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Formation of a novel tritrophic system: an invasive plant (*Robinia pseudoacacia*) and its host shifted consumers

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Lakatos Tímea Klára

Témavezető

Tóthmérész Béla
Egyetemi tanár

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Tanúsítom, hogy **Lakatos Tímea Klára** doktorjelölt 2012-2015 között a fent megnevezett Doktori Iskola **Kvantitatív és Terresztris Ökológia** programjának keretében irányításommal végezte munkáját. Az értekezésben foglalt eredményekhez a jelölt önálló alkotó tevékenységével meghatározóan hozzájárult. Az értekezés elfogadását javasolom.

Debrecen, 2017.

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Dr. Tóthmérész Béla
témavezető

Az invazív fehér akác (*Robinia pseudoacacia*) és európai magfogyasztó közössége. Egy új, gazdaváltó tritrófikus rendszer

Formation of a novel tritrophic system: an invasive plant (*Robinia pseudoacacia*) and its host shifted consumers

Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a Környezettudomány tudományágban

Írta: Lakatos Tímea Klára okleveles biológus
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Témavezető: Dr. Tóthmérész Béla

A doktori szigorlati bizottság:
elnök: Dr. Nagy Sándor Alex …………………………
tagok: Dr. Várbíró Gábor …………………………
Dr. Horváth Roland …………………………

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Az értekezés védésének időpontja:.…………………

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Introduction

Human activities cause economic and environmental problems worldwide, altering the environment by climate change, habitat loss and by introduction of alien species (Harvey et al. 2010). The introduction of alien plants often modifies habitats and biodiversity, thus composition and functioning of native ecosystems (Harvey et al. 2010; Bezemer et al. 2014). Changes in community composition of the invaded areas are mainly achieved through two processes. Firstly, the invaders may arrive with their native herbivores and the herbivores' natural enemies. Secondarily, host shifting herbivores and natural enemies may form novel ecosystems (Seastedt et al. 2008; Mascaro et al. 2013).

In response to the presence of a potential host plant, native consumers (herbivores) may adapt and shift to the consumption of the introduced plant, thus new insect - plant associations emerge through ecological fitting (Agosta 2006). These novel ecosystems are often compound by a few species, thus also being small ecosystems (Bascompte and Melián 2005). By adapting to an introduced host plant, herbivores may or may not lose their natural enemies (parasitoids) which may follow them to the new host plant (Cronin and Abrahamson 2001) or may gain new parasitoids (Harvey et al. 2010). Thus, formation of new communities and modification of ecosystem composition and functioning may be favored by host-shifts to introduced alien plants (Agosta 2006; Bezemer et al. 2014).

Conforming to the enemy release hypothesis, invasive plant species may show low herbivore diversity in their new habitats. This suggests that such species escaped their native herbivores, and that herbivore species of the new area are incompatible with the alien plant species due to their taxonomic distance from native host plants or the strong host-specificity of insects (Keane and Crawley 2002). Thus, invasive species often constitutes newly available niches for native herbivorous insects of the invaded area, facilitating their host plant shift (Carroll 2007). The study of invasive species and associated community characteristics can help further our understanding of how to develop methods to control invasions (Shea et al. 2002; Harvey et al. 2010).

Host plant shift of such phytophagous insects is enhanced by the taxonomic (Cagnolo et al. 2011) or chemical relatedness of plant species, the rarity of the formerly used host plant or by the advantages from lack of competition or predation on the new host plant (Jaenike 1990; Cagnolo et al. 2011). Ecological fitting is an underlying mechanism of the formation of new communities which contributes to the structuring of plant-insect associations (Janzen 1985). Species that evolved under different conditions can colonize new habitats, adapt to new conditions and form new associations. Native herbivores can shift to introduced plants, if they recognize the potential host plant as a feeding or oviposition site (Agosta 2006).

Not only herbivores, but also the parasitoids and other natural enemies of herbivores may be affected by the invasive host plant (Harvey et al. 2010) and vice versa. These novel host plants may affect parasitoids through plant allelochemicals or via herbivore fitness (Bezemer et al. 2014). Parasitoids may respond differently to introduced plants than its host shifted herbivores (Cronin and Abrahamson 2001). Insect parasitoids also influence the tritrophic interactions by reducing herbivory (van Loon et al. 2000). Optimally foraging parasitoids may favor patches with large prey abundance, thus patches with low prey abundance may become partial refuges from parasitism (Comins and Hassell 1979).

Dynamics of insect herbivore populations depend on trophic interactions with other species in their community, being controlled by their predators or host plants (Denno et al. 2003). Bottom-up controlled herbivores are mostly affected by the availability of their host plants (both quantity and quality of resources), while top-down controlled herbivores are limited due to predation or parasitism by their natural enemies. The relative strength of bottom-up and top-down forces can be altered by disturbance, invasive species and habitat structure components (Denno et al. 2003) like isolation (Chase et al. 2010).

Another set of factors influencing strength of bottom-up and top-down forces on insect herbivores are their traits such as behaviour, life history and strategies like dispersal, life cycle and environmental factors such as host plant density or patch size (Nylin 2001). Disturbance is influencing the abundance of species, the species composition (structure), and dynamics of communities. It may increase resource availability for herbivores (Hobbs and Huenneke 1992), but in turn disturbance may also cause high parasitism by reducing habitat complexity, thus making refuges of herbivores less common (Wilkinson and Feener 2007). Disturbance also can make communities more prone to invasion of alien species (Cohen 2002).

Insect communities are good model systems to test responses to disturbance such as alterations or changes in habitat because of their short generation time and high variability (Osborne, J.L., Loxdale, H.D. and Woiwod 2002). Spatial structure of patches is also an important factor influencing population and trophic dynamics of insects (Denno et al. 2003). Isolation usually decreases population sizes and diversity of communities, mostly by its effect of reducing dispersal and/or colonization. Isolation can also influence trophic dynamics of patches; it weakens top-down control (Chase et al. 2010), as higher trophic levels are more limited by habitat fragmentation (Cronin and Haynes 2004) and dispersal than herbivores (Elzinga et al. 2007).

Herbivore species show various responses to host plant density without a general pattern (Kareiva 1983); with known examples of different herbivore species having highest herbivory at large, small (Kareiva 1983) or intermediate densities (Underwood and Halpern 2012), while some species are independent of host plant density (Kareiva 1983). Density of host plants influences herbivores indirectly through individual characteristics of trees like the size (height and trunk diameter) (Shea et al. 2000) or the amount of pods (Arista and Talavera 1996). A positive relationship between abundance of herbivores and host plants may be hypothesized if large patches are more prone to occupation, but the density in patches is determined by a combination of migration and population growth processes (Hambäck and Englund 2005; Hambäck et al. 2007). As more host plants provide more resources, the resource concentration hypothesis (Root 1973) predicts that large plant patches are easier to be found so more herbivores immigrate into them (Kunin 1999). However, several herbivore species show resource dilution, being mostly present in sparse and small patches of host plants (Otway et al. 2005; Stephens and Myers 2012). Resource concentration of herbivores, when the host plant is invasive, leads to the persistence of the insect-plant system. It is predicted that weak resource dilution can accelerate invasive plant population decline, while strong resource dilution leads to population growth of the invasive plant in the large patches (Stephens and Myers 2012). Parasitoids in the invasive plant patches appear in low densities compared to native plant patches (Cronin and Haynes 2004).

Host specificity is another major factor affecting herbivores in the formation of new communities. A majority of herbivore insects show strong host specificity (Janzen 1970), feeding on one (monophagy) or a few (oligophagy) plant species. Specialist species are more sensitive to host plant patch size, and will colonize fewer small patches than generalist herbivores (Jaenike 1990; Zabel and Tscharntke 1998).

Novel communities of invasive plants may contain herbivores belonging to several feeding guilds, like sap-suckers, chewers, leaf-miners, gall inducers and seed predators (Singer and Stireman 2005). Seed predators decrease seed production of their host plant through their consumption, thus seed predation is a major biotic factor influencing invasive plant species. Seed predator insects may be acting before seed dispersal (pre-dispersal seed predators) or after seed dispersal (post-dispersal seed predators) (Janzen 1971). Beside seed consumption, seed predation may trigger seed or seedpod abortion in infested plants as the host plant’s reaction (Janzen 1971). Thus specialist seed predators are potential biocontrol agents of invasive plants (Dennill and Donnelly 1991), contributing substantially to the decrease of the invasive plant’s potential range (Sallabanks and Courtney 1992), also being less threatening to other parts of the host plant or to other plant species than generalist herbivores (Dennill and Donnelly 1991). So pre-dispersal seed predators can influence host plant abundance (Stephens and Myers 2012) and vice versa (Kolb et al. 2007).

The North-American black locust (*Robinia pseudoacacia* L.) was introduced to Europe without its native seed predators, but gained new consumer species. No herbivores consuming black locust seeds in North-America are present in Europe; therefore, there must have been a host shift of native Eurasian consumers (Hargrove 1986; Perju 1998). In Eastern - Europe black locust can be found in large patches like plantations or as single individuals (escaped plantations) or were planted as ornamental trees.

The studied novel ecosystem of black locust includes the pre-dispersal seed predator *Bruchophagus°robiniae* Zerova, 1970 and its parasitoids. The seed predator was studied from ecological, taxonomical and faunistic perspectives (Zerova 1970; Farkas and Terpó-Pomogyi 1974; Perju 1998). *B. robiniae* and its parasitoids together with black locust form an ideal model for studying effects of introduced plants on native consumers and their parasitoids, since it arrived without these consumers. Moreover, the separate occurrence of black locust individuals can be considered as a stage of escaping from cultivation. This makes black locust an ideal model organism from the viewpoint of introduced plants' spreading effects (becoming invasive) on native consumers (herbivores) and their community (parasitoids).

This tritrophic system also provides an excellent model system for measuring effects of disturbances on insect populations. Seedpods can be regarded as a concentration of resources in time and space (Osborne, J.L., Loxdale, H.D. and Woiwod 2002). Prior to emergence seed predator and parasitoid individuals are closed inside the infested seed and seedpod in which they developed (Batiste 1967). Due to this isolation, insects are spatially separated so the total removal of individuals from selected patches is feasible by the removal of all the seedpods of black locust.

There is a need for studies investigating the dispersal and the population dynamics of insect communities in altered environments, and especially for those involving invasive species and their insect meta-communities (Cronin and Haynes 2004; Bezemer et al. 2014). It is especially important to study several insect generations (Bezemer et al. 2014) and higher trophic levels (Cronin and Haynes 2004) as host plants interact not only with their herbivores, but even with the natural enemies of their herbivore (Price et al. 1980).

Aims of the studies

Resource dependence

We aimed to study how seed predators and their parasitoids respond to the escape of an introduced plant (Lakatos et al. 2016). We tested the influence of host plant resource abundance on the tritrophic system of the invasive black locust *R. pseudoacacia*, its pre-dispersal seed predator *B. robiniae*, and two parasitoid species: *Eupelmus* *urozonus* Dalman, 1820 and *Mesopolobus* sp. Westwood, 1833. We tested the following predictions: (1) Small patches of host plants show lower herbivore density than large patches because are harder to be found and provide less resources. (2) Besides the decreasing density of herbivores, the decreasing size of host plant patches also decreases specialist parasitoid ratio. (3) In contrast to specialized parasitoids, the density of generalist parasitoids shows no dependence on the patch size of host plant.

Disturbance induced dynamics

To simulate the effect of disturbance and to study the dispersal of insects we created experimentally vacated, and thus disturbed black locust patches (Lakatos et al. 2017). Our study provides a model ecosystem to analyse the effect of disturbance on the dynamics of a tritrophic system. The concept was to generate local extinctions in selected black locust patches by removing all pods, hereby also removing the insects hibernating inside them. We predict that vacated patches, which are close enough to a potential insect source, will be recolonized successfully. The seed predator and the parasitoid species may follow different patterns and dynamics recolonizing the vacated patches, due their various responses to disturbance. By rearing insects from the collected pod samples, we can get data about the initial occupation and diversity of patches, and abundance of species. In our field experiment it is particularly important that the host plant of the system is an invasive alien plant, with a host-shifted herbivore and parasitoids. Such communities provide the opportunity to study dynamics of systems, before they reach an equilibrium stage.

Our study hypothesis was that disturbance affects the spread of black locust. Study predictions: when all seedpods are removed from selected black locust patches: (1) Recolonization patterns of seed predators and their parasitoids in vacated (disturbed) patches will be different: both will recolonize, but parasitoids will appear in larger amounts because are less adapted to black locust than seed predators e.g. they also can be found on the plants surrounding black locusts. (2) Quantities of seed predators and their parasitoids are significantly affected by isolation of vacated patches. (3) Host plant density also has a significant effect (bottom-up control) on the quantities of the seed predators and their parasitoids. (4) Parasitoids will have a significant effect (top-down control) on the quantities of seed predators.

