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Research article

The demise of enemy release associated with the invasion of specialist folivores on an invasive tree

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There is a long history of humans either intentionally or accidentally moving plant species to areas outside of their native ranges. In novel environments, populations of many of these plant species exhibit explosive population growth and spread, in part due to the absence of coevolved enemies such as herbivorous insects. However, over time such enemies can 'catch up' with their host and re-establish host–herbivore relationships. Though this phenomenon has been documented in several systems, little evidence exists on how this re-assembly of enemies results in increased levels of herbivory. In this study we focus on the case of black locust *Robinia pseudoacacia*, a sparsely populated tree species when growing on undisturbed sites in its limited native range in the eastern USA but a highly invasive species, especially in disturbed environments, in most temperate world regions. We recorded folivore damage on invasive populations in five continents, including both native and invaded portions of North America. Here, we investigated 1) how total foliage damage and damage caused by different groups of folivores differs among regions; 2) how seasonal development of folivore damage differs among regions; 3) how folivory varies with distance from the native range within North America; and 4) how the number of recorded specialist folivores correlates with the amount of folivory. We observed strong differences among regions in the amount and type of folivore damage, with the native range experiencing the highest damage, especially that caused by the native chrysomelid beetle *Odontota dorsalis*, which is limited to the native and invaded North American range of *R. pseudoacacia*. Among world regions, total folivory is negatively associated with the distance from the native range and positively associated with the number of established *R. pseudoacacia* specialist folivore species, supporting the hypothesis that global patterns of herbivore invasions are associated with diminished enemy release.

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Keywords: biological invasion, black locust, folivory, leaf damage, *Robinia pseudoacacia*, species richness

Introduction

When plants invade new regions, they typically benefit from the absence of insect herbivores that feed on them in their native range. The enemy release hypothesis (ERH) has been advanced to explain how this release contributes to the establishment and spread of invasive plants (Keane and Crawley 2002, Blumenthal 2005). Under ERH, non-native plants are subjected to lower rates of herbivory than they experience in their native range, and this may result in exceptionally high growth and reproduction. An illustrative example is provided by *Acer platanoides,* which experiences lower levels of herbivory in North America than in its native European range (Adams et al. 2009). Furthermore, herbivory levels on *A. platanoides* in North America are much lower than on its native congener *A. saccharum* (Cincotta et al. 2009).

This escape from herbivory may, however, be short-lived; over time, native herbivorous insects may adapt to feeding on non-native plants and specialist herbivores from the plants' native range may invade and become reunited with their host plants (Strong et al. 1977, Hawkes 2007, Crous et al. 2016). Insect host plant preference is strongly influenced by phylogeny: most insects are only able to feed upon closely related plant species (Forister et al. 2015, Gougherty and Davies 2021). When non-native plants are more closely related to native plants in a region, native insects in that region are more likely to be able to adopt these non-native plants as novel hosts (Branco et al. 2015).

When a non-native plant becomes widespread in a region, either through its invasiveness or as a result of it being extensively planted for agricultural, horticultural or forestry purposes, specialist herbivores often invade from its native range and reunite with their host (Wingfield et al. 2015, Crous et al. 2016). Hawkes (2007) documented how this pattern slowly erodes enemy release in non-native plants across many different systems, such as widely planted tree species used in forestry and agriculture (Hurley et al. 2016, Brockerhoff et al. 2023) and invasive plants (Medzihorský et al. 2023).

This accumulation of additional specialist herbivores through invasions may ultimately lead to an erosion of the benefits of enemy release experienced by non-native plants, causing a reduction in fitness and competitive status. While the phenomenon of increasing numbers of insect herbivores with time has been well-documented in several different systems (Hurley et al. 2016, Brockerhoff et al. 2023, Medzihorský et al. 2023), little evidence exists on whether this translates into increases in levels of herbivory over time experienced by non-native tree species. There are, however, examples of individual pests originating from the native range of agricultural crop species, reuniting with their host crops in non-native regions and causing considerable damage (Gutierrez and Ponti 2013), but such information is lacking on entire assemblages of herbivores. Herbivory by insects on trees is a complex process known to be affected by many different factors such as the diversity of insect natural enemy populations and tree growing conditions (Schowalter et al. 1986), so it is difficult to predict that increases in herbivore species richness necessarily translate into increased herbivory.

The global spread of black locust, *Robinia pseudoacacia*, is an excellent system for studying how the accumulation of insect herbivores translates into increased herbivory levels. This tree species has a relatively small native range in North America but has spread into other temperate regions of North America as well as virtually every other continent except Antarctica, and has become the most widely distributed invasive tree in the world (Vítková et al. 2017, Delavaux et al. 2023). Mally et al. (2021) and Medzihorský et al. (2023) showed that the spread of this tree in North America as well as in other global regions has been accompanied by parallel, though delayed, invasions by specialist insect herbivores.

