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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Using a botanical garden to assess factors influencing the colonization of exotic woody plants by phyllophagous insects

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Abstract The adoption of exotic plants by indigenous herbivores in the region of introduction can be influenced by numerous factors. A botanical garden in Western Siberia was used to test various hypotheses on the adaptation of indigenous phyllophagous insects to exotic plants invasions, focusing on two feeding guilds, external leaf chewers and leaf miners. A total of 150 indigenous and exotic woody plant species were surveyed for insect damage, abundance and species richness. First, exotic woody plants were much less damaged by chewers and leaf miners than native plants, and the leaf miners' species richness was much lower on exotic than native plants. Second, exotic woody plants having a congeneric species in the region of introduction were more damaged by chewers and hosted a more abundant and species-rich community of leaf miners than plants without native congeneric species. Third, damage by chewers significantly increased with the frequency of planting of exotic host plants outside the botanical garden, and leaf miners' abundance and species richness significantly increased with residence time in the garden. Finally, no significant relationship was found between insect damage or abundance and the origin of the exotic plants. Besides the ecological implications of the results, this study also illustrates the potential of botanical gardens to test ecological hypotheses on biological invasions and insect–plant interactions on a large set of plant species.

Keywords Invasion ecology · Arboretum · Siberia · Exotic trees · Folivore response

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Introduction

Botanical gardens, arboreta and, more generally, plantations of exotic plants are considered to play an important role in the introduction of invasive species worldwide (Wester 1992; Dawson et al. 2008a; Heywood 2011; Hulme 2011; Richardson and Rejmánek 2011). However, they are also increasingly recognized as an important tool for research on invasive species (Kenis et al. 2009; Pearse 2010; Barham et al. 2015). Exotic plants in botanical gardens or in plantations can be used as sentinel plants to identify future threatening plant pests or diseases from a specific area (Britton et al. 2010; Tomoshevich et al. 2013; Barham et al. 2015; Roques et al. 2015). Botanical gardens can also help to evaluate the potential invasiveness and impact of newly introduced plants (Richardson and Rejmánek 2011) or plant pests (Baranchikov et al. 2014). Moreover, the gathering of large numbers of native and exotic plant species from different botanical and floristic regions in botanical gardens and arboreta allows to test various ecological hypotheses on biological invasions, for example, on plant–herbivore interactions (Dawson et al. 2008b; Pearse and Hipp 2009, 2014; Pearse 2010; Kirichenko et al. 2013) or plant–pollinator interactions (Razanajatovo et al. 2015).

One of the most commonly tested hypotheses is the enemy release hypothesis that suggests that invasive species do better in their area of introduction, because they are released from natural enemies that control them in the area of origin (Keane and Crawley 2002). Through surveys in botanical gardens in Russia and Switzerland, we showed that leaf mining insects were more likely to attack indigenous woody plants than exotic plants of the same genus, but also that damage by leaf chewing insects was not significantly different between the two groups of plants (Kirichenko et al. 2013). This was attributed to the higher host specificity in leaf miners than in leaf chewers. However, in that study, we only considered congeneric host plants and did not take into account other potential factors that may influence the adaptation of indigenous insects to exotic plants, such as taxonomic relationship between the exotic host plants and the native flora, the date of introduction of the exotic plant and its abundance in the region. Many insects are specific to a single genus or closely related genera within a family. Exotic plants are more likely to recruit new herbivores when they have congeneric native species in the region of introduction than when they are taxonomically isolated in this region (Connor et al. 1980; Dalin and Björkman 2006; Roques et al. 2006; Dawson et al. 2008b; Harvey et al. 2012). A high species richness within the host genus may also positively influence the recruitment (Pearse and Hipp 2014).

In addition, the recruitment of native herbivores by exotic plants does not necessarily occur at the time of arrival. It has already been shown that the level of herbivory and species richness of herbivorous insects increase with time since introduction of exotic host plants (Siemann et al. 2006; Hawkes 2007; Brändle et al. 2008; Harvey et al. 2013). Similarly, it is likely that the recruitment of insect herbivores by exotic plants is more rapid if the plant species or genus is locally abundant or widely distributed (Leather 1986; Brändle and Brandl 2001; Brändle et al. 2008). Furthermore, the biogeographic origin of the plant may also play a role in its ability to recruit new herbivores, i.e., plants originating from neighboring regions are more likely to be attacked by insects with broad geographic ranges (Kirichenko et al. 2013).