Although black locust is a widespread invasive species with a huge economic importance, until now the herbivore communities typical to its native regions were not compared to the novel ones on its new areas (Lakatos et al. manuscript a). Neither were compared the seed predator-parasitoid communities of native European shrub and tree legumes to the novel communities on introduced or invasive ones. The seed predator community of black locust is scarcely and deficiently studied albeit it is one of the most common invasive tree species of Europe. The parasitoid community linked with the seed predator *B. robiniae* is apparently unknown from both taxonomic and quantitative aspects. The study of this novel tritrophic ecosystem provides a unique opportunity to trace the evolution and coevolution process of species on human timescale.

We tested the process of co-evolution in the novel seed predator-parasitoid community of black locust to answer the following questions: (1) How does the diversity of herbivores belonging to different insect orders differ between native and novel areas of black locust? (2) How does the diversity of seed predators differ between native and invasive shrub and tree legumes in Europe? (3) What is the species composition of the black locust’s seed predator community in the eastern Carpathian Basin? (4) What is the species composition of the seed predator’s parasitoid community on black locust in the eastern Carpathian Basin? (5) Is there a common parasitoid composition pattern between *B. robiniae* and other *Bruchophagus* species? (6) Is there a common parasitoid composition pattern between the black locust's and other legume species hosted seed predator communities?

Materials and methods

Literature data collection

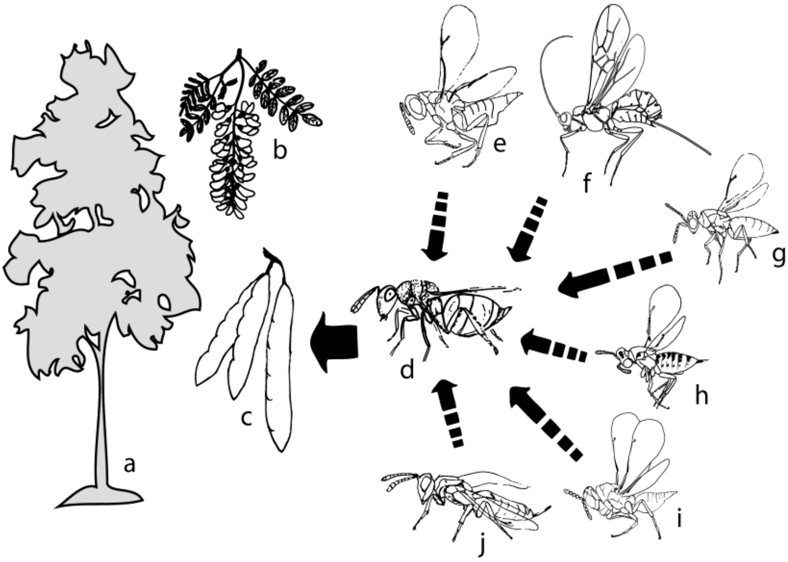
Parasitoid community of Bruchophagus robiniae

All available data regarding herbivores and parasitoids of black locust and other introduced and/or invasive and native shrub and tree legumes from Europe were searched in the Universal Chalcidoidea Database (UCD) (Noyes 2017), Scopus, Web of Knowledge and Google Scholar. Further data about the leguminous plants occurring in Europe were compiled from the Atlas of seeds and fruits of central and east European flora (Bojnanský and Fargašová 2007), with accepted names, synonyms and grow habits checked in the online databases of the International Legume Database & Information Service (White 2016) and The Plant List (List 2013).

Study system

The analyzed tritrophic system is composed by black locust as host plant, *Bruchophagus robiniae* as specialist seed predator and several parasitoid species (Figure 1). Black locust (*Robinia pseudoacacia* Linnae 1753; Fabaceae), native to the east coast of North-America (Call and Nilsen 2003), is one of the most widely distributed alien plants (Lambdon et al. 2008), introduced to and naturalized in the west coast of North-America, Europe, Asia (Boring and Swank 1984), Africa (Samecka-Cymerman et al. 2009) and Australia (Atkins et al. 1991). Since its introduction to Europe in the 17th century (Rédei et al. 2011) it is often planted for agricultural (as shelterbelt for wind- and snow protection) and commercial uses, sand fixing and soil improvement (Rédei et al. 2011); also an important honey tree, timber and firewood (Boring and Swank 1984). Seedpods of black locust contain 1-15 dark brown, kidney-shaped seeds. The species produces huge amount of hard-coated seeds with long viability, accumulating in soil for many years. It also reproduces through vegetative root suckering (Rédei et al. 2011).

Figure 1. The studied system: a) host plant: black locust tree, b) flowers, c) seedpods, d) seed predator: *B. robiniae*; parasitoids: e) *Mesopolobus robiniae*, f) *Bracon* sp. g) *Baryscapus* sp., h) *Aprostocetus venustus*, i) *Pediobius bruchicida*, j) *Eupelmus urozonus.*



Relatively few insect consumers of black locust seeds are known. Its native seed predators (in Appalachian Mountains, North-America) are *Spermophagus hoffmannseggi* Gyllenhal, 1833 (Bruchidae) and an *Apion* species (Curculionidae) (Hargrove 1986), but these species were not introduced to Europe. In Eastern Europe the following species are reported as seed predators: *Aphis craccivora* Koch, 1854 (Hemiptera: Aphididae) (Kiss 1895; Perju 1998); *Etiella zinckenella* Treitschke, 1832 (Lepidoptera: Pyralidae (Perju 1998; Bartha et al. 2015), *Bruchophagus robiniae* Zerova, 1970 (Hymenoptera: Eurytomidae) (Zerova 1970; Farkas and Terpó-Pomogyi 1974; Perju 1998) and *Bruchidius cisti* Fabricius, 1775 (Coleoptera, Bruchinae)(Bartha et al. 2015). These species cause loss in seed production of black locust populations. Moreover, there was found an apparently new insect community linked with the seed predator *Bruchophagus robiniae*, which is a new consumer of black locust seeds being not present in the eastern shores of North-America (Zerova 1970; Hargrove 1986; Lakatos et al. 2016).

Bruchophagus robiniae (Hymenoptera: Chalcidoidea: Eurytomidae) is a monophagous pre-dispersal seed predator of black locust (Perju 1998). The native host of *B. robiniae* is not known. Since *B. robiniae* was described from Crimea, Armenia and Middle Asia (Zerova 1970) it may not be native to Europe. *B. robiniae* has one generation per year. Oviposition occurs in the early stages of pod development; females lay their eggs on green seedpods containing immature seeds (Batiste 1967). Each larva feeds and develops inside one infested seed (Batiste 1967), hibernates inside the seed throughout the winter and the next spring it pupates and adults emerge (Traveset 1995). *Bruchophagus* pre-dispersal seed predators are widely distributed in crops of legume species (Leguminosae or Fabaceae), thus having economic impact (Soroka and Otani 2011). A plenty of pre-dispersal seed predators are attacking not only herbaceous legumes (Soroka and Otani 2011) but also shrubs and trees (Szentesi and Jermy 1995; Delobel and Delobel 2006; Noyes 2017). Most species are univoltine and to date most of them seem to be highly host-specific (Traveset 1995; Neser and Prinsloo 2004).

The abundance of the seed predators is moderated by parasitoids from the superfamilies of Chalcidoidea and Ichneumonoidea (Hymenoptera) (Yu et al. 2005; Noyes 2017). Chalcid species parasitize larval or pupal stage of the herbivorous host, controlling the population dynamics of seed predators. The parasitoid community of *B. robiniae* has not been studied until now.

Study sites and data collection

Resource dependence

Study sites were in two areas of Romania, Bihor (near Oradea city, BH) and Cluj (in and near Cluj-Napoca city, CJ) counties (Figure 2). We collected samples of black locust from 19 separated plots (Appendix 1). Many hymenopteran seed predators and parasitoids have a winter diapause, without which many specimens fail to complete their development. We therefore collected black locust pods in March 2009. This way we assured that we will rear the community belonging only to *B. robiniae*, as those parasitizing *Etiella* emerge from pods before autumn of the previous year (year of oviposition).

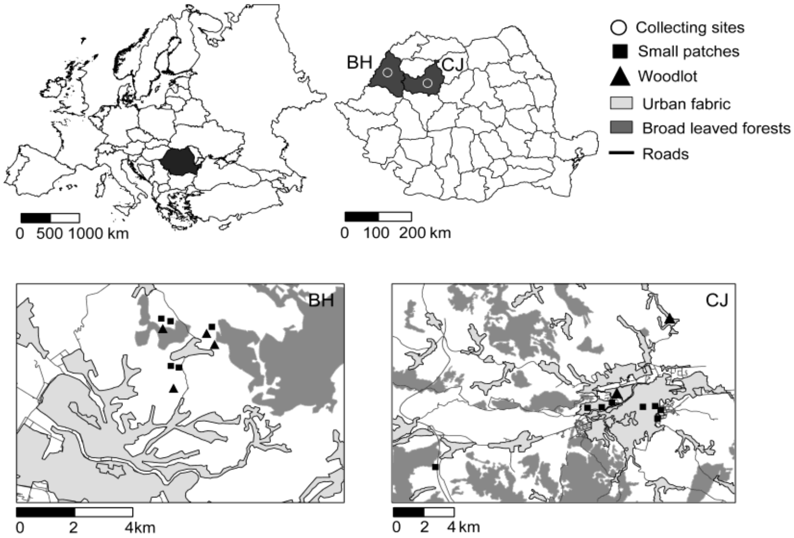


Figure 2. Map of data collection sites in Romania. BH: Bihor county; CJ: Cluj county. Urban fabric patches are the discontinuous urban fabric patch type of the Corine land cover seamless vector data.

Samples were taken from trees with two host plant abundance types: small patches and woodlots (Appendix 1, Figure 2). The studied woodlots were monoculture plantations of black locust. The woodlots varied in number of trees, some being part of young or mostly abandoned and thinned (partially cut) plantations. The smallest woodlot was a patch of 10-15 black locust trees in a park, surrounded by a number of other tree species (approximated black locust individuals in woodlots from Cluj: median=40, inter-quartile range 15–40; from Bihor: median=100, inter-quartile range 50–200). Trees in woodlots were at a maximum of a few meter distance from each other, while trees in small patches were at least 25 meters from each other.

During sample collection, ripened dried pods of black locust were chosen randomly. As the amount and availability of pods varied between trees, each sample (N=65) contained 18 to 119 pods, collected from one tree specimen. In every woodlot, we sampled multiple trees. All emerged insects were pooled per species per sample. In order to exclude the effect of pod characteristics, we measured: length of pods and the number of seeds for each sampled pod. For rearing insects, collected seedpod samples were placed in plastic cups, covered with punched plastic wrap (ventilation). The samples were kept for 8 months in a covered balcony with constant ventilation, in a temperature slightly more favorable/constant than outdoor. The emergence of insects stopped by the next fall. The emerged insects were removed from samples monthly and preserved in Eppendorf tubes with 70% ethanol or mounted on cards for identification. The insect specimens were identified by T. Lakatos with the supervision of Z. László.

Disturbance induced dynamics

Experimentally vacated black locust patches were created near plantations to investigate the effect of disturbance on the colonization abilities and dynamics of the insect species (Figure 3). Choosing distant patches from plantations we ensured treatment effectiveness and simulation of escaped invasive plant patches. In November 2010, we monitored black locust plantations to find suitable patches for the treatment near Oradea (Bihor County, Romania). Using a GPS device, we marked the edges of black locust patches. Based on the collected information, four patches (as spatial replicates) were selected where the removal of all pods from trees and from the soil was possible. This resulted in four vacated patches and four control patches nearby vacated ones (Figure 3, Appendix 2). In March 2011, we collected black locust pod samples from the eight selected patches. These samples represent the initial stage of the system. After sample collection, we experimentally vacated four selected patches by removing all the available pods from trees. Also, by using rakes we collected all of the litter from vacated patches, containing fallen pods. Sampling of pods was repeated in March of 2012, 2013, 2014 and 2015 to gain data about the recolonization and dynamics of insect species.

To calculate the tree density in the patches (number of trees/area of patches) we registered the tree specimens with GPS and calculated the area of patches using Google Earth Pro^{TM} version 7.1.2.2041 (http://earth.google.com/; © 2015 Google). The distances of patches from the surrounding black locust plantations were calculated with the determination of the centroids of each vacated patch using QGIS (QGIS Development Team 2015).

