth Century (Slavík 1995), and was widely planted in warm areas, particularly on barren rocky slopes, for the stabilization of soil, and for wood and honey production (Vítková et al. 2017). Due to its nitrogen-fixing ability, it enriches habitats with nitrogen and supports the spread of nitrophilous herbs and shrubs (Benesperi et al. 2012; Vítková and Kolbek 2010; Vítková et al. 2017).

Study area and design

The fieldwork for this study was carried out in a forested lowland area of ca. 600 km² (approximately between 49°56′N and 50°08′N, and 14°09′E and 14°26′E; 200–400 m a.s.l.) in central Bohemia, the Czech Republic, Europe (Fig. 1). This area is predominantly covered by stands of deciduous forests, human settlement, farmland and grassland. The forests are formed by native species of oak (*Quercus* spp.), hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*), maples (*Acer* spp.) and limes (*Tilia* spp.). In the first half of the 20th
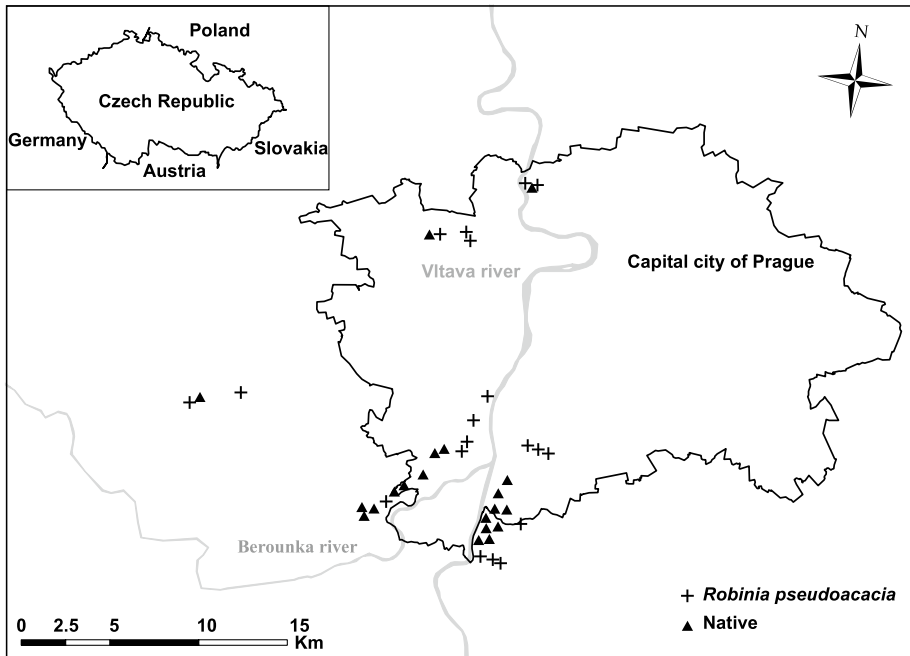
Fig. 1 Map showing locations of the study plots (19 plots in the stands of *Robinia pseudoacacia* and 20 plots in native stands)

century, large parts of this area were planted with *R. pseudoacacia*, which further spread spontaneously to the surroundings (Nožička 1957).

We established 20 study plots (100 m × 100 m) in stands of native deciduous trees (dominated by *Quercus* spp.; henceforth "native stands") and 19 study plots in stands dominated by the invasive *R. pseudoacacia* (comprising more than 95% of tree cover; henceforth "*R. pseudoacacia* stands") (Fig. 1, Online Resource 1). These study plots were established at least 100 m from the forest edges and the minimum distance between adjacent plots was 500 m (Beck and Linsenmair 2000; Hanzelka and Reif 2015). Mixed stands with both alien and native trees were avoided.

This study focused on moths of the superfamilies Hepialoidea, Cossoidea, Zygaenoidea, Drepanoidea, Lasiocampoidea, Bombycoidea, Geometroidea and Noctuoidea. To sample moths in both stand types, we used 39 modified, automatic, portable light traps (Heaths 1965) with similar specifications as used by Brehm and Axmacher (2006). Moths were attracted to traps with two 8 W UV LED strip lights (total luminous flux of 400 lm in the wavelength range of 400–420 nm, powered by 7.2 Ah/12 V lead batteries) and then euthanized by evaporated chloroform. At each plot, a single portable trap was placed on the ground, approximately in the middle of the plot. All traps were exposed on the same night at the beginning of each month from April to November 2014, from dusk until dawn, when the weather was suitable (i.e. no strong wind and no strong rainfall) and the moon was quarter-sized at maximum. Such traps attract flying insects within a radius of a few tens of metres (Truxa and Fiedler 2012). Therefore, they should have attracted moths occurring almost exclusively within the area of the study plots, without sampling individuals from

the surrounding habitats. Such a sampling design allowed us to cover all major phenological phases of moth species richness, throughout the part of the year when the moths were actively flying (e.g. Jonason et al. 2014; Tropek et al. 2014), and also to avoid short-term effects that may possibly affect the light trapping (Yela and Holyoak 1997).

Moth data and traits

The samples from the light traps were stored in paper bags and frozen at −22 °C. In the laboratory, all moths from the target groups were identified to the species level. To measure their biomass (in terms of dry weight), the moths were dried in an oven at 80 °C for 12 h and then weighed on an analytical scale (van Langevelde et al. 2011). For each species, the evidence of its utilization of *R. pseudoacacia* as a host plant was determined from the literature (Kulfan 2012).

To analyse the possible effects of *R. pseudoacacia* resulting from differences in habitat characteristics, a species-traits approach was adopted (Pavlikova and Konvicka 2012). For each species, the following ecological characteristics were recorded (Table 1): (i) general traits, not specific to any particular stage of life cycle (voltinism, overwintering stage, preferred structure of habitat and vegetation layer), (ii) traits specific for the larval stage (length of larval development, diet specialisation and feeding guild) and (iii) traits specific for adults (wing span as a measure of body size and mobility, life span).

Habitat characteristics and environmental variables

To describe differences in the habitat structure of both *R. pseudoacacia* and native stands, 14 habitat characteristics expected to affect the diversity of arthropods (Strong et al. 1984; Gardner et al. 1995; Hartley 2002; Highland et al. 2013) were recorded in June 2014. At each plot, the age of the forest was recorded. Fallen (FALLEN TREES) and dead (DEAD TREES) trees were counted and other vegetation characteristics were estimated in three equal-sized subplots of 100 × 33 m, and mean values for each parameter were calculated (see Hanzelka and Reif 2016 for details). Specifically, by walking through the whole subplots, we visually estimated the percentage cover of herbs < 0.5 m height (HERB1), herbs > 0.5 m (HERB2), shrubs from 1 to 5 m in height (SHRUB), trees from 5 to 10 m (TREE1), trees > 10 m (TREE2), canopy cover (CANOPY) and clearings (CLEARINGS). Further we estimated the proportion of the number of trees with diameter at breast height (dbh) < 0.2 m (TREES); trees with dbh 0.2–0.5 m (TREEM) and trees with dbh > 0.5 m (TREET). We expressed the light conditions as the presence of a continuous canopy (CANYES/CANNO).

Finally, we considered six environmental variables known to affect arthropod communities (Novotny et al. 2015) expressed as proportions of the following land cover types in the surroundings of study plots: ARABLE—arable land; WATER—water bodies; ROCK; GRASS—grassland; URBAN—urban area; BROAD—broad-leaved forest; CONIF—coniferous forest. The proportions of these land cover types were estimated within a circular buffer of 500-m radius around each plot using ArcGIS version 10.2 (ESRI 2011).

Data analysis

To reduce the complexity of habitat and environmental data without substantial loss of information, the major dimensions of habitat structure and land cover characteristics of

Table 1 Presumed relationships of ecological traits of the general, larval and adult stages of selected species of nocturnal Lepidoptera, according to the type of studied forest stands, dominated by either native trees (mainly oaks) or by the invasive *Robinia pseudoacacia* (*RP*)

Traits and trait categories	Predicted relationship
(i) General traits (not specific to any particular stage of life cycle)	

Voltinism
  VOLTIN_G1—one generation per year
  VOLTIN_G2—mostly two generations
	more generations per year in *RP* stands (faster larval development in *RP* stands due to warmer conditions)

Overwintering stage EGG, LARVA, CHRYSALIS, ADULT	moths overwintering as eggs more common in the native stands (mostly tree leaf-chewers)

Preferred habitat structure
  OPEN HABITATS—grassland dwellers
  FOREST-STEPPE—forest steppes and scrubland
  FOREST—forest stands
  GENERALISTS—without habitat preference
	forest species more dominant in the native stands, habitat generalist more dominant in *RP*

Preferred vegetation layer HERB, SHRUB, CANOPY	species of the canopy layer more dominant in the native stands
(ii) Larval traits	

Length of larval development
  DEVELOP_SHORT: < 2 months
  DEVELOP_MED: 2–6 months
  DEVELOP_LONG: > 6 months
	shorter larval development in *RP* stands (warmer conditions in *RP* stands caused by the more open habitat structure)

Diet specialisation
  MONOPHAGY—feeding on a single plant species
  OLIGOPHAGY—feeding on plants belonging to one family
  POLYPHAGY—feeding on many species across plant families or on plant residues
	more specialized species in the native stands

Feeding guild
  LEAF—leaf-chewing larvae
  VEG_PARTS—larvae feeding on other vegetative parts of plants (roots and stems)
  GEN_PARTS—on flowers and seeds
  THALLUS—on mosses and lichens
  CARNIVOROUS—carnivorous larvae
  DET_HS—detritivores mainly on herbal or shrub residues and litter
  DET_T—detritivores on dead tree leaves or leaf litter
	higher proportion of herbivorous species in the native stands, no differences in the proportion of detritivorous moths

(iii) Adult traits	

Body size and Mobility (according to wing span; Berwaerts et al. (2002), Öckinger et al. (2010))
  SMALL: mean wing span < 25 mm
  MEDIUM: 26–40 mm
  LARGE: 41–100 mm
	larger and more mobile moths with higher proportions in the native stands (mostly tree leaf-chewers and also more permeable environment in the native stands due to the absence of a shrub layer)

Life span
  LIFE_SHORT: adults live < 2 months
  LIFE_MED: 2–4 months
  LIFE_LONG: > 4 months
	shorter in *RP* stands (faster development caused by warmer conditions)

All traits were taken from Macek et al. (2007, 2008, 2012)

the *R. pseudoacacia* and native stands were determined by principal component analysis (PCA) in Canoco 5.0 (ter Braak and Šmilauer 2012). We ran two separate PCAs: one for vegetation structure and second for land cover characteristics. To determine the number of principal components, we used the screeplot method (Jackson 1993). Based on this criterion, we used the plot scores from the first two principal components of habitat structure (further called "VEG1" and "VEG2") and land cover characteristics (further called "LAND1" and "LAND2").

Since our data may have suffered from problems of spatial autocorrelation, we applied a method of generalized least squares (GLS) from the package "nlme" (Pinheiro et al. 2017) in all following univariate models. Geographic coordinates of plot centres were used to express the possible spatial effects, and different autocorrelation structures within the residuals (Gaussian, exponential, linear, rational quadratics and spherical) were compared. The parsimony of these models, as well as a model without residual autocorrelation, were assessed using the Akaike Information Criterion, AIC (Zuur et al. 2009). By comparing the AIC values, we selected the most appropriate autocorrelation structure. In all cases, the most parsimonious models (i.e. those with the lowest AIC value) turned out to be the models without spatial effects. Thus, we used linear models without accounting for spatial autocorrelation in further analyses.

To compare the habitat characteristics of native versus *R. pseudoacacia* stands, linear models were fitted with the principal components of habitat characteristics (VEG1 or VEG2) as respective response variables and the stand type (STAND: native trees or *R. pseudoacacia*) as the predictor.

To compare the species richness, abundance and biomass between the native and *R. pseudoacacia* stands, we used the number of moth species in each plot (SPECIES), number of all moth individuals per plot (INDIVIDUALS) and the total dry mass of moths per plot (BIOMASS; in grams) as the respective response variables, all transformed using the natural logarithm.

At first, a full linear model with all main predictors—stand type (STAND: native or *R. pseudoacacia*), LAND1 and LAND2 (principal components of land cover characteristics), VEG1 and VEG2 (principal components of habitat structure)—was constructed for each of the response variables (i.e. SPECIES, INDIVIDUALS, BIOMASS). Plots of the standardized residuals were checked against each continuous variable for possible polynomial trends. We thus added a quadratic term for VEG2 into the models. Interactions were not included, because there were no meaningful interpretations related to our hypotheses. In the next step, a multi-model inference framework was used (package "MuMIn", Bartoń 2016) to obtain a minimum adequate set of predictors for each response variable. Due to the small sample size relative to the number of estimated parameters, the candidate models containing all possible predictor combinations were compared by AIC corrected for small sample sizes (AICc—Akaike 1974; Burnham and Anderson 2002). Models with ΔAICc (i.e. the difference between the AICc value of the focal model with the lowest AICc value) < 2 were selected as the best performing models. The predictors that appeared in these best performing models were considered as the minimum adequate set and were used for interpretations. All models were further validated for the assumption of normal distribution of errors, based on a visual inspection of the distribution of standardized residuals (Crawley 2013). All univariate models were fitted in the program R version 3.3.1 (R Core Team 2016).

To test if the stand types differed in the traits of the moths assemblages, redundancy analyses (RDA) were performed in Canoco 5.0 (ter Braak and Šmilauer 2012). However, this method does not take the geographic positions of study plots into account and thus

its results may suffer from spatial autocorrelation in the data (Šmilauer and Lepš 2014). Therefore, we combined RDA with principal coordinates of neighbour matrices (PCNM) to account for spatial autocorrelation (Dray et al. 2006; Peres-Neto et al. 2006), following recommendations from the developers of this technique (Šmilauer and Lepš 2014).

In PCNM, the Euclidean distance matrix based on geographical distances of neighbouring sample plots was first calculated. This matrix was then processed by a principal coordinate analysis (PCoA) to obtain the spatial variables represented by respective PCoA axes (Šmilauer and Lepš 2014). Monte Carlo permutation tests (999 runs) were used to test the significance of each axis in the PCoA. From the PCoA output, we extracted the positions of each study plot along the significant PCoA axes (called "PCo scores") and these scores were further used in all subsequent RDAs as covariate variables capturing the spatial information in the data.

In the next step, we fitted three RDA models, where each contained the functional traits as the response variables. The value of a particular functional trait for each plot was quantified as the number of all trapped individuals on a particular plot sharing an identical level of a given trait (e.g. SMALL body size; Table 1). These response variables were centred and standardized in all models. The first model (STAND model) included a single predictor, the stand type, and PCo scores as covariables. The second model (COVARIATE model) included land cover characteristics, LAND1 and LAND2, as predictors and PCo scores as covariables. The third model (STAND │ COVARIATE model) included the stand type as a predictor and land cover characteristics and PCo scores as covariables.

In addition to RDA models we used variation partitioning (Peres-Neto et al. 2006) to distinguish the marginal, conditional and shared effects of the three groups of predictors—stand type (native/*R. pseudoacacia*), habitat structure (VEG1 and VEG2) and environmental variables (significant PCo scores from PCNM and land cover characteristics, LAND1 and LAND2)—on the distribution of the ecological traits of moths. Marginal effects are the effects of a given predictor variable (or a group of variables) without taking the other predictors into account; conditional effects quantify the effects of a given predictor variable after controlling for the effects of other predictors; shared effects are the effects shared between a given predictor variable and the other predictors (Šmilauer and Lepš 2014).

Results

Habitat characteristics of native and invaded forest stands

Native and invaded forest stands differed in habitat characteristics (Fig. 2a). The first PC axis, VEG1 (explaining 55.42% of the variation in habitat characteristics), reflected a gradient from older stands with taller trees and a more developed and continuous canopy to younger, open stands with smaller trees, a more developed shrub layer and a higher number of fallen trees (Fig. 2a). Native stands had lower VEG1 scores than *R. pseudoacacia* stands ($t = -9.075$, $p < 0.001$). The second axis, VEG2 (18.96%), reflected a gradient from plots with a more developed lower herb layer and small area of clearings to plots with a more developed taller herb layer and larger area of clearings (Fig. 2a), and was not significantly different between the native and the *R. pseudoacacia* stands ($t = -1.933$, $p = 0.061$).

In case of the land cover characteristics, the first axis, LAND1 (63.45%), reflected mainly the gradient from a landscape with a large portion of broad-leaved forest to a landscape with a larger cover of urban area (Fig. 2b). The second axis, LAND2 (20.73%),
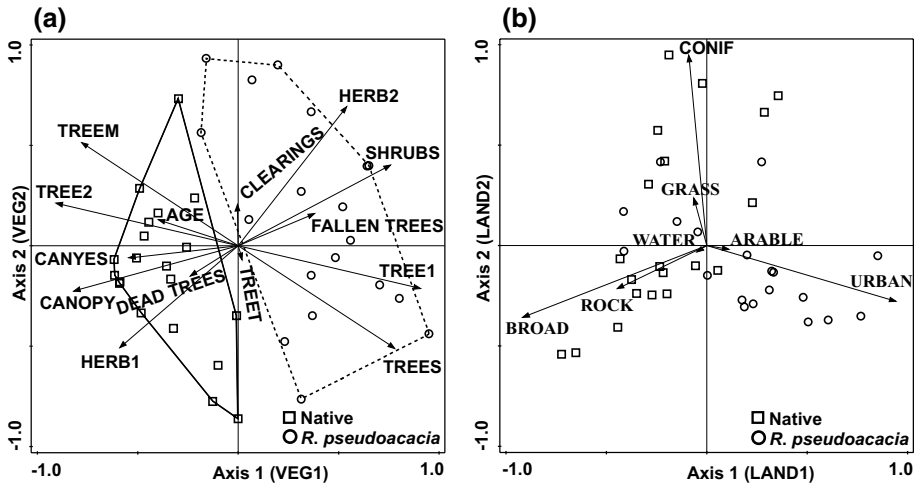
Fig. 2 Principal components analysis (PCA) of **a** habitat and **b** land cover characteristics between the 20 plots dominated by native trees and 19 plots dominated by *R. pseudoacacia*. Polygons indicate convex hulls separately bounding the native and *R. pseudoacacia* plots

reflected mainly the gradient from a landscape with a large share of coniferous forests to a landscape without coniferous forests.

Moth species richness, abundance and biomass

In total, 18,556 individuals of 384 moth species were captured (Online Resource 2), of which 346 species (mean ± s.e. [range] = 122 ± 27 [81–165]) were trapped in native stands and 304 species (90 ± 16 [61–120]) in *R. pseudoacacia* stands, with 266 species occurring in both stand types. Seventy eight species were more common in *R. pseudoacacia* and 164 species were more common in native stands. A total of 18 species that had been previously documented to feed on *R. pseudoacacia* were recorded, 15 of them in both stand types, two species only in native stands and one species only in *R. pseudoacacia* stands.