Here we hypothesize that *R. pseudoacacia* illustrates the phenomenon of diminishing enemy release in an invasive plant. Specifically, we hypothesize that as *R. pseudoacacia* has become increasingly dominant across the globe, specialist herbivores associated with this tree species in its native range have spread into the *R. pseudoacacia* invaded range, inflicting increasing levels of damage. We test this hypothesis by comparing folivory levels on *R. pseudoacacia* across different world regions where the tree has existed for varying periods of time and reached varying levels of abundance. We compare data from these same regions to also test the hypothesis that folivory levels are related to the number of *R. pseudoacacia* specialists that are locally established.

Material and methods

Sampling

Foliage was sampled from *R. pseudoacacia* trees at several localities in each of six study regions: Czech Republic (8 localities), Japan (2 localities), New Zealand (9 localities), South Africa (5 localities) and North America (30 localities) (Fig. 1). These locations were selected to provide information from each of the major biogeographic regions where *R. pseudoacacia* is abundant. In North America, sampling was conducted both in the native range of *R. pseudoacacia* (7 localities) and in the *R. pseudoacacia* invaded range (23 localities). See Supporting information for descriptions (including coordinates) of sample localities. At each locality, sampling was conducted in late summer (corresponding to the last part of the vegetation season). At a subset of locations, sampling was conducted on several occasions from early to late summer (18-week period in both the Northern and Southern Hemispheres) with 2–4 weeks between each sampling interval in order to quantify the seasonal distribution of folivory (Supporting information). All sampling in the Czech Republic and Japan was made in 2021. Sampling inside the

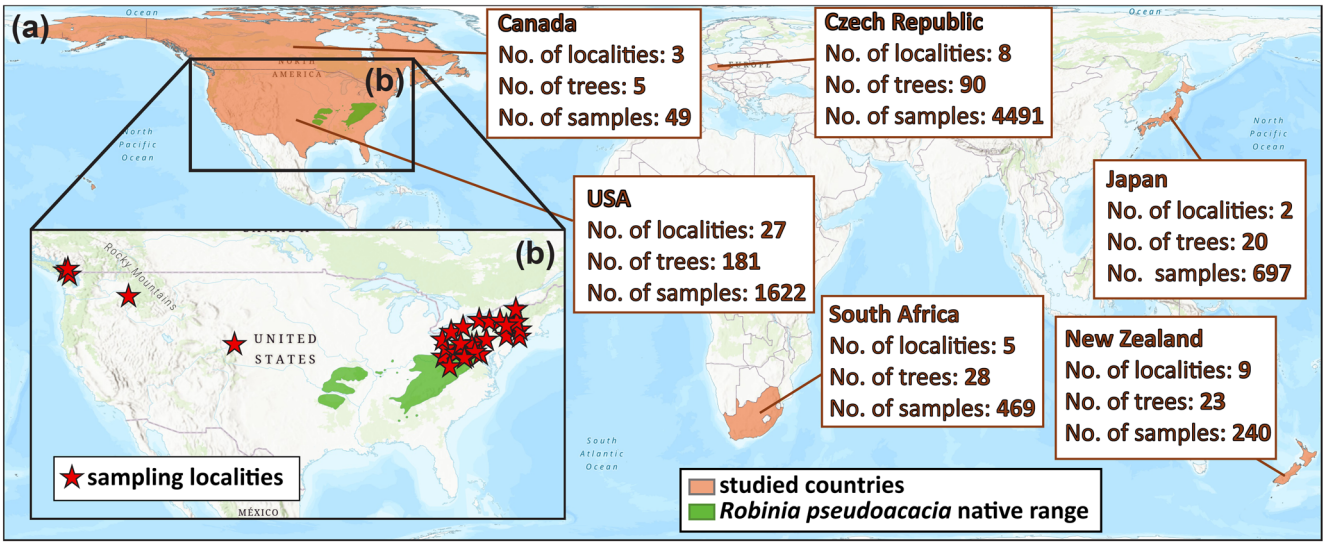

Figure 1. Study regions (a) and distribution of sampled locations in North America (b).

native range in North America was performed in both 2021 and 2022, but sampling outside the native range in North America was done only in 2022. Sampling in South Africa and New Zealand was conducted in 2021 and 2022.

At each locality, 5–10 trees with height over 3 m were selected for sampling. Foliage was sampled from a height of 3–5 m using pole pruners. From each tree, two branch tips (20–30 cm) were sampled from opposing sides of the tree crown. From these branch tips, 5–10 leaves were randomly selected. Each leaf was digitally photographed or scanned, generally with the leaf underside facing up (Fig. 2). Herbivore damage on the upper leaf side was documented by turning the respective leaflets to face up; when damage on both sides of a leaflet occurred, photos of both sides were taken. When leaflets overlapped, they were detached from the rachis and spread out in order to obtain a complete image of every leaflet (Fig. 2a). The total number of evaluated leaves was 7568 (Fig. 1).