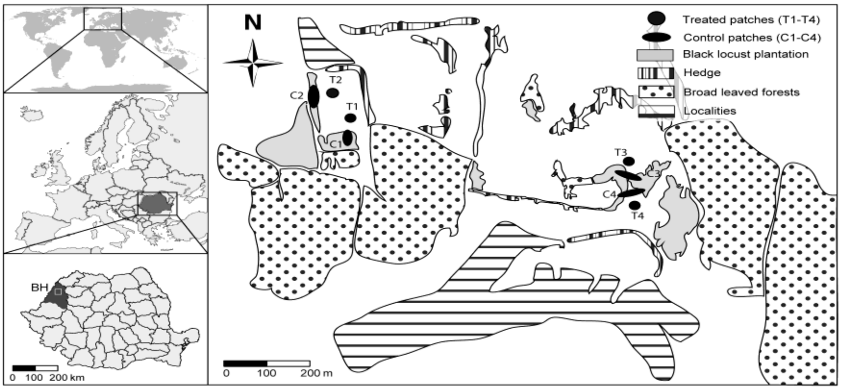


Figure 3. Map of data collection sites near Oradea, Romania. Vacated black locust patches are marked as black circles while control patches are elliptic-shaped patches near vacated ones. All neighbouring patches that contained any black locusts were treated as black locust patches. Native broadleaf forests (mainly oak and hornbeam woodlands) and shrub belts without black locust are also presented.

To rear insects, collected pod samples were placed into plastic containers, containing an average of 230 pods of the same tree. To assure the ventilation of samples, the containers were covered with punched plastic wrap. We counted monthly the emerged insects from the samples. At each census pod samples were poured out from plastic containers individually on a blank sheet of paper. Living specimens were caught with a brush dipped in ethanol. Then we searched for dead insect specimens between pods, and placed seedpods back into their container. The collected insects were stored in Eppendorf tubes with 70% ethanol or mounted on cards for identification.

Parasitoid community of Bruchophagus robiniae

Hungary and Romania are important cultivators of black locust in Europe (Sandu et al. 2005; Rédei et al. 2008). In the 1960’s Hungary had more black locust plantations than the rest of Europe altogether (Rédei et al. 2008). Large plantations of cultivated, introduced plants provide important meeting points with native insect species of the invaded area. Black locust seedpod samples were collected from Hungary in March of 2013-2015 and from Romania in March of 2009, 2011, 2013-2015. Study sites were numbered based on an East-West gradient. Study site 1 is located in Cluj County (N 46.801424, E 23.611978) and site 2 is located in Bihor County, Romania (N 47.098173, E 31.975356). Site 3 is located in Hajdú-Bihar County, Hungary (N 47.570120, E 21.560905).

After sample collection, hibernating insects were reared from seedpod samples. Each collected pod sample was placed in a plastic cup, containing 20-200 pieces of pods collected from the same tree. To ensure the ventilation of samples, plastic cups were covered with punched wrap. Emerged insects were collected monthly from seedpod samples and stored in Eppendorf-tubes with 70% ethyl alcohol.

Data analysis

Resource dependence

Outcome variables were (i) densities of seed predators or parasitoids (the mean abundances of seed predators or parasitoids per single pod); (ii) the mean incidences of seed predators or parasitoids per single pod; (iii) seed predation by *B. robiniae* and parasitism by the two parasitoids. Abundances were counts of seed predators and parasitoids from pod samples. Incidence was one if at least one seed predator or parasitoid of a given species was present, and zero if no seed predator or parasitoids emerged from a pod sample. Mean abundances and incidences per pods were calculated by dividing abundances per pod samples by the number of pods from the respective sample. Seed predation was the ratio between the total number of inhabitants and seed number from the pod sample, while parasitoid ratio was the ratio between the number of all emerged specimens of a given community member and the total number of inhabitants from the same pod sample.

The fixed explanatory variable was the natural logarithm of the host plant abundance. Since we were interested in the effect of host plant abundance irrespectively of length of black locust pods, we used this variable as a covariate in an ANCOVA design. We used area (Bihor (BH) versus Cluj (CJ)) as a random factor in our models. We also used plot id as a random factor to control for the different numbers of collected samples per plots. Plot id was nested in area. The relationships between outcome variables and host plant abundance were not linear, thus we have used second degree polynomials (Figure 4). In the case of seed predator abundance and seed predation we used linear models since relationships has not shown curved forms. To investigate the effect of host patch sizes of black locust on seed predator and parasitoid densities, incidence and ratios, we used generalized linear mixed effects models (GLMM) with binomial error structure. Binomial GLMMs on all outcome variables were performed with package lme4 (Bates et al. 2012), function *glmer*, using Laplace approximation of the maximum likelihood and logit link function. GLMMs were performed using the statistical computing environment R version 3.0.2 (R Development Core Team 2013).

Disturbance induced dynamics

Outcome variables were the seed predation by *B. robiniae* and the parasitism of *B. robiniae*. Seed predation was defined as the ratio of consumed seeds and seed numbers per samples. Parasitism was the ratio between abundance of parasitoid specimens and abundance of all emerged specimens per samples. Explanatory variables were the disturbance (factorial variable with two levels: CONTROL and VACATED), the isolation of patches (continuous variable containing distances (m) between patch centroids: vacated versus control, control versus nearby black locust plantations), and the density of black locusts in patches (continuous variable: number of black locusts in the area of analyzed patches). The abundance of parasitoids was used as explanatory variable in the models of seed predation, while the abundance of *B. robiniae* was used as an explanatory variable in the model of parasitism. The variance inflation factors for all explanatory variables were between 1.13 and 2.40. Therefore, there was no multicollinearity, and we could retain all variables in the models.

The number of collected pods multiplied by the median seed number was used as a covariate in the models, because numbers of pods and seeds differed between host plants. We used years as a random factor (factorial variable with five levels: 2011, 2012, 2013, 2014, and 2015). We also used a blocking factor because the spatial arrangement of the patch pairs (factorial variable with two levels: block1 and block2) (Figure 3). We used patch id as a random factor to control for the different number of collected samples per patches. Patches were nested in blocks and blocks were nested in years, therefore we used a nested design for random factors.

To investigate the effect of disturbance on seed predation and parasitism of black locust we used logistic GLMMs with a repeated measures and also an ANCOVA designs using the statistical computing environment R version 3.2.2 (R Development Core Team 2015). Logistic GLMMs were performed with the function *glmer*, using Laplace approximation of the maximum likelihood and logit link function from the package *lme4* (Bates et al. 2012). For multiple comparisons we used the function *glht* from the package *multcomp* (Hothorn et al. 2008). For the GLMMs the outcome variables were prepared as a two column data frame containing the successes and total observations (successes and failures) (Crawley 2012).

Parasitoid community of Bruchophagus robiniae

After data collection regarding herbivores and parasitoids of black locust and other introduced and/or invasive and native shrub and tree legumes from Europe we categorised the species. The herbivores of black locust were categorised by nativeness and herbivore orders (native Lepidoptera, introduced Coleoptera, novel Hymenoptera). The seed predator species of legumes were categorised by herbivore order and host plant nativeness and habitus (native shrub Coleoptera, native tree Hymenoptera, invasive tree Lepidoptera etc.). After categorisation, we compared the number of species between categories. All statistical analyses were performed in R Statistical Environment (R Development Core Team 2017).

Results

Resource dependence

*Black locust pod characteristic*s – We collected a total of 4325 seedpods from 65 black locust trees from the two host plant abundance types (woodlots: 2719 seedpods from 38 trees, small patches: 1606 seedpods from 27 trees, Appendix 1). The mean number of collected pods per sample was 66.54 (SD=27.33, min.=18, max.=119). The mean length of pods per sample was 5.17 cm (SD=0.92 cm, min.=3.8 cm, max.=7.86), and the mean number of seeds per pod per sample was 4.4 (SD=1.51, min.=2.87, max.=9.16). We found positive correlation between the number of seeds and length of pods (GLM with gamma error distribution: t=14.92, p<0.01, intercept=-2.68, slope=1.36). Therefore, we considered only the length of pods to determine if pod characteristics differed between tree samples. The most abundant emerged species were the seed predator *B. robiniae* (695 individuals: 359 males, 336 females) and two parasitoid species: *E. urozonus* (19 individuals: 3 males, 16 females) and *Mesopolobus* sp. (53 individuals: 23 males, 30 females).

Seed predation by B. robiniae – We found significant positive relationship with the host plant abundance for *B. robiniae* (Table 1, Figure 4a). Namely there were more seed predators per pods in woodlots than in small patches of black locust (resource concentration). There was a significant increase in the incidence of *B. robiniae* along host plant abundance, but in the woodlots compared to small patches their incidence decreased (Table 1, Figure 4d). The seed predation showed a marginally significant increase along host plant abundance (Table 1, Figure 4g).

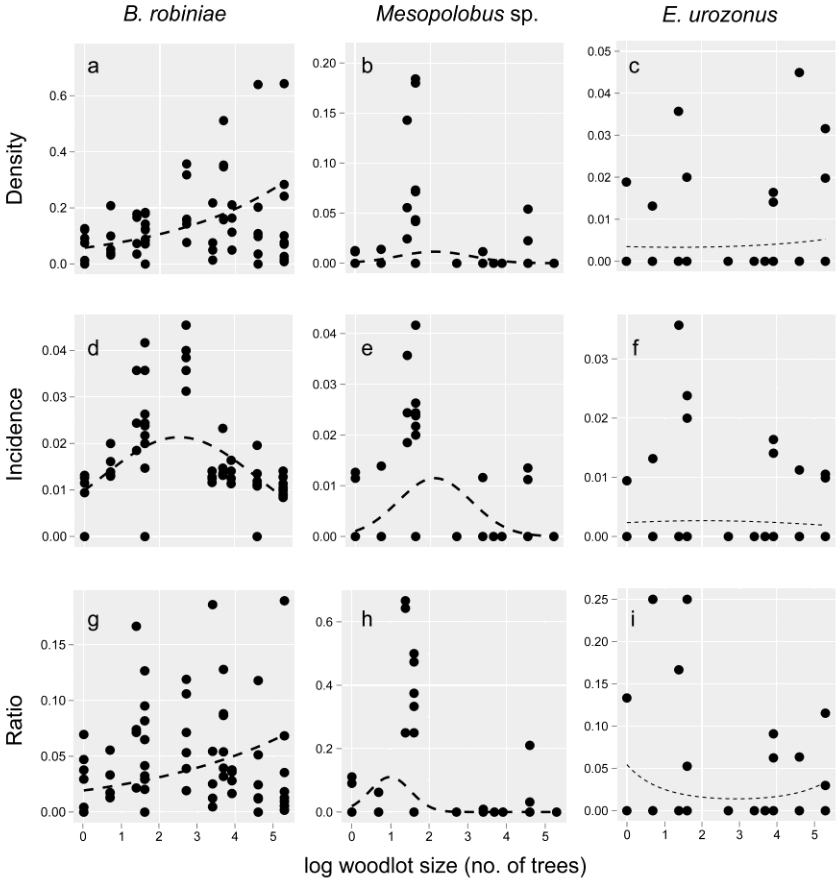


Figure 4. Scatterplots of the black locust plot size effect on seed predation and parasitism of the seed predator by *Mesopolobus* sp. and *Eupelmus urozonus*. Curves are fitted based on the logistic GLMM estimates for the seed predator (*Bruchophagus robiniae*: a, d, g) and its parasitoids (*Mesopolobus* sp.: b, e, h; *Eupelmus urozonus*: c, f, i) density (specimen counts / pod number), incidence (presence / absence) and ratio (total individuals / number of seeds for *B. robiniae,* analyzed group individuals / total individuals per number of pods for parasitoids).