Using observations on phyllophagy by leaf chewers and leaf miners in a botanical garden in Western Siberia, we tested the following hypotheses: (1) exotic woody plants are less damaged by chewers and leaf miners than indigenous plants, and the leaf miners' species richness is lower in exotic plants; (2) exotic woody species having a congeneric species in the region of introduction are more likely to be attacked by leaf chewers and leaf miners than species without congeneric species; (3) herbivory by the two functional groups on exotic woody plants increases (3.1) with the time of introduction of the plant species in the region, (3.2) with the local abundance of the exotic host plant, and (3.3) with the biogeographic proximity of the region of origin, e.g., East Asian and European plants being more damaged than American species.

Materials and methods

Arboretum

Field data were gathered in August 2013 in the arboretum of Central Siberian botanical garden of the Siberian Branch of the Russian Academy of Sciences (CSBG SB RAS) in Novosibirsk, Western Siberia, Russia (54°49′33 N; 83°06′34E; 157 m a.s.l.). Established in 1946, it is the biggest botanical garden in Asian Russia. The CSBG covers an area of 1000 ha and hosts about 5000 plant species, including 566 woody plant species, sub-species and cultivars originating from various biogeographic regions (Koropachinskiy and Vstovskaya 2012; Central Siberian Botanical Garden 2015). The arboretum is situated in a forested area. Trees usually grow naturally and pesticides are very rarely used—no insecticide was used in the study year (M. Tomoshevich: personal communication). Climatically, the year 2013 was rather ordinary for Novosibirsk, with an average temperature of −16 °C for January and +19 °C in July. The yearly precipitation was ca. 600 mm, which is slightly higher than the average precipitation (450 mm) (The climate of the Novosibirsk Region and Novosibirsk 2016).

Host plants

We examined 251 individuals of 150 woody plant species (trees and shrubs) from 21 families and 43 genera (see summary in Table 1 and details in Supplementary Material, Table S1). Eighty-five plant species, thereof mostly exotic plants, were represented by only one individual tree. When more than one tree or shrub per species was available, we examined from two to five individuals per species. The botanical garden collection is largely organized by family and genus; and thus, native and exotic plants of the same genera are found in the same areas. Thirty-four plant species from 19 genera were native to the region (Western Siberia), and the 116 other species from 41 genera were exotic, i.e., introduced from Europe, North America or other parts of Asia (including Eastern Siberia and the Russian Far East) (Koropachinskiy and Vstovskaya 2012; Germplasm Resources Information Network 2013; Flora Europaea 2015) (Table 1). Three other parameters were gathered for each exotic plant species included in the observations. First, we assessed whether the introduced plant species had native congeneric species in Western

Table 1 Woody plants involved in the study in the Central Siberian botanical garden SB RAS, Novosibirsk, Russia