Relationships of moth species richness, abundance and biomass to the characteristics of the forest stands were estimated by linear models with performance assessed by AICc. Stand type was included in all except one of the best performing models (ΔAICc < 2) for all of the response variables (Table 2). Specifically, the species richness, the number of individuals, and the total biomass of captured moths were higher in native stands than in invaded stands (Table 3, Fig. 3). In addition, the best performing models for moth species richness, abundance and biomass also included VEG2 and the quadratic term of VEG2 (Table 2). The highest number of species and highest biomass were recorded in stands with intermediate values of VEG2 (Table 3a, c), i.e. with moderate proportions of clearings and both taller and shorter herbs in the understorey. Moreover, one model for moth abundance contained the effect of VEG1 (Table 3b), with increasing numbers of individuals towards stands with a closed canopy and less-developed shrub layer. Finally, the best performing models for moth species richness and abundance also included the effects of LAND2 (Table 2), with the number of species and individuals increasing towards stands surrounded by a higher coverage of coniferous trees (Table 3a, b). Some of the best performing models (m54 for moth abundance and m54 for moth biomass, see Table 2)

Table 2 Characteristics of the best models (ΔAICc < 2) relating (a) number of species, (b) number of individuals and (c) total dry biomass of moths to particular predictors

Model/predictors	Intercept	STAND[a]	LAND1[b]	LAND2[b]	VEG1[c]	VEG2[c]	VEG2^2[d]	K[e]	AICc[f]	ΔAICc	AICc weight
(a) Number of species											
m54	+	+	−	+	−	+	+	6	− 14.100	0.270	0.466
(b) Number of individuals											
m50	+	+	−	−	−	+	+	5	25.900	0.000	0.149
m54	+	+	−	+	−	+	+	6	26.000	0.140	0.139
m6	+	+	−	+	−	−	−	4	27.200	1.270	0.079
m57	+	−	−	−	+	+	+	5	27.800	1.960	0.056
(c) Total dry biomass											
m50	+	+	−	−	−	+	+	5	39.300	0.000	0.315
m54	+	+	−	+	−	+	+	6	40.600	1.210	0.172

The ± symbols indicate if the predictor was included (+) or not (−) in the model

[a] STAND—stand type of the study plots (stands of *R. pseudoacacia* compared to native stand)

[b] LAND1 and LAND2—PC1 and PC2 scores of land cover characteristics in the surroundings of the study plots

[c] VEG1 and VEG2—PC1 and PC2 scores of habitat characteristics of the study plots

[d] VEG2^2—quadratic term of VEG2

[e] K—number of estimable model parameters

[f] AICc—Akaike information criterion corrected for small sample sizes

Table 3 Estimates of the effects of particular predictors from the best models (ΔAICc < 2) on the number of species, number of individuals and total dry biomass of moths from the 20 plots in native forests and 19 plots dominated by the invasive *Robinia pseudoacacia*

Model/Predictors	Intercept		STAND[a]		LAND2[b]		VEG1[c]		VEG2[c]		VEG2^2[d]	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
(a) Number of species												
m54	4.564	0.051	0.254	0.062	0.067	0.030	–	–	0.046	0.031	−0.057	0.024
(b) Number of individuals												
m50	6.026	0.087	0.332	0.104	–	–	–	–	0.090	0.052	−0.040	0.052
m6	5.958	0.074	0.280	0.105	0.098+	0.052	–	–	–	–	–	–
m57	6.204	0.065	–	–	–	–	−0.142	0.050	0.042	0.052	−0.102	0.406
(c) Total dry biomass												
m50	2.471	0.103	0.683	0.124	–	–	–	–	0.109	0.062	−0.109	0.047

[a] STAND—the effects of the stand type, specifically, the stands formed by the native tree species, on response variables

[b] LAND2—PC2 scores of land cover characteristics in the surroundings of the study plots

[c] VEG1 and VEG2—PC1 and PC2 scores of habitat characteristics of the study plots
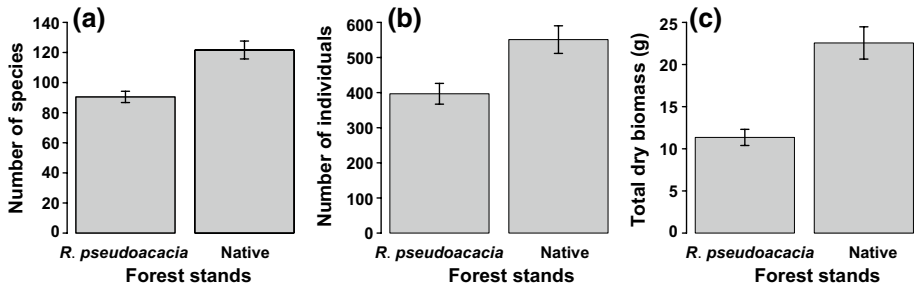
[d] VEG2^2—quadratic term of VEG2

Fig. 3 Comparisons of moth **a** species richness, **b** numbers of captured individuals and **c** total biomass between the 20 study plots with native trees and 19 plots dominated by *R. pseudoacacia*. Columns show means and bars show 95% confidence intervals

contained "masquerading" variables and were thus not used for inference. Such variables are included among the terms of the best performing models, but do not improve the fit sufficiently to offset the penalty for their addition, compared to the more parsimonious models without this variable (Anderson 2008; Arnold 2010).

Composition of moth communities

The stand type explained 16.8% of the variation of moth traits (Table 4), and its effect remained significant even after controlling for environmental variables (STAND│COVARIATE models; Table 4). Moth communities in the native stands were characterised by a higher presence of univoltine moths, which are specialists of forest habitats and are associated with the canopy layer, and by habitat generalists (Fig. 4a). On the contrary, forest-steppe moths, which are associated with more open habitats or herb and shrub layers, with more generations per season and with chrysalis as an overwintering stage, were more numerous in the *R. pseudoacacia* stands. Adult moths in the native stands were larger, more mobile and longer-living, while the stands of *R. pseudoacacia* predominantly supported moths with a faster life cycle and a higher proportion

Table 4 Results of redundancy analysis comparing the functional trait composition of nocturnal Lepidoptera between the 20 plots in native forests and 19 plots dominated by the invasive *Robinia pseudoacacia*

Model	Eigenvalues				Test of all canonical axes			
	Axis 1	Axis 2	Axis 3	Axis 4	Trace	F	p	adj. VAR (%)[a]
~STAND[b]	0.161	0.167	0.092	0.085	0.161	8.268	0.001	16.8
~COVARIATE[c]	0.097	0.019	0.165	0.130	0.116	2.732	0.002	8.8
~STAND│COVARIATE[d]	0.087	0.129	0.088	0.076	0.087	4.776	0.001	10.3

All models were controlled for spatial autocorrelation, using the method of principal coordinates of neighbour matrices

[a]adj.VAR (%)—adjusted percent variance explained by the predictors

[b]STAND—stand type (native/*R. pseudoacacia*)

[c]COVARIATE—LAND1 and LAND2 as predictors

[d]STAND│COVARIATE—the conditional effects of the stand type, after including LAND1 and LAND2 into the model. In all models, significant PCo scores from PCNM analyses were included as covariables
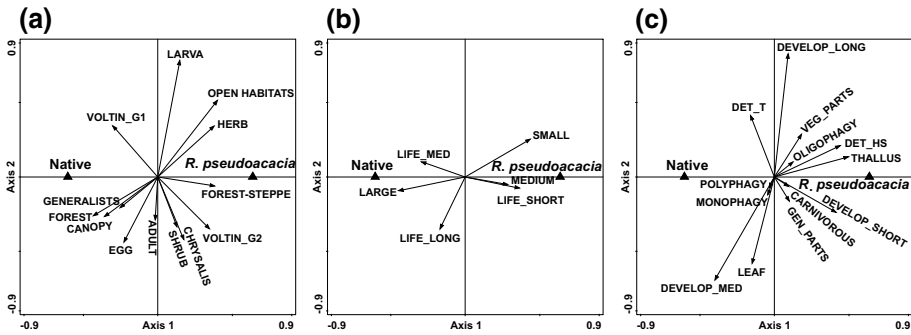
Fig. 4 Redundancy analysis (RDA) relating the **a** general, **b** adult and **c** larval-stage ecological and biological traits of nocturnal Lepidoptera to the two types of stands studied: 20 plots of native stands and 19 plots dominated by the invasive *Robinia pseudoacacia*. Spatial autocorrelation and significant environmental variables were included as covariables in all these models. See the "Methods" section for plot characteristics and details on traits

of short-living adults of smaller body sizes (Fig. 4b). With respect to larval feeding guilds, larvae feeding on herb and shrub litter or on thallus were more common in *R. pseudoacacia* stands (Fig. 4c). Other feeding guilds showed weaker responses to stand type.

Shared and marginal effects of all three groups of predictors (stand type, habitat structure, environmental variables) explained a substantial proportion of the variability in moths functional trait composition (Table 5). While the conditional effects of stand type and habitat characteristics were rather weak relative to the marginal effects (8.7 vs. 21.6% and 4.6 vs. 19.8%, respectively; Table 5), the effects of land cover characteristics, controlled for the spatial positions of plots, explained nearly half of the variability compared to the marginal effects (10.6 versus 22.7%; Table 5).

Table 5 The results of variation partitioning showing the shared, marginal and conditional effects of the groups of environmental variables on the functional trait composition of nocturnal Lepidoptera

Factor groups	Marginal effects			Conditional effects			Shared effects		
	F	p	adj.VAR[a]	F	p	adj.VAR[a]	F	p	adj.VAR[a]
STAND[b]	11.5	0.001	21.6	4.2	0.001	8.7			
HABITAT[c]	5.7	0.001	19.8	1.8	0.028	4.6	3.3	0.001	32.6
LAND COVER[d] + SPA-TIAL[e]	3.2	0.001	22.7	2.4	0.001	10.6			

[a]adj.VAR (%)—adjusted percent variance explained by the predictors

[b]STAND—stand type (native/*R. pseudoacacia*)

[c]HABITAT—VEG1 and VEG2 scores

[d]LAND COVER—LAND1 and LAND2 scores

[e]SPATIAL—significant PCo scores from PCNM

Discussion

Stands formed by native trees differed significantly in their habitat structure from stands of the invasive *R. pseudoacacia*. The native stands were mostly formed by taller trees with a closed canopy and with a higher cover of shorter herbs. On the other hand, *R. pseudoacacia* stands were characterized by a more open canopy, with a higher coverage of shrubs and taller herbs in the understorey. Similar to our study, Buchholz et al. (2015) reported a more developed understorey vegetation in *R. pseudoacacia* stands compared to stands of the native birch *Betula pendula* (with a significant effect on the cover of herbs and a marginally significant effect on the cover of shrubs). These effects are probably caused by the nitrogen-fixing ability of *R. pseudoacacia* enriching the soil in nitrogen (Boring and Swank 1984; Cierjacks et al. 2013; Vítková et al. 2017) and by the more open canopy of its stands, which allows for a better transmission of solar radiation into the understorey and consequently supports the growth of herbs and shrubs in the understorey layer.

Based on the light-trapping data, we found significantly lower total species richness, abundance and biomass of nocturnal Lepidoptera in stands dominated by the invasive *R. pseudoacacia*. This is in accordance with the general pattern of decreasing diversity, abundances or biomass of herbivores caused by invasive plants (Liu and Stiling 2006; Gerber et al. 2008; Spafford et al. 2013; Litt et al. 2014; van Hengstum et al. 2014; Schirmel et al. 2016). Similarly, Degomez and Wagner (2001) found in northern Arizona a nearly 30% loss of species diversity in stands of non-native *R. pseudoacacia* in contrast to stands of native *Robinia* species. However, some of the studied groups, e.g., the hyperdiverse Hymenoptera and Diptera, did not exhibit losses in diversity (Degomez and Wagner 2001). Also, other studies comparing the diversity of native and *R. pseudoacacia* stands did not find differences in species diversity of predators (Buchholz et al. 2015) or saproxylic beetles (Rocca et al. 2016). Based on these findings and on the results of our study, it seems that the response of arthropods to the invasion of *R. pseudoacacia* depends on their feeding strategy, with prevailing negative effects on herbivores.

The lower species richness and lower number of individuals observed in *R. pseudoacacia* stands could be explained by the paucity of canopy moths, which are also mostly leaf-chewing herbivores (Degomez and Wagner 2001). Despite three centuries of occurrence in Central Europe (Slavík 1995), the spectrum of species able to feed on *R. pseudoacacia* remains limited (Kulfan 2012). Higher abundances of canopy dwellers in the native stands could also explain the higher proportion of moths overwintering in the egg stage found in the native stands, including polyphagous forest pests with generally higher population densities (Alford 2000). In contrast to understorey species, canopy species are often strongly associated with spring leaf germination (Van Asch and Visser 2007; Hikisz and Soszyńska-Maj 2015), when leaves are more palatable. Since they are probably not able to feed on the alien *R. pseudoacacia,* they lack a suitable feeding niche in canopies dominated by this tree. Differences in the number of leaf-chewing moths between *R. pseudoacacia* stands and native stands could also affect the frequency distribution of adult body sizes, because species restricted to the canopy of native trees tend to be larger in body size (Heleno et al. 2008). Thus the lack of canopy species in *R. pseudoacacia* stands can also explain lower total biomass of moths in these stands.

The species diversity and the number of individuals were also weakly positively affected by the proportion of coniferous stands in the surroundings of the study plots (represented by LAND2). This is in accordance with the known effects of woody plant diversity in the surroundings of traps on the diversity and abundance of moths (Novotny et al. 2015). Even

among forest species specialized on coniferous trees, larger and mobile moths can be found (e.g. larger geometrids, hawkmoths, lappets), dispersing occasionally to deciduous stands and thus increasing the total species diversity and abundance.

Our results also showed that aspects of habitat structure, not accounted for by the distinction between native and invaded stands, had important effects on species diversity, abundance and total biomass. Specifically, sites with an intermediate proportion of clearings and an intermediate proportion of lower and taller herbs in the herb layer (the quadratic term of VEG2) had the highest number of species and individuals and the highest biomass of moths. We also detected the direct effects of vegetation structure on the functional composition of moths. Therefore, vegetation structure plays an important role in moth community assembly.

The moth assemblages of native forests were only partly formed by forest canopy specialists. Another guild occurring more frequently in the native stands were generalists, without distinctive habitat specialization. This is not consistent with some studies on ubiquitous species (Yoshioka et al. 2010, 2014), showing a higher abundance of generalists in invaded habitats. However this discrepancy may be due to the fact that those studies were conducted in non-forest habitats while our research was performed in forest stands. A majority of generalists in our study were migrants or pests with good dispersal ability (Slade et al. 2013). Such species probably disperse more easily through the more permeable native stands, formed by tall trees and without a well-developed shrub layer, than through stands of *R. pseudoacacia*, with a dense understorey. The more complex structure of invaded forests may therefore represent a dispersal barrier for insect habitat generalists (Barbaro et al. 2005). Similarly, in contrast to predictions and results showing a higher occurrence of diet specialists in native stands (Liu and Stilling 2006; Burghardt et al. 2010; Litt et al. 2014), we found no difference in preferences for stand type in the herbivore monophages and oligophages. This is probably because the loss of canopy diet specialists in *R. pseudoacacia* stands is compensated by dietary specialists gained in the better developed understorey.

Many studies on detritivores in invaded habitats have shown that the diversity or abundances of detritivores is higher in invaded stands than in native stands due to the higher amount of ground litter and decaying vegetation in non-native vegetation (Standish 2004; Levin et al. 2006; Litt et al. 2014). Interestingly, we found that moths with larvae feeding on litter leaves of herbs or shrubs were more common in stands of *R. pseudoacacia*. This may be related to the higher cover of shrubs and taller herbs, dominated by native plant species (Hejda et al. 2017), in the *R. pseudoacacia* stands.

It is interesting that moths with faster life-cycles (i.e. those having shorter larval development, shorter adult lifespans and more generations per season) occurred more frequently in *R. pseudoacacia* stands. This may be caused by a warmer and drier microclimate in these stands because leaves of *R. pseudoacacia*, unlike the leaves of native trees, rotate during strong summer heat to be less exposed to solar radiation (Xu et al. 2009), making them less effective in buffering heat stress in the understorey than native trees.

Overall, moth assemblages in *R. pseudoacacia* stands were similar to those of open-forests or forest-steppe habitats with better light conditions, but lacked canopy species, while forest and canopy dwellers dominated in native stands.

Conservation implications

The lower moth species richness in stands dominated by the invasive *R. pseudoacacia* indicates that this habitat does not favour Lepidopteran species richness in central European forests. Moreover, we did not record any moth species of conservation concern (sensu

Farkač et al. 2005) in the invaded stands, while several such species were recorded in the native stands. Therefore, we suggest that the further spread of this invasive tree should be prevented and its eradication from sites of conservation concern should be prioritized.

At the same time, we found remarkable differences in the proportions of various ecological groups of moths between the native and invasive stands, which were likely caused by differences in habitat structure. Specifically, the native forests had more closed canopies and a less developed understorey than the studied invasive stands. Due to the higher light availability and well-developed understorey vegetation (Buchholz et al. 2015), stands of *R. pseudoacacia* resembled open forests, which are among the most threatened and vanishing habitats in Europe (Miklín and Čížek 2014). Therefore, from the perspective of moths restricted to the forest understorey, forest-steppe and open habitats, the conservation potential of the studied native stands with the currently prevailing vegetation structure is limited. The second message from our study for the conservation of moths in central European lowland forests is therefore the need to increase the heterogeneity of the habitat structure and canopy openness of native forests (see also Sebek et al. 2015). Even though the composition of native stands supports the diversity of some functional groups of moth fauna due to long-term adaptations (e.g. canopy feeders), the diversity of moth fauna and its functional guilds may be limited by the large-scale homogeneity of native stands, with closed canopies and relatively homogenous age structure. In this respect, the management of native lowland forests may consider active measures (planned clearings, coppicing, disturbances, grazing, creating small-scale gaps or selective cutting) to promote the patch dynamics of new versus old stands, as well as closed canopies versus more open areas (Merckx et al. 2012; Pavlikova and Konvicka 2012; Sebek et al. 2015).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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4.3 Studie III

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

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<u>**Abstrakt článku:**</u>

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.

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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 & Tscharntke, 1994; Tscharntke, 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 (Carvalheiro, 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; Tscharntke, 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 m^2 up to several hectares) but even the smallest ones contribute to local biodiversity (Carvalheiro 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, Hooftman, 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)
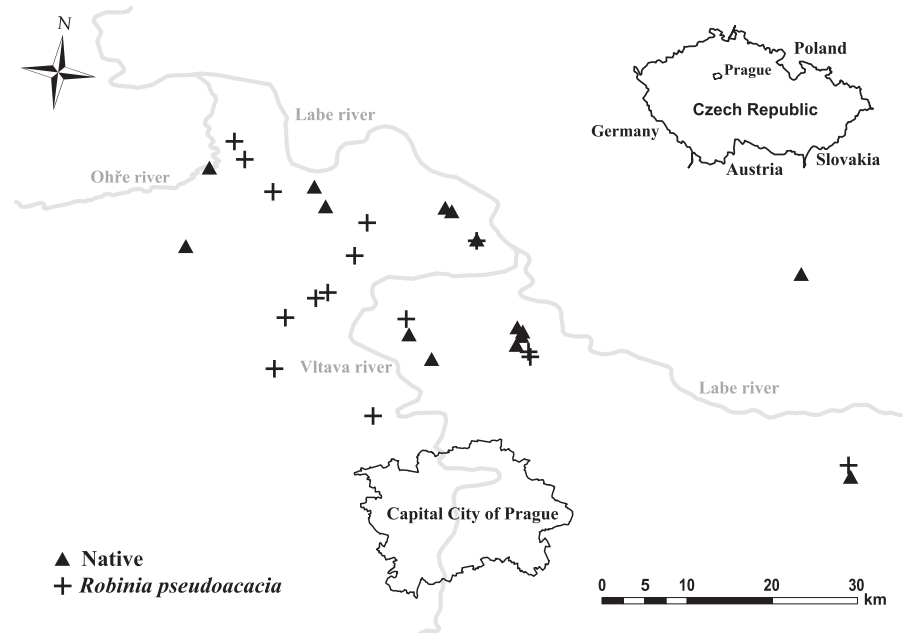
1. Similar to large forest stands, *R. pseudoacacia* will create a more open-habitat structure of isolated woodlots in agricultural landscapes than native tree species.