Table 1. Seed predation and parasitism of the seed predator by *Mesopolobus* sp. and *Eupelmus urozonus* in function of black locust (*Robinia pseudoacacia*) plot sizes. Plot sizes are log transformed. Number of analyzed pod samples N=65. Estimates: b_0 - model intercepts, b_x - linear slopes, b_{x2} - quadratic terms of the second order polynomials. Density means mean abundance per single pod; incidence means presence or absence per single pod; ratio means seed predation in case of *B. robiniae* (total emerged specimens/number of seeds) and analyzed group individuals/total individuals per single pod for parasitoids.

		estimate	se	z	p
B. robiniae					
density	b_0	2.85	0.23	-12.42	0.000
	b_x	0.30	0.08	3.56	0.000
incidence	b_0	-4.61	0.32	-14.28	0.000
	b_x	0.61	0.28	2.18	0.029
	b_{x2}	-0.12	0.05	-2.38	0.017
ratio	b_0	-3.95	0.33	-12.07	0.000
	b_x	0.24	0.13	1.85	0.064
Mesopolobus sp.					
density	b_0	-6.84	1.16	-5.89	0.000
	b_x	2.24	1.24	1.80	0.072
	b_{x2}	-0.53	0.26	-1.99	0.046
incidence	b_0	-5.87	0.72	-8.16	0.000
	b_x	1.28	0.72	1.77	0.076
	b_{x2}	-0.35	0.16	-2.19	0.028
ratio	b_0	-3.99	1.06	-3.75	0.000
	b_x	3.61	1.84	1.96	0.050
	b_{x2}	-1.82	0.91	-2.00	0.045
E. urozonus					
density	b_0	-5.66	0.66	-8.55	0.000
	b_x	-0.07	0.57	-0.13	0.894
	b_{x2}	0.03	0.10	0.28	0.784
incidence	b_0	-6.06	0.67	-8.69	0.000
	b_x	0.13	0.64	0.20	0.839
	b_{x2}	-0.03	0.12	-0.27	0.786
ratio	b_0	-2.91	0.69	-4.21	0.000
	b_x	-0.93	0.60	-1.56	0.119
	b_{x2}	0.16	0.11	1.46	0.144

Parasitoids of B. robiniae – The parasitoid *Mesopolobus* sp. showed a non-linear relationship with the host plant abundance (Table 1, Figure 4b). The density of *Mesopolobus* sp. increased in the range of small patches, but decreased from small patches to woodlots. Thus, *Mesopolobus* sp. was present in black locust pods infested by *B. robiniae* in a significantly smaller number in pods collected from patches with higher black locust abundances than in pods collected from small patches. As in the previous relationship there was a negative association between the incidence of *Mesopolobus* sp. and the abundance of host plants (Table 1, Figure 4e). Incidence of *Mesopolobus* sp. increased in the range of small patches, but decrease from small patches to woodlots. The parasitism of *Mesopolobus* sp. was also smaller in woodlots than in the case of small patches (Table 1, Figure 4h). The parasitoid *E. urozonus* showed no relationship with the host plant abundance (Table 1, Figure 4c). Incidence of *E. urozonus* also showed no significant relationship with the host plant abundance (Table 1, Figure 4f). The parasitism of *E. urozonus* was also the same in the black locust woodlots as in the case of small patches (Table 1, Figure 4i).

Disturbance induced dynamics

In the initial stage herbivores were abundant, while parasitoid species were present in a low number in both type of patches (vacated and control). The number of emerged individuals suggests that at the initial stage vacated patches were better habitats for the seed predators, while control patches were better habitats for parasitoids (Table 2).

We found that the seed predator and its parasitoids dispersed into vacated patches of black locust and recolonized them (Figure 5). In the 1st year after the disturbance the decrease in seed predation and parasitism was almost 100% in both vacated and control patches, after which the seed predation slowly increased to 3-5% and also the parasitism to 30-40% (from now on we will consider this period the abundance growth phase), than dropped in the last year (4th year after disturbance) to the size of seed predation measured in the 1st year after the disturbance, but parasitism of vacated patches remained much higher than at the initial stage (Table 2).

Table 2. Number of collected seedpods and number of species in the five study years.

Year of collection	2011		2012		2013		2014		2015		Sum
Patches	Initial Control	Initial Vacated	Control	Vacated	Control	Vacated	Control	Vacated	Control	Vacated	
Seed median / pod	3	3	3	4	4,5	3	5,25	3	5	4	
No. of collected pods	1129	1915	3864	6388	2450	4524	3010	5156	2507	4386	35329
B. robiniae	396	1829	125	79	230	205	529	774	163	257	4587
Mesopolobus sp.	0	0	0	0	0	2	24	42	0	14	82
Eupelmus urozonus	7	13	4	1	22	37	82	153	5	34	358
Braconidae	2	6	0	0	0	1	3	0	0	0	12
Pediobius bruchicida	4	1	0	0	6	10	25	58	2	18	124
Aprostocetus venustus	2	1	0	0	67	330	178	1105	8	108	1799
Total Parasitoids	15	21	4	1	95	380	312	1358	15	174	2375
Total Hymenoptera	411	1850	129	80	325	585	841	2132	178	431	6962
median of % seed predation	4.16	4.66	0.19	0.21	1.33	1.45	3.46	5.32	1.47	0.8	
median of % parasitoids	2.39	0.54	0.00	0.00	9.82	18.33	32.86	37.84	0.00	11.76	

Black locust pods collected in 2011 (initial stage) yielded 32.47% of the total hymenopterans (Table 2). Pods collected in 2012 (1st year after the disturbance) yielded only 3% of the total hymenopterans. Pods collected in 2013 (2nd year after the disturbance) yielded 13% of the total hymenopterans. Pods collected in 2014 (3rd year after the disturbance) yielded 42.7% of the total hymenopterans. In 2015 (4th year after disturbance) collected pods yielded only 8.75% of the total hymenopterans.

Disturbance and dynamics – We found significant year effect in seed predation (logistic GLMM: χ^2=87.42, df=4, p<0.001, Figure 5A and Figure 6B), and parasitism (logistic GLMM: χ^2=130.81, df=4, p<0.001, Figure 5B and Figure 6D). After controlling with years, we found insignificant changes in seed predation due to the disturbance (Figure 5C, Figure 6A, Table 3). After controlling with years, the parasitism was significantly higher in disturbed patches compared to control ones (Figure 5D, Figure 6C, Table 4).

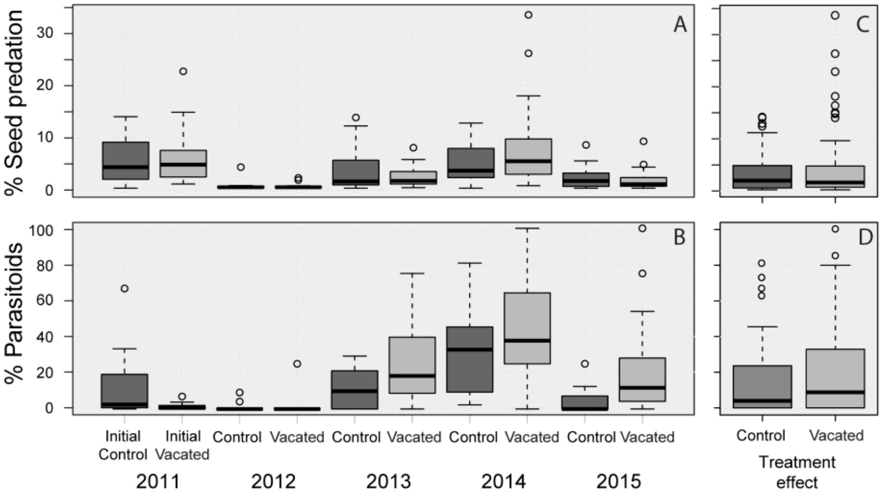


Figure 5. Proportions of seed predation (A, C) and parasitism (B, D) in the seed predator community of black locust (*R. pseudoacacia*). Dark boxplots denote control patches, while grey ones denote vacated patches. Boxplots show the medians, interquartile-ranges, minimum and maximum values of the seed predation and parasitism. Open circles are outliers.

Table 3. Logistic GLMM for the seed predation by *Bruchophagus robiniae* in the pods of black locust (*R. pseudoacacia*) (N=164) in four replicates of vacated and control patches.

	estimate	SE	z	p
intercept	-4.10	0.48	-8.58	<0.001
Disturbance	-0.09	0.23	-0.38	0.70
Isolation	0.14	0.14	0.99	0.32
Host plant density	-0.17	0.06	-2.91	0.004
Parasitism	0.003	0.004	0.81	0.42

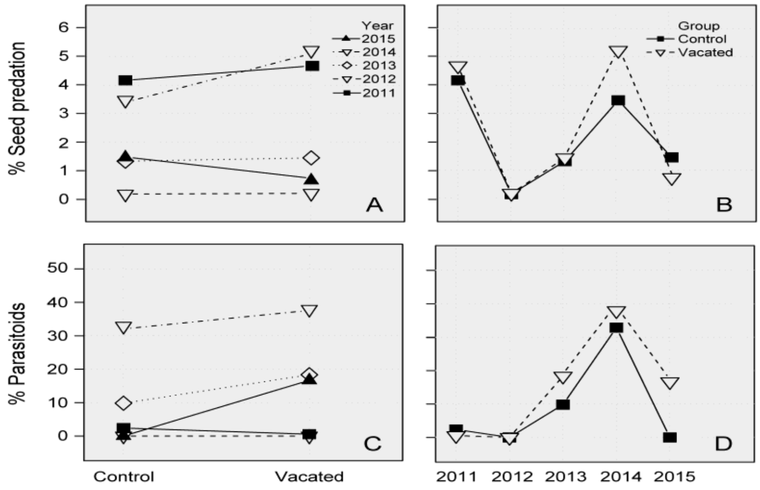


Figure 6. Changes in seed predation and parasitism of the seed predator *B. robiniae* in the seed predator community of black locust (*R. pseudoacacia*). Changes are plotted against treatment (A, C) and years (B, D). Points present medians of seed predation and parasitism for the given treatment – year combination

Isolation, host plant density and parasitoid effect – Seed predation was not affected by the isolation of patches (Table 3). The parasitism of this seed feeding insect community was affected negatively by patch isolation (Table 4). Seed predation decreased significantly with the increasing density of host plants in patches (Table 3), while parasitism was not affected by the density of host plants in patches (Table 4). The correlation between seed predation and parasitism was not significant (Table 3), but the number of parasitoids had a significantly negative effect on the percentage of herbivores (logistic GLMM: estimate=-0.09, SE=0.02, z=-5.3, p<0.001). The number of herbivores correlated negatively and significantly with the parasitism (Table 4).

Disturbance effect on the extent of change in seed predation and parasitism – The seed predation and parasitism showed significant changes in both vacated and control patches through the period of the experiment (year effect). But vacated patches showed larger changes than control ones: both in the case of seed predation (repeated measures ANCOVA: estimate=0.31, SE=0.1, z=3.24, p=0.01), and parasitism (repeated measures ANCOVA: estimate=0.58, SE=0.24, z=2.4, p=0.016).

Table 4. Logistic GLMM for the proportion of parasitoids in the seed predator insect community in the pods of black locust (*R. pseudoacacia*) (N=164) in four replicates of vacated and control patches.

	estimate	SE	z	p
intercept	-3.16	0.54	-5.87	<0.001
Disturbance	1.07	0.37	2.88	0.004
Isolation	-0.40	0.19	-2.01	0.04
Host plant density	-0.10	0.11	-0.89	0.37
B. robiniae	-0.25	0.08	-3.25	0.001

We reviewed and categorised the insect herbivore species of black locust by orders and nativeness. We found that the largest herbivore group is Lepidoptera, followed by Coleoptera and Hemiptera, with least species belonging to gall midges (Diptera) and sawflies (Hymenoptera) (Figure 7). The native herbivores of black locust also mostly belong to the orders Lepidoptera, Hemiptera and Coleoptera, but only few species were introduced with/able to follow black locust into its new areas. Regarding the black locust's novel, host shifting herbivores most of them also belong to the order Lepidoptera with a large drop to the order Coleoptera. The other three orders have no documented novel black locust herbivores in its invaded areas (Figure 7). Based on literature data we categorized the seed predator diversity on legume species by nativeness and habitus; we found a strong correlation: number of seed predator species increases with the increasing number of plant species (Spearman-rho=0.89, p<0.001) (Figure 8). There is no significant difference between native and invasive species (Wilcoxon-W=12, p=0.36) nor shrubs and trees (Wilcoxon-W=16, p=0.63) considering the seed predators per plant species.

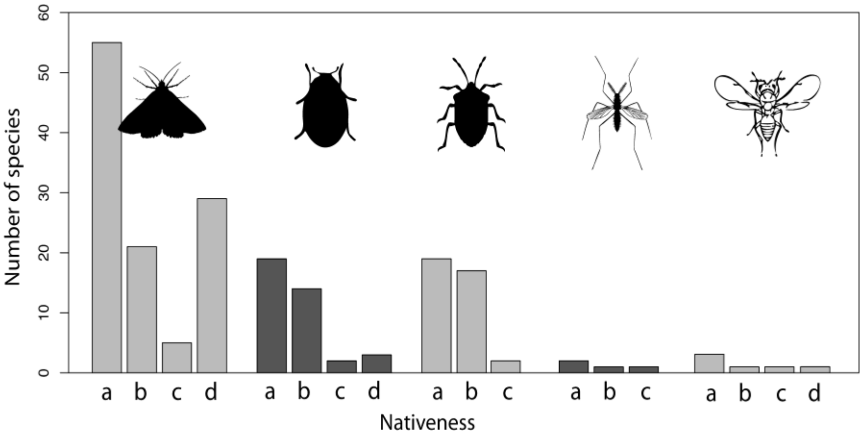


Figure 7. Categorisation of insect herbivore species of black locust by orders (Lepidoptera, Coleoptera, Hemiptera, Diptera and Hymenoptera) and nativeness: letter 'a' represents all species belonging to an order, 'b' is for native herbivores, 'c' is for native herbivores which were introduced together with black locust and 'd' represents novel herbivore species, gained in the invaded areas.