No.	Family	Genus	Presence of native congeneric plant species in Western Siberia	Number of surveyed species	
				Exotic	Native
1	Aceraceae[a]	*Acer*	No	8	0
2	Actinidiaceae[a]	*Actinidia*	No	1	0
3	Adoxaceae	*Sambucus*	Yes	1	1
4	Adoxaceae	*Viburnum*	Yes	2	1
5	Araliaceae[a]	*Eleutherococcus*	No	1	0
6	Berberidaceae[a]	*Berberis*	No	4	0
7	Betulaceae	*Alnus*	No	3	0
8	Betulaceae	*Betula*	Yes	4	3
9	Betulaceae	*Carpinus*	No	1	0
10	Betulaceae	*Corylus*	No	4	0
11	Caprifoliaceae	*Lonicera*	Yes	10	3
12	Caprifoliaceae	*Symphoricarpos*	No	2	0
13	Celastraceae[a]	*Euonymus*	No	1	0
14	Cornaceae	*Cornus*	Yes	1	1
15	Elaeagnaceae	*Elaeagnus*	No	1	0
16	Elaeagnaceae	*Shepherdia*	No	1	0
17	Ericaceae	*Rhododendron*	Yes	1	0
18	Fabaceae	*Amorpha*	No	1	0
19	Fabaceae	*Caragana*	Yes	3	1
20	Fabaceae	*Chamaecytisus*	Yes	1	1
21	Fagaceae[a]	*Quercus*	No	2	0
22	Grossulariaceae	*Ribes*	Yes	5	2
23	Hydrangeaceae[a]	*Philadelphus*	No	2	0
24	Juglandaceae[a]	*Juglans*	No	1	0
25	Malvaceae	*Tilia*	Yes	2	0
26	Oleaceae[a]	*Fraxinus*	No	1	0
27	Oleaceae[a]	*Syringa*	No	3	0
28	Rosaceae	*Amelanchier*	No	1	0
29	Rosaceae	*Cotoneaster*	Yes	0	1
30	Rosaceae	*Crataegus*	Yes	7	1
31	Rosaceae	*Malus*	Yes	4	0
32	Rosaceae	*Pentaphylloides*	Yes	1	1
33	Rosaceae	*Physocarpus*	No	3	0
34	Rosaceae	*Prinsepia*	No	1	0
35	Rosaceae	*Prunus*	Yes	4	1
36	Rosaceae	*Rhamnus*	Yes	2	0
37	Rosaceae	*Rosa*	Yes	1	4
38	Rosaceae	*Sorbaria*	Yes	0	1
39	Rosaceae	*Sorbus*	Yes	2	1
40	Rosaceae	*Spiraea*	Yes	5	3
41	Salicaceae	*Populus*	Yes	3	1
42	Salicaceae	*Salix*	Yes	13	6
43	Ulmaceae	*Ulmus*	Yes	2	1
Total			Yes—25; no—18	116	34

[a] Plants having no relative at family level in Western Siberia (according to Peschkova 2006; Bakulin et al. 2008; Koropachinskiy and Vstovskaya 2012)

Siberia: 81 exotic species had congeners and 35 had not (Peschkova 2006; Bakulin et al. 2008; Koropachinskiy and Vstovskaya 2012). Woody plants from nine families had no relative at family level in Western Siberia (Table 1). Second, the year of first introduction in the botanical garden was obtained from the garden's archives. All species involved in our study were introduced first to the botanical garden in the period 1965–2000. Finally, the exotic plant species were classified into four groups according to their frequency of planting outside the botanical garden in the city and surroundings of Novosibirsk: 0—not found outside the botanical garden; 1—found occasionally outside the botanical garden (i.e., in less than 10 % of the 22 parks and other green areas within the city of Novosibirsk); 2—found rather frequently outside the botanical garden (i.e., in 10–50 % of the parks and other green areas); 3—found very frequently outside the botanical garden (i.e., in more than 50 % of the parks and other green areas) (Tomoshevich and Banaev 2011; Tomoshevich 2015; M. Tomoshevich: personal communication).

The list of the woody plant species included in the study, with information on origin, year of introduction in the botanical garden, frequency of planting outside botanical garden and existence of congeneric species in Western Siberia, is provided as Supplementary Material (Table S1).

Herbivory assessments

Two functional groups of phyllophagous insects were considered, leaf chewers and leaf miners. Assessments were made directly on the plants. In general, 500 leaves per plant were selected haphazardly on a minimum of five branches per plant in the lower part (<2 m) of a tree crown or on a whole shrub. On trees with large compound leaves (e.g., *Fraxinus*, *Juglans* spp.), 500 leaflets were examined. On some trees with very large simple leaves (e.g., some *Acer* spp.), less leaves were surveyed (i.e., 200–400 leaves). On plants with small leaves (e.g., *Berberis, Caragana, Chamaecytisus*, some *Salix* spp., etc.), we checked 700–1000 leaves per individual plant, according to the size. For each individual plant, herbivory was expressed per 100 leaves. In most cases, herbivory was assessed on a singly tree or shrub. However, for some species, up to five individual plants were examined, in which case, the data were averaged to provide a single herbivory assessment per plant species following the method used in our previous study (Kirichenko et al. 2013).

Herbivory assessments were carried out on 13–18 August, 2013. In Western Siberia, mid-August is the best time for such assessments, because most of the damage by leaf miners and chewers that accumulated during spring and summer is still visible, and leaves have not yet fallen (Kirichenko et al. 2013).