The photographs/scans of each leaf were visually evaluated by the same person (M. Medzihorská) to maintain consistency of scoring. We recorded the number of leaflets per leaf, as well as the damage caused by insects from four main feeding categories: 1) free feeders (chewing insects that consume continuous portions of a leaflet), 2) skeletonizers (insects that feed on the leaf parenchyma and epidermis tissue, leaving veins intact), 3) gall makers (insects that induce abnormal leaf growth; mostly *Obolodiplosis robiniae*) and 4) leafminers (insects that feed on leaf parenchyma but leave epidermis intact). Leafminers were further subdivided into two groups of damage: larval *Odontota dorsalis* leafmines, and all other leafmines, mostly caused by the larvae of Gracillariidae moths. For each category, the percent of leaflet surface area damage (attributed to the above categories) was estimated at 5% increments. For each leaf, damage was calculated as an average of leaflet damage (sum of leaflet damage / number of leaflets) for each damage category. Total leaf damage area was calculated as the sum of average damage in each category.

Statistical analyses

The seasonal distribution of foliage damage was summarized across the growing season (ordinal dates 140–270 – i.e. 20 May–27 September – in the Northern Hemisphere; at Southern Hemisphere sites sampling was based on the same range starting 22 September) using data from four regions (Czech Republic, Japan, native range in North America, South Africa). For each category of damage, plots of mean damage per tree for each region, including standard error (SE), were created to describe the temporal accumulation of damage at each of the studied regions.

Based on the samples collected from late summer (ordinal date of sampling > 200), foliage damage levels for each of the four feeding categories and two subcategories were calculated as means across all trees sampled at each sampling location in each of the six world regions. For each category, damage was expressed as logit transformed percentage of leaf area using the *logit* function from the R package 'car' (ver. 3.1-1, Fox and Weisberg 2019), and a linear model (assuming a Gaussian distribution) was used to estimate the effect of region on damage using the *lm* function in R (www.r-project.org). Pairwise Tukey tests were used to make pairwise comparisons among estimates from each region using the *glht* function and the *cld* function to assign letters for statistical differences; both functions were from the R package 'multcomp' (ver. 1.4-22, Hothorn et al. 2008).

In order to explore the effect of proximity to the native range of *R. pseudoacacia* on folivory levels across North America, plots were made of damage in each of the six categories versus distance from the nearest edge of the native range. For this purpose, we used average damage in each of the five categories at 14 localities inside the native range and 20 localities in the invaded *R. pseudoacacia* range in North America (Fig. 1b). Distance from the native range was calculated using ArcGIS Pro 10.1 (ESRI 2022) based on a digitalized version of the *R.*

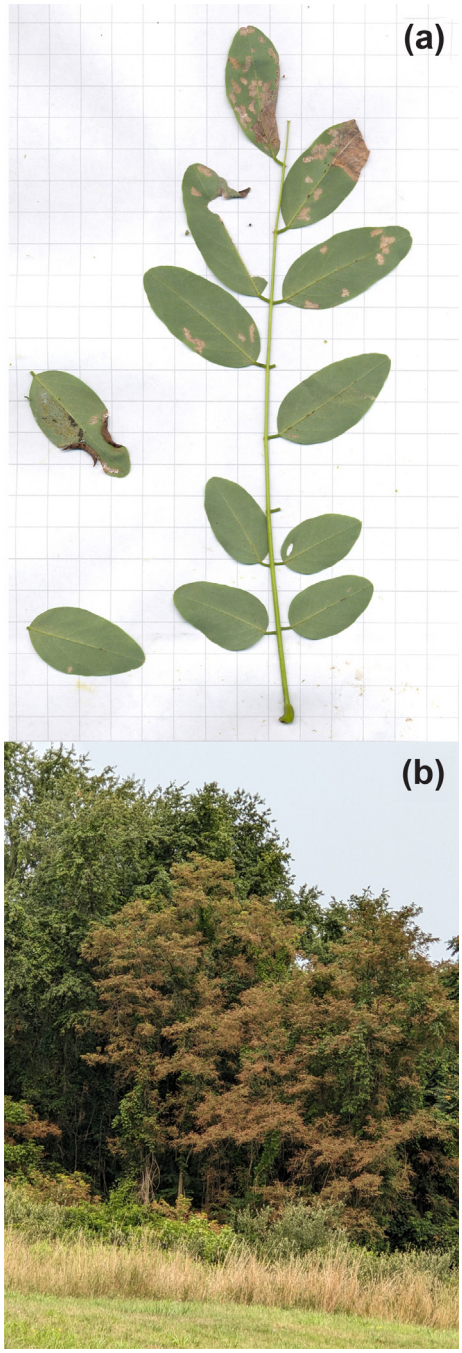

Figure 2. Photos of damaged *Robinia pseudoacacia* leaves. (a) Sample leaf used for scoring folivory sampled inside of the *R. pseudoacacia* native range (17 July 2020, Morgantown, USA) exhibiting free-feeding folivory, skeletonization (caused by *Odontota dorsalis* adults) and gall-making (caused by *Obolodiplosis robiniae*). (b) Trees affected mostly by *Odontota dorsalis* feeding, inside of the *R. pseudoacacia* native range (1 August 2023, Morgantown, West Virginia, USA).

pseudoacacia native range from Little (1971). For each of the five damage categories, the effect of distance was tested based on linear regression with damage as dependent variable and logarithm (base 10) of distance from the native range as a predictor variable using the *lm* function in R (www.r-project.org).