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.), hornbean (*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**
	Robinia	−0.397	−0.631	−0.162		*Robinia*	−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**
						Robinia	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**
	Robinia	−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
						Robinia	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**
	Robinia	−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
	Robinia	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**
	Robinia	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**		*Robinia*	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**
	Robinia	−0.840	−1.078	−0.602		*Robinia*	−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**		*Robinia*	−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**
	Robinia	−0.456	−1.284	0.371		Area	−0.666	−1.902	0.570
	Land1	−0.217	−0.631	0.196		*Robinia*	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**		*Robinia*	−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**
	Robinia	−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).

[a]Model 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 ΔAICc < 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 ± SD = 1,782 ± 479) was lower than that in the native woodlots (2,665 ± 887; $z = -3.497$, $p < .001$), while the total species richness did not differ between the *Robinia* (mean ± SD =217 ± 22) and native woodlots (220 ± 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
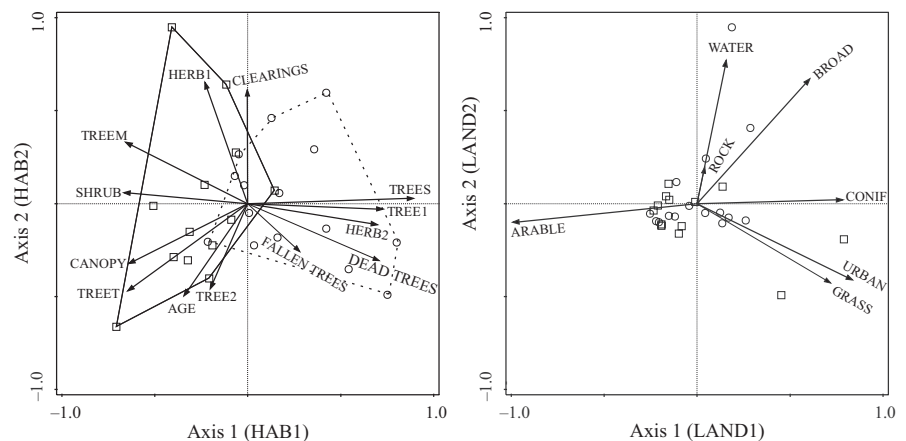

FIGURE 2 Principal components analysis (PCA) of (a) habitat structure and (b) land cover characteristics between the native and *Robinia* woodlots. Polygons indicate convex hulls bounding the native and *Robinia* plots

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	*p*
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.
[a]Adj. VAR (%): adjusted percent variance explained by the predictors.
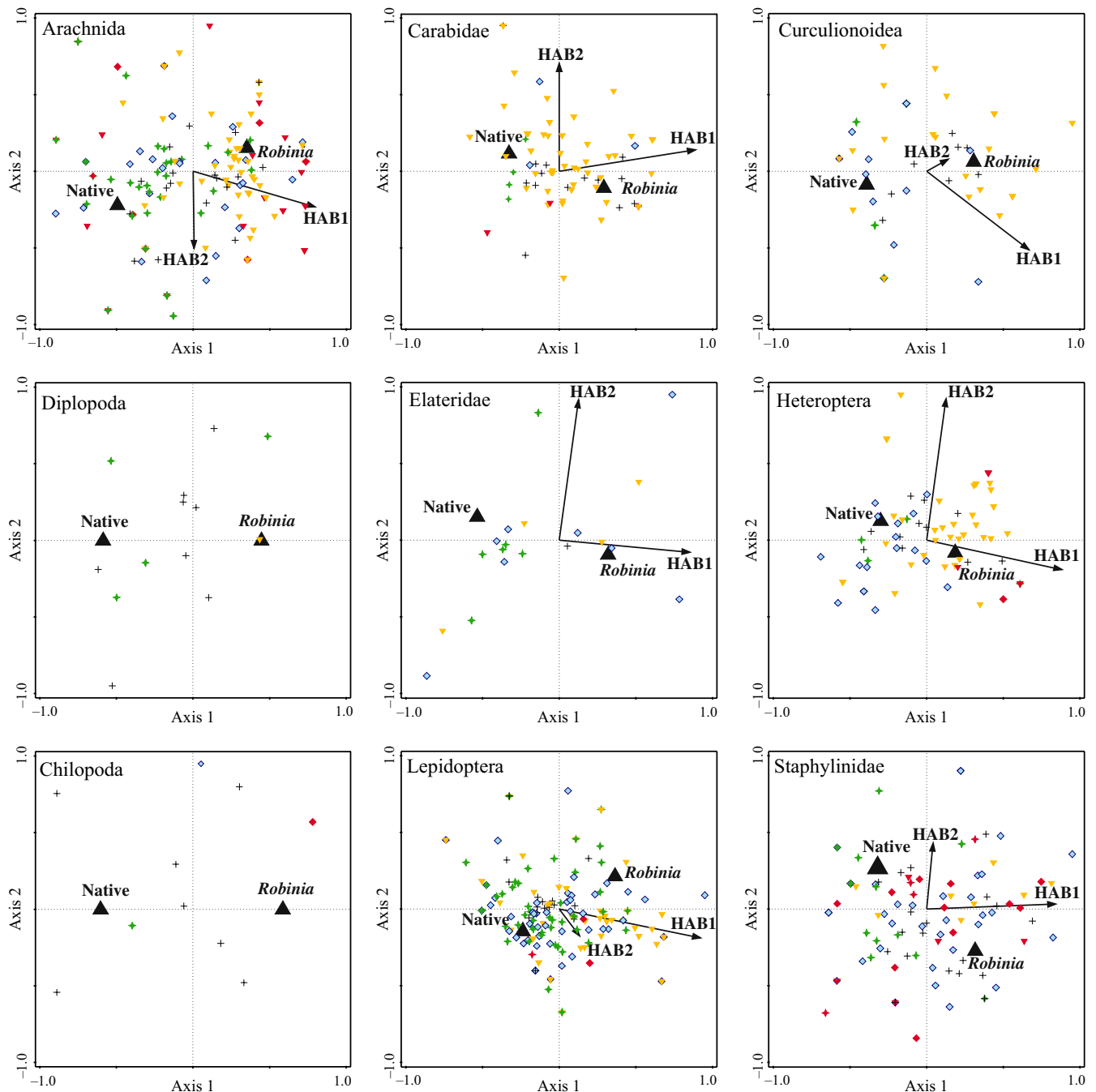[b]Habitat structure (HAB1, HAB2) was included in the analyses.

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 (Irmler, 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-Boyero, 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-Boyero, 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).

DATA AVAILABILITY STATEMENT

The data are provided in the 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 Curculionoidea; 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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

4.4 Studie IV

Conservation implications of cascading effects among groups of organisms.

Jiří Reif, Jan Hanzelka, Tomáš Kadlec, **Martin Štrobl**, Martin Hejda

Abstrakt článku:

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

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

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ABSTRACT

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

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1. Introduction

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

Invasive plants can change the invaded community's composition in terms of niche breadth. A narrow niche breadth means that a species is adapted to a limited set of environmental conditions (Godet et al., 2015). Therefore, we can expect that a narrow niche breadth limits

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

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

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

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

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

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

Based on this framework, we tested the following predictions using data on bird occurrence, the food supply for birds and the habitat structure in native forest stands and in stands invaded by *R. pseudacacia* in the Czech Republic. (i) Habitat structure will differ between native stands and the stands dominated by the invasive *R. pseudacacia*. (ii) Food supply for birds will be more diverse in the native stands than in the stands of the invasive *R. pseudacacia*. (iii) The number of specialist bird species will be higher in the native stands, whereas the number of generalists will be higher in the stands of the invasive *R. pseudacacia*. (iv) Birds feeding on invertebrates and canopy foragers will have higher species richness in the native stands, whereas the species richness of birds with a mixed diet and shrub foragers will be higher in the *R. pseudacacia* stands.

In addition, we can expect a tight relationship of bird species richness to habitat characteristics rather than to food supply if the altered habitat structure drives changes in bird community composition due to woody plant invasion. Taken together, these tests should help uncover the mechanisms of how invasive plant species, represented by *R. pseudacacia* in the Czech Republic, impact native bird communities.

2. Materials and methods

2.1. The invasive alien R. pseudacacia

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

2.2. Study area and field surveys

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

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

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

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

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

was considered unbroken at the whole plot level when all subplots were classified as unbroken.

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

2.3. Bird community metrics

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

2.3.1. Habitat specialization

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

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

2.3.2. Diet and foraging techniques

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

Concerning the foraging techniques, we used information in Cramp (1977–1994) to classify the species into groups recognizing (i) major foraging strata: canopy, shrub and ground; and (ii) parts of vegetation most often used for feeding: ground, foliage and bark (Table A.1). Note that we finally obtained five groups of species according to their

feeding techniques because ground foragers appeared in both types of classification. Three species that mainly catch flying insects (*Ficedula albicollis*, *Muscicapa striata* and *Phoenicurus phoenicurus*) were not sorted according to the latter classification. They do not match any of the above categories, and a separate category of flying insect catchers would be too species poor for further analysis.

2.4. Characteristics of the study plots

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

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

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

2.5. Statistical analysis

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

Table 1
Factor loadings of original variables along the first two most important principal components (PC1 and PC2), as revealed by principal component analysis performed separately for (a) the habitat structure on study plots and (b) the land cover composition in the 500-m surroundings of study plots. DBH — diameter at breast height. Variables with loadings of higher values than 0.70 are in bold.

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

2.5.1. Gradients in the species composition of bird communities

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

2.5.2. Comparisons of invaded and native stands

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

2.5.3. Relating bird community metrics to plot characteristics

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

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

3. Results

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

(native stands: mean $= 2.26$, SD $= 0.25$; stands of *R. pseudacacia*: mean $= 2.33$, SD $= 0.25$; SAR model: F $= 0.71$, P $= 0.406$).

3.1. Characteristics of the study plots

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

3.2. Species composition of bird communities

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

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

3.3. Habitat specialist and generalist birds

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

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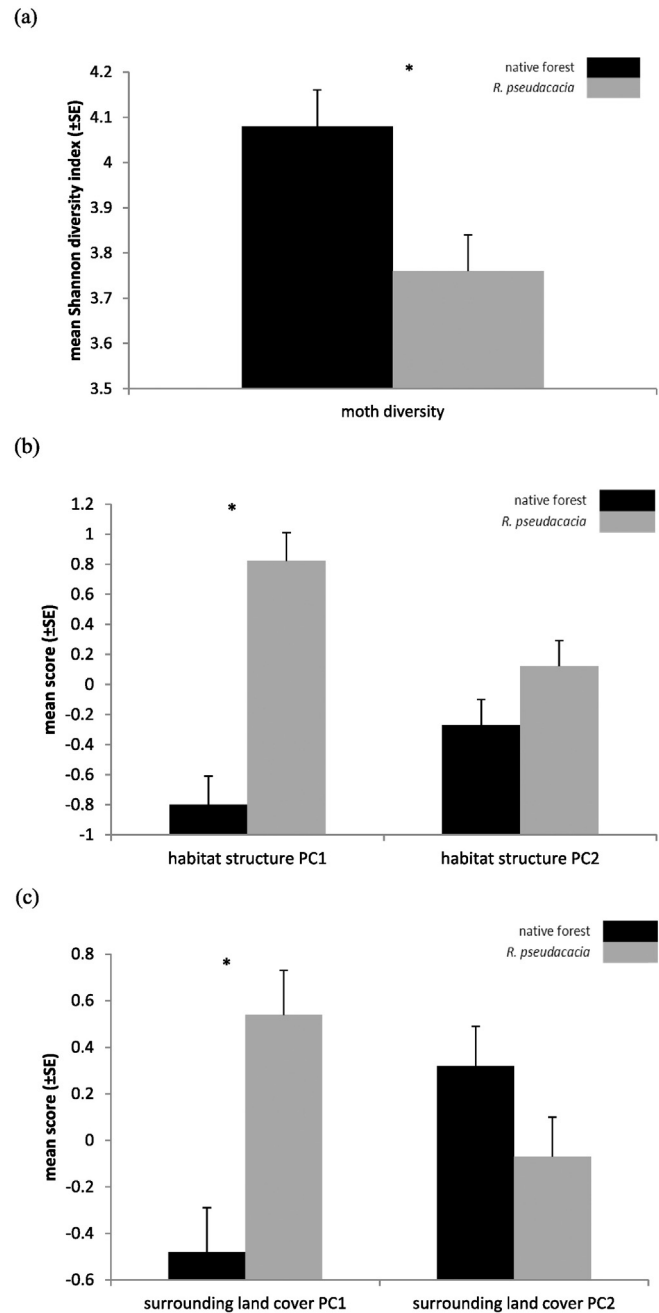

Fig. 1. Comparison of (a) the Shannon diversity index of moths, (b) habitat structure (PC1 and PC2 from principal component analysis on 13 variables describing habitat structure in the study plots) and (c) land cover composition in a 500-m radius surrounding the plots (PC1 and PC2 from principal component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

Shannon diversity of birds instead of bird species richness (Appendix A.1).

Habitat structure affected the species richness of generalist birds (Table 2d–f). The significant effect of PC1 (Table 2d) indicated that more habitat generalists were breeding in plots with a more developed shrub layer, a higher amount of dead wood, and trees of lower stature and lower canopy coverage. Strong and moderate generalists both showed the same significant pattern (Table 2e, f). The species richness
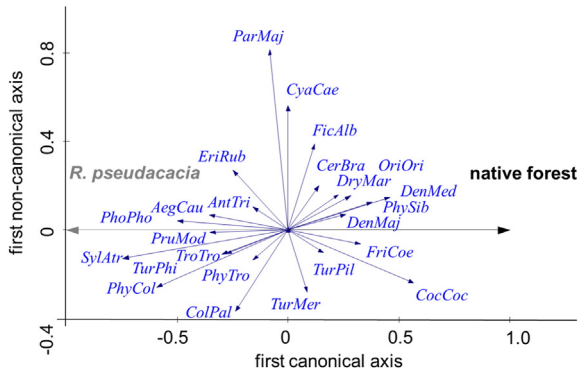
Fig. 2. Bird species' (blue arrows) associations with native forest stands (black arrow) and with stands of invasive *Robinia pseudacacia* (grey arrow) as revealed by redundancy analysis. The closer the position of a species' arrow to the extreme part of the x-axis, the higher the association of a given species with a given stand type. Species with unclear associations (i.e. those close to the centre of the plot) are not depicted. Birds are abbreviated by first three letters of their scientific names (see Table A.1 for full names). Note that positions of some species'identifiers were moved to improve readability. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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

3.4. Diet and foraging techniques of birds

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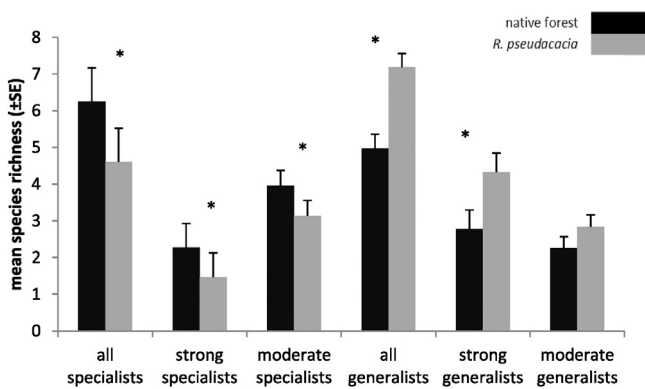

Fig. 3. Species richness of bird groups defined by habitat specialization in native forest stands and stands of invasive *Robinia pseudacacia*. The values are the least-square means estimated by simultaneous autoregressive models. A separate model was run for each species group. Asterisks indicate significant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

Table 2

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

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

effect of the surrounding habitat composition was found in the case of the Shannon diversity index of bird species feeding exclusively on invertebrates (Appendix A.1).

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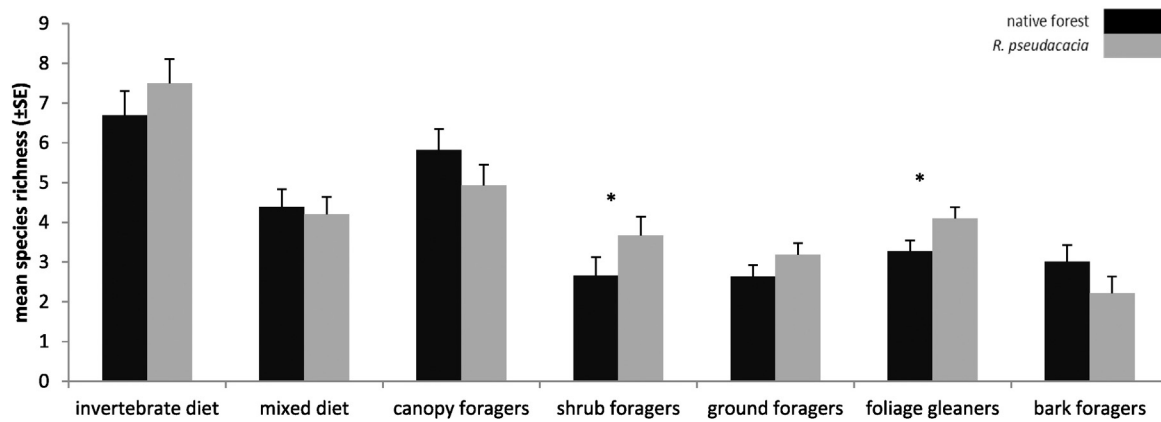
Fig. 4. Species richness of bird groups defined by diet and foraging techniques in native forest stands and stands of invasive *Robinia pseudacacia*. The values are the least-square means estimated by simultaneous autoregressive models. A separate model was run for each species group. Asterisks indicate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

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

4. Discussion

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

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

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

ability to colonize new environments, such as urban areas (Evans et al., 2011), and benefit from new food types (Ducatez et al., 2015).

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

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

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

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

Table 3

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

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

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

We also classified the birds according to their feeding strategies to gain further insight into species' sorting between invaded and native forest stands. Bark foragers and canopy foragers were more represented in native stands and their richness and diversity increased with the diversity of moths. On the other hand, species feeding in foliage were more species-rich in invaded stands. Because native oaks have a well-developed canopy and host many species of xylophagous insects (Vodka et al., 2009), bark foragers (such as *D. medius*, *D. martius* and *Certhia brachydactyla*) and canopy foragers (such as *O. oriolus* and *Coccothraustes coccothraustes*) find rich food resources in native stands,

while *R. pseudacacia* lacks phytophagous insect species (Kuflan, 2012). The higher species richness and diversity of foliage gleaners in invaded stands might be surprising given the limited development of *R. pseudacacia* foliage and lack of phytophagous insects. However, this pattern is most likely driven by birds feeding in the shrub layer formed by native plants such as *S. nigra*, which is abundant in *R. pseudacacia* stands and rather scarce or even lacking in native forest stands. This also corresponds to the increasing diversity of birds foraging in the shrub layer, which are represented by species typical for *R. pseudacacia* stands like *S. atricapilla*, *P. collybita* and *A. caudatus*, with a higher shrub cover on study plots.

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

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

Our results should be interpreted with caution because the data were collected over a single year and the study area covered only 600 km². It might be possible that repeating our survey in subsequent years and extending the study area would reveal different patterns. However, we consider this possibility quite improbable. Climatic conditions of the year of data collection were close to the long-term average: the mean temperature in May was only 0.4 °C warmer and the mean temperature in June was only −0.4 °C colder than mean temperatures between 1961 and 1990 (http://portal.chmi.cz/historicka-data/pocasi/uzemni-teploty#). Therefore, we think that adding more years would likely result in stronger conclusions, but not in reversed patterns. The observed effect of *R. pseudacacia* on specialist and generalist birds is in accord with ecological theory (Futuyma and Moreno, 1988) and the proposed mechanisms fit well the observed patterns. It would be very

difficult to imagine a mechanism, for example, of how specialized bird species or exclusive invertebrate feeders would benefit from a limited food supply in invaded stands. Higher moth diversity in the native stands is also very intuitive and supported by ecological theory predicting a lack of insect species adapted to a novel host plant due to the short time since introduction (Liu and Stiling, 2006). Therefore, although a high level of detail in our study was compromised by limited spatial and temporal replication, we are convinced that our conclusions present real mechanisms of the impact of *R. pseudacacia* on birds.