To assess herbivory by chewers, the number of leaves with signs of at least 5 % of their leaves eaten by leaf chewers was counted on the total number of leaves and averaged for 100 leaves. Skeletonized leaves, i.e., leaves with intact leaf epidermis, were not counted, and very minor leaf surface reductions (<5 %) were not considered, since it was not possible to assign these to leaf chewers.

Leaf miners were assessed in two ways, following the method described in Kirichenko et al. (2013). First, the abundance of leaf miners was monitored by counting the number of mines on the total number of leaves and averaged for 100 leaves. Mines of the same leaf miner species in a single leaf were counted only once to avoid the overestimation of gregarious species. In contrast, leaves hosting two or more species of leaf miners were counted two or more times. Second, leaf miners' species richness was calculated by counting the number of species present in the samples. For taxonomic identification, we photographed and collected leaves with representative and questionable mines. In most cases, leaf miners can be identified through their mines, and the different developmental stages were further examined in the laboratory to confirm species determination (Gerasimov 1952; Hering 1957; Spencer 1976; Gusev 1984; Ler 1997; Kuznetzov 1999; Edmunds et al. 2015; Ellis 2015). However, in some cases, a proper identification was not possible. Therefore, in this study, species richness was based on morpho-species rather than on true species.

Statistic analysis

Damage by leaf chewers, leaf miner abundance and leaf miner species richness were log-transformed prior to analyses. These three dependent variables were then analyzed separately in various ways. First, damage, abundance and species richness on native woody plants were compared with those on exotic plants (all origins included), using t tests. The subsequent tests were carried out only with observations made on exotic plants. Second, general linear models were performed for the three dependent variables with the origin of the plant (Europe, Asia outside Western Siberia and North America), frequency of planting (classed as described above) and absence/presence of congeners in Siberia as fixed factors. When the results of the GLM were significant, multiple comparisons of means were performed with the post hoc Tukey HSD test. Finally, the effect of year of first introduction in the botanical garden was assessed for the three dependent variables by performing linear regressions based only on plant species not found outside of the botanical garden, because it was impossible to obtain information on the year of first introduction in the region for the plants planted outside of the botanical garden. All statistics were carried out using IBM SPSS 22.0.

Results

From the 150 woody plant species, 134 (89 %) had at least some signs of damage by external chewers and 40 (27 %) had more than 10 % of their leaves with more than 5 % of their surface eaten. Seventy-five plant species (50 %) hosted at least one morpho-species of leaf miner, and 49 plant species (33 %) hosted at least two morpho-species. These leaf miners belonged to 73 morpho-species, 29 genera, 13 families and four orders (Lepidoptera, Diptera, Hymenoptera and Coleoptera). Sixty-four percent of the morpho-species were Lepidoptera, and 45 % belonged to the family Gracillariidae.

Exotic woody plants were less damaged by chewers ($t = 4.511$; $df = 148$; $P < 0.001$), were less attacked by leaf miners ($t = 4.836$; $df = 148$; $P < 0.001$) and supported a lower leaf miner richness ($t = 3.202$; $df = 148$; $P = 0.002$) than native plants (Fig. 1a, b).

On exotic plants, damage by chewers was significantly influenced by the presence of a congeneric plant species in Siberia ($F_{1,92} = 27.740$; $P < 0.001$) (Fig. 2a) and by the frequency of planting ($F_{3,92} = 6.124$; $P = 0.001$) (Fig. 2b) but not by the origin of the exotic plant ($F_{2,92} = 0.486$; $P = 0.617$) (Fig. 2c). Chewers' damage increased with the presence of congenerics (Fig. 2a) and the frequency of planting (Fig. 2b) in the region. Leaf miners' abundance significantly increased with the presence of congeneric species ($F_{1,92} = 16.742$; $P < 0.001$) (Fig. 3a) but not with the frequency of planting ($F_{3,92} = 1.144$; $P = 0.336$) (Fig. 3b). Leaf miners' abundance was not significantly influenced by the origin of the plant ($F_{2,92} = 0.098$; $P = 0.907$) (Fig. 3c). Similarly, leaf miners' richness was much higher in the presence of congeneric species ($F_{1,92} = 19.179$; $P < 0.001$) (Fig. 4a) but was not affected by the frequency of planting ($F_{3,92} = 0.595$; $P = 0.620$) (Fig. 4b) nor by the origin of the plant ($F_{2,92} = 0.766$; $P = 0.468$ (Fig. 4c). Among woody plants that have not been planted outside the botanical garden, the year of first introduction in the garden was inversely correlated with leaf miners' abundance ($R = -0.272$; $F_{1,67} = 5.346$; $P = 0.024$), and species richness ($R = -0.306$; $F_{1,67} = 6.924$; $P = 0.011$), i.e., plant species, were increasingly colonized by leaf miners with time. No significant pattern was found for defoliators ($R = -0.190$; $F_{1,67} = 2.507$; $P = 0.118$).