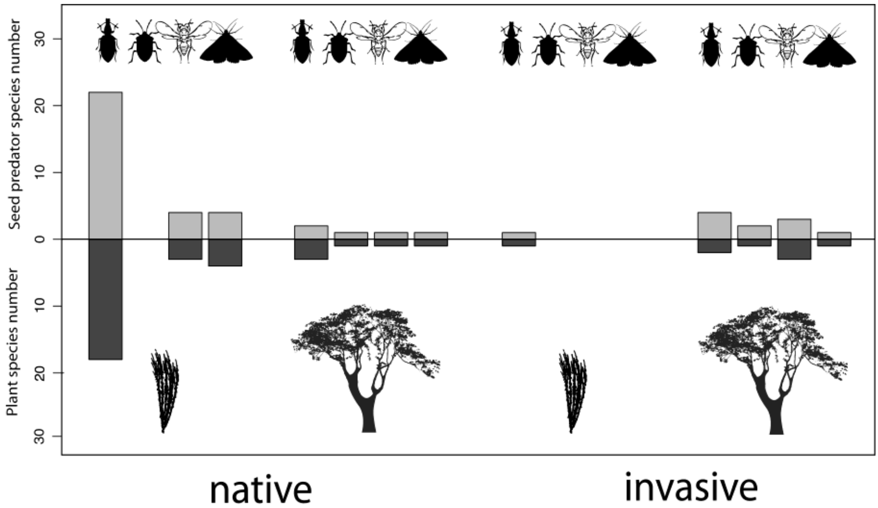


Figure 8. Comparison of seed predator (categorised into the major insect orders: Coleoptera, Hemiptera, Hymenoptera and Lepidoptera) and plant species numbers between native and invasive legume shrubs and trees.

From black locust seedpod samples, we reared the chalcid *Bruchophagus robiniae* (as seed predator) in large abundances. From the black locust seedpod inhabiting community *B. robiniae* was the most abundant species (Table 5.). Over the five study years we also encountered some of the other known seed predators of black locust, but they were present only with a few individuals. One of them is *Aphis craccivora*, the black legume aphid, which occurred haphazardly with altogether 78 individuals (mean=8.67, SD=7.07). From all samples only four coleopteran seed predators emerged, belonging to four species (2 Curculionidae, 1 Apionidae and 1 Bruchidae). Over the five study years no *Etiella zinckenella* individuals emerged. Compared to the parasitoid communities of other herbivores on legume host plants (*Etiella zinckenella*: 27, *Bruchidius villosus*: 9, *Ectomyelois ceratoniae*: 13, *Aphis craccivora*: 15) the parasitoid community of *B. robiniae* on *R. pseudoacacia* is composed by a relatively few species (N=7). The composition of the parasitoid community was consistent throughout the study years. Parasitism ratio was largely fluctuating between study years and study sites, so was the number of individuals and proportion of parasitoid species (Table 5).

The reared parasitoid species were: *Eupelmus urozonus* Dalman, 1820, *Mesopolobus robiniae* Lakatos and Laszló, 2017, *Pteromalus sequester* Walker, 1835, *Aprostocetus venustus* (Gahan, 1914), *Pediobius bruchicida* Rondani, 1872, two *Baryscapus* species (Gahan, 1913) and four Braconidae species (Table 5, Figure 1). *Eupelmus urozonus* and *Mesopolobus robiniae* were the most frequent parasitoids, present in almost all study years with relatively large individual numbers. *Pteromalus sequester* was mostly present, but with only a few individuals. *Aprostocetus venustus* was present in most samples in a largely fluctuant number. *Pediobius bruchicida* and the two *Baryscapus* species and emerged only sporadically from the samples. The Braconidae species were the most underrepresented in the parasitoid community (Table 5).

Table 5. The total number, mean and standard deviation of collected seedpods, number of Hymenopteran individuals (seed predator and parasitoids), number and percentage of the seed predator *B. robiniae*, percentage of parasitoids (sum of individual parasitoid species) and the number and percentage of individual parasitoid species.

	total	%	mean	%	sd	%
Number of seedpods	70145		5845.4		3986.7	
Hymenoptera	17687		1473.9		1166.5	
Bruchophagus robiniae	12196	68.95	1016.3	70.3	771.9	17.9
Parasitoids	5491	31.05	457.6	29.7	560.4	17.9
Eupelmus urozonus	1021	5.77	85.1	6.9	104.0	8.2
Mesopolobus robiniae	383	2.17	31.9	3.2	31.8	3.9
Pteromalus sequester	46	0.26	3.8	0.4	7.2	0.6
Aprostocetus venustus	3728	21.08	310.7	17.2	446.6	18.2
Baryscapus sp.	39	0.22	3.3	0.6	5.7	1.3
Pediobius bruchicida	248	1.40	20.7	1.3	30.2	1.0
Braconidae	26	0.15	2.2	0.1	3.1	0.1

Comparing the parasitoid community of *B. robiniae* to parasitoids of other *Bruchophagus* species (Appendix 3) we found a similar pattern with several common parasitoid species and several frequent common genera. The species appearing as parasitoid of several *Bruchophagus* species is *Pteromalus sequester. E. urozonus* and *A. venustus* also appeared in other similar communities, while the *Mesopolobus* parasitoid of other *Bruchophagus* species is mostly *M. bruchophagi,* not *M. robiniae*. Moreover, the composition of the parasitoid communities attacking seed predators of native and invasive legume species is similar with several common species and genera (Appendix 4).

The most frequent parasitoid species of seed predators, also present in *B. robiniae*'s community are *Pteromalus sequester* and *Eupelmus urozonus*. *Pediobius bruchicida* and *Aprostocetus venustus* were also present in some cases. Moreover, all genera of the reared parasitoids occur in seed predator-parasitoid communities of other legume species (Appendix 4).

Discussion

Resource dependence

We reared one species of the potential seed predators of black locust and two parasitoid species. The seed predator species was the most abundant in the community. Testing the influence of the black locust's abundance (prediction 1), we found that the seed predator *B. robiniae* was present with greater numbers in large patches of host plants (woodlots) than in small patches of host plants (individuals). Corroborating the resource concentration hypothesis, we found a positive association between the seed predator and the host plant abundance. Large patches of black locust carry large amounts of seedpods and provide more resources to seed predators than individual trees.

Behavioral characteristics as searching strategy can influence host plant choice of herbivores. Some species with no in-flight detection are independent of host plant abundance. Several herbivorous species that use visual cues are negatively related to host plant abundance, while some olfactory searchers show a more positive relation with host plant abundance (Bukovinszky et al. 2005; Andersson and Hambäck 2011). Thus, for *B. robiniae* being a potential olfactory searcher like other species of the genus *Bruchophagus* (Kamm and Buttery 1983), the search type can facilitate the host plant finding (Bukovinszky et al. 2005) and may lead to a positive relation with host plant abundance. Based on the findings of Stephens & Myers (2012) the persistence of plant populations is influenced by the distribution pattern of herbivores among host plant patches with different abundance. The found positive association of the seed predator *B. robiniae* with the host plant abundance follows the resource concentration distribution, and its consumption may decrease seed production of large patches.

Our results did not support prediction 2, which states that with the decreasing abundance of host plants specialist parasitoid ratio also decreases. The response of the specialist parasitoid *Mesopolobus* sp. was unimodal to host plant abundance. However, the parasitoid emerged with a significantly lower density from woodlots samples than from pods collected in small patches. This relationship of *Mesopolobus* sp. with the host plant abundance shows that its density is higher in small patches of host plant than in large patches. Moreover, *Mesopolobus* sp. had a higher parasitization ratio on the seed predator *B. robiniae* in small black locust patches. The high abundance and incidence in small patches with small prey populations is advantageous for a later arrived or less dominant parasitoid species, because this species avoids interference with other parasitoids in abundant patches (Lessells 1985).

Fulfilling the prediction 3, we found no relationship with the host plant for the generalist parasitoid *E. urozonus*. Incidence of *E. urozonus* showed no significant difference between black locust seedpods infested by *B. robiniae* collected from the two host plant patch types. The lack of association of this parasitoid with the abundance of its prey’s host plant may be due to the small amount of emerged specimens or to its extreme polyphagy. The search for actual prey starts only after landing on a host plant (Harvey et al. 2010). So, at low abundance of the seed predator *B. robiniae*, individuals of *E. urozonus* are parasitizing other prey species, being not associated with the abundance of the host plant. Another point regarding generalists is that under some conditions (Hambäck and Englund 2005) they do not necessarily show density independence to host plant abundance. They may also show a negative relationship. A habitat generalist is likely to have no relationship with host plant abundance, while a trophic generalist may have other relationships (Hambäck et al. 2007).

The only seed predator species that emerged from the collected pods of black locust was *B. robiniae*. The other known seed predators – from Eastern Europe *A. craccivora* and *E. zinckenella* (Perju 1998) and native consumers from North America *S. hoffmannseggi* and *Apion* spp. (Hargrove 1986) – were not present in our samples of black locust pods. Considering the studied community there are no previous investigations regarding parasitoids on *B. robiniae*. Of the insect species that emerged from the samples in our study, the seed predator *B. robiniae* and the parasitoids *Mesopolobus* sp. and *E. urozonus* responded differently to the abundance of the host plant *R. pseudoacacia*.

Several studies of introduced plants' and their insect consumer systems deal only with two-trophic interaction of host plant and herbivores (Harvey et al. 2010). However, through herbivores, parasitoid species are influenced by host plants (Doak 2000), so different effects of introduced plants can also manifest in higher trophic levels (Harvey et al. 2010). Specialization of herbivores on a novel host plant may provide in some cases (e.g. when other herbivores have not already colonized the novel host plant) the benefits of lowering the rate of competition and the risk of parasitization (Jaenike 1990), if parasitoids are not following the host shift of herbivores (Cronin and Abrahamson 2001). In this study, we observed as seed predator only *B. robiniae*, therefore it can be considered that there is no interspecific competition in seed predation of the black locust.

The species *B. robiniae* was described by Zerova (1970) as a species closely related to *Bruchophagus coluteae* Bouček, 1954, which is the seed predator of *Colutea arborescens* (Zerova 1970). Phytophagous species of *Bruchophagus* are strongly host specific with host plants within a genus (Neser and Prinsloo 2004). The black locust has no native *Bruchophagus* seed predators, while other *Robinia* species (*Robinia viscosa*, *Robinia hispida*, *Robinia neomexicana*) have absolutely no *Bruchophagus* seed predators (Noyes 2017). The likely host plant shift of the ancestor *Bruchophagus* species and initiation of a new community is of interest because of the hidden advantages and the taxonomic distance of black locust from native plant species in Europe.

According to the Enemy Release Hypothesis, it is advantageous for the introduced host plant to be taxonomically different because it enables the formation of the Enemy-Free Space, and it leads to low infestation levels and to low parasitism levels of the herbivores (Keane and Crawley 2002). Our point is that besides the taxonomic and chemical host plant characteristics, resource abundance may shape the herbivore-parasitoid communities in a cascading manner (von Zeipel et al. 2006). In the case of black locust herbivore frequency increased while parasitoid frequency (in one case) decreased in woodlots. This may be also a cascading effect or the consequence of asynchrony due to community novelty.

Disturbance induced dynamics

In vacated patches, we found that the abundance of insects was lower in most of the years following the disturbance (2012, 2013, 2015, except in 2014), than in 2011. In 2014 the abundance exceeded the initial values found in 2011, which suggest that there is a periodicity in the found changes, and in 2014 the system showed a local maximum. Species of this tritrophic system dispersed into vacated patches and recolonized them. We found that the disturbance affected only the levels of parasitism (Figure 5D, Table 2 and 4). After the disturbance parasitism in vacated patches was significantly larger compared to control patches. Seed predation in vacated and control patches did not differ significantly.

In the first year after treatment parasitoid species recolonized vacated patches in a low number. Although many parasitoid species have good dispersal and flight abilities (Yu et al. 2009), the recolonization by parasitoids may be slower than that of their hosts (Elzinga et al. 2007), because higher trophic levels need the conditions to be favorable for multiple (lower) trophic levels (Cronin and Haynes 2004). Parasitoids need their herbivorous host to recolonize vacated host plant patches, and host plant patches have to be suitable for that (Elzinga et al. 2007). After the successful recolonization of vacated patches by the seed predators the accumulation of parasitoid species takes more growing seasons.