5. Conservation implications

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

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

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4.5 Studie V

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

Martin Hejda, Jan Hanzelka, Tomáš Kadlec, **Martin Štrobl**, Pyšek P., Jiří Reif

Abstrakt článku:

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.

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

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Abstract

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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 co-exist 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, & Vincente, 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 & Wesołowski, 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.
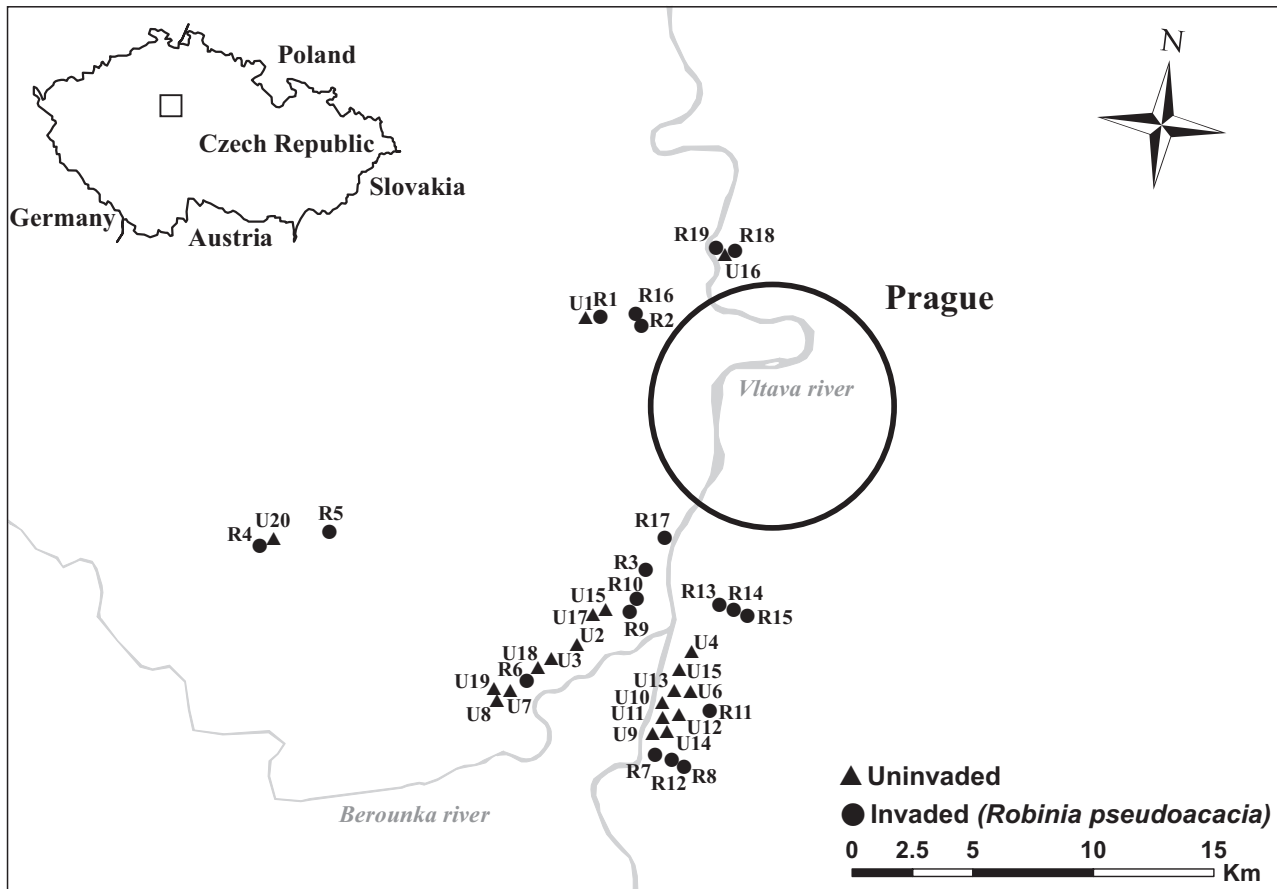
FIGURE 1 Map showing the location of study plots (19 invaded and 20 uninvaded)

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 ~20 × 30 km is located close to Prague, the capital of the Czech Republic, central Europe (coordinates of central point: 50°01′N; 14°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 uninvaded 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
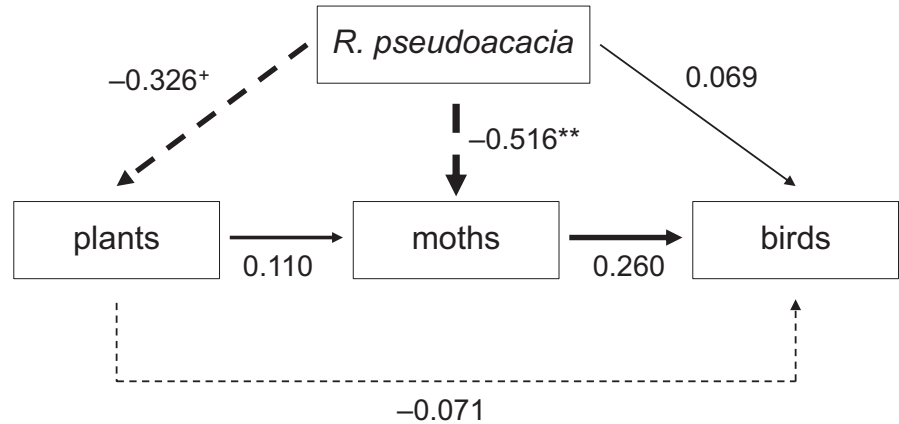
species excluding neophytes for plants—see Pyšek, Danihelka, et al., 2012) was the response variable and the stand type (invaded vs. uninvaded) was the predictor variable. The geographic coordinates were used to model the possible inter-plot similarity, given by their spatial arrangement. This was included 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			Moths				Birds			
	DE	*p*-value	IE	DE	*p*-value	IE	*p*-value	DE	*p*-value	IE	*p*-value
R. pseudoacacia	−0.326	.050	–	**−0.516**	**<.001**	**−0.036**	**<.001**	0.069	.730	**−0.120**	**<.001**
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 ± 7.0 and 15.3 ± 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 ± 17.4 and 121.7 ± 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 ± 2.6 and 10.9 ± 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	*p*-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
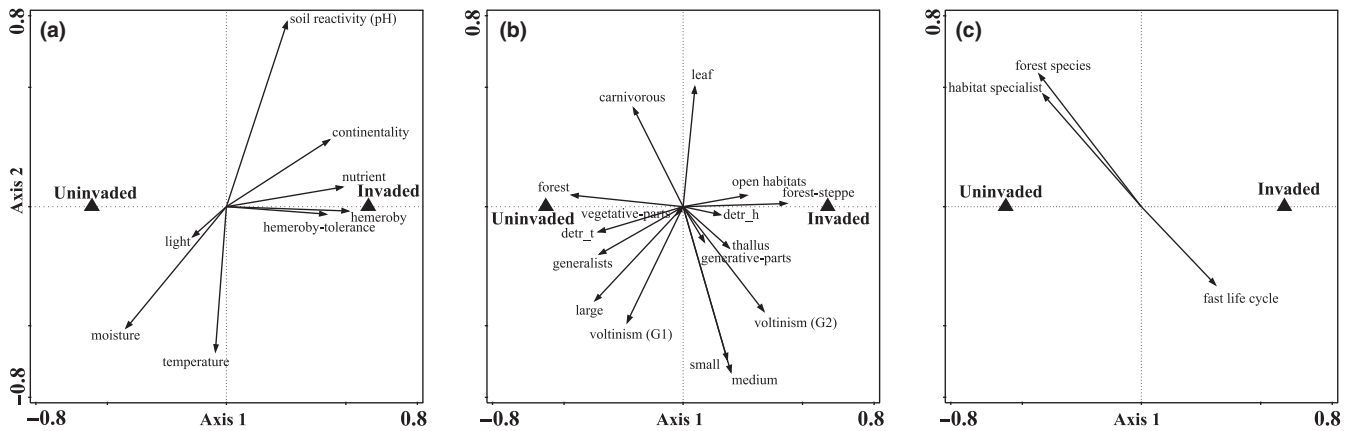
FIGURE 3 Ordination plots presenting the analyses on the differences in the distribution of species' ecological traits between the invaded and uninvaded stands for plants (3a – RDA, p = .002), moths (3b – RDA, p = .002) and birds (3c – RDA, p = .012). Geographic and surrounding habitat characteristics 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 understorey plants are context-dependent (Vítková & Kolbek, 2010). If the productivity is stress-limited (usually by drought), understorey 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 schoenoprassum* 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 expertize 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.

4.6 Studie VI

A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland.
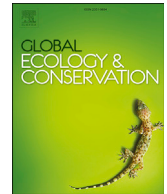
Javier Rivas Salvador, **Martin Štrobl**, Tomáš Kadlec, Pavel Saska, Jiří Reif

Abstrakt článku:

Agricultural intensification seriously threatens European biodiversity. To mitigate this threat, farmland habitat suitability should be improved. Mid-field woodlots surrounded by intensively cultivated fields or grasslands, represent one of the promising tools for such improvement. However, woodlots can be dominated by non-native plants and their impacts on woodlot function as refugees for biodiversity remains unclear. Therefore, we studied the impact of the invasive black locust (*Robinia pseudoacacia* L.) on bird species richness in woodlots in intensively cultivated Central European farmland. We surveyed 27 mid-field woodlots (13 covered by native vegetation and 14 dominated by black locust) in the Czech Republic, relating the species richness of all birds, habitat specialists and habitat generalists to woodlot characteristics: black locust occurrence, distance to the main forest, age of the woodlot, vegetation structure, arthropod biomass (representing food supply for birds), surrounding habitats and type of crops in which they are embedded. Our results suggest that the woodlots covered by the black locust had lower species richness of all birds, habitat specialists and habitat generalists than the woodlots covered by native tree species. The negative impact of the invasive woody plant on birds was likely driven by changes in vegetation structure since such woodlots had lower coverage of the shrub layer and less continuous canopy. This mechanism was particularly supported in habitat generalists, whereas habitat specialists additionally showed positive relationships to the other vegetation characteristics (namely the coverage of herbs in the ground layer and the proportion of medium-sized trees). Our study shows that even though mid-field woodlots host numerous bird species, their role in the delivery of conservation benefits for breeding birds is compromised if non-native woody plants dominate the vegetation. Therefore, from the perspective of breeding birds' conservation, the native woody plant species should be used for woodlot establishment.

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Original Research Article

A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland

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ABSTRACT

Agricultural intensification seriously threatens European biodiversity. To mitigate this threat, farmland habitat suitability should be improved. Mid-field woodlots surrounded by intensively cultivated fields or grasslands, represent one of the promising tools for such improvement. However, woodlots can be dominated by non-native plants and their impacts on woodlot function as refugees for biodiversity remains unclear. Therefore, we studied the impact of the invasive black locust (*Robinia pseudoacacia* L.) on bird species richness in woodlots in intensively cultivated Central European farmland. We surveyed 27 mid-field woodlots (13 covered by native vegetation and 14 dominated by black locust) in the Czech Republic, relating the species richness of all birds, habitat specialists and habitat generalists to woodlot characteristics: black locust occurrence, distance to the main forest, age of the woodlot, vegetation structure, arthropod biomass (representing food supply for birds), surrounding habitats and type of crops in which they are embedded. Our results suggest that the woodlots covered by the black locust had lower species richness of all birds, habitat specialists and habitat generalists than the woodlots covered by native tree species. The negative impact of the invasive woody plant on birds was likely driven by changes in vegetation structure since such woodlots had lower coverage of the shrub layer and less continuous canopy. This mechanism was particularly supported in habitat generalists, whereas habitat specialists additionally showed positive relationships to the other vegetation characteristics (namely the coverage of herbs in the ground layer and the proportion of medium-sized trees). Our study shows that even though mid-field woodlots host numerous bird species, their role in the delivery of conservation benefits for breeding birds is compromised if non-native woody plants dominate the vegetation. Therefore, from the perspective of breeding birds' conservation, the native woody plant species should be used for woodlot establishment.

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1. Introduction

In Europe, massive biodiversity loss is well documented in agricultural landscapes (Donald et al., 2001; BirdLife International, 2004; Attwood et al., 2008). Once heterogeneous, extensively cultivated farmland providing a fine mosaic of environments for various kinds of species occupying different habitats became dominated by large blocks of intensively managed arable fields and grasslands occupied by a few generalist taxa (Shultz et al., 2005; Devictor et al., 2008). Such a landscape is inhospitable for the majority of species adapted to the mosaic of environments created by traditional diversified farmland management (Kosicki and Chylarecki, 2012). Under these circumstances, woodlots provide important harbours for species unable to live in the intensively managed homogenous farmland (Herzon and O'Hara, 2007; Štrobl et al., 2019). Their intended establishment might represent a useful tool to improve the state of biodiversity in such landscapes (Marr and Howley, 2018).

However, woodlots may differ in habitat quality (Orlowski and Nowak, 2005) and it is thus of utmost importance to evaluate these habitat features in respect to their importance for biodiversity. From this perspective, it is particularly interesting that woodlots were frequently created using non-native woody plant species (Fortier et al., 2015). The woodlots dominated by the non-native woody plants might be better for local species richness than the complete absence of such landscape features in farmland (Benton et al., 2003). However, if the non-native woody plants form woodlots of a suboptimal habitat quality for the majority of local species, the function of such woodlots as biodiversity refuges is questionable and their intended establishment should be avoided. This latter possibility is suggested by various recent studies showing adverse impacts of plant invasions on the species richness in open habitats (Skórka et al., 2010; Hajzlerová and Reif, 2014; Rogers and Chown, 2014). Thereby, the ecological role of such woodlots calls for a comprehensive assessment.

In order to elucidate the biodiversity consequences of plant invasions in woodlots, we focused on birds in woodlots scattered over intensively cultivated lowland farmland in the Czech Republic, Central Europe. In this area, woodlots are scarce, albeit important habitat for birds species providing breeding opportunities, food resources and migratory stopover sites (Rajmonová and Reif, 2018). However, a large part of these woodlots is dominated by invasive tree species, mainly black locust (*Robinia pseudoacacia*). The black locust was introduced in the second half of the 18th century as an exotic species; since then it has expanded its distribution and has been considered one of the most widely distributed invasive plant in Central Europe (Vítková et al., 2017). It has generally negative impacts on native organisms which scale across trophic levels from primary producers to secondary consumers (Hejda et al., 2017). In the case of birds, recent studies showed that even though the species richness remains unchanged (Hanzelka and Reif, 2016), increasing abundance of the black locust in forest stands results in changes of species composition (Kroftová and Reif, 2017). Specifically, habitat specialist species are replaced by habitat generalists (Hanzelka and Reif, 2015). Changes in invertebrate food supply were hypothesised as a possible driver (Reif et al., 2016a) when the occurrence of particular arthropod species in invaded and native forest stands was largely determined by alteration of vegetation structure following the black locust invasion (Kadlec et al., 2018). On the other hand, woodland landscape including a moderate presence of black locust stands in its mosaic, seems to contribute not only to higher bird biodiversity but also to improve the functional connectivity of the landscape (Porro et al., 2020).

Although the studies cited above gained some knowledge about possible consequences of the black locust dominance on bird populations, most of these studies were conducted in large forest tracts and thus their applicability to the farmland context and specifically to the small-sized mid-field woodlots remains limited. To fill this knowledge gap, we surveyed breeding bird communities, vegetation structure and arthropod food supply for birds in 27 woodlots (13 consisting of native tree species and 14 dominated by the invasive black locust). Using these data, we test two alternative hypotheses. Either, (i) woodlots provide breeding habitat for birds irrespective to native/non-native origin of the dominant tree species or (ii) black locust woodlots offer less suitable breeding habitat for birds. Based on the first hypothesis, we can formulate two alternative predictions: (a) bird species richness, as well as the richness of habitat specialists and generalists do not differ between native and black locust-dominant woodlots because neither of both habitat types differs in vegetation structure and/or invertebrate food supply. Although this scenario is unlikely, some studies from other systems of invasive species suggest its theoretical plausibility (e.g. Kuebbing and Nuñez, 2015; Simberloff, 1981). An alternative prediction of this first hypothesis is that (b) bird species richness does not differ between the native and black locust woodlots, even though the vegetation structure and/or food supply do differ. This might be caused by a lack of alternatives for bird breeding in the inhospitable intensively cultivated farmland (Chamberlain and Fuller, 1999). Respective to the second hypothesis, if black locust woodlots do not provide suitable breeding habitats for birds, we predict that (c) bird species richness, and especially the richness of habitat specialists, will be lower in black locust than in native woodlots. Such woodlots should also provide limited food supply and should have a simplified vegetation structure.

2. Material and methods

2.1. Study area and study plots

Our study was carried out in the intensive agricultural landscape of Central Bohemia, Czech Republic, Central Europe (latitude 49°53′–50°07′; longitude 14°09′–14°27′; 160–330 m a.s.l.; annual rainfall total 500–600 mm; annual mean temperature 8–9 °C). Study area (~1200 km^2) is dominantly formed by intensive cultivated arable fields and woodland habitat fragments create ca. 15% of this area (ca. 85% of these forests are formed by native tree species and 15% are formed by

invasive *Robinia pseudoacacia*). For our study, we selected 27 mid-field woodlots (average size: 0.38 ha; range: 0.12−1.32 ha; average age: 78 years; sd:12 years; range: 50−110 years, see Fig. 1), 14 of them were dominated by the invasive black locust (*R. pseudoacacia*; henceforth: "black locust woodlots") while the remaining ones were composed by native deciduous tree species: dominantly by oaks (*Quercus* spp.) and European ash (*Fraxinus excelsior* L.), mixed by hornbeam (*Carpinus betulus* L.), maples (*Acer* spp.), limes (*Tilia* spp.) and elms (*Ulmus* spp.), henceforth: "native woodlots". Mean distance among adjacent woodlots was 2.40 km (range 0.31−12.30 km). All woodlots were completely surrounded by intensively managed blocks of arable land, major part of them were completely or partially surrounded by cereals (n = 20 woodlots), and in lesser number by rapeseed (n = 7), maize (n = 3) and poppy (n = 1) plantations (please note than one woodlot may be surrounded by more crop types). In the study area, farmland was cultivated at least since the beginning of the Middle Ages in the second half of the first millennium, but presumably even earlier since the Neolitic era (Sádlo and Štorch, 1999). After the World War II, the agricultural production greatly intensified and strong inputs of nutrients to sustain large monoculture fields and heavy machinery for management are required (Lerman, 2001).