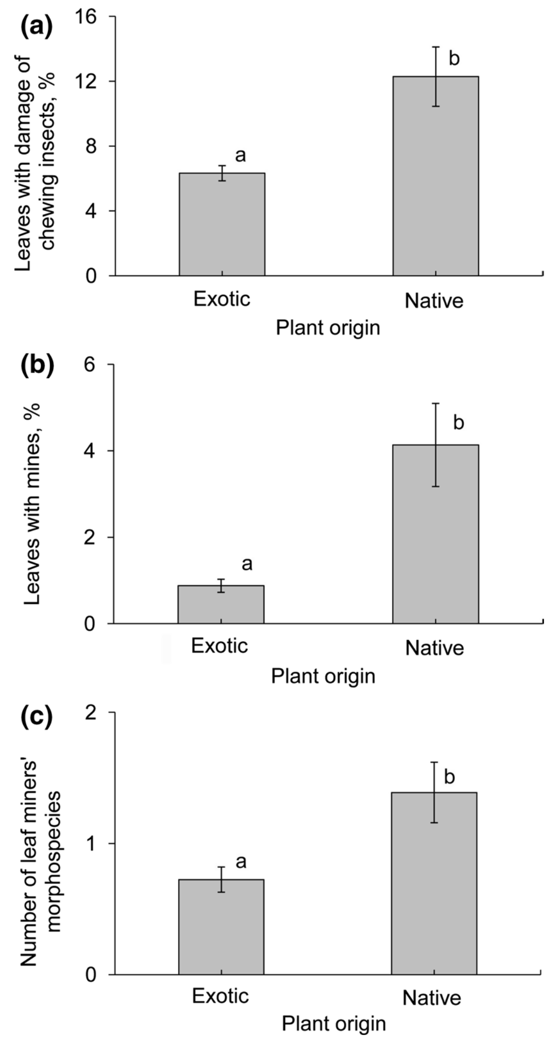

Fig. 1 Damage by external chewers (**a**), abundance of leaf mining insects (**b**), and taxonomic richness of leaf mining insects (**c**) on leaves of exotic and native woody plants species in the Central Siberian botanical garden, Novosibirsk, Russia in August 2013, (mean ± SE). *Different letters above bars* indicate significant differences at $P < 0.01$

Discussion

In accordance with the enemy release hypothesis, our study showed that exotic woody plants are, on average, much less attacked by leaf miners and leaf chewers than native plants. Similar observations had been previously made by a large number of authors (e.g., Carpenter and Cappuccino 2005; Liu and Stiling 2006; Parker and Gilbert 2007; Proches et al. 2008; Sugiura 2010; Harvey et al. 2012; Litt et al. 2014; van Hengstum et al. 2014; Cronin et al. 2015). However, in a significant amount of other studies, no difference in herbivory damage or abundance was found between native and exotic plants, especially when only congeneric native and exotic plant species were compared (e.g., Novotny et al. 2003; Hawkes 2007; Sugiura et al. 2008; Chun et al. 2010; Dostál et al. 2013), suggesting that the release from herbivory in the region of introduction is not a general pattern for exotic plants (Bezemer et al. 2014). The herbivores' feeding guild also plays a role, with endophagous insects, such as leaf miners, bud borers or gall makers,