To test the hypothesis that the amount of folivory on *R. pseudoacacia* is related to the richness of foliage feeding specialists, we used specialist occurrence records compiled from all world locations in Medzihorský et al. (2023). The number of recorded specialists in a 100 km radius from each study site was used to calculate the species richness at each location. These spatial analyses were performed using ArcGIS Pro 10.1 (ESRI 2022). We then regressed total late season foliage damage as a function of specialist species richness. Two separate regressions were performed: the first regression was on total leaf damage, and the second was on leaf damage excluding leafmines and skeletonization caused by *O. dorsalis*, which was the largest source of leaf damage in most North American sampling locations.

Results

Seasonal distribution of folivory

Seasonal patterns of the timing of various types of feeding damage on *R. pseudoacacia* leaves are shown in Fig. 3. In the North American native range of *R. pseudoacacia* and in the Czech Republic, the total damaged area increased during the vegetation growing season, with a minor decrease at the end of the season in the North American native range (Fig. 3a). In Japan and South Africa, total damage was approximately constant throughout the season, with generally very low damage in South Africa.

Damage by free feeding insects in South Africa and the Czech Republic was ≤ 1% during the entire season (Fig. 3b). Conversely, in Japan free feeding damage remained moderately high through the entire season. In the native range, free feeding damage increased during the first half of the season and then remained approximately constant at a high level (Fig. 3b).

North America is the only region where the locust leafminer *O. dorsalis*, a chrysomelid beetle, is present. This species is present throughout the native range of *R. pseudoacacia* but has also invaded a large portion of the North American continent following the invasion of *R. pseudoacacia* (Medzihorský et al. 2023). Its larvae mine leaflets, whereas the adults skeletonize the leaflet lamina. We observed substantial damage by *O. dorsalis* adults (Fig. 3c) and larvae (Fig. 3e). Skeletonization damage increased through early August and decreased towards the end of the growing season. Damage by the leafmining beetle larvae increased in early summer and then exhibited two peaks.

Galling damage, caused exclusively by *O. robiniae* in the sampled regions, was present in every region except South Africa, where the species is absent (Fig. 3d). Damage was most severe in Japan during mid-summer. Temporal patterns of damage indicate two peaks through the season, though the damage was low in most regions and did not exceed 0.5%.

Leafmines other than those created by *O. dorsalis* larvae are caused mostly by specialist micromoth species of the