2.2. Bird data

Both types of woodlots (i.e. black locust and native) were surveyed in spring 2017 to gather information about bird occurrence. Each woodlot was visited 3 times corresponding to early (late March), middle (mid-April) and late spring (mid-June) to capture all phases of the peak breeding season. During each visit, the observer walked slowly first through the whole perimeter and later through the inner area of the woodlot recording every bird species which was heard or seen in the woodlot, the survey finished once the whole area of the woodlot has been surveyed. Thus, due to the complete coverage of the whole woodlot, our sampling effort was proportional to woodlot area. Bird surveys were conducted between dawn and 11:00 during favourable weather conditions (no rain, no strong wind). The recorded species (n = 29, see Online Resource Table 1) were classified according to their habitat specialization index (SSI) obtained from Reif et al. (2010) as generalists and specialists, respectively. SSI was introduced by Julliard et al. (2006) as a coefficient of variation of density of a given species across different habitats (the higher the density variation across the habitats, the more specialized species) and Reif et al. (2010) calculated SSIs for 137 bird species breeding in the Czech Republic using data on species' densities collected within a national common bird monitoring scheme of country-wide coverage. For purposes of this study, we ranked all species according to their SSI values in descending order and considered the first half of species as specialists and the second half as generalists following Reif et al. (2016a). Birds species richness was calculated as the total number of bird species registered in a given
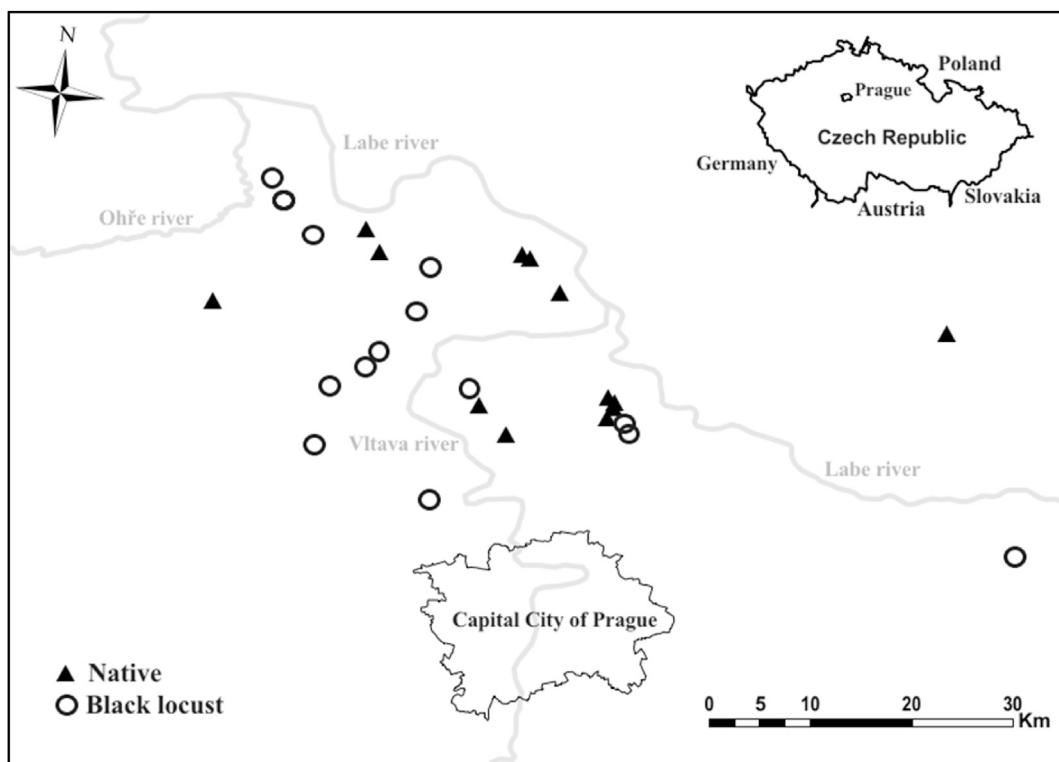

Fig. 1. Map showing the location of the surveyed woodlots (13 of them with native vegetation and 14 of them dominated by the black locust *Robinia pseudoacacia*).

woodlot across all visits. We expressed the richness separately for all birds, specialists and generalists. To account for possible of effects of sampling on the observed species richness (Shimadzu, 2018) we applied rarefaction using the R-package iNEXT (Hsieh et al., 2020). These rarefied species richness estimates (for all species, habitat generalists and specialists) were used for further analysis.

2.3. Arthropod food supply for birds

For information about the food supply for birds, arthropods were collected in the same woodlots where the birds were surveyed. Three different sampling methods were used to obtain information about different arthropod taxa taken by birds: (i) light trapping (a single light trap equipped with two 8 W UV LED strip lights powered by 7.2 Ah/12 V lead batteries); (ii) pitfall trapping (5 pitfall traps consisting of two nested plastic cups, 94 mm in diameter and 144 mm in height, containing 4% formaldehyde solution, and spaced 5 m apart along a straight line across each woodlot); and (iii) sweep-netting (vegetation lower than 3 m along the lane of pitfall traps was swept by a net 35 cm in diameter, area covered 25 × 5 m). To minimize the trapping of moths from surrounding habitats, each light trap was situated in the middle of the woodlot. As the used light sources attract the moths from the distance of few tens of metres (Truxa and Fiedler, 2012) we got samples of moths living directly in the woodlots or moths which flew through the woodlots. The transect with pitfall traps avoided the edges as the marginal traps were located minimally 10 m from the edge (Roume et al., 2011). The samples from sweeping were collected from vegetation in close vicinity of pitfall traps.

Arthropod sampling took place 5 times during 2016 at monthly intervals from April to September covering the main period of arthropod activity (Štrobl et al., 2019). Through these complementary approaches we collected information for the major taxa included in bird food supply (Lopes et al., 2016): Chilopoda, Diplopoda, Arachnida (Aranea and Opiliones), Orthoptera, Heteroptera, Neuroptera, Coleoptera (Carabidae, Elateridae, Staphylinidae, Silphidae, Curculionoidea) and Lepidoptera. All captured arthropods were determined to the species level. Arthropod food supply for birds was defined as the total arthropod biomass for each woodlot (Gullan and Cranston, 1994). It was calculated using the species-specific body lengths (extracted from literature) and the equations relating the length to body mass described by Hódar (1996). The total arthropod biomass (in mg) was calculated as the sum of all individuals of each arthropod species multiplied by the species-specific weight.

2.4. Woodlot characteristics

Each woodlot was characterized by the area of woodlot and two sets of environmental variables: the first set described woodlot vegetation structure and the second set land cover composition surrounding the woodlot. The area of each woodlot (in ha) was computed from aerial photographs using ArcGis 10.2 software (ESRI, 2011). Variables describing the vegetation structure (see Table 1 for the summary information) were assessed by visual inspection on-site following Hanzelka and Reif (2016). We estimated percentage cover of herbs <0.5 m (herb 1), herbs > 0.5 m (herb 2), shrubs and small trees 1−5 m (shrub), trees 5−10 m height (tree 1), trees > 10 m height (tree 2), the canopy and clearings (proportion of the woodlot area without woody plant cover). We also estimated the proportion of trees with a diameter at breast height <0.2 m (treeS), 0.2−0.5 m (treeM) and >0.5 m (treeT), and the numbers of dead and fallen trees were counted (Table 1). Surrounding land cover composition was assessed in a 500 m buffer around the woodlot recognizing the following land cover types using aerial photographs in ArcGis 10.2 (ESRI, 2011): proportion of arable land, grassland, urban habitat, rock, broad-leaved forest, coniferous forest and water body. Additionally, we registered the age of forest cover at woodlots (extracted from forest management maps downloaded from the Forest Management Institute, www.uhul.cz), area of each woodlot and the distance to the nearest continuous forest block (calculated using aerial photographs in ArcGis 10.2; ESRI, 2011). Moreover, we expressed the variable crop type (with categories cereals, maize, rapeseed, and poppy) to account for the type of arable land where a given woodlot was located in (Table 1).

2.5. Statistical analysis

As the first step, we tested whether the vegetation structure differed between the two woodlot types (i.e. black locust and native). For this purpose, we conducted a redundancy analysis (RDA) in CANOCO 5 statistical software (ter Braak and Smilauer, 2012) where the response variables were those describing the vegetation structure and the explanatory variable was the type of woodlot. Secondly, we reduced the number of variables using a principal component analysis (PCA) using R 3.6.0 (R Core Team, 2015), performed separately for each set of variables, i.e. woodlot vegetation structure variables and surrounding land cover composition variables. For the selection of the axes we have applied a parsimony criterion to maximize the explained variance with the lower number of axis. These axes (hereafter called vPCs based on the analysis of the vegetation structure variables, and sPCs based on the analysis of the surrounding land cover composition variables) were taken for further analyses. Because we were specifically interested in the effects of woodlot vegetation on birds and the variables defining the surrounding habitat and those describing the vegetation composition were not highly correlated, using two separated set of PCA's was the best approach to understand the possible effects that they could present over the bird species richness.

Additionally, we conducted a biserial correlation analysis, using R package ltm (Rizopoulos, 2006), to check whether the woodlot type and the vPC's were correlated. Furthermore, after a prior correlation analysis (see Online Resource Table 2) we

tested for differences in food supply (expressed as arthropod biomass) between the woodlot types generalized least squares (GLS) using the R-package nlme (Pinheiro et al., 2017) with the type of woodlot and woodlot area (log-transformed) as predictors. GLS models allow us to deal with spatial autocorrelation by adding a correlation matrix to the model. In this case we tested four different correlation structures (spherical, linear, exponential, and Gaussian) and also a null correlation structure indicating the absence of spatial autocorrelation in data. Based on the Akaike Information Criterion (AIC), we selected the correlation structure with the best fit and used that model type for inference. In all occasions, the models without a correlation structure were more supported than the models containing a correlation structure indicating that spatial autocorrelation was not an issue in these data (see Online Resource Table 3). Therefore, we report all results based on the models without a correlation structure.

To test for differences in bird species richness between black locust and native woodlots, we used GLS in the same way as described above to deal with the spatial autocorrelation (see Online Resource Table 3). Separate models were run for the rarefied richness of all bird species, habitat specialists and habitat generalists, respectively, and woodlot area (log-trans-formed) was included in all models. Finally, to gain deeper insights into the factors driving the bird species richness variation across the woodlots, we modelled the species rarefied richness for all the bird species, generalists and specialists separately, as a function of woodlot area (log-transformed), woodlot type, age, food supply (expressed as arthropod biomass), distance to the closest continuous forest block, crop type, vegetation structure (vPCs) and the surrounding land cover composition of a given woodlot (sPCs). For this purpose, we also used GLS models with the assessment of the correlation structure. After selection of the most supported correlation structure, we composed a global model containing all the explanatory variables together and performed variable selection via model dredging in R-package MuMIn (Barton, 2015) based on AIC corrected for small sample sizes (AICc). From all the possible combinations of variables we selected the best subset (ΔAICc < 2) of models. Moreover, we calculated relative importance of every variable included in the most supported models by summing Akaike weights across all models. All the models were conducted in R 3.6.0 (R Core Team, 2015). More details about each of the variables used in our analyses can be found in Table 1.

3. Results

3.1. Reduction of environmental variables using PCA

The results of the PCA to reduce the number of variables describing surrounding land cover composition showed that 93% of the variance can be explained by the first two principal components (sPC1 and sPC2, respectively). The sPC1 described a gradient discriminating arable land from the rest of surrounding habitats, while the sPC2 showed a gradient between broad-leaved forest versus the urban habitat and grassland (Fig. 1, see Online Resource Table 4a).

In the case of the PCA for the vegetation structure variables, the first four principal components (vPC1, vPC2, vPC3 and vPC4) explained 83% of the variance. The vPC1 described a gradient from woodlots dominated by tall herbs to those with a developed shrub layer (Fig. 2). The vPC2 expressed a gradient between woodlots with the thinner trunks and woodlots with tall trees (Fig. 2). The vPC3 showed a gradient from woodlots with tall trees to woodlots with medium sized trunks and tall herbs (Fig. 2). The vPC4 showed a gradient from woodlots without clearings to woodlots with developed shrub layer (Fig. 2, see Online Resource Table 4b). The results of the biserial correlation test showed that vPC1 and the woodlot type (i.e. black locust dominated vs, native woodlots) are strongly correlated (r = 0.79), while the rest of vPCs did not show any correlation with the woodlot type (vPC2: r = − 0.06; vPC3: r = −0.15; vPC4: r = 0.17).

3.2. Habitat and food supply

According to the RDA, the vegetation structure significantly differed between native and black locust woodlots (P = 0.006; 19.5% of the explained variance). Black locust woodlots contained higher herbs, thinner trees and higher number of dead trees, while native ones had higher continuity of the canopy (Fig. 3). The bush layer was generally more prominent in native woodlots and frequently absent in black locust ones (Fig. 3). We did not find any significant difference between black locust and native woodlots with respect to total arthropods biomass (Table 2, see Fig. 4).

3.3. Bird species richness

In our surveys, we recorded 24 bird species in native woodlots and 18 species in black locust woodlots. The mean bird species richness per a woodlot was 6 species (±standard deviation = 1.73 species) in native woodlots, while 3 species (±3.23) in black locust woodlots. The rarefied species richness of all birds, habitat specialists and habitat generalists was significantly higher in native woodlots than in black locust woodlots (Table 2).

After including all variables describing woodlot characteristics, the model dredging for the species richness of all birds identified one model with ΔAICc <2 (Table 3); without any correlation structure (Online Resource Table 5a). This model used the woodlot type (relative importance = 0.98; Online Resource Table 6), the log transformed area (relative importance = 0.7; Online Resource Table 6) and the vPC3 (relative importance = 0.63; Online Resource Table 6) as the best predictors. All of them with positive effects over the species richness (Table 4). Hence, woodlots with higher number of bird species are the

Table 1
List of all variables, their description and their role in respective analyses.

Variable	Definition	Analysis
Woodlot type	Discrimination between woodlots dominated by black locust from those covered by native trees	Explanatory variable for GLS models and for RDA
Herb1	Percentage of herbs coverage (>0.5 m)	PCA on vegetation structure, response for RDA
Herb2	Percentage of herbs coverage (<0.5 m)	PCA on vegetation structure, response for RDA
Shrub	Percentage of shrub coverage (1−5 m)	PCA on vegetation structure, response for RDA
Tree1	Percentage of tree coverage (5−10 m)	PCA on vegetation structure, response for RDA
Tree2	Percentage of tree coverage (>10 m)	PCA on vegetation structure, response for RDA
Canopy	Percentage of the woodlots area covered by the canopy of tree	PCA on vegetation structure, response for RDA
Clearings	Percentage of the woodlot area where the canopy is disrupted	PCA on vegetation structure, response for RDA
TreeS	Proportion of trees with a diameter at breast height < 0.2 m	PCA on vegetation structure, response for RDA
TreeM	Proportion of trees with a diameter at breast height 0.2−0.5 m	PCA on vegetation structure, response for RDA
TreeT	Proportion of trees with a diameter at breast height > 0.5 m	PCA on vegetation structure, response for RDA
Dead_t	Number of dead trees within the woodlot	PCA on vegetation structure, response for RDA
Fallen_t	Number of fallen trees within the woodlot	PCA on vegetation structure, response for RDA
Arable_land	Coverage of arable land in 500 m radius around woodlot	PCA on surrounding land cover composition
Grassland	Coverage of grassland in 500 m radius around woodlot	PCA on surrounding land cover composition
Urban_habitat	Coverage of urban habitat in 500 m radius around woodlot	PCA on surrounding land cover composition
Rock	Coverage of rocks in 500 m radius around woodlot	PCA on surrounding land cover composition
Water	Coverage of water bodies in 500 m radius around woodlot	PCA on surrounding land cover composition
Broad.leaved_forest	Coverage of broad-leaved forest in 500 m radius around woodlot	PCA on surrounding land cover composition
Coniferous_forest	Coverage of coniferous forest in 500 m radius around woodlot	PCA on surrounding land cover composition
All bird richness	Rarefied Species richness of all birds	Response variable for GLS models
Specialist richness	Rarefied richness of habitat specialist birds	Response variable for GLS models
Generalist richness	Rarefied richness of habitat generalist birds	Response variable for GLS models
Area	Woodlot area (ha)	Explanatory variable for GLS models
Distance	Distance to the nearest continuous forest block (m)	Explanatory variable for GLS models
Age	Woodlot age (years)	Explanatory variable for GLS models
Arthropods Biomass	Total biomass of arthropods captures in woodlot (mg)	Explanatory variable for GLS models*
Crop type	Category of arable land where the woodlot is located in (cereals, maize, rapeseed, poppy)	Explanatory variable for GLS models
vPC1	Fist principle component obtained by PCA on vegetation structure	Explanatory variable for GLS models
vPC2	Second principle component obtained by PCA on vegetation structure	Explanatory variable for GLS models
vPC3	Third principle component obtained by PCA on vegetation structure	Explanatory variable for GLS models
vPC4	Fourth principle component obtained by PCA on vegetation structure	Explanatory variable for GLS models
sPC1	First principle component obtained by PCA on land cover type composition	Explanatory variable for GLS models
sPC2	Second principle component obtained by PCA on land cover type composition	Explanatory variable for GLS models

* Also used as a response variable in a GLS model comparing arthropod biomass between native and black locust dominated woodlots.

larger ones, dominated by native trees, and with a developed bush layer and with a high number of trees with a breast diameter of 0.2−0.5 m.

In the case of habitat specialist bird species, the model dredging showed four models with ΔAICc <2 (Table 3); without any correlation structure (Online Resource Table 5b). The variables included in all the models were the woodlot type (relative importance = 0.9; Online Resource Table 6) and the vPC3 (relative importance = 0.86; Online Resource Table 6). Additionally, the vPC2 (relative importance = 0.18; Online Resource Table 6), the age of the woodlot (relative importance = 0.1; Online Resource Table 6) and the arthropod biomass (relative importance = 0.14; Online Resource Table 6) were included in just one of the best performing models and their large standard errors indicated their low importance (Table 4). By contrast, the woodlot type and the vPC3 showed positive effects (Table 4) meaning that native woodlots with a well-developed shrub layer contain higher number of habitat specialist bird species.

The analysis of species richness of habitat generalist birds showed a subset of six models with ΔAICc <2 (Table 3) which did not include any correlation structure (Online Resource Table 5c). All the best performing models included the log transformed area (relative importance = 1; Online Resource Table 6) as one of the best predictor, followed by the woodlot type (relative importance = 0.37; Table 4) present in four out of the six best performing models, the vPC1 (relative importance = 0.36;
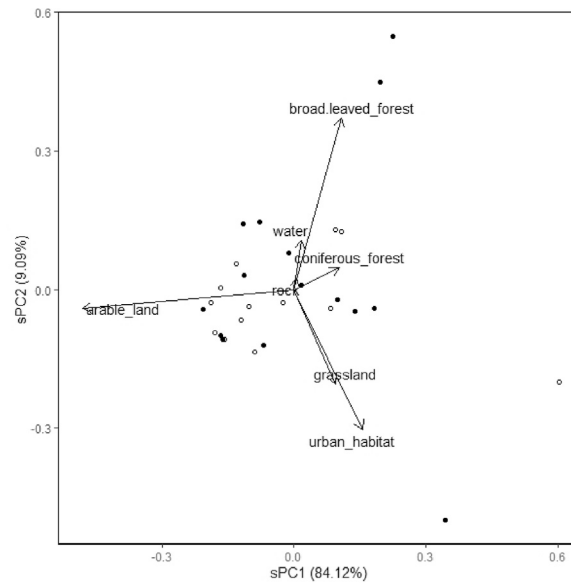
Fig. 2. Positions of variables corresponding to particular land cover types surrounding the woodlots along the first two axes (sPC1 and sPC2) resulting from the principal component analysis. Native woodlots are represented by open circles, while the black locust woodlots are represented by closed circles.

Online Resource Table 6) and the vPC4 (relative importance = 0.28; Online Resource Table 6) present in two out four. Additionally, the arthropod biomass (relative importance = 0.21; Table 4) and the vPC2 (relative importance = 0.16; Online Resource Table 6) were included in just one of the best performing models. All the included variables showed positive effects on the habitat generalist species richness (Table 4). However only the effects of the area, the woodlot type and vPC1 were important meaning that habitat generalists are more abundant in native and larger woodlots (Table 4).

4. Discussion

Mid-field woodlots are traditionally considered as landscape features creating heterogeneity in farmland and thus enhancing its value for biodiversity (Benton et al., 2003). However, our results provide important indication that such delivery of conservation benefits by woodlots may be compromised by the dominance of an invasive woody plant supporting the prediction of our second hypothesis, which predicted that black locust woodlots would not provide suitable habitat for birds. Specifically, woodlots covered by the invasive black locust were typical with less developed canopy and shrub layers than the native woodlots. These differences in vegetation structure at least partly translated into the differences in bird species richness as we found that the black locust woodlots hosted lower number of bird species than the woodlots dominated by the native species of trees. At the same time, the invertebrate food supply did not differ between both woodlot types and was unrelated to bird species richness.