An interesting result is how parasitoid species responded to disturbance (Table 2, Figure 5). After the setback due to treatment, in the second and third year after treatment (2013 and 2014) the number of parasitoids was increasing. This high consumption may have been the main cause of the second drop in seed predator abundance. This pattern of recolonization looks like a host – parasitoid dynamic. In many occasions disturbance causes high parasitism by its effect of ruining refuges of herbivores (Wilkinson and Feener 2007). *Bruchophagus* species are known to suffer from various levels of parasitism between 3.2 and 98% (Soroka and Otani 2011).

With the isolation of vacated patches seed predation showed no changes, while parasitism was decreased significantly by isolation. This suggests that herbivores have better dispersal or resource finding abilities, and that isolation can weaken top-down control (Chase et al. 2010), or that parasitoid species are less adapted to this host-shifted community, and are still using their previous hosts as alternatives.

Regarding the host plant *R. pseudoacacia* density we found, that denser patches had significantly lower seed predation than less dense patches (Table 3). A possible cause of this result is a negative correlation between tree density and the availability of seedpods. In dense patches trees are more resource and space limited, with decreased leaf area per tree for photosynthesis, bearing smaller amount of fruit then trees in sparse patches (Arista and Talavera 1996). During fieldwork we observed, that relatively dense patches of black locust carry fewer seedpods (pers. obs.). So, bottom-up control has an important impact on seed predation, but not on the parasitism. We found that the host plant density of patches had no influence on the proportion of parasitoids. Our results suggest that the seed predator is not only affected by bottom-up effect of its host plant density, but the herbivore of this community is also the subject of top-down control by its parasitoids, especially in disturbed (vacated) patches.

The recolonization of vacated patches, and probably the decline in control patches, suggests that vacated and control patches are connected. Albeit, this connectivity was not too strong as vacated and control patches differed in abundances of species even in the initial stage (Cronin and Haynes 2004). If insects in a patchy habitat form a patchily distributed population than the dynamics of patches are linked together by the dispersal of insects (Pannell and Obbard 2003) and thus populational changes may be also linked. Active dispersal of small insects is a short-term movement from a few meters up to a kilometer (Elzinga et al. 2007). Most *Bruchophagus* seed predator species feed on herbaceous legume plants (Soroka and Otani 2011), so they do not need to disperse for long distances to find another host plant. Although the dispersal of small insects can be enhanced by the air flow, this passive dispersal is not a directional movement (Compton 2002). The monophagy of *Bruchophagus* species (Kamm 1989) makes their recolonization and dispersal more difficult. Population dynamics of *Bruchophagus* species are known to fluctuate between years resulting variable seed consumption and parasitism (Soroka and Otani 2011).

Parasitoid community of Bruchophagus robiniae

For the in-depth study of novel ecosystems it is a must to include higher trophic levels (parasitoids, hyperparasitoids) beside the host plant and its host shifting herbivores (Bezemer et al. 2014). It is also essential to study several consecutive insect generations (Bezemer et al. 2014) to detect and eliminate the parasitoid species appearing sporadically and not belonging to the community. The consistent presence of seven parasitoid species confirms the community's coherence. However, the fluctuation of the seven species in abundance suggests the novelty of the parasitoid community of *B. robiniae*, a novel seed predator of black locust. The herbivores of black locust are belonging mainly to Lepidoptera and Coleoptera, less to Hemiptera, Diptera and Hymenoptera. Its novel herbivores are also belonging to Lepidoptera and Coleoptera with a single exception the seed predator *B. robiniae*, belonging to Hymenoptera. The number of seed predators regardless of insect orders was conforming the number of leguminous species regardless of being native or invasive.

Herbivores and seed predators – The expectable patterns of seed predator diversity is a decrease from native to invasive species conforming to the natural enemy release hypothesis (Keane and Crawley 2002), and from tree to shrub legume species conforming the host plant size effect on herbivores (Neuvonen and Niemelä 1981; Schlinkert et al. 2015). The diversity pattern of the reviewed seed predators shows no difference between native and invasive, nor between shrub and three legumes. One explanation of the found pattern is that the enemy release do not works in all cases or its effects are ameliorated with time (Harvey et al. 2015; Schultheis et al. 2015). Regarding host plant size and herbivore load the possible explanations for the lack of correlation are, that plant odours (allelochemicals) hide the size effect so trees and shrubs have similar odours or their odours are not different enough from the surrounding plant matrix (the importance of neighbouring plant species).

Seed predators of black locust – Black locust arrived to Europe as a new, potential host plant without its native seed predators (Hargrove 1986). None of the species were reared from European seedpods of black locust (Perju 1998; Bartha et al. 2015; Lakatos et al. 2016). The novel seed predator *Bruchophagus robiniae* is not present between the native seed predators of black locust (Hargrove 1986), so after the contact with the new, unused host plant, the species *B. robiniae* shifted to the consumption of black locust seeds. Before its host shift, the species may have been a pre-dispersal seed predator of a Eurasian legume species, and being compatible and pre-adapted to the consumption of black locust seeds. *B. robiniae* presumably has a narrow host specificity, but there is no another known host plant of the species. The listed European seed predator species may have Palaearctic origin, so it looks like black locust gain new seed predators from the Eurasian fauna after its introduction.

B. robiniae individuals at our current knowledge feed only with black locust seeds. Based on our rearings, adult emergence peaks in April-May-June, and stops in late summer. Even when samples were reared for several years, no individual emerged after the first summer, not even in the next spring. Like other *Bruchophagus* species, each *B. robiniae* individual is feeding and developing inside one infested seed, so prior to emergence individuals are closed inside the seed in which they developed (Batiste 1967). Prior to emergence each fully developed *B. robiniae* individual chews a visible exit hole on the infested seed and usually on the seedpod wall. In multiple times, despite the presence of exit holes, we observed dead *B. robiniae* individuals trapped inside seeds. This suggests that individuals perform their whole development, even pupation inside the infested seed they consumed and developed in. Due the consumption damaged seeds are softened and their colour became lighter than that of intact seeds, and may lose their germination capability (Farkas and Terpó-Pomogyi 1974). Insects trapped inside the seeds can be taken out by gradually splitting the seed.

The distribution of *B. robiniae* in Europe: Ukraine (Zerova 1970), Bulgaria (Fallahzadeh et al. 2009), Greece (Boyadzhiev 2006), Hungary (Farkas and Terpó-Pomogyi 1974) and Romania (Perju 1998). Its distribution in Asia: Caucasus, Iran, Armenia (Zerova 1970), Uzbekistan (Fallahzadeh et al. 2009) and Turkey (Çam 2012). The species is not present between the native seed predators of black locust in North-America (Hargrove 1986). In Hungary *B. robiniae* was firstly detected by Farkas and Terpó-Pomogyi (1974). The presence of the species in Romania was first published by Perju (1998). These data are not present in the distribution map of the *B. robiniae* in the UCD (Noyes 2017) so we confirm the presence of the species in these regions. The species *Aphis craccivora* is a phloem feeding herbivore with a wide host plant range, polyphagous on Fabaceae. When vegetative parts of the host plant are too mature, individuals damage immature pods causing shrinkage by feeding with the phloem of pods (Ofuya 1989), thus causing seed production loss (Ofuya 1989) and reducing the number of developing seedpods in inflorescences to 1-2 seedpods (instead of the normal 8-10) (Kiss 1895). Over the years we observed some traces in seedpods, suggesting the presence and early emergence of *E. zinckenella,* such as the damage of multiple seeds in a row and a big, irregular exit hole chewed on the pod wall (Szentesi and Jermy 1998).

Parasitoid community of black locust's seed predator – The novelty of the parasitoid community of *B. robiniae* is a possible explanation of the observed low number of parasitoid species and of the fluctuating parasitism level (Table 5). Host shift of phytophagous insects does not trigger necessarily the specialization of parasitoids (Cronin and Abrahamson 2001). At higher trophic levels of this system were parasitoid and hyperparasitoid species from two superfamilies of Hymenoptera: Chalcidoidea and Ichneumonoidea. *Eupelmus urozonus* has a wide host range being extremely polyphagous; individuals were reared from galls, larvae of Coleoptera and Lepidoptera and Hymenoptera: Eurytomidae species (e.g. *Bruchophagus roddi*) (Noyes 2017). *Mesopolobus robiniae* is a new species to science, recently described from the seedpods of black locust (Lakatos et al. manuscript b). The genus *Mesopolobus* also has a wide host range but certain species are host-specific on a particular herbivore feeding guild. Several Eurytomidae (Hymenoptera) seed predator species has *Mesopolobus* parasitoids (Noyes 2017). *Pteromalus sequester* is a polyphagous parasitoid, with several seed predator hosts from the orders of Coleoptera (Apionidae, Bruchidae, Curculionidae), Lepidoptera and Hymenoptera (Eurytomidae: *Bruchophagus*) and with also several Fabaceae plant associates (Soroka and Otani 2011; Noyes 2017). Several species of the genus *Aprostocetus* were reared from different *Bruchophagus* species (ex. *B. oddi*) (Graham 1991; Noyes 2017), and *Aprostocetus venustus* Gahan, 1914 was reared from black locust seeds along with *B. robiniae* individuals (Boyadzhiev 2006). *Baryscapus* species are host-specific parasitoids of hosts from orders Lepidoptera, Hymenoptera and Coleoptera (Graham 1991) and several species of the genus often acts as hyperparasitoid too (Askew and Shaw 2005) on species of Ichneumonidae, Braconidae, Cynipoidea and Chalcidoidea (Graham 1991). In our samples two species of *Baryscapus* were present. *Baryscapus (Tetrastichus) bruchophagi* Gahan, 1913, is a known parasitoid of *Bruchophagus* species (*B. roddi, B. gibbus*, *B. kobolovae*, *B. platypterus*) (Graham 1991; Noyes 2017). The species *Pediobius bruchicida* has a wide host range, being parasitoid of herbivores from the orders Lepidoptera, Coleoptera (Bruchidae, Curculionidae) and Hymenoptera (Cynipidae) and often acts as hyperparasitoid of other parasitoid species. The genus *Pediobius* has a cosmopolitan distribution with numerous species (Bouček 1965). The Braconidae species are belonging to *Glabrobracon* sp., *Bracon* sp. and to 2 other genera. The found composition of our parasitoid community is confirmed by the fact, that all of the reared genera of the suspected parasitoids of *B. robiniae* were present in the parasitoid community of other *Bruchophagus* species (Appendix 3).

Conclusions

Resource dependence

The studied pre-dispersal seed predator *B. robiniae* consumed more seeds in woodlots than in small patches, while the specialist parasitoid *Mesopolobus* sp. preferred small patches of host plant to large patches (woodlots) and the generalist *E. urozonus* showed independence from patch size. The low species number of parasitoids and the lack of competitor seed predators support the presumed novelty of this introduced plant - seed predator - parasitoid system and that *R. pseudoacacia* is in early stages of species accumulation from the local fauna of Europe. We show that the patch size of an invasive plant has an important effect on the formation of its novel seed predator community. Such an effect is likely to influence the structure of herbivore communities and should be considered in the evaluation of potential biocontrol agents of invasive plants.

Disturbance induced dynamics

The top-down control in the studied system was fortified by the disturbance. Since the host plant of the system is an invasive species, partial disturbances of habitat patches of such species (as part of invasive species management) may contribute to the severity of the top-down control (high parasitism) which may lower the effects of seed predators. On the contrary to the expected, the total removal of seedpods from black locust patches may increase the amount of black locust seeds as less of them might be consumed, so more seeds can accumulate in the soil facilitating its spread. This effect of disturbance on black locust may be useful designing a biological control against invasive species.

Parasitoid community of Bruchophagus robiniae

Considering shrub and tree legumes we cannot confirm the enemy release hypothesis, since we did not found significant differences between invasive and native species regarding seed-predator communities. Based on our findings we also falsified the host plant size – insect diversity hypothesis. Among the herbivores of black locust, the most specious were the Lepidoptera, while least specious were the Diptera and the Hymenoptera. The main seed predator of black locust in East-Central Europe is the seed wasp *Bruchophagus robiniae.* Parasitoids of *B. robiniae* are *Eupelmus urozonus, Mesopolobus robiniae, Pteromalus sequester*, *Aprostocetus venustus, Pediobius bruchicida*, two *Baryscapus* species and several *Bracon* species. The found parasitoid composition of the black locust seed predator *B. robiniae* is validated by its analogy with the parasitoid communities of other seed predators and *Bruchophagus* species.