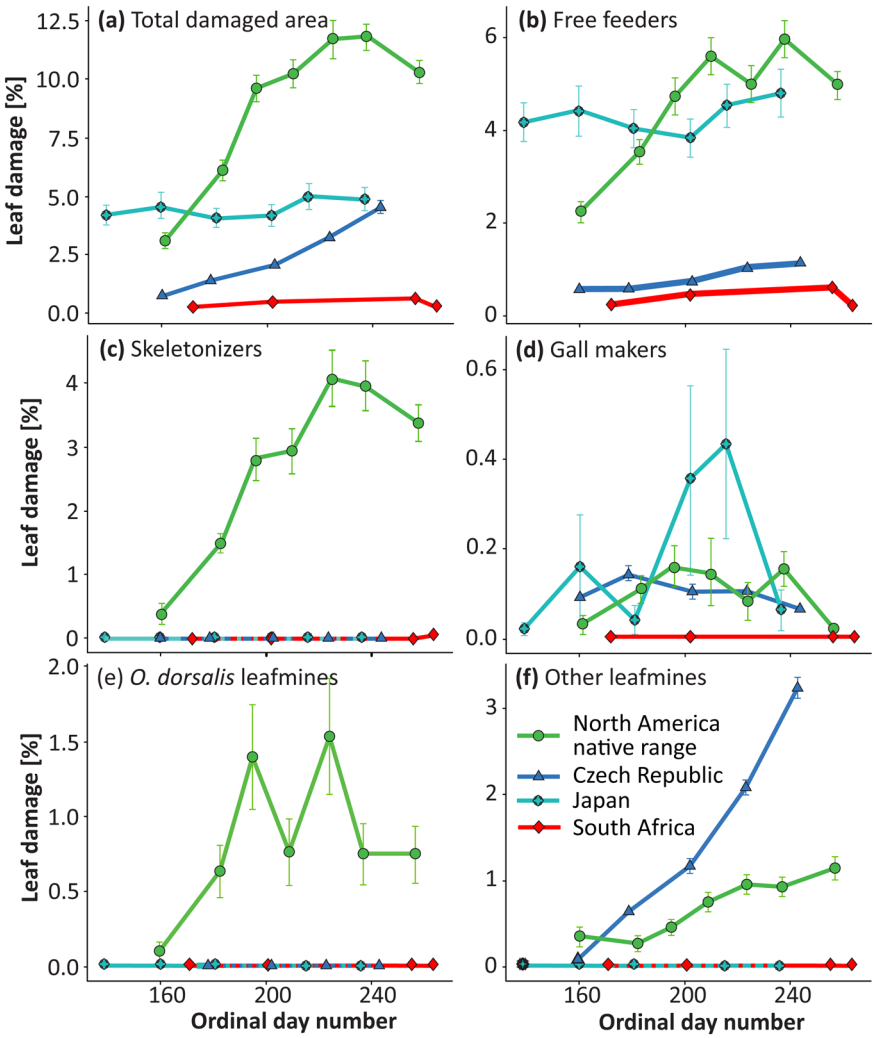

Figure 3. Temporal development of leaf damage (expressed as percent damage) caused by different feeding guilds compared among studied regions across the vegetative season of *Robinia pseudoacacia*; points represent average damage across all plots in region and error bars corresponding SE; (a) total leaf area damaged; (b) damage by free feeding insects; (c) damage by leaf-skeletonizing insects (primarily adult *Odontota dorsalis*); (d) damage by gall-making insects; (e) damage by larval *O. dorsalis*; (f) damage by other larval leafminers.

Gracillariidae family, which are currently not present in South Africa and Japan (Medzihorský et al. 2023). Accordingly, their damage was only observed in North America and the Czech Republic (Fig. 3f). In both regions, damage increased through the entire vegetation season, especially in the Czech Republic.

Global variation in folivory

Total damage recorded at the end of the growing season was much greater in the native range than in any of the other investigated regions (Fig. 4, Table 1). In the native range, the greatest quantity of damage was skeletonization, mostly caused by adults of *O. dorsalis,* along with damage caused by its leafmining larvae (Fig. 4b, Table 1). In the North American invaded range of *R. pseudoacacia*, the damage caused by *O. dorsalis* was significantly less than in the *R. pseudoacacia* native range (Fig. 4b, Table 1). The leafmining caterpillars of gracillariid micromoths caused significantly more leaf damage in the Czech Republic than in any of the other regions (Fig. 4b, Table 1). Gall makers, represented by *O. robiniae*, were present in every studied region except South Africa. This species caused marginal damage in all studied regions except New Zealand, where it was responsible for the majority of leaf damage (Fig. 4b, Table 1). Free feeders are the most species-diverse group (Fig. 4b); their damage had significantly less impact in the Czech Republic and South Africa compared to Japan and North America, where their damage reached much higher levels of 3.6–5.1% (Table 1). There are eight free feeding specialists recorded in North America (five Lepidoptera and three Hymenoptera) but only *Euura tibialis* (Hymenoptera) is recorded outside of North America (it has invaded both the European and Asian Palearctic) (Medzihorský et al. 2023).

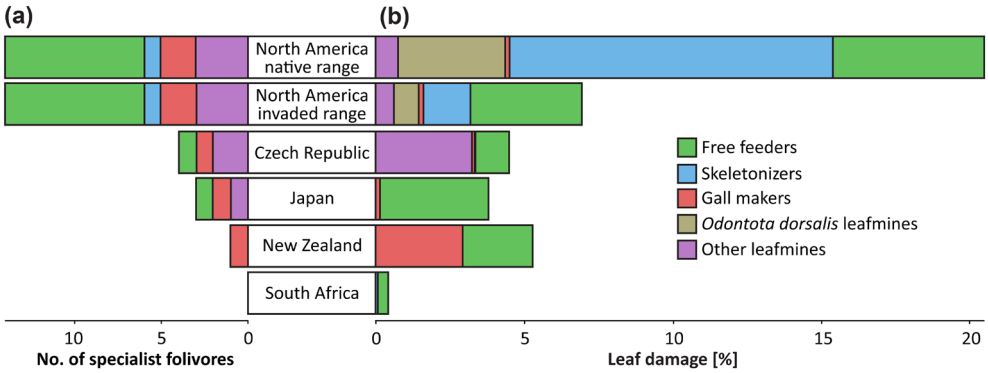

Figure 4. Regional differences in folivore diversity and *Robinia pseudoacacia* leaf damage: (a) number of specialist insect folivores established in each region (taken from Medzihorský et al. 2023); (b) average levels of late-season folivory (%) caused by different feeding groups on *R. pseudoacacia* in each region.

Folivory in relation to distance from native range

The relationships of late season damage levels with distance from the native range at sites sampled in North America (21 outside and 14 inside the native range of *R. pseudoacacia*) is shown in Fig. 5. Total damage is significantly negatively correlated with distance from the native range of *R. pseudoacacia* ($R^2 = 0.52$, $p < 0.01$) (Fig. 5a). Leaf skeletonizers (adult *O. dorsalis*) are most strongly and negatively correlated with distance from the native range ($R^2 = 0.43$, $p < 0.01$) (Fig. 5c), followed by *O. dorsalis* larval leafminers ($R^2 = 0.25$, $p < 0.01$) (Fig. 5e). The damage by free feeders is not significantly correlated with the distance from the native range ($R^2 = 0.1$, $p = 0.1$) (Fig. 5b). Damage caused by gall makers ($R^2 = 0$, $p = 0.9$) and other leafminers (mostly Gracillariidae) ($R^2 = 0$, $p = 0.8$) had insignificant relationships with distance from the native range (Fig. 5d).