The lower richness of bird species in black locust woodlots concerned all species, habitat generalists and habitat specialists. We suggest that the changes in vegetation structure caused by the invasive black locust dominance may be a driver of impoverishment bird species richness in invaded woodlots. Specifically, black locust woodlots had thinner trees with less continuous canopy, more deadwood and less developed shrub layer than native woodlots. These vegetation characteristics are indeed those structuring communities of European woodland birds (Moning and Müller, 2008; Whytock et al., 2018). Their effects were particularly strong in the case of habitat generalists where these vegetation characteristics were present in the most supported models. Indeed, among European birds, habitat generalists are typically those originally breeding in forests with well-developed understory such as the blackcap (*Sylvia atricapilla* L.), common blackbird (*Turdus merula* L.) or song thrush (*Turdus philomelos* B., Reif et al., 2016b; Tomiałojć, 2000). Therefore, it is not surprising that the species richness of habitat generalists was highest in the native woodlots with a well-developed shrub layer.

Interestingly, in the case of species richness of all birds and particularly in the case of species richness of habitat specialists, we found the influence of several variables related to the vegetation structure, namely the proportion of trees with a trunk of an intermediate size and the coverage of herbs up to 0.5 m height, in addition to the significant effect of the black locust dominance. Therefore, the changes in vegetation structure due to the black locust dominance are unable to fully account for the number of the specialist species in woodlots and the other vegetation factors play a role as well. The positive effect of the herb layer may be explained by its function as a provider of food resources for seed-eating bird species because such species (including corn bunting *Miliaria calandra* L., linnet *Carduelis cannabina* L. and tree sparrow *Passer montanus* L.) were largely represented among habitat specialists. The effect of trees with intermediate trunk size is less obvious. We can speculate about
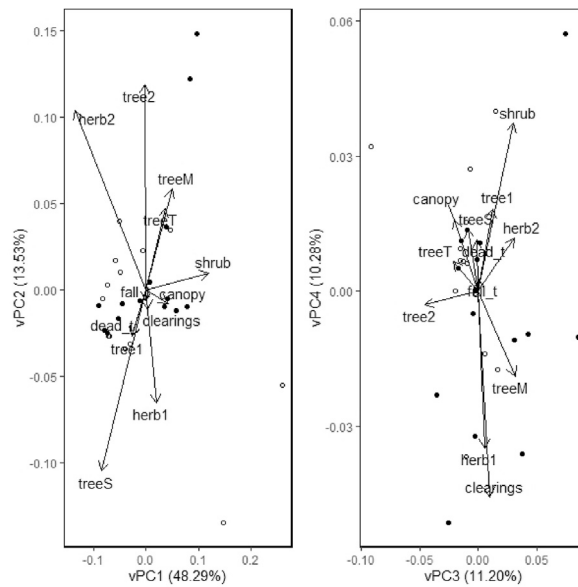
Fig. 3. Positions of variables corresponding to particular vegetation characteristics of the woodlots along the first four axes (vPC1−vPC4) resulting from the principal component analysis. See Table 1 for definitions of particular variables. Native woodlots are represented by open circles, while the black locust woodlots are represented by closed circles.
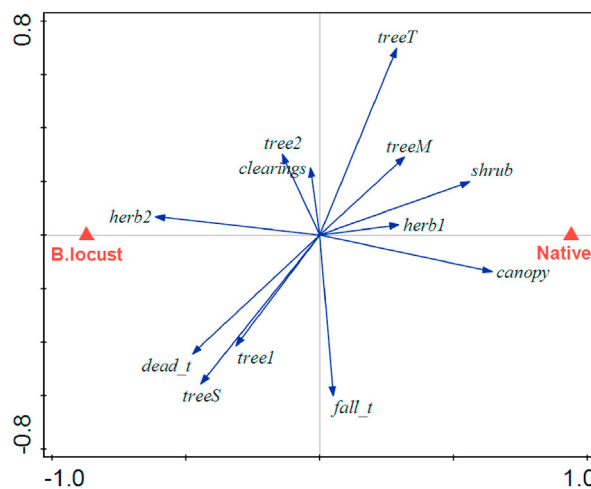

Fig. 4. First two ordination axes of the redundancy analysis showing the differences in vegetation structure between the woodlots covered by native woody plant species (Native) and the woodlots dominated by black locust (*R. pseudoacacia*). See Table 1 for definitions of particular variables.

their role as perching posts for some specialist birds with the sit-and-wait preying strategy such as the red-backed shrike (*Lanius collurio* L.) and pied flycatcher (*Ficedula hypoleuca* Pallas, 1764).

On the other hand, our results do not provide any support for the possibility that the black locust woodlots provide less food resources, represented by invertebrates, for birds. This was indicated by the absence of a significant difference in invertebrate food supply between the black locust and native woodlots observed in our data, and by the lack of support for this variable in models explaining patterns in bird species richness. Although this lack of support must be taken with caution due to the limited sample size and the possibility that our methods of invertebrate sampling may not cover the food types preferred by birds, it adds to the indirect line of evidence that the negative impact of the tree invasion on birds is mediated by changes in vegetation and not by changes in food supply in our study system.

Our results obtained in woodlots strikingly differ from findings of the earlier studies focused on the consequences of the black locust dominance performed in continuous forest stands. In these studies, habitat generalists indeed benefited from the black locust dominance in terms of their species richness, while habitat specialists showed a negative impact (Hanzelka and Reif, 2015). As a consequence, an overall effect of the black locust on the total bird species richness was absent in forest (Reif

Table 2
Result for the generalized least square models to estimate the effects of the woodlot type (black locust vs. native) and the woodlot area (log-transformed) on the rarefied species richness of all bird species, habitat specialist birds, habitat generalist birds and arthropod biomass, respectively. In the table are detailed the estimate effect of each variable (coef), its standard error (SE), its t-value and the level of statistical significance (p-vale).

All bird richness	coef	SE	t-value	p-value
(Intercept)	7.888	2.024	3.898	0.001
Woodlot Type (native)	7.084	1.623	4.365	<0.001
log(Area)	3.071	1.268	2.421	0.023
Specialist richness	**coef**	**SE**	**t-value**	**p-value**
(Intercept)	0.856	0.646	1.325	0.198
Woodlot Type (native)	1.323	0.518	2.555	0.017
log(Area)	0.015	0.405	0.036	0.971
Generalist richness	**coef**	**SE**	**t-value**	**p-value**
(Intercept)	8.047	1.353	5.947	<0.001
Woodlot Type (native)	2.521	1.085	2.324	0.029
log(Area)	3.768	0.848	4.444	<0.001
Arthropod biomass	**coef**	**SE**	**t-value**	**p-value**
(Intercept)	40.943	12.059	3.395	0.002
Woodlot Type (native)	15.647	9.670	1.618	0.119
log(Area)	0.008	7.557	0.001	0.999

et al., 2016a). These differences can be explained by two important ecological drivers. First, the black locust dominance had different consequences on vegetation structure in forests than in woodlots because the black locust forest stands had highly developed shrub layer (Hejda et al., 2017; Kadlec et al., 2018), while the opposite was true in the case of woodlots. Since habitat generalists benefit from shrub layer development (Hanzelka and Reif, 2015), their species richness increased due to the black locust dominance in forests in contrast to the opposite pattern in woodlots. Second, black locust-dominated forest stands were surrounded by the continuous forest consisting of native trees providing suitable habitat for numerous bird species (Hanzelka and Reif, 2016). Therefore, even though the birds might suffer to some extent from the presence of the invasive woody plant in forests (Kroftová and Reif, 2017), its adverse effect might be buffered by the surrounding suitable habitats. Even in forest fragments, non-native trees did not have a negative effect on bird richness if a large amount of native forest habitat was present in landscape (Porro et al., 2020). Such a buffering effect cannot be expected to act for the mid-field woodlots surrounded by of arable fields creating an inhospitable environment for the vast majority of breeding birds. As a result, the adverse impact of the invasive woody plant can be thus magnified by the isolation of woodlots (Štrobl et al., 2019). Another non-mutually exclusive explanation is that the relatively small size of our woodlots compared to forest stands might underpin the differences in species richness patterns (Fahrig, 2013).

For all bird species together and habitat generalists, we found out that the most important variable affecting their species richness was the size of the woodlot, whereas it was not related to species richness of specialists. Ideally, the effect of variation in woodlot area, which was not of primary research interest in this study, would be best controlled by establishment of small study plots of the same area in all woodlots. However, this solution was not applicable because such study plots would be too small for bird surveys given relatively small size of the whole focal woodlots. Therefore, we surveyed birds by covering whole woodlots, keeping the per unit area sampling effort approximately constant and then we used species-area relationship to account for the area effects by the means of statistical analysis. This approach is recommended to avoid oversampling of small habitat fragments (Fahrig, 2020). On the other hand, the area effects observed in our models can be also biologically interesting given the difference between generalists and specialists. According to the species-area relationship and the island biogeography theory (Macarthur and Wilson, 1967), larger islands keep larger population sizes of the species and thereby reduce their extinction probabilities (Storch et al., 2018). This may be the case of habitat generalists originating from the forest bird species pool for which woodlots represent fragments of their preferred habitat (Hofmeister et al., 2017). By contrast, the absence of any significant area effects in habitat specialists may be explained by the frequently observed preference of such species for forest edges and non-forest woody vegetation (Rajmonová and Reif, 2018). Availability of such habitats does not increase with woodlot size resulting in its no effect on the specialists' species richness (Bellamy et al., 1996).

Although, our sampling focused on the breeding season since it is a crucial period for maintaining birds' population sizes (Newton, 1998), but the census technique we applied cannot prove whether the observed individuals really bred in the woodlots. It is possible that a (unknown) part of the recorded species in some woodlots were not breeders. However, although this fact may somewhat reduce the relevance of our results in the understanding of the woodlot characteristics to support breeding bird populations, it does not mean that the findings are not important for environmental management. In fact, woodlots may act as steppingstones (Štrobl et al., 2019) facilitating dispersal of bird individuals through unsuitable environment of intensively cultivated farmland (Rajmonová and Reif, 2018). Therefore, management of their habitat to maximize bird species richness is still relevant from a perspective of conservation biology.

Table 3

Characteristics of the generalized least squares models relating rarefied species richness of all bird species, habitat specialist birds and habitat generalist birds, respectively, to woodlot area (log-transformed), type (black locust and native), age, arthropod biomass, and vegetation structure (vPC1-vPC4 − see Fig. 2 for their meaning). The models are ranked according to the Akaike information criterion corrected for small samples (AICc) and only the top ranking models (ΔAICc < 2) are shown.

All birds richness	df	logLik	AICc	delta	weight
Woodlot Type + log(Area)+vPC3	5	−70.600	154.056	0.000	0.252
Specialist richness	**df**	**logLik**	**AICc**	**delta**	**weight**
Woodlot Type + vPC3	4	−39.458	88.735	0.000	0.108
Woodlot Type + vPC2+vPC3	5	−38.343	89.544	0.809	0.072
Woodlot Type + Arthropods Biomass + vPC3	5	−38.499	89.854	1.119	0.062
Woodlot Type + Age + vPC3	5	−38.936	90.730	1.995	0.040
Generalist richness	**df**	**logLik**	**AICc**	**delta**	**weight**
log(Area)+vPC1+vPC4	5	−61.326	135.510	0.000	0.077
Woodlot Type + log(Area)	4	−63.490	136.799	1.289	0.041
log(Area)+vPC1	4	−63.496	136.810	1.300	0.040
Woodlot Type + log(Area)+vPC4	5	−62.038	136.933	1.423	0.038
Woodlot Type + log(Area)+vPC2	5	−62.234	137.325	1.816	0.031
Woodlot Type + log(Area)+Arthropod Biomass	5	−62.288	137.433	1.923	0.030

Table 4

Effects of each variable over the rarefied species richness included in the best subset of generalized least squares models (ΔAICc < 2) produced by the model dredging. Result shown for all species, habitat specialist and habitat generalist. For each variable, both estimated effect (coef) and standard error (SE) are shown. The effects with confidence intervals not overlapping zero are shown in bold. Notate that the effects of variables distance, sPC1, sPC2, and the crops are not shown since they do not were considered in any of the best models.

All species richness

Woodlot Type		log(Area)		Age		Arthropods Biomass		vPC1		vPC2		vPC3		vPC4	
coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE
7.708	**1.456**	**3.145**	**1.127**	NA	NA	NA	NA	NA	NA	NA	NA	**0.107**	**0.039**	NA	NA

Specialists richness

Woodlot Type		log(Area)		Age		Arthropods Biomass		vPC1		vPC2		vPC3		vPC4	
coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE
1.520	**0.431**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	**0.035**	**0.012**	NA	NA
1.486	**0.423**	NA	NA	NA	NA	NA	NA	NA	NA	−0.015	0.011	**0.035**	**0.012**	NA	NA
1.717	**0.451**	NA	NA	NA	NA	−0.012	0.009	NA	NA	NA	NA	**0.037**	**0.012**	NA	NA
1.519	**0.432**	NA	NA	0.017	0.018	NA	NA	NA	NA	NA	NA	**0.037**	**0.012**	NA	NA

Generalists richness

Woodlot Type		log(Area)		Age		Arthropods Biomass		vPC1		vPC2		vPC3		vPC4	
coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE	coef	SE
NA	NA	3.736	0.792	NA	NA	NA	NA	**0.034**	**0.013**	NA	NA	NA	NA	0.059	0.029
2.521	1.085	3.768	0.850	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NA	NA	**4.097**	**0.818**	NA	NA	NA	NA	**0.033**	**0.014**	NA	NA	NA	NA	NA	NA
2.328	**1.057**	**3.516**	**0.836**	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.049	0.030
2.558	**1.058**	**3.895**	**0.831**	NA	NA	NA	NA	NA	NA	0.039	0.026	NA	NA	NA	NA
2.009	1.116	**3.768**	**0.828**	NA	NA	0.033	0.022	NA	NA	NA	NA	NA	NA	NA	NA

From the applied perspective, our results support the idea of high impact of black locust on the woodlot vegetation structure and are thus consistent with our second hypothesis: black locust woodlots do not offer suitable habitat for birds in the breeding season. It is possible that such negative impacts would be the case also for other non-native woody plant species, although the studies focused on such impacts are lacking in this landscape context (Nelson et al., 2017). Our findings are important in the context of recent efforts to improve the value of farmland for biodiversity (Pe'er et al., 2019), since the establishment of non-forest woody vegetation patches is one of the important tools frequently adopted within agri-environmental schemes (Pe'er et al., 2017). When such landscape features are created, it is essential to use solely native woody plant species for this purpose, to achieve conservation benefits for birds in farmland. Defining plausible management options for the existing black locust woodlots is another important conservation issue.

5. Conclusions

Our results showed significant changes in the vegetation structure of the mid-field woodlots when they are dominated by the black locust. This alteration of the vegetation structure decreases the species richness of all birds, generalist species as well as specialist species. According to our results, these woodlots are unsuitable for breeding birds and thus the usage of native

woody plant should be encouraged for creation of woodlots. Similarly, conservation efforts aiming to preserve bird species, might target preferentially woodlots dominated by the native vegetation since its presence in arable land plays a major role in bird ecology. However, Strobl et al. (2019) found positive effects of black locust woodlots over the insect communities. Thereby, a broader assessment based on a multitaxonomic approach is required to determine the real ecological impact of woodlots dominated by the black locust.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2021.e01458.

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5. Diskuse

Výsledky studií tvořící tuto disertační práci a zabývající se vlivem nepůvodních dřevin, zejména invazního trnovníku akátu, na společenstva členovců, spíše podporují názor, že invazní rostliny mohou být jedním z faktorů způsobujících recentně pozorovaný úbytek členovců na lokální úrovni (Cardoso et al., 2020; Tallamy et al., 2020; Wagner, 2020).

Prostřednictvím multi-taxonomického přístupu jsme zaznamenali jednak negativní vliv trnovníku akátu na celkovou abundanci i biomasu členovců v souvislých lesních celcích (Štrobl et al., in prep.), tak jsme rovněž prokázali jeho negativní dopad na celkovou abundanci i celkový počet druhů členovců v izolovaných lesních fragmentech situovaných v intenzivní zemědělské krajině, v porovnání s porosty tvořenými původními druhy listnatých dřevin (Štrobl et al., 2019). Tyto výsledky jsou v souladu s recentními poznatky o obecně negativním vlivu invazních rostlin na společenstva členovců (Litt et al., 2014; Spafford et al., 2013; van Hengstum et al., 2014) a souvisejí zejména s úbytkem herbivorního hmyzu v porostech trnovníku akátu (Degomez & Wagner, 2001; Kadlec et al., 2018; Štrobl et al., 2019; Štrobl et al., in prep.). I když jsme prokázali negativní vliv trnovníku akátu na celkový počet druhů členovců v izolovaných lesních fragmentů, jeho role v kontextu diverzity členovců v intenzivně zemědělsky využívané krajině nebyla pouze negativní (Štrobl et al., 2019). V průměru jsme totiž nezaznamenali nižší počet druhů členovců ani jejich nižší biomasu v akátových fragmentech oproti fragmentům tvořených původními druhy dřevin (Rivas-Salvador et al., 2021; Štrobl et al., 2019). Hlavním důvodem byl fakt, že fragmenty trnovníku akátu byly tvořeny světlými porosty s dobře vyvinutým bylinným patrem, a tudíž se staly refugiem druhů vázaných na otevřené biotopy napříč studovanými taxonomickými skupinami členovců, které nahradily úbytek členovců vázaných na lesní prostředí, způsobený trnovníkem akátem (Štrobl et al., 2019). Je tedy zřejmé, že efekt invazního trnovníku akátu na společenstva původních členovců se skládá jednak z jeho přímého dopadu na hmyzí herbivory a následných kaskádových efektů na vyšší trofické úrovně členovců, tak z nepřímých dopadů plynoucích z odlišné struktury habitatu oproti původním druhům dřevin (Buchholz et al., 2015; Kadlec et al., 2018; Štrobl et al., 2019; Štrobl et al., in prep.), stejně jako tomu bylo prokázáno i u jiných druhů invazních dřevin (Harris et al., 2004; Pawson et al., 2010). Dopady trnovníku akátu se rovněž často zásadně lišily mezi jednotlivými taxony a trofickými gildami členovců, což je v souladu s výsledky globálních studií o vlivu invazních rostlin na členovce (Litt et al., 2014; Schirmel et al., 2016; Spafford et al., 2013; van Hengstum et al., 2014).