Summary

The introduction of alien species is one of the most threatening consequence of human activities (Harvey et al. 2010; Bezemer et al. 2014). The introduction of alien plants promotes the formation of new insect-plant associations (Agosta 2006). Ecosystems are modified when herbivores are introduced along with the new plant, or when herbivores of the area recognize the potential host plant (Agosta 2006) and shift to its consumption (Seastedt et al. 2008; Mascaro et al. 2013). Natural enemies (parasitoids) may or may not follow the herbivore into its new ecosystem (Cronin and Abrahamson 2001) or it may gain new parasitoid species (Harvey et al. 2010). Dynamics of insect herbivore populations depends on their trophic interactions (Denno et al. 2003). Bottom-up controlled herbivores are mostly affected by their host plants (both quantity and quality of resources), while top-down controlled herbivores are limited due to predation or parasitism. The relative strength of bottom-up and top-down forces are often altered by disturbance, invasive species, habitat structure (Denno et al. 2003) such as isolation, density or size of host plant patches and herbivore traits such as behaviour and life cycle (Nylin 2001).

Novel communities of invasive plants may contain herbivores belonging to several feeding guilds, like sap-suckers, chewers, leaf-miners, gall inducers and seed predators (Singer and Stireman 2005). Seed predators decrease seed production of their host plant species, and also may trigger selective abortion of infested seeds or seedpods (Janzen 1971). Thus, specialist seed predators are potential biocontrol agents of invasive plants (Dennill and Donnelly 1991). We studied a novel, European, tritrophic system composed by the invasive black locust as host plant, *Bruchophagus robiniae* as host shifted, host-specific seed predator and its parasitoids. Parasitoids are lowering the effect of herbivory, interacting with their herbivorous prey and also with the host plant (Price et al. 1980).

Black locust (*Robinia pseudoacacia* Linnaeus, 1753) is native to North-America. After its introduction to Europe black locust was intensively planted for reforestation and erosion control, naturalised and became invasive. Seeds of black locust are hard-coated, accumulate in soil and remain viable for many years (Rédei et al. 2011). Black locust seeds have few known consumers. Its native seed predators are *Spermophagus hoffmannseggi* and an *Apion* spp. seed predator (Hargrove 1986), and until now none of these species were reared from European black locust seeds. The new, European seed predators of black locust are *Etiella zinckenella* (Perju 1998; Bartha et al. 2015), *Bruchidius cisti* (Bartha et al. 2015), *Bruchophagus robiniae* (Farkas and Terpó-Pomogyi 1974; Perju 1998) and *Aphis craccivora* (Perju 1998). These species cause seed loss and may reduce the invasion rate of black locust. *Bruchophagus robiniae* Zerova, 1970 (Hymenoptera: Chalcidoidea: Eurytomidae) is a monophagous (Perju 1998), host shifted pre-dispersal seed predator. Parasitoids of seed wasps (Eurytomidae) are from the superfamilies of Chalcidoidea and Ichneumonoidea (Hymenoptera) (Yu et al. 2005; Noyes 2017).

Resource dependence – We investigated the influence of host plant abundance on the above presented tritrophic system, including the seed predator *B. robiniae* and the two parasitoid species: *Eupelmus urozonus* and *Mesopolobus* sp. (Lakatos et al. 2016). We collected black locust seedpod samples in March 2009 from Bihor and Cluj Counties, Romania, from small patches and woodlots. Insect inhabitants were reared out from samples and identified. We found that the abundance of the host plant effected the seed predator and the two parasitoid species differently. The seed predator *B. robiniae* was present in higher density in woodlots than in small patches of black locust. The density of the specialist parasitoid *Mesopolobus sp.* was lower in woodlots than in small patches, while the generalist parasitoid *Eupelmus urozonos* was evenly distributed between woodlots and small patches of black locust. *B. robiniae* followed the resource concentration distribution suggesting, that its seed predation mostly decrease seed production of woodlots. The found pattern of *Mesopolobus* sp. might be advantageous for a less dominant parasitoid species, avoiding interference with other parasitoid species. The lack of association of the generalist parasitoid *E. urozonus* with the abundance of the host plant may be due to its extreme polyphagy, also parasitizing other prey species, not associated with this host plant. We show that parasitoid species are influenced by the patch size of an invasive host plant, thus characteristics of introduced plants also manifest in higher trophic levels.

Disturbance induced dynamics – To investigate disturbance driven dynamics of the above presented tritrophic system (Lakatos et al. 2017), we created seed-vacated, thus disturbed host plant patches in a black locust plantation near Oradea, Bihor County, Romania. We removed all pods from selected patches of black locust resulting in an induced local extinction of seed predators and their parasitoids. In this field experiment four patches were selected for vacation and for each vacated patch, we selected a near control patches. We collected black locust seedpod samples in March 2011 from all eight patches. After sample collection, we removed all pods from trees and from the soil of the four patches selected for vacation. We repeated the sample collection in March of 2012, 2013, 2014 and 2015 in all eight patches. The inhabitant insects were reared out from the samples and identified. We found that disturbance modified the seed predator-parasitoid ratio in the studied system. Seed predation was not affected by disturbance, but it increased parasitism, thus it strengthened top-down control. Seed predation was also affected by the bottom-up control of the host plant’s density. It decreased with increasing density, but was not affected by the isolation of patches. Parasitism decreased with increasing patch isolation, but was not affected by the density of host plants. Since the host plant of the system is an invasive plant, partial habitat disturbance of such species may increase the severity of parasitoid top-down control, reducing seed predation. On the contrary to the expected, the total removal of seedpods from black locust patches may increase the amount of seeds, so more seeds accumulate in the soil, facilitating the invasive plant's spread.

Parasitoid community of Bruchophagus robiniae – To gain information about the European seed predators of black locust and the parasitoid community of *B. robiniae,* we collected black locust seedpods in five years and reared the insects hibernating inside them (Lakatos et al. manuscript a). We collected seedpod samples from Romania in March of 2009, 2011, 2013-2015 and from Hungary in March of 2013-2015. We found, that in Eastern-Europe the most abundant seed predator of black locust is the seed wasp *Bruchophagus robiniae*. Over the five years we encountered a few individuals of the other known European seed predators of black locust (*Aphis craccivora* and four species of Coleoptera seed predators), but they occurred haphazardly. Our observations on the biology of *B. robiniae*: (i) The emergence of insects' peaks in May and stops in late summer, even when samples were reared for several years. (ii) Individuals perform their whole development, even pupation inside the infested seed they developed. Our observations on the parasitoid community of *B. robiniae*: (i) At higher trophic levels of this system are parasitoid and hyperparasitoid species from two superfamilies of Hymenoptera: Chalcidoidea and Ichneumonoidea. (ii) We found seven parasitoid species, present in all years and sites. (iii) The main parasitoid species of *B. robiniae* are: *Eupelmus urozonus*, *Mesopolobus robiniae* sp. n., *Pteromalus sequester, Aprostocetus venustus*, *Pediobius bruchicida*, two *Baryscapus* species and several Braconidae species. (iv) The parasitism ratio and the abundance of parasitoid species was highly variable between years and study sites. The consistent presence of the seven parasitoid species throughout the study years confirms the community's coherence. It is also confirmed by the presence of several frequent common genera and some common parasitoid species with the parasitoids of other seed predators of legume plants and of other *Bruchophagus* species. However, the parasitism ratio was largely fluctuating between study years and study sites, so was the proportion and abundance of parasitoid species. This variability supports the presumed community novelty, suggesting that it is still in formation. Moreover, one species in this parasitoid community, *Mesopolobus robiniae* is a new species to science, recently described from the seedpods of black locust (Lakatos et al. manuscript b).

Összefoglaló

Az idegenhonos fajok behurcolása és elterjesztése az emberi tevékenység egyik legsúlyosabb következménye (Harvey et al. 2010; Bezemer et al. 2014). Az idegenhonos növényekhez kapcsolódva új rovar-gazdanövény társulások jönnek létre (Agosta 2006), amennyiben a növénnyel őshonos fogyasztói is átkerülnek az új területre, illetve ha az új terület herbivórjai felismerik az új, potenciális gazdanövényt (Agosta 2006) és képesek áttérni a fogyasztására (Seastedt et al. 2008; Mascaro et al. 2013). A gazdaváltó herbivórt új közösségébe követhetik a természetes ellenségei (parazitoidok) (Cronin and Abrahamson 2001). De új parazitoid fajok is bekapcsolódhatnak a közösségbe (Harvey et al. 2010). Az invazív növények új, gazdaváltó ökoszisztémáinak tanulmányozásával lehetőségünk nyílik betekinteni a közösségek formálódásának folyamatába.

A herbivór rovarok populációdinamikája a rendszer trófikus kapcsolatai függvényében változik (Denno et al. 2003). A fentről-lefelé ható szabályozás által kontrollált herbivórokra legnagyobb hatással a gazdanövényük van. A felülről-lefelé ható szabályozás által kontrollált herbivórokat a ragadozóik, illetve a parazitoidok fogyasztása korlátozza. A két típusú szabályozási típus egymáshoz viszonyított erősségét befolyásolja és megváltoztathatja a zavarás, az invazív fajok megjelenése és az élőhely struktúrája (Denno et al. 2003), a gazdanövényfoltok izolációja, sűrűsége és mérete, valamint a herbivór faj viselkedésbeli és életciklusuk jellegzetességei (Nylin 2001).

Az invazív növények új közösségeiben jelenlevő herbivór fajok több táplálkozási guildbe tartozhatnak, így lehetnek nedvszívó, rágó, levélaknázó, gubacsokozó, valamint magpredátor fajok (Singer and Stireman 2005). A magfogyasztók magkárosításuk mellett a gazdanövény válaszreakciójaként további, indirekt magkárokat is kiválthatnak, ami a fertőzött termések vagy magok szelektív aborciójában nyílvánul meg (Janzen 1971). Ennek köszönhetően a specialista magfogyasztók közül számos faj az invazív növények elleni védekezés biokontroll ágense (Dennill and Donnelly 1991).

Vizsgálataink modellrendszerének egy új, európai magfogyasztó-parazitoid közösséget választottunk, amelyben a gazdanövény az invazív fehér akác, a gazdaváltó magfogyasztó az akácmagdarázs *Bruchophagus robiniae*, valamint ennek parazitoidjai vannak jelen. A rovarközösségek átfogó tanulmányozásához a magasabb trófikus szintek bevonása is szükséges (Cronin and Haynes 2004), hiszen csökkentve a herbivórok hatását befolyásolják úgy a herbivórokat, mint rajtuk keresztül a rendszer gazdanövényét is (Price et al. 1980). Továbbá szintén fontos több rovar-generáció tanulmányozása (Bezemer et al. 2014).

A fehér akác (*Robinia pseudoacacia* L, 1753) Észak-Amerikában, az Appalach-hegység terülén őshonos. Európába kerülését követően intenzíven telepítették az újraerdősítések valamint a talajerrózió megfékezésére, majd meghonosodott és invazívvá vált. Kemény héjú magvai felhalmozódnak a talajban és hosszú ideig életképesek maradnak (Rédei et al. 2011). A fehér akácnak viszonylag kevés magfogyasztó faja van. Őshonos, észak-amerikai magfogyasztói a *Spermophagus hoffmannseggi* és *Apion spp*. (Hargrove 1986), amely fajok hatása alól megszabadult a behurcolásnak köszöhetően, hiszen ezek egyike sem volt még európai akáctermésekből kinevelve. Viszont az akác új magfogyasztó fajokra tett szert az Eurázsiai faunából, gazdaváltó fogyasztókat szerezve (Hargrove 1986; Perju 1998). Európában ismert magfogyasztói: *Etiella zinckenella* (Perju 1998; Bartha et al. 2015), *Bruchidius cisti* (Bartha et al. 2015), *Bruchophagus robiniae* (Farkas and Terpó-Pomogyi 1974; Perju 1998) és *Aphis craccivora* (Perju 1998). A magfogyasztók jelentősége az akác magkárosításából, valamint az ez általi terjedéscsökkenésből tevődik össze. *Bruchophagus robiniae* Zerova, 1970 (Hymenoptera: Chalcidoidea: Eurytomidae) kizárolóag az akác magvaival táplálkozó, monofág (Perju 1998) pre-diszperziós, gazdanövény váltó magpredátor.