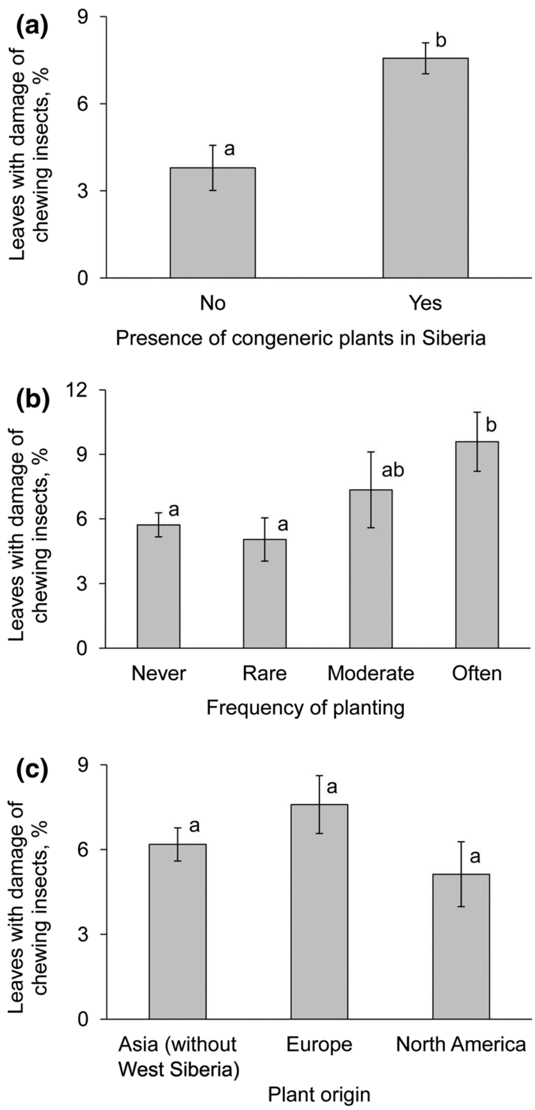

Fig. 2 Damage by external chewers on exotic woody plants depending on the presence or absence of congeneric plants in Siberia (**a**), frequency of planting in Novosibirsk (**b**), and plant species origin (**c**), (mean ± SE). *Different letters above bars* indicate significant differences at $P < 0.05$

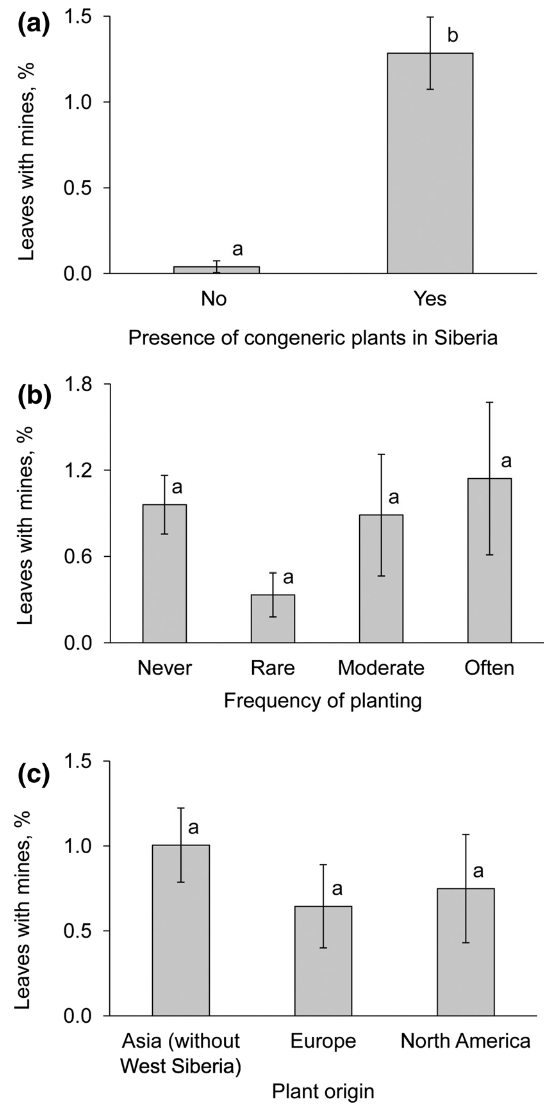

Fig. 3 Abundance of leaf mining insects on exotic woody plants depending on the presence or absence of congeneric plants in Siberia (**a**), frequency of planting in Novosibirsk (**b**), and plant species origin (**c**), (mean ± SE). *Different letter above bars* indicate significant differences at $P < 0.01$

showing a stronger preference for native plants than external feeders, probably because of their higher specificity (Kulfan et al. 2010; Burghardt and Tallamy 2013; Kirichenko et al. 2013).