Struktura lesních porostů trnovníku akátu se signifikantně lišila v porovnání s porosty původních druhů listnatých dřevin (Kadlec et al., 2018; Reif et al., 2016; Rivas-Salvador et al., 2021; Štrobl et al., 2019; Štrobl et al., in prep.). I v našich studiích byly potvrzeny dosavadní publikované poznatky o tom, že trnovník akát tvoří v sekundárním areálu velmi světlé porosty s dobře vyvinutým podrostem (Campagnaro, Nascimbene et al., 2018; Šibíková et al., 2019; Vítková et al., 2017). To je dáno fyziognomií trnovníku akátu, který přes svojí řídkou korunu propouští velké množství slunečního záření do podrostu (Xu et al., 2009), a rovněž faktem, že se akát olisťuje později než původní druhy dubů (Šibíková et al., 2019). V souvislých akátových porostech jsme zaznamenali vyšší podíl vysoké bylinné vegetace i keřového patra v porovnání s porosty původních dřevin (Kadlec et al., 2018; Reif et al., 2016; Štrobl et al., 2019; Štrobl et al., in prep.). Naopak v akátových lesních fragmentech bylo sice rovněž více vyvinuté vyšší bylinné patro, ale vyšší podíl keřového patra byl zaznamenán v lesních fragmentech tvořených původními druhy dřevin (Rivas-Salvador et al., 2021; Štrobl et al., 2019). Tento rozdíl pravděpodobně souvisí se skutečností, že ve většině akátových fragmentů zahrnutých v této studii, byl jejich podrost dominantně tvořen kompetitivními druhy trav, jako je např. ovsík vyvýšený *Arrhenatherum elatius* (L.) J. Presl et C. Presl), které mohou efektivně potlačovat klíčení a růst semenáčků keřů. Většina těchto porostů byla totiž situována v Polabské nížině (Rivas-Salvador et al., 2021; Štrobl et al., 2019), kde v podloží převládají váté písky a fluviální písčito-štěrkové náplavy, na kterých trnovník akát vytváří společenstva asociace *Arrhenathero elatioris-Robinietum pseudoacaciae* Šimonovič et al. ex Vítková et Kolbek 2010 (Vítková & Kolbek, 2010). Jak v případě porostů původních dřevin v souvislých lesních celcích, tak v lesních fragmentech v zemědělské krajině měly porosty původních dřevin vyvinutější a zapojenější korunové patro (Kadlec et al., 2018; Reif et al., 2016; Rivas-Salvador et al., 2021; Štrobl et al., 2019; Štrobl et al., in prep.). Rozdílná struktura mezi porosty invazního trnovníku akátu a původních druhů dřevin se odrazila do statisticky průkazné rozdílné struktury složení společenstev členovců mezi porosty (Kadlec et al., 2018; Štrobl et al., 2019). Napříč studovanými taxony členovců jsme prokázali, že druhy otevřených biotopů, včetně ohrožených druhů, byly dominantně spjaty s lesními fragmenty tvořenými invazním trnovníkem akátem. Naopak lesní druhy členovců v nich byly zastoupeny pouze minimálně, přičemž ty dominovaly v lesních fragmentech tvořených původními druhy dřevin (Štrobl et al., 2019). Stejné trendy v rozdílné struktuře složení společenstev mezi porosty trnovníku akátu a původních druhů dřevin byly rovněž zjištěny i v souvislých lesních celcích u nočních motýlů (Kadlec et al., 2018).

Z jednotlivých trofických gild členovců má trnovník akát nejvíce negativní dopad na herbivory, a to jak v souvislých lesních porostech, tak v lesních fragmentech izolovaných ornou půdou (Degomez & Wagner, 2001; Hejda et al., 2017; Kadlec et al., 2018; Štrobl et al., 2019; Štrobl et al., in prep.). Většina druhů herbivorního hmyzu, a především lesní specialisté s vazbou na korunové patro, se totiž pravděpodobně nebyli schopna troficky adaptovat na nepůvodní invazní rostlinu, jelikož s ní během evoluce vlivem přirozených bariér nepřišli do styku (Bezemer et al., 2014; Keane & Crawley, 2002; Liu & Stiling, 2006).

Nejintenzivněji jsme zdokumentovali vliv trnovníku akátu na společenstvo převážně herbivorních nočních motýlů, u kterých jsme prokázali jeho negativní dopad na abundanci, diverzitu i biomasu velkých nočních motýlů (noční „Macrolepidoptera"; Hejda et al., 2017; Kadlec et al., 2018; Štrobl et al., 2019). Tyto trendy jsou způsobeny přímým dopadem akátu spojeným s úbytkem herbivorních specialistů korunového patra (Degomez & Wagner, 2001; Hejda et al., 2017; Kadlec et al., 2018; Štrobl et al., 2019), jelikož pouze několik málo druhů nočních motýlů je schopno přijímat akát jako hostitelskou rostlinu v larválním stadiu (Kulfan, 2012). U nočních motýlů jsme rovněž testovali nepřímý efekt trnovníku akátu na diverzitu nočních motýlů skrze jeho dopady na diverzitu cévnatých rostlin (Hejda et al., 2017), protože je zdokumentováno, že úbytek hebivorů může být zčásti způsoben poklesem diverzity rostlin v důsledku rostlinné invaze (Litt et al., 2014; Schirmel et al., 2016; Simao et al., 2010). Zjistili jsme sice statisticky průkazný nepřímý efekt trnovníku akátu na diverzitu nočních motýlů v důsledku nepatrného poklesu rostlinné diverzity v akátových porostech, ale tento efekt byl velmi slabý v porovnání s jeho přímým efektem, který vyústil ve výrazný pokles diverzity nočních motýlů kvůli úbytku motýlů vázaných na korunového patro (Hejda et al., 2017). Naše studie zabývající se rozložením funkčních vlastností nočních motýlů v lesních porostech trnovníku akátu (Kadlec et al., 2018), je jedna z prvních prací poskytující komplexní poznatky o vlivu invazních dřevin na funkční diverzitu členovců. Rozložení funkčních vlastností nočních motýlů se statisticky průkazně lišilo mezi porosty trnovníku akátu a původními dubovými porosty (Hejda et al., 2017; Kadlec et al., 2018). I když bylo v porostech akátu zaznamenáno průkazně méně nočních motýlů vázaných na korunové patro, tak jsme v kontrastu s naším očekáváním a dosud publikovanými výsledky o vyšším podílu potravně specializovaných motýlů v porostech původních dřevin (Burghardt et al., 2010; Jahner et al., 2011) nezaznamenali preferenci monofágních a oligofágních motýlů k původním porostům (Kadlec et al., 2018). Motýli s vazbou na bylinné patro a otevřené biotopy společně s lesostepními druhy silně tíhli ke světlým akátovým porostům s dobře vyvinutým podrostem. Naopak v důsledku zapojeného patra v porostech původních druhů dřevin dominovali lesní specialisté (Hejda et

al., 2017; Kadlec et al., 2018). V akátových porostech byly ve srovnání s dubovými porosty více zastoupeny vícegenerační druhy motýlů s rychlejším životní cyklem – kratší larvální periodou i kratší délkou života dospělců (Kadlec et al., 2018). To mohlo být způsobeno teplejším a sušším mikroklimatem v porostech trnovníku akátu v důsledků propustnosti velkého množství slunečního záření skrz jeho řídkou korunu do podrostu (Xu et al., 2009), který je zejména v letních měsících vystaven velkému tepelnému a vodnímu stresu (Šibíková et al., 2019; Vítková et al., 2017). V porostech invazního trnovníku akátu byly zaznamenáni motýli menších velikostí, což může být spojeno opět s úbytkem motýlů vázaných na korunové patro (Kadlec et al., 2018). Heleno et al. (2008) totiž prokázali, že hmyzí herbivoři s vazbou na korunové patro původních druhů dřevin mají větší velikost těla oproti herbivorům kolonizujících korunové patro invazních dřevin. V případě srovnání společenstev nočních motýlů se zahrnutím motýlů i ze skupiny tzv. drobných motýlů „Microlepidoptera", nebyl mezi porosty invazního akátu a původních druhů dřevin zjištěn rozdíl v celkové abundanci nočních motýlů (Štrobl et al., in prep.). Tento výsledek je v kontrastu s poznatky Kadlece et al. (2018), což je pravděpodobně způsobeno vyšším počtem jedinců ze skupiny drobných motýlů („Microlepidoptera") v akátových porostech. Tento jev pravděpodobně souvisí s velkým zastoupením jedinců několika málo druhů drobných motýlů potravně vázaných na trnovník akát (*Parectopa robiniella* a *Phyllonorycter robiniella*) ve vzorcích, či faktem, že mnoho zástupců této skupiny motýlů je vázaných na bylinný a keřový podrost, jenž byl rozvinutější v akátinách. Jelikož ale u motýlů této skupiny nebyla provedena druhová determinace, není možné tyto efekty jednoznačně interpretovat. Naopak stejně jako ve studii Kadlece et al. (2018) jsme prokázali nižší biomasu nočních motýlů v porostech trnovníku akátu i v případě zahrnutí motýlů ze skupiny Microlepidoptera (Štrobl et al., in prep.), což patrně souvisí opět s úbytkem motýlů korunového patra, kteří mají větší velikost těla, a tím pádem i vyšší tělesnou hmotnost (Kadlec et al., 2018).

U převážně herbivorních nosatců jsme v lesních fragmentech zaznamenali negativní dopad trnovníku akátu na jejich abundanci, který byl opět způsoben úbytkem lesních druhů vázaných na korunové patro a na dřeviny obecně (Štrobl et al., 2019). V souvislých akátových lesích jsme rovněž zaznamenali nižší abundanci i biomasu převážně herbivorních brouků z podřádu Polyphaga, kteří byli více spjati s dubovými porosty (Štrobl et al., in prep.). Tyto trendy byly spojeny nejspíše s vysokým zastoupením brouků živících se listy dřevin (např. nosatci (Curculionoidea) či chrousti (Melolonthinae); Štrobl et al., in prep.), kteří pravděpodobně stejně jako noční motýli nedokážou přijímat akát jako svou hostitelskou rostlinu (Kadlec et al., 2018). Rovněž jsme zachytili nižší abundanci i biomasu štíhlopasých blanokřídlých (Apocrita)

v porostech trnovníku akátu (Štrobl et al., in prep.). Většinu zachycených jedinců štíhlopasých ve vzorcích tvořili zástupci parazitoidních lumků (Ichneumonoidea) a parazitoidních i hálkotvorných žlabatek (Cynipoidea). Úbytek štíhlopasých blanokřídlých v akátových porostech patrně souvisí s úbytkem brouků ze skupiny Polyphaga a nočních motýlů, které např. lumci dominantně využívají jako své hostitele (Quicke, 2015). Tato interpretace odpovídá dosud známým poznatkům o obecně negativním dopadu invazních dřevin na parazitoidní skupiny členovců (Bezemer et al., 2014; Harvey & Fortuna, 2012; Siamo et al., 2010). Kdybychom měli k dispozici podrobná druhová data o saproxylických broucích ze skupiny Polyphaga, tak bychom mohli nepřímo podpořit či vyvrátit výsledky studie Della Rocca et al. (2016), ve které její autoři zjistili, že v mrtvém dřevě trnovníku akátu se nevyskytuje průkazně menší počet jedinců ani druhů saproxylických brouků v porovnání s původními druhy dřevin (dubem letním a topolem bílým (*Populus alba* L.). To je obecně limitem studie Štrobl et al., in prep., ve které jsme nedeterminovali jedince členovců do druhové úrovně, a z výsledků této studie tedy nelze vždy úplně jednoznačně zobecnit závěry o vlivu trnovníku akátu na saproxylické brouky. V případě kovaříků (Elateridae) jsme neprokázali negativní vliv trnovníku akátu na jejich druhovou diverzitu ani abundanci v lesních fragmentech v zemědělské krajině (Štrobl et al., 2019). Naopak jsme zachytili více jedinců kovaříku v akátových fragmentech než v lesních fragmentech tvořenými původními druhy dřevin, přičemž tento trend byl dán vysokými četnostmi druhů kovaříků (zejména *Agriotes* spp.) vázaných na dobře vyvinuté bylinné patro v akátinách (Štrobl et al., 2019).

Abundance, druhová diverzita ani biomasa převážně herbivorních ploštic (Heteroptera) nebyla v našich studiích negativně ovlivněna invazí trnovníku akátu (Štrobl et al., 2019; Štrobl et al., in prep.). Tyto výsledky jsou v kontrastu s poznatky Degomeze & Wagnera (2001), kteří prokázali negativní dopad trnovníku akátu na abundanci i diverzitu hemipterních skupin hmyzu. Tento rozdíl může být způsoben použitou metodou sběru členovců, kdy Degomez & Wagner (2001) zvolili pouze metodu sklepávání členovců z větví akátů do 3 m výšky, a naopak my jsme v našich studiích použili kombinaci více metod odchytu členovců (světelné lapače, smýkání bylinného a keřového patra, zemní pasti) vhodných i k zachycení ploštic z ostatních vegetačních pater lesního porostu (Štrobl et al., 2019; Štrobl et al., in prep.). Podstatná část druhů ploštic totiž zjevně profitovala zejména z dobře vyvinutého bylinného patra v akátových porostech (Štrobl et al., 2019).

S výjimkou střevlíkovitých brouků (Carabidae) a síťokřídlých (Neuroptera), jsme neprokázali žádný negativní vztah mezi invazním trnovníkem akátem a abundancí, diverzitou ani biomasou predátorů (Štrobl et al., 2019; Štrobl et al., in prep.) Tyto výsledky jsou v souladu

se slabým dopadem invazních dřevin na společenstva karnivorních členovců, který byl obecně potvrzen v mnoha dalších studiích (Buchholz et al., 2015; Hartley et al., 2010; Litt et al., 2014; Van der Colff et al., 2015). Nižší abundance střevlíků zaznamenaná v akátových lesních fragmentech (Štrobl et al., 2019) je v kontrastu s výsledky Buchholze et al. (2015), kteří nezaznamenali negativní vliv trnovníku akátu na společenstvo střevlíkovitých brouků. Vyšší abundance střevlíků v porostech původních dřevin může být spojena s příznivějšími mikroklimatickými podmínkami, konkrétně s vyšší relativní vlhkostí půdy související se silně zapojeným korunovým patrem v těchto porostech, díky kterým zde mohou střevlíci nalézat větší množství potravy, jako jsou žížaly, plži či chvostoskoci (Collembola). V rozporu s výsledky Buchholze et al. (2015) jsme nezjistili žádný efekt trnovníku akátu na diverzitu a abundanci stonožek (Chilopoda; Štrobl et al., 2019). Naopak stejně jako Buchholz et al. (2015) jsme neprokázali negativní dopad trnovníku akátu na diverzitu a abundanci pavouků (Araneae). V naší studii dokonce abundance pavouků pozitivně korelovala s vyvinutějším bylinným patrem a otevřeností korunového patra v akátových lesních fragmentech, a obecně v nich dominovaly druhy otevřených biotopů (Štrobl et al., 2019). To je v kontrastu se srovnáním společenstev pavouků mezi porosty trnovníku akátu a břízy bělokoré, kde akátové porosty měly mírně zapojenější korunové patro než porosty břízy bělokoré, a byly v nich více zastoupeny lesní a stínomilné druhy pavouků (Buchholz et al., 2015). Rozdílný výsledek může být způsoben i odlišným přístupem ke sběru pavouků. Buchholz et al. (2015) se totiž zabývali pouze epigeickými pavouky, přičemž v naší studii (Štrobl et al., 2019) jsme provedli mnohem komplexnější sběr pavouků včetně smýkání bylinného a keřového patra. U síťokřídlých jejich abundance rostla se zvyšujícím se zápojem korunového patra a s rostoucím podílem keřového patra v lesních fragmentech původních druhů dřevin (Štrobl et al., 2019). To může být spojeno se zvýšenou dostupností jejich potravy, kterou z velké části tvoří mšice (Aphidoidea), jejichž společenstva jsou početnější i druhově bohatší na původních druzích dřevin. Trnovník akát totiž hostí pouze 16 druhů mšic, což je mnohem méně druhů ve srovnání s původním druhy dubů (39 druhů mšic na dubu letním a 25 druhů na dubu zimním; Holman, 2009).

U detritovorních mnohonožek (Diplopoda) jsme nezaznamenali žádný rozdíl v jejich abundanci a diverzitě mezi lesními fragmenty tvořenými trnovníkem akátem a původními druhy dřevin (Štrobl et al., 2019). Stejně tak Buchholz et al. (2015) nezaznamenali žádný vliv trnovníku akátu na četnosti mnohonožek v městských lesích. V případě detritovorních členovců jsme předpokládali pozitivní vliv akátu na jejich diverzitu i abundanci, protože ve velkém množství případů detritovorní členovci z invaze nepůvodních dřevin dokonce profitují (Harris et al., 2004; Litt et al., 2014). Detritovoři totiž mohou profitovat z velké produkce biomasy

v porostech invazních rostlin (Ehrenfeld, 2010; Vilà et al., 2011), následně většího množství rostlinného opadu s často větší rychlostí rozkladu (Standish et al., 2004). I když v porostech trnovníku akátu bylo výrazně méně mnohonožek specializovaných na lesní prostředí (např. špičanka dlouhoocasá, *Ophyiulus pilosus* (Newport, 1842)), tak jejich úbytek kompenzovaly zejména eurytopní druhy mnohonožek, jako je např. mnohonožka lesní či oblanka sídelní (*Cylindroiulus caeruleocinctus* (Wood, 1864); Štrobl et al., 2019). Tyto eurytopní druhy mohly pravděpodobně profitovat ze značného množství dusíku v opadu akátu (Tateno et al., 2007) a z velkého množství rozkládající se rostlinné vegetace v jeho podrostu (Vítková et al., 2017). Z usychajícího a rozkládajícího se podrostu v souvislých akátových porostech profitovaly i detritovorní druhy nočních motýlů s vazbou na rostlinný opad a zavadající listy keřů a bylin (např. *Hoplodrina respersa* (Denis & Schiffermüller, 1775)), které v dubových porostech chyběly z důvodu absence podrostu v těchto lesích (Kadlec et al., 2018).

U převážně omnivorních rovnokřídlých jsme neprokázali žádný rozdíl v abundanci, diverzitě, biomase ani druhovém složením mezi porosty trnovníku akátu a porosty původních druhů dřevin (Štrobl et al., 2019; Štrobl et al., in prep.). Z omnivorních skupin pouze škvoři (Dermaptera) a zejména jejich biomasa byla spjata s porosty trnovníku akátu (Štrobl et al., in prep.). I když jsou škvoři vyskytující se v ČR omnivorní, tak jejich značnou část potravy tvoří rostlinné zbytky (Kočárek & Holuša, 2005). Z tohoto důvodu mohli škvoři teoreticky profitovat z velkého množství odumřelé vegetace v podrostu akátin v důsledku tepelného a vodního stresu pro vegetaci v akátových porostech v letních měsících.

Oproti srovnání celkové abundance a biomasy členovců s noční aktivitou mezi porosty invazního trnovníku akátu a porosty původních druhů dubů jsme neprokázali signifikantní rozdíl v celkové abundanci a biomase členovců v lesních porostech nepůvodní borovice černé ve srovnání s porosty původní borovice lesní (Štrobl et al., in prep.). Tyto trendy budou pravděpodobně nejvíce spojeny se skutečností, že se oba borovicové porosty nelišily v zastoupení herbivorních skupin hmyzu, zejména nočních motýlů a brouků z podřádu Polyphaga (Štrobl et al., in prep.). Tyto výsledky tedy nepřímo podporují tvrzení, že většina původních druhů hmyzích herbivorů se dokáže nepůvodní kongenerické rostlině rychle přizpůsobit, a dokážou jí často přijímat jako svou hostitelskou rostlinu, jelikož její pletiva obsahují velmi podobné složení fytochemikálií jako pletiva původní druhů rostlin stejného rodu (Agrawal & Kotanen, 2003; Agrawal et al., 2005; Burghardt et al., 2010; Dostál et al., 2013; Zuefle et al., 2008). Porosty nepůvodní borovice černé se sice statisticky průkazně lišily ve struktuře vegetace od porostů původní borovice lesní, ale tyto rozdíly nebyly tak značné jako v případě srovnání struktury vegetace invazního trnovníku akátu a původních druhů dubů (Štrobl et al.,

in prep.). To je způsobeno podobnou ekologií a fyziognomií u obou studovaných druhů borovic (Křivánek., 2006). Nicméně jsme zaznamenali vyšší podíl keřového patra a více světlin v porostech borovice černé v porovnání s borovicí lesní (Štrobl et al., in prep.). Větší podíl světlin a keřového patra v porostech borovice černé může být důvodem pro vyšší abundanci i biomasu rovnokřídlých, poněvadž majoritu rovnokřídlých ve vzorcích tvořila kobylka křovištní (*Pholidoptera griseoaptera* (De Geer, 1773)), která je často vázaná např. na ostružiní v lesních světlinách i keřové patro lesních porostů (Kočárek et al., 2015).