Forrás függés a vizsgált rendszerben – Vizsgálatunk során a gazdanövény abundanciájának magfogyasztóra és két, leggyakoribb parazitoidjára (*Eupelmus urozonus* és *Mesopolobus* sp.) kifejtett hatását tanulmányoztuk (Lakatos et al. 2016). 2009 márciusában fehér akác terméseket gyűjtöttünk Bihar és Kolozsvár megyében (Románia) kis facsoportot alkotó, valamint erdőfoltot alkotó akácfákról, majd kineveltük a begyűjtött termésmintákból kirepülő rovarokat. A vizsgálat során azt találtuk, hogy a gazdanövény tömegessége eltérő módon befolyásolta a magfogyasztót és két parazitoidját. Az akácmagdarázs *B. robiniae* nagyobb egyedsűrűségben volt jelen az erdőfoltokban, mint a kis foltokban. A specialista parazitoid *Mesopolobus* sp. egyedsűrűsége viszont alacsonyabb volt az erdőfoltokban, mint a kis foltokban. A generalista parazitoid *Eupelmus urozonos* pedig egyforma arányban volt jelen mindkét típusú akácfoltban. A magdarázs *B. robiniae* forrás koncentrációt követő eloszlása arra utal, hogy magfogyasztása leginkább a nagy erdőfoltok magtermelését csökkenti. A specialista *Mesopolobus* sp. nagyobb egyedsűrűségben a kis foltokban volt jelen, kis magfogyasztó egyedsűrűség mellett. Ez az eloszlás egy később érkező, kevésbé domináns parazitoid faj számára előnyös, ilyen módon elkerülve a többi parazitoid fajjal való versengést. A generalista *E. urozonus* akác abundancia függetlensége valószínűleg erős polifágiája következménye, hiszen akác és magdarázs hiányában más fajokat fogyaszt. Vizsgálatunkkal kimutattuk, hogy az invazív gazdanövény foltmérete hatással van magfogyasztójának parazitoidjaira is. Az invazív növények tehát a herbivór mellett hatással vannak a magasabb trófikus szintekre is, több szinten befolyásolva új, formálódó közösségeiket.

Zavarás hatása a vizsgált rendszerben – Terepi kísérletünk során mesterséges zavarás hatását és az általa rovarpopulációkban kiváltott dinamikai változásokat vizsgáltuk a már bemutatott tritrófikus rendszerben (Lakatos et al. 2017). A kísérletes zavarást egy Nagyvárad melletti (Bihar Megye, Románia) akácültetvény foltjaiban végeztük el, terméseltávolítás formájában. A termések eltávolításával a kezelt akácfoltokban a magfogyasztó és parazitoidjainak lokális kihalását idéztük elő. Vizsgálati hipotézisünk szerint a zavarás felerősíti a parazitoidok felülről-lefelé ható szabályozását, lecsökkentve a magpredációt és ezáltal elősegítve a gazdanövény terjedését. A vizsgálati elrendezés négy megüresítéshez kiválasztott (kezelt foltok) akácfoltból állt, valamint 1-1 (összesen négy) kontroll foltból, minden kezelt folt közelében. 2011 márciusában akáctermés mintákat gyűjtöttünk mind a nyolc foltból, majd a négy kezelt foltból eltávolítottuk az összes termést, úgy a fák, mint a talaj szintjéről. A termésgyűjtést megismételtük 2012, 2013, 2014 és 2015 márciusában mind a nyolc foltból, majd kineveltük és meghatároztuk a termésekben hibernáló rovarokat. Eredményeink szerint a zavarás megváltoztatta a vizsgált gazdaváltó rendszer magfogyasztó - parazitoid arányát, viszont gazdaváltó nem befolyásolta a magpredáció mértékét. Ezzel szemben a zavarás hatására megnőtt parazitizmus mértéke, felerősítve a fentről-lefelé ható szabályozást. A magfogyasztót a gazdanövény alulról-felfelé ható szabályozással befolyásolta. A foltok sűrűsége csökkentette a magfogyasztást, míg a foltok izoláltsága nem volt rá hatással. A parazitizmus viszont csökkent a foltok izolációjával, míg a foltok sűrűsége nem befolyásolta. Mivel a vizsgált rendszer gazdanövénye egy invazív faj, kimutattuk, hogy az invazív növények élőhelyeinek részleges zavarása megnövelheti a felülről-lefelé ható szabályozás erejét, lecsökkentve a magpredációt. Tehát a várttal ellentétben, a teljes termésmennyiség akácfoltokból való eltávolítása hosszú távon megnöveli a magmennyiséget, mivel kevesebb mag lesz elfogyaszta, megnövelve a talajban felhalmozó magbankot és elősegítve az invazív faj terjedését.

Az akácmagdarázs parazitoid közössége – Akácterméseket gyűjtöttünk be öt évben, majd kineveltük és meghatároztuk a termésekben fejlődő rovarokat annak érdekében, hogy azonosítsuk a fehér akác európai magfogyasztóit, valamint az akácmagdarázs *B. robiniae* parazitoid közösségében jelen levő fajokat (Lakatos et al. manuscript a). A termesztett, idegenhonos növények kiterjedt ültetvényei jelentős találkozási felületet biztosítanak új élőhelyeik őshonos rovarfajaival. Európában Magyarország és Románia a fehér akác jelentős termesztői (Sandu et al. 2005; Rédei et al. 2011), így termésmintáink begyűjtését Románia (2009, 2011-2015 márciusa) és Magyarország (2013-2015 márciusa) több területén végeztük. Rovarkineveléseink alapján a fehér akác magvainak leggyakoribb fogyasztója Közép-Kelet Európában az akácmagdarázs, *Bruchophagus robiniae*. Az öt vizsgált év folyamán további magpredátor fajok is kirepültek a mintáinkból, mint az *Aphis craccivora* levéltetű és négy bogár faj (Coleoptera) egy-egy egyede, de ezek csak kis egyedszámban és szorványosan jelentek meg. A magdarázs

B. robiniae biológiájával kapcsolatos megfigyeléseink: (i) A kifejlett rovarok kirepülése májusban tetőzik, majd nyár végére megszűnik, még abban az esetben is, amikor a rovarok kinevelését több éven keresztül végeztük. (ii) Az egyedek teljes fejlődésüket, így a bebábozódást is egy-egy kiválasztott, fertőzött magon belül végzik. A magdarázs *B. robiniae* parazitoid közösségével kapcsolatos megfigyeléseink: (i) A közösség magasabb trófikus szintjein fémfürkész (Chalcidoidea, Hymenoptera), valódi fürkész (Ichneumonidae, Hymenoptera) és gyilkosfürkész (Braconidae, Hymenoptera) családokba tartozó parazitoid és hiperparazitoid fajok vannak jelen. (ii) Hét parazitoid faj volt jelen minden vizsgált évben és helyen. (iii) A jelen lévő parazitoid fajok: *Eupelmus urozonus*, *Mesopolobus robiniae* sp. n., *Pteromalus sequester, Aprostocetus venustus*, *Pediobius bruchicida*, két *Baryscapus*, valamint több Braconidae faj. (iv) A parazitizmus aránya, valamint a parazitoid fajok abundanciája folyamatosan változott a különböző vizsgált évek és helyek között. A hét parazitoid faj következetes jelenléte a különböző vizsgált években és helyeken megerősíti a fajok egy közösségbe való tartozását. A közösség összetételét alátámasztja továbbá az érintett parazitoid génuszok és néhány faj jelenléte más *Bruchophagus* fajok, valamint egyéb, Pillangósvirágúakon előforduló magevők közösségeiben. A parazitizmus arányának folyamatos fluktuálása a vizsgált évek és helyek között viszont a vizsgált rendszer feltételezett új, gazdaváltó igazolja, utalva arra, hogy a rendszer formálódása még folyamatban van. Továbbá, a rendszer parazitoid fajainak egyike, a *Mesopolobus robiniae* tudományra új faj és a közelmúltban lett leírva, mint az akác terméseiből kinevelt faj (Lakatos et al. manuscript b).

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Appendix

Appendix 1. Distribution of sample number between the two collecting areas and plot types. Woodlot size = number of tree individuals in woodlots. N of samples = number of tree individuals sampled. N of seedpods = amount of seedpods collected from sites. Coordinates are given in decimal degrees (DD).

Area	Plot type	N	E	Woodlot size	Samples per plot	Pods per plot	Total samples	Total pods
Cluj county	small patches	46.761636	23.618103	2	2	152	22	1126
		46.770948	23.576595	4	4	151		
		46.768185	23.559914	5	5	163		
		46.768111	23.568950	5	5	221		
		46.773839	23.580611	1	1	102		
		46.767017	23.618161	2	2	122		
		47.086450	21.971764	1	1	76		
		46.768753	23.615867	2	2	139		
	woodlot	46.826167	23.629297	15	6	161	13	648
		46.768742	23.604356	40	7	487		
Bihor county	small patches	47.086458	21.971578	1	1	106	5	480
		47.086453	21.971494	1	1	79		
		47.098969	21.984856	1	1	87		
		47.100983	21.967483	1	1	106		
		47.101100	21.965989	1	1	102		
	woodlot	47.093958	21.987850	30	5	394	25	2071
		47.097514	21.985047	50	4	300		
		47.079314	21.971067	100	6	408		
		47.098539	21.965108	200	10	969		

Appendix 2. Coordinates of vacated and control patch centroids (decimal degrees in WGS84) with host plant densities (per m^2) and distances (m) between patch centroids (vacated versus control, control versus nearby black locust plantations).

	Patches	N	E	density	distance
Vacated	1	47.10089	21.96752	0.22	99.35
	2	47.10156	21.96585	0.25	87.91
	3	47.09624	21.98492	0.13	65.99
	4	47.09852	21.98478	0.18	109.97
Control	1	47.10035	21.96734	0.26	37.88
	2	47.10141	21.96534	0.34	40.08
	3	47.09655	21.98492	0.35	33.41
	4	47.09785	21.98513	0.30	46.36

Appendix 3. The known parasitoid associates of *Bruchophagus* species listed in the Universal Chalcidoidea Database (Noyes 2017). *Bruchophagus* sp. represents data from literature where species were identified to genus level only.

Bruchophagus species	Nr. of parasitoid species	Common parasitoid species with *B. robiniae*	Common parasitoid genera *with B. robiniae*
Bruchophagus sp.	15	*Aprostocetus venustus, Pteromalus sequester*	*Aprostocetus, Baryscapus, Eupelmus, Mesopolobus, Pteromalus*
B. astragali	1	-	-
B. ater	2	-	-
B. caraganae	7	*Pteromalus sequester*	*Mesopolobus, Eupelmus*
B. ephedrae	1	-	-
B. fellis	2	-	-
B. funebris	4	*Pteromalus sequester*	-
B. gibbus	20	*Aprostocetus venustus, Pteromalus sequester*	*Aprostocetus, Baryscapus, Eupelmus, Mesopolobus*
B. kolobovae	8	*Pteromalus sequester*	*Baryscapus, Eupelmus, Mesopolobus*
B. mellipes	4	-	*Pteromalus*
B. mexicanus	1	-	*Mesopolobus*
B. onobrychidis	1	*Aprostocetus venustus*	-
B. platypterus	9	*Pteromalus sequester*	*Baryscapus, Eupelmus, Mesopolobus*
B. roddi	20	*Aprostocetus venustus, Pteromalus sequester, Eupelmus urozonus*	*Baryscapus, Eupelmus, Mesopolobus, Pteromalus*
B. tauricus	1	-	-

Appendix 4. Legume species categorised by nativeness and habitus and number of their seed predator species and common parasitoid species and genera with *B. robiniae*

Host plant type	Seed predator order	Common species with *B. robiniae*	Common genera with *B. robiniae*
native shrub	Coleoptera	*Pteromalus sequester*, *Eupelmus urozonus*	*Aprostocetus*, *Baryscapus*, *Mesopolobus*, *Pediobius*, *Pteromalus*
native shrub	Hymenoptera	*Pteromalus sequester*	*Eupelmus*, *Mesopolobus*
native shrub	Lepidoptera	*Eupelmus urozonus*, *Pteromalus sequester*	*Aprostocetus*, *Pediobius*, *Pteromalus*, *Mesopolobus*
native tree	Coleoptera	*Eupelmus urozonus*, *Pteromalus sequester*	*Aprostocetus*, *Baryscapus*, *Eupelmus*, *Mesopolobus*, *Pediobius*
native tree	Hemiptera	-	-
native tree	Hymenoptera	*Pteromalus sequester*	*Eupelmus*, *Mesopolobus*
native tree	Lepidoptera	*Eupelmus urozonus*	*Aprostocetus*, *Pediobius*, *Pteromalus*
invasive shrub	Coleoptera	-	*Eupelmus*, *Pteromalus*, *Mesopolobus*
invasive tree	Coleoptera	*Pteromalus sequester*	*Aprostocetus*, *Baryscapus*, *Eupelmus*, *Mesopolobus*
invasive tree	Hemiptera	-	-
invasive tree	Hymenoptera	*Pteromalus sequester*, *Eupelmus urozonus*, *Pediobius bruchicida*, *Aprostocetus venustus*	*Eupelmus*, *Pteromalus*, *Mesopolobus*, *Baryscapus*
invasive tree	Lepidoptera	*Eupelmus urozonus*	*Aprostocetus*, *Pediobius*, *Pteromalus*