Factors affecting the recruitment of exotic plants by indigenous herbivores have been studied through literature reviews and meta-analyses (e.g., Leather 1986; Brändle and Brandl 2001; Liu and Stiling 2006; Brändle et al. 2008; Bezemer et al. 2014), or field data on single or a small group of species (e.g., Siemann et al. 2006; Parker and Gilbert 2007; Ando et al. 2010; Harvey et al. 2013; Castells et al. 2014), but rarely through field data collected on a large number of species at the same place and the same time (Dietz et al. 2004; Carpenter and Cappuccino 2005; Burghardt and Tallamy 2013; Dostál et al. 2013). The examination of damage, population density and species richness in two functional groups of phyllophagous insects, leaf chewers and leaf miners allowed us to confirm the importance of some factors affecting the recruitment of exotic plants by phyllophagous insects, but not others.

The most important and undisputed factor is clearly the presence of congeneric species in the region of introduction. Native insects more likely shift to exotic host plants having congenerics in the area of introduction, rather than to taxonomically isolate exotic plants (Connor et al. 1980; Brändle and Brandl 2001; Dalin and Björkman 2006;

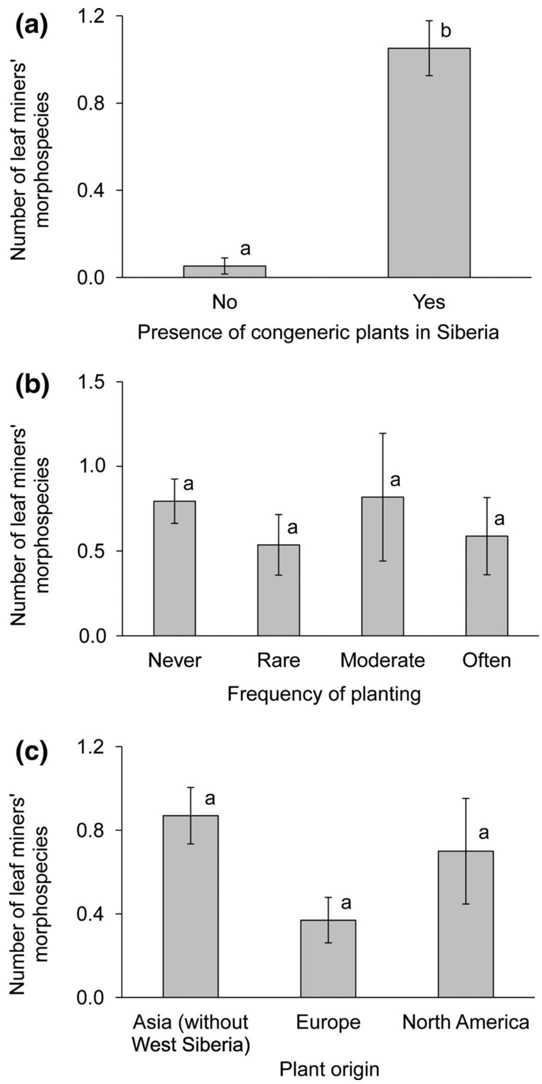

Fig. 4 Taxonomic richness of leaf mining insects on exotic woody plants depending on the presence or absence of congeneric plants in Siberia (**a**), frequency of planting in Novosibirsk (**b**), and plant species origin (**c**), (mean ± SE). *Different letters above bars* indicate significant differences at $P < 0.01$