Pro komplexnější budoucí studium vlivu nepůvodních dřevin na společenstva členovců by bylo ideální vybrat tři druhy jehličnatých i tři druhy listnatých dřevin – vždy jeden druh původní dřeviny, k němu kongenerický druh nepůvodní dřeviny a nepůvodní druh více fylogeneticky vzdálený od původní druhu dřeviny. V prostředí ČR by teoreticky přicházely v úvahu z listnatých dřevin původní dub letní/zimní, nepůvodní kongenerický dub červený (*Quercus rubra* L.) a fylogeneticky nejvzdálenější nepůvodní trnovník akát. Z jehličnatých dřevin by mohly přicházet v úvodu původní borovice lesní, nepůvodní kongenerická borovice černá nebo borovice vejmutovka (*Pinus strobus* L.) a fylogeneticky vzdálenější douglaska tisolistá (*Pseudotsuga menziesii* (Mirb.) Franco). Zásadní problémem je ale fakt, že v ČR nejspíše nenajdeme oblast, kde by se všechny tyto potenciálně vhodné druhy studijních dřevin vyskytovaly ve větších výměrách pohromadě.

V souvislých lesních porostech byly prokázány kaskádové efekty způsobené invazním trnovníkem akátem mezi rostlinami – primárními producenty, nočními motýly – primárními konzumenty a ptáky – sekundárními konzumenty (Hejda et al., 2017). Tyto efekty byly spíše nepřímé, a funkční vztahy mezi jednotlivými trofickými úrovněmi nebyly samy o sobě klíčovou determinantou jejich druhové diverzity. Trnovník akát sice skrz druhovou diverzitu rostlin signifikantně negativně ovlivňoval druhovou diverzitu nočních motýlů, ale tento efekt byl velmi slabý. Naopak statisticky průkazný přímý dopad trnovníku akátu na druhovou diverzitu nočních motýlů byl velmi silný, a to z důvodu úbytku druhů korunového patra, jelikož většina z nich nedokáže přijímat akát jako svojí hostitelskou rostlinu (Kulfan, 2012). Rovněž byl zjištěn nepřímý negativní efekt trnovníku akátu na druhovou diverzitu ptáků skrze diverzitu nočních motýlů (Hejda et al., 2017), který byl spojen s poklesem diverzity habitatově specializovaných ptáků v důsledku úbytku diverzity nočních motýlů vázaných na korunové patro v jeho porostech (Reif et al., 2016). Naopak habitatoví generalisté nebyli ovlivněni potravní nabídkou členovců vyjádřenou diverzitou nočních motýlů, a diverzita habitatových generalistů byla vyšší v porostech trnovníku akátu než v porostech původních druhů dřevin. Habitatoví generalisté byli totiž pozitivně spjati s více vyvinutým keřovým patrem v akátových porostech, které jim

poskytovalo větší hnízdní možnosti (Reif et al., 2016). Tyto protikladné trendy tedy byly nejspíše důvodem, proč nevyšel průkazný přímý efekt druhové diverzity nočních motýlů na druhovou diverzitu ptáků v rámci path analýzy (Hejda et al., 2017).

V lesních fragmentech situovaných v zemědělské krajině byla prokázána signifikantně nižší druhová diverzita všech ptačích druhů, habitatových specialistů i habitatových generalistů, v porostech trnovníku akátu v porovnání s lesními fragmenty tvořenými původními druhy dřevin (Rivas-Salvador et al., 2021). Dokonce zde nebyl zaznamenán pozitivní efekt vegetační struktury v akátových porostech na habitatové generalisty, jelikož v akátových fragmentech bylo velmi málo vyvinuté keřové patro (Rivas-Salvador et al., 2021; Štrobl et al., 2019). V kontrastu se souvislými lesními porosty trnovníku akátu (Reif et al., 2016) jsme nezjistili žádný průkazný vztah mezi druhovou diverzitou ptáků a jejich potravou, která byla vyjádřena celkovou biomasou všech členovců zachycených na konkrétní studijní lokalitě (lesním fragmentu; Rivas-Salvador et al., 2021). A to zejména proto, že se celková biomasa členovců nelišila mezi studovanými typy lesních ostrůvků (Rivas-Salvador et al., 2021). Dalším důvodem může být skutečnost, že jsme nedokázali dokonale podchytit všechny typy potravy tvořenou členovci stávajícími metodami sběru členovců, i když jsme použili kombinaci tří metod sběru členovců (zemní pasti, smýkání vegetace, a světelné lapače). Většina biomasy členovců byla totiž tvořena zejména epigeickými členovci a v mnohem menší míře jsme zde zachytili biomasu létavého hmyzu (s výjimkou nočních motýlů; Štrobl et al., 2019). Proto by bylo do budoucna vhodné použít např. i metody sběru členovců pomocí Mörickeho misek či Maleiseho pastí, díky kterým by byly zachyceny i dvoukřídlé a blanokřídlé skupiny hmyzu tvořící podstatnou složku potravy ptáků (Sottas et al., 2020; Wilson et al., 1999).

Výsledky této práce potvrzují, že vliv invazních rostlin na společenstva členovců se liší mezi jednotlivými taxony (Litt et al., 2014; Schirmel et al., 2016, Spafford et al., 2013; van Hengstum et al., 2014), a podtrhují důležitost multi-trofického a multi-taxonomického přístupu při studiu problematiky (Seibold et al., 2018). Jedním z limitů této práce je, že jsme se nezabývali vlivem trnovníku akátu na opylovače. Trnovník akát je významná nektarodárná rostlina (Somme et al., 2016) a je pravděpodobné, že zejména během jeho kvetení může mít pozitivní vliv na lokální diverzitu zejména nespecializovaných druhů opylovačů. Tento jev byl totiž pozorován i u jiných invazní dřevin s velkou produkcí nektaru (Bezemer et al., 2014; Emery & Doran, 2013). Nezbytným a často opomíjeným faktorem při studiu vlivu invazních rostlin na členovce (van Hengstum et al., 2014), ale i v ekologicko-ochranářských studiích obecně, je správný výběr a kombinace použitých metod sběru členovců (Knapp et al., 2020; Yi et al., 2012). Limitem studie Štrobl et al. (2019) zabývající se vlivem invazního trnovníku akátu

na společenstva členovců v souvislých nížinných lesích je použití pouze jedné metody sběru členovců – světelných lapačů. Pro komplexnější posouzení těchto dopadů je nutné použít více metod sběru členovců s cílem zachycení široké diverzity členovců s vazbou na jednotlivá vegetační patra lesního porostu a pracovat s druhovými daty, tzn. provést determinaci jednotlivých taxonomických skupin do druhové úrovně. Přílišná generalizace výsledků o dopadech invazních rostlin na biotu plynoucí ze zaměření na jednu taxonomickou skupinu, či přehlížení druhů s určitými funkčními vlastnostmi plynoucí z použití pouze jedné metody sběru, může vést i ke špatným rozhodnutím v ochranářské praxi (Pyšek, Jarošík, et al., 2012; van Hengstum et al., 2014). Z tohoto pohledu je dobré zvolit ve výzkumu této problematiky přístup studia dopadů invazních rostlin na funkční vlastnosti druhů napříč společenstvem členovců, který nám může poskytnout lepší nástroj pro generalizaci výsledků pro ochranářskou praxi. Proto jsme se rozhodli v další fázi výzkumu zaměřit na studium dopadů trnovníků akátu na členovce v zemědělské krajině prostřednictvím funkčních vlastností druhů stanovených napříč společenstvy členovců zachycenými různými metodami sběru. Předběžné výsledky analýz ukazují, že se rozložení funkční vlastností členovců mezi porosty trnovníku akátu a původních druhů dřevin mění v závislosti na použité metodě sběru členovců (nepublikovaná data), a podtrhují důležitost komplexního přístupu ke studiu problematiky.

6. Závěr

Invazní trnovník akát celkově negativně působil zejména na hmyzí herbivory a lesní specialisty, což vedlo zejména v souvislých lesních porostech k poklesu celkové abundance, diverzity i biomasy členovců. Rovněž jsme zjistili, že trnovník akát negativně ovlivňuje strukturu potravních sítí v souvislých lesních porostech. Zde totiž snižuje diverzitu habitatově specializovaných ptáků prostřednictvím úbytku hmyzí potravy vázané na korunové patro. Na druhou stranu jsme neprokázali jeho negativní dopad na většinu taxonů karnivorních členovců a někteří detritovoři dokázali z jeho invaze dokonce profitovat. Trnovník akát ve srovnání s porosty původních druhů dřevin vytváří světlé porosty s nezapojeným korunovým patrem a dobře vyvinutým podrostem. Z tohoto důvodu byli členovci s vazbou na otevřené a lesostepní biotopy, včetně ohrožených druhů, dominantně spjati s porosty trnovníku akátu. Tato skutečnost, kdy invazní dřevina poskytuje pro určitou část druhů členovců v krajině lepší podmínky než původní druhy dřevin, poukazuje na palčivý problém v nastavení managementu nížinných lesů v České republice, a to zejména v chráněných územích (Miklín & Čížek, 2014; Sebek et al., 2015). Většina nížinných lesů se totiž v České republice pěstuje ve formě zapojených stinných lesních porostů, ve kterých nemohou společenstva členovců vázaná na otevřené lesní porosty prosperovat (Miklín & Čížek, 2014; Sebek et al., 2015). Především izolované porosty trnovníku akátu obklopené ornou půdou slouží jako refugium diverzity těchto druhů a v kombinaci se zastíněnými porosty původních druhů dřevin můžou biodiverzitu členovců v intenzivní zemědělské krajině lokálně zvyšovat. Proto doporučuji trnovník akát tolerovat jako dřevinu tvořící izolované neprodukční biotopy situované v intenzivně obhospodařované zemědělské krajině. V neprodukčních biotopech izolovaných ornou půdou je totiž šíření akátu minimalizováno a jeho přínosy v kontextu biodiverzity členovců, ale i jeho potenciál pro biodiverzitu obecně (Vítková et al., 2017), dle mého názoru, převažují nad jeho negativy. Nelze totiž očekávat, že v těchto izolovaných lesních fragmentech v zemědělské krajině bude do budoucna docházet ke zlepšení struktury porostů tvořených původními druhy dřevin. Eradikace trnovníku akátu je samozřejmě velmi žádoucí v lučních a lesostepních biotopech, zejména v chráněných územích, u kterých je vhodné trnovník akát likvidovat i v jejich okolí právě kvůli jeho dobré schopnosti se šířit (Sádlo et al., 2017; Vítková, 2014). V běžných hospodářských, a zejména v biologicky cennějších lesích, by bylo vhodné trnovník akát postupně nahradit původními druhy dřevin a obecně zlepšit strukturu nížinných lesů v ČR a alespoň v chráněných územích dosáhnout jejich otevřenější struktury (Miklín & Čížek, 2014;

Sebek et al., 2015). Nejen z pohledu členovců nedoporučuji provádět nové výsadby trnovníku akátu, ani jiných druhů nepůvodních dřevin, ve volné krajině (tzn. mimo městské parky, zahrady a arboreta). S ohledem na výsledky této disertační práce se přikláním k názoru, že je třeba posuzovat vliv nepůvodních rostlin na biodiverzitu co nejkomplexněji, protože jejich dopady na biotu se mohou značně lišit mezi jednotlivými taxony a silně závisí na kontextu (Pyšek et al., 2012).

Studium problematiky dopadů invazních dřevin na členovce by se dalo rozvinout o výzkum zabývající se vlivem invazních dřevin na tělesnou kondici členovců. Jelikož jsme zjistili negativní dopad trnovníku akátu na abundanci střevlíkovitých brouků v lesních fragmentech, tak by bylo zajímavé zjistit, zda tento trend nějak souvisí s tělesnou kondicí lesních druhů střevlíků, např. na základě zhoršené potravní nabídky v porostech akátu. Rovněž by bylo zajímavé studovat, jak trnovník akát ovlivňuje tělesnou kondici málo mobilních druhů píďalek (Geometridae) potravně vázaných na bylinný a keřový podrost trnovníku akátu. Trnovník akát ovlivňuje chemické vlastnosti půd (Lazzaro et al., 2018; Vítková et al., 2015) a rostliny v jeho podrostu jsou v letních měsících vystaveny častému vodnímu a tepelném stresu (Vítková et al., 2017). Tyto faktory by se mohly promítnout do nutriční kvality hostitelských druhů rostlin a následně zhoršené tělesné kondice na ně vázaných málo mobilních druhů píďalek.

Rovněž zcela chybí poznatky o tom, jak se mění diverzita členovců na gradientu procentuálního zastoupení invazní dřeviny v lesním porostu. Touto problematikou se zabývali Kroftová & Reif (2017) u ptáků ve smíšených porostech trnovníku akátu a původních druhů dřevin, a zjistili, že diverzita ptáků byla nejvyšší v porostech s přibližně 50% zastoupením trnovníku akátu. Princip i design jejich studie by šel dobře implikovat do případové studie zaměřené na společenstvo nočních motýlů, přičemž očekávám, že bychom mohli dojít k obdobným výsledků i u nočních motýlů, protože jsme zjistili, že i přes nižší diverzitu nočních motýlů v porostech trnovníku akátu bylo v jeho porostech zastoupeno mnoho druhů s vazbou na bylinné a keřové patro, které v porostech původních dřevin chybí (Kadlec et al., 2018). Ve smíšeném porostu původních druhů dřevin s přibližně 50% zastoupením trnovníku akátu by tak mohla být diverzita nočních motýlů nejvyšší.

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Vzdělání

2015–dosud	Česká zemědělská univerzita v Praze, Fakulta životního prostředí, Ph.D., obor: Ekologie (předpokládaný termín dokončení: rok 2021). **Disertační práce:** *Ekologie a diverzita členovců v porostech invazních dřevin.*
2013–2017	Česká zemědělská univerzita v Praze, Institut vzdělávání a poradenství, obor: Souběžné doplňující studium učitelství odborných předmětů. **Závěrečná práce:** *Didaktický projekt ve výuce odborných předmětů pro obor ekologie a životní prostředí.*
2013–2015	Česká zemědělská univerzita v Praze, Fakulta životního prostředí, magisterské studium, obor: Ochrana přírody. **Diplomová práce:** *Ekologie a diverzita hmyzu v akátových porostech.*
2010–2013	Česká zemědělská univerzita v Praze, Fakulta životního prostředí, bakalářské studium, obor: Aplikovaná ekologie. **Bakalářské práce:** *Vliv letního a podletního léčení varroázy na spady roztočů Varroa destructor po 1. podzimní fumigaci.*

Praxe

2018–dosud	Vědecko-technický pracovník na Fakultě životního prostředí ČZU v Praze působící ve výzkumném týmu ekologie hmyzu: administrace a koordinace výzkumných projektů, sběr a analýza biologických dat, laboratorní práce, publikační činnost, spoluřešitel dvou grantů na podporu projektů ke zlepšení stavu životního prostředí hl. m. Prahy.

2016–dosud	Pedagogická činnost v rámci doktorského studia na Fakultě životního prostředí ČZU v Praze (výuka cvičení předmětů „Obecná ekologie" a „Zoologie bezobratlých"; vedení terénní praxe; vedoucí 2 bakalářských prací, oponent 4 BP, konzultant 3 BP a 2 DP, lektor „Letní dětské univerzity na ČZU" a projektu „Hurá na vysokou").
2017–dosud	OSVČ – management chráněných území, biologické průzkumy se zaměřením na hmyz.
2016	Hlavní řešitel interního grantu na Fakultě životního prostředí ČZU v Praze „Diverzita členovců izolovaných akátových fragmentů v intenzivně obhospodařované zemědělské krajině".
říjen 2016	Pedagogická praxe na SOŠ ekologické a potravinářské ve Veselí nad Lužnicí (výuka předmětů Biologie a Ekologie a životní prostředí).
2009–2016	Odborný pracovník na včelí farmě s uznaným šlechtitelským chovem včelích matek (náplň práce: obhospodařování produkčních včelstev, chov včelích matek).

Znalosti a dovednosti

Jazykové dovednosti: anglický jazyk – komunikace písmem i slovem; **německý jazyk –** začátečnická konverzace a komunikace písmem.

Počítačové dovednosti: program ArcGis – analýza vektorových a rastrových dat; program R – analýza jednorozměrných dat (lineární modely, zobecněné lineární modely, GLS); program CANOCO 5. 0 – pokročilé analýzy mnohorozměrných dat.

Řidičský průkaz: skupina B – aktivní řidič (15–20 tis. km ročně).

Ostatní zájmové činnosti: včelařství (člen ZO ČSV Vodňany, momentálně chov 20 včelstev), ochrana přírody (člen České entomologické společnosti).

Publikační činnost

Publikace v časopisech s IF:

Štrobl M., Hanzelka J., Hejda M., Kadlec T. Impacts of non-native trees *Robinia pseudoacacia* and *Pinus nigra* on arthropod communities. in prep.

Knapp, M., **Štrobl, M.,** Venturo, A., Seidl, M., Jakubíková, L., Tajovský, K., Kadlec, T., & González, E. Importance of grassy and forest islands for overwintering of ground-

dwelling arthropods in agricultural landscapes: a multi-taxa approach. *Agriculture, Ecosystems and Environment*, submitted.

Knapp, M., González, E., **Štrobl, M.,** Seidl, M., Jakubíková, L., Čížek, O., Balvín, O., Benda, D., Teder, T., & Kadlec, T. Artificial field defects: A low-cost measure to support arthropod diversity in arable fields. *Ecological Applications*, submitted.

González, E., **Štrobl, M.,** Janšta, P., Hovorka, T., Kadlec, T., & Knapp, M. Artificial temporary non-crop habitats support natural enemies within arable fields. *Journal of Applied Ecology*, under review.

Rivas-Salvador, J., **Štrobl, M.,** Kadlec, T., Saska, P., & Reif, J. (2021). A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland. *Global Ecology and Conservation*, 26, e01458 https://doi.org/10.1016/j.gecco.2021.e01458

Štrobl, M., Saska, P., Seidl, M., Kocian, M., Tajovský, K., Řezáč, M., Skuhrovec, J., Marhoul, P., Zbuzek, B., Jakubec, P., Knapp, M., & Kadlec, T. (2019). Impact of an invasive tree on arthropod assemblages in woodlots isolated within an intensive agricultural landscape. *Diversity and Distributions,* 25(11), 1800–1813. https://doi.org/10.1111/ddi.12981

Kadlec, T., **Štrobl, M.,** Hanzelka, J., Hejda, M., & Reif, J. (2018). Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure. *Biodiversity and Conservation,* 27(10), 2661–2680. https://doi.org/10.1007/s10531-018-1560-8

Hejda, M., Hanzelka, J., Kadlec, T., **Štrobl, M.,** Pyšek, P., & Reif, J. (2017). Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. *Diversity and Distributions*, 23(9), 997–1007. https://doi.org/10.1111/ddi.12596

Reif, J., Hanzelka, J., Kadlec, T., **Štrobl, M.,** & Hejda, M. (2016). Conservation implications of cascading effects among groups of organisms: The alien tree *Robinia pseudacacia* in the Czech Republic as a case study. *Biological Conservation,* 198, 50–59. https://doi.org/10.1016/j.biocon.2016.04.003

Příspěvky na konferencích

Aktivní účast na pěti tuzemských konferencích formou prezentace:

- Zoologické dny 2016, 2019
- Kostelecké inspirování 2015, 2017

- Biodiverzita 2016

Aktivní účast na dvou zahraničních konferencích formou posteru:

- Neobiota 2018 (Dublin, Irsko)

- Carabids in extreme environments. 19th European Carabidologists Meeting (Primiero San Martino di Castrozza, Itálie)

V Praze dne 17. 3. 2021   Martin Štrobl