Folivory in relation to specialist folivore richness

Regression of mean percent foliage damage on foliage feeding *Robinia* species richness (summarized in a 100 km radius around each damage sampling location) indicated a significant positive relationship (Fig. 6). This pattern was significant both for total leaf damage ($R^2 = 0.29$, $p < 0.01$) and leaf damage excluding damage caused by *O. dorsalis* ($R^2 = 0.15$, $p < 0.01$).

Discussion

Enemy release is a phenomenon common among many non-native species (Keane and Crawley 2002). Although there are some questions about its ubiquity (Williams et al. 2010, Roy et al. 2011), most invasive plants are associated with fewer insect herbivores and are subjected to lower levels of herbivory in their invaded ranges compared to their native range (Liu and Stiling 2006). Here we document this phenomenon in *R. pseudoacacia*; in its invaded range in North America, the Czech Republic, Japan, New Zealand and South Africa, total herbivory levels are less than in its native range (Fig. 4b, Table 1).

The enemy release phenomenon can be broken down into multiple component phenomena (Heger and Jeschke 2014). Here we provide evidence of two of these phenomena: 1) lower herbivory levels in a plant's invaded range than its native range (described above), and 2) lower richness of specialist herbivore species in the invaded range than in the native range. The latter phenomenon is detailed in Medzihorský et al. (2023) but is also summarized here (Fig. 4a). Furthermore,

Table 1. Variation among sampled regions in amounts of late season folivory broken down as damage caused by different feeding groups and expressed as the percent of leaf area that is damaged. Coefficients of determination (R^2) and p-values (p) correspond to the model testing the effect of region on damage for each damage category. Means in the same column followed by different letters are significantly different ($\alpha = 0.05$) based on pairwise comparisons derived from the model.

Region	Total damaged area	Free feeders	Skeletonizers	Gall makers	*Odontota dorsalis* leafmines	Other leafmines
North America, native range	20.5a	5.1a	11.0a	0.1b	3.6a	0.8b
North America, invaded range	7.0b	3.8b	1.6b	0.2b	0.8b	0.6b
Czech Republic	4.5c	1.1d	0.0c	0.1b	0.0c	3.3a
Japan	3.8c	3.7b	0.0c	0.2b	0.0c	0.0c
New Zealand	5.3c	2.3c	0.1c	2.9a	0.0c	0.0c
South Africa	0.4d	0.3e	0.1c	0.0b	0.0c	0.0c
R^2	0.38	0.24	0.46	0.21	0.15	0.40
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01