Roques et al. 2006; Harvey et al. 2012; Burghardt and Tallamy 2013). Taxonomically related plants have similar structural and chemical leaf characteristics that are crucial for phyllophagous insects and facilitate the acceptance of new plant species (Connor et al. 1980). In our study, hardly, any leaf miner was found on plant species without congenerics in the region. This was expected, since leaf miners have developed very specialized plant–insect relationships, and most species are known to be specific at genus level (Connor and Taverner 1997). However, there were two exceptions in our survey. First, the North American *Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem. (Rosales: Rosaceae) was attacked by the local leaf mining moth *Bucculatrix bechsteinella* (Bechstein & Scharfenberg) (Lepidoptera: Bucculatricidae), a polyphagous species feeding on many genera of the family Rosaceae. Second, the Hungarian lilac, *Syringa josikaea* J. Jacq. ex Rchb. (Lamiales: Oleaceae) was colonized by the moth *Gracillaria syringella* F. (Lepidoptera: Gracillariidae), mining exclusively on Oleaceae (Ellis 2015). No plant of this family occurs in Siberia, and thus, *G. syringella* is most probably invasive, having arrived with *Syringa* spp., which are widely planted as ornamental plants in Siberia and particularly in the studied region. Interestingly, the supposedly more generalist leaf chewers also neglected exotic plants without congenerics, albeit the differences in the herbivory rate between native and exotic plants were less marked than in leaf miners (Figs. 2a vs. 3a). Even within a genus, the phylogenetic relationship between introduced and native host plants may play a role. In their survey on chewing and mining insects on oaks (*Quercus* spp.) in North America, Pearse and Hipp (2009) found that introduced oaks that are more closely related to the local native oak experienced more chewing and mining damage than distantly related oaks.

Damage by chewers, but not by leaf miners, significantly increased with the frequency of planting of the exotic woody host plant in Western Siberia. These field results are remarkably similar to those gathered in Germany from literature data by Brändle and Brandl (2001), who observed that the herbivore's species richness was positively related to exotic tree abundance in the country, and that the proportion of specialists showed a negative relationship with tree abundance. In another literature survey, Leather (1986) found that the number of insect species feeding on British Rosaceae generally increases with the size of the geographical range of the host species.

Leaf miners abundance and species richness increased with the years of the presence of the plant in the botanical garden, in contrast to chewers' damage, which showed not significant relationship with the year of first planting. It is unclear why chewers reacted more to tree abundance and leaf miners to the history of introduction. However, both groups reacted in the same direction to the two factors, i.e., insect damage and abundance, tend to increase with residence time and local abundance of the host plant. Other studies observed a positive relationship between insect damage/abundance and host plant residence time. For example, using a meta-analysis, Hawkes (2007) found that time since introduction was a significant nonlinear predictor of enemy release for plant herbivores and pathogens, with initial release in recently arrived species and little to no release after 50–200 years. Similar results were gathered from plant–insect records from the literature (Leather 1986; Brändle et al. 2008). In contrast, no relationship between insect damage/abundance and residence time of introduced plants was found in another meta-analysis (van Hengstum et al. 2014) and a large field survey in Canada (Carpenter and Cappuccino 2005).

We found no significant difference in the level of insect damage, abundance and richness between exotic plants from different continents, although we had hypothesized that plants originating from neighboring regions (i.e., other parts of Asia) would be more attacked, since many insects have a distribution range that covers other Asian regions and Europe. Similarly, Kirichenko et al. (2013) did find clear differences in herbivore damage and abundance between exotic plants of different origins.

Only few studies investigating the interactions between exotic plants and native insects involved field observations and experiments on large numbers of plant species (Bezemer et al. 2014). Botanical gardens and arboreta are excellent tools for such studies, because they hold large collections of exotic and native plants in a single location and keep historical records on their identification, origin, time of introduction, establishment success, etc. Our study provided field results that would have been very difficult to gather in Siberia outside the botanical garden, and possibilities to test further ecological hypotheses on the same systems are numerous. Thus, the use of botanical garden collections for investigations on invasion ecology should be encouraged, in particular in regions where field work is logistically difficult. However, it should be kept in mind that the use of botanical gardens for ecological studies also has some limitations. The main one is the low number of individual plants per species. For example, in this study, the majority of the plants were represented by a single individual, which limited the options for robust statistical analyses. Furthermore, as in Novosibirsk, native species are often planted more abundantly than exotic species, which may introduce another bias when comparing exotic versus native species. Finally, in the botanical gardens, the plants are often well maintained, e.g., they can be watered, fertilized or protected with pesticides, and competition with other plants is limited. Therefore, the conditions in botanical gardens differ from natural ecosystems, which may, for instance, result in differences in susceptibility to herbivory, invasiveness, etc. These limitations should be taken into the account when interpreting data obtained in the botanical gardens.

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Author contribution statement MK and NK designed the experiment, NK conducted field work and NK & MK analyzed the data and wrote the manuscript together.

Compliance with ethical standards

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

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