



## Original article

## Resource dependence in a new ecosystem: A host plant and its colonizing community

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## ABSTRACT

The introduced black locust (*Robinia pseudoacacia*) has become an invasive plant species in Europe. The introduction of alien plants such as the black locust may modify ecosystem composition and functioning. In response to the presence of a potential host plant, herbivores can adapt and shift to the consumption of the new host plant. In Eastern-Central Europe, the seed predator *Bruchophagus robiniae* (Hymenoptera: Eurytomidae) is an important consumer of black locust seeds which presumably shifted from its formerly host species to black locust. We tested the influence of host plant abundance on a seed predator – parasitoid community. We found that the seed predator *B. robiniae* was present in higher numbers 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. We found that parasitoid species are influenced by the patch size of host plants, thus characteristics of introduced host plants can also manifest in higher trophic levels.

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## 1. 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 can lead to the formation of novel ecosystems (Mascaro et al., 2013) as new insect–plant associations can emerge through ecological fitting and initiate adaptation of herbivores in response to the presence of a new host plant (Agosta, 2006).

The introduction of alien plants may also modify ecosystem composition and functioning (Bezemer et al., 2014). In response to the presence of a potential host plant, native consumers (herbivores) can adapt and shift to the consumption of the new host plant. 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, the 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).

In their new habitats, the low consumer number on introduced plants suggests that such species often 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). The study of invasive species and associated community characteristics can help further our understanding of how to develop methods to control invasions (Harvey et al., 2010; Shea et al., 2002).

Host plant shift of specialist 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). 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

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host plant as a feeding or oviposition site (Agosta, 2006). Not only herbivores, but also the parasitoids of herbivores may be affected by the introduced plants. These host plants may affect parasitoids through plant allelochemicals or via herbivore fitness (Bezemer et al., 2014). Parasitoids can respond differently to introduced plants than the herbivores of introduced plants (Cronin and Abrahamson, 2001). Insect parasitoids also influence seed predators, lowering the impact of seed predation on host plants (Gómez & Zamora, 1994; Munguía-Rosas et al., 2013). 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).

Another major factor affecting herbivores in the formation of new communities or leading to modified community composition is the herbivore's response to host plant abundance. Different species of herbivores respond differently to resource abundance. 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 seeds of 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 predators (Jaenike, 1990; Zabel and Tscharnatke, 1998). Specialist herbivores are less threatening to other plant species than generalist herbivores, so they are potential biocontrol agents of invasive plants (Dennill and Donnelly, 1991).

Seed predation is a major biotic factor influencing invasive plant species. Beside seed consumption, seed predation leading to fruit abortion in infested plants, may contribute substantially to the decrease of the invasive plant's potential range (Sallabanks and Courtney, 1992). 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 (Perju, 1998). No herbivores consuming black locust seeds in North-America are present in Europe; therefore, there must have been a host shift of native consumers (Hargrove, 1986; Perju, 1998). In Eastern Europe black locust can be found in large patches like plantations or as single individuals which escaped plantations or were planted as ornamental trees. The seed predator of black locust *Bruchophagus robiniae* Zerova, 1970 (Hymenoptera: Eurytomidae) was studied from ecological, taxonomical and faunistic perspectives (Farkas and Terpó-Pomogyi, 1974; Zerova, 1970; Perju, 1998). *B. robiniae* and its parasitoids together with the 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).

We aimed to study how seed predators and their parasitoids respond to the escape of an introduced plant. 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.

## 2. Material and methods

### 2.1. Study system

Black locust, *R. pseudoacacia* L. (Leguminosae), is a widely distributed alien plant in Europe, which reproduces through vegetative root suckering or by seed propagation. Black locust produces 5–11 cm long seedpods, which persist on trees throughout winter. Pods contain 3–15 seeds that remain viable in soil for years (Perju, 1998).

Few insect consumers of black locust seeds are known in Europe. In black locust's native range (North America) its seed predators are *Spermophagus hoffmannseggii* Gyllenhal, 1833 and *Apion* spp. Herbst, 1797 (Hargrove, 1986); while in Eastern Europe the following species are reported as seed predators: *Aphis craccivora* Koch, 1854 (Hemiptera: Aphididae); *Etiella zinckenella* Treitschke, 1832 (Lepidoptera: Pyralidae); *B. robiniae* (Perju, 1998). *B. robiniae* is a monophagous pre-dispersal seed predator of black locust that produces one generation per year (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. Oviposition occurs in the early stages of pod development and larvae feed and develop inside one seed (Batiste, 1967). Adults emerge during the following spring. Parasitoids of eurytomid seed predators are mainly from the families of Chalcidoidea and Ichneumonoidea (Hymenoptera) (Noyes, 2012; Yu et al., 2005), but the parasitoid community of *B. robiniae* has not been studied until now.

### 2.2. Study area and data collection

Study sites were in two areas of Romania, Bihor (near Oradea city, BH) and Cluj (in and near Cluj-Napoca city, CJ) counties (Fig. 1). We collected samples of black locust from 19 separated plots (Table 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).

Samples were taken from trees with two host plant abundance types: small patches and woodlots (Table 1, Fig. 1). 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,

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