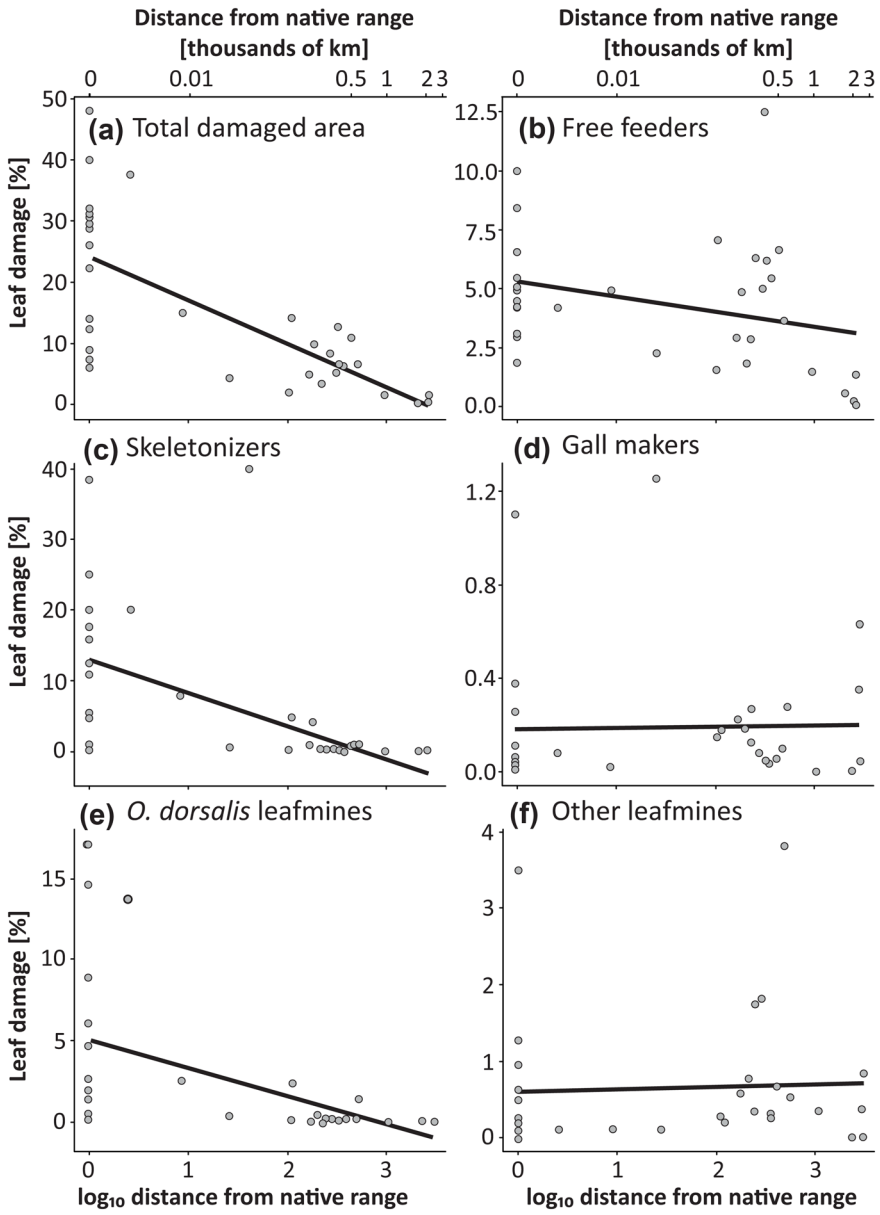

Figure 5. Folivore damage in North America: relationship between $\log_{10}$ distance from the *Robinia pseudoacacia* native range and type of leaf damage: (a) mean total leaf area damage (%) ($R^2 = 0.52$, $p < 0.01$); (b) mean damage by free-feeding insects (%) ($R^2 = 0.1$, $p = 0.1$); (c) mean damage by skeletonizing insects (%) ($R^2 = 0.43$, $p < 0.01$); (d) mean damage by gall-making insects (%) ($R^2 = 0$, $p = 0.9$); (e) mean damage by *Odontota dorsalis* leafmines (%) ($R^2 = 0.25$, $p < 0.01$); (f) mean damage by other leafmining insects (%) ($R^2 = 0$, $p = 0.8$).

we document that these two phenomena are linked; global variation in folivory levels are significantly correlated with the richness of *R. pseudoacacia* specialist species (Fig. 6). The correlation between insect herbivore diversity and herbivory is a general trend seen worldwide (Carvalho et al. 2014) although the evidence presented here regarding herbivory on an invasive plant provides new information.

Our analysis indicates that enemy release declines as more specialist herbivores invade the *R. pseudoacacia* invaded range. In its native range, there are more specialist folivore species feeding on *R. pseudoacacia* than in any region outside of North America (Fig. 4). Patterns of folivory track these patterns of folivore richness, with greatest levels of folivory in the native range. Furthermore, within North America, there is a significant decline in total folivory levels with increasing distance from the native range (Fig. 5a). This pattern is seen both in total herbivory and in damage caused by free feeding insects (Fig. 5b) as well as skeletonization (Fig. 5c) and leafmines (Fig. 5e) made by *O. dorsalis*. The observed decrease in folivory levels with distance most likely reflects the spatial spread of specialist folivores from the *R. pseudoacacia* native range described in Medzihorský et al. (2023).

Among sites located in different continents, total levels of folivory were greatest in the *R. pseudoacacia* native range, and

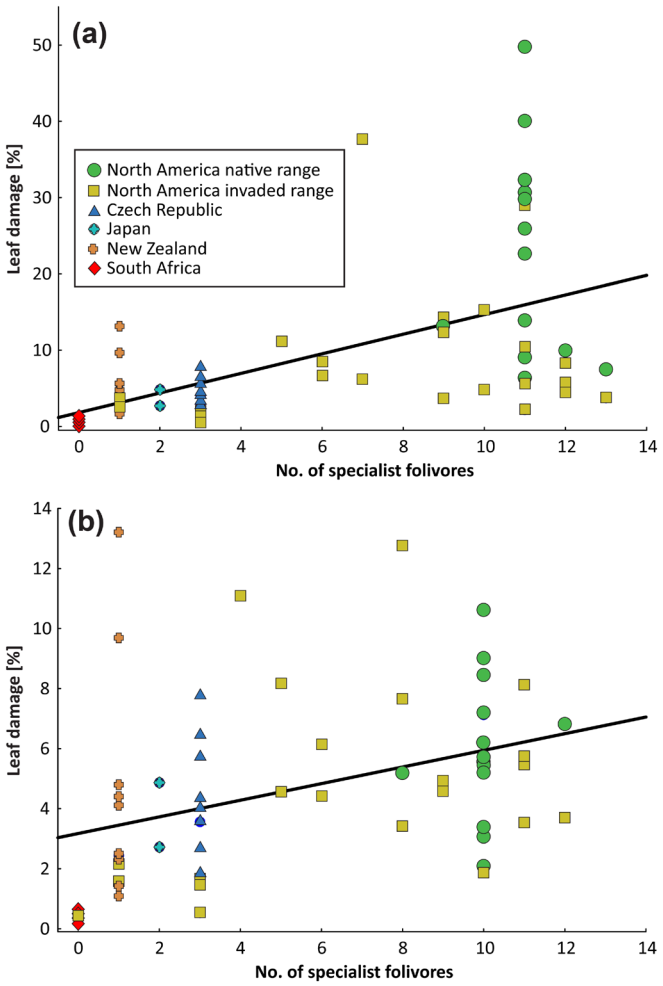

Figure 6. Relationship between foliage damage and number of foliage feeding *Robinia* specialist species among all sampling sites. Number of species (richness) was summarized from occurrence records described in Medzihorský et al. (2023) found in a 100 km radius circle around each foliage damage sampling location. (a) total late-season foliage damage, (b) total late season foliage damage excluding damage caused by *Odontota dorsalis* (larval leafmining and adult leaf skeletonizing).

least in South Africa (Fig. 4b). The history of *R. pseudoacacia* range expansion across the globe is poorly documented. It is likely that it began to spread in North America as soon as Europeans began colonization and large-scale forest clearing in around 1650 (Thompson et al. 2013). Subsequent *R. pseudoacacia* first records in other continents are 1720 in the European Palearctic, 1843 in Australasia, 1858 in the Afrotropics and 1873 in the Asian Palearctic (Medzihorský et al. 2023). This order approximately coincides with decreasing levels of herbivory and decreasing levels of specialist herbivore species richness among regions (Fig. 4, 6).

Differences in specific types of folivory among regions can be largely explained by differences in which specialist folivores are established in each region. For example, substantial levels of leaf skeletonization and *O. dorsalis* leafmines were only found in the *R. pseudoacacia* native range and the North American invaded range (Fig. 4b). This would appear to be the result of specialist leaf skeletonizers (e.g. *O. dorsalis*) only being present in those regions. Furthermore, within the invaded range, there was a distinct pattern of declining levels of skeletonization with increasing distance from the native range (Fig. 5c). This pattern most likely reflects a parallel pattern of declining incidence of *O. dorsalis* presence with increasing distance from the native range (Medzihorský et al. 2023). In more distant locations, *O. dorsalis* either has not yet invaded or populations have not yet built to high densities so skeletonization damage is low. It remains unclear whether, over time, *O. dorsalis* populations in these more distant locations will increase to the high levels seen in the native range. While outbreaks of this species in the native range are typically intense, occurring every year in the same location, little is known about their causes and it is unclear how *O. dorsalis* populations are affected by variation in the abiotic conditions that they experience across North America.

Substantial damage from leafmines created by species other than *O. dorsalis* was only present in the native range, the North American invaded range and the Czech Republic. This most likely reflects the pattern that specialist leafminers (*Macrosaccus robiniella*, *Parectopa robiniella*) have only invaded the non-native *R. pseudoacacia* range in North America and Europe (Medzihorský et al. 2023). However, the gracillariid leafminer moth *Chrysaster ostensackenella* was reported recently from eastern China, where foliage damage caused by this species was reported to be up to 80% (Liu et al. 2015), from South Korea (Koo et al. 2019) and more recently also from Europe (Huemer and Mayr 2022).

Total damage to leaves increased throughout the season in both the North American native range and the Czech Republic (Fig. 3a). Total leaf damage remained relatively constant in both Japan and South Africa (Fig. 3a). Aside from the presence of *O. robiniae* and *E. tibialis* (a sawfly with free feeding larvae) in Japan, there are no specialist folivore species present in these two regions, so damage would have been caused by generalist folivores. Either these agents completed feeding early in the season or leaves damaged by early season feeding fell off and were not included in subsequent samples.

The seasonal distribution of *O. dorsalis* leafmines in the native range was bimodal (Fig. 3e). This may reflect bivoltinism, which has been observed in all but the northernmost distribution of this species in North America (Wheeler 1980). In theory, however, leafmines from the first generation would be retained, so cumulative damage should continuously increase through the season. However, it is possible that leaves or leaflets with mines from the first generation may have fallen off and therefore not have been recorded when the second generation peaked. There was a trend of increasing damage through the season in both North America and the Czech Republic for both free feeding insects (Fig. 3b) and leafminers (Fig. 3f). This most likely reflected the seasonal accumulation of feeding damage caused by *E. tibialis* and/or lepidopteran leafminers.

Damage caused by the gall-maker *O. robiniae* peaked at mid-season in Japan, North America and the Czech Republic (Fig. 3d). This most likely reflected the large numbers of new galls in early summer with damaged leaves, or leaflets falling from trees later in the season. This species is globally the most successful invader among all specialist species (Medzihorský et al. 2023), recorded first in the early 2000s from Japan (Kodoi et al. 2003), in 2007 from the Czech Republic (Skuhravá et al. 2007) and in 2009 from New Zealand (Anonymous 2009). This species causes marginal damage in both the native and invaded region of North America, the Czech Republic and Japan (Fig. 4b–5d, Table 1), but in New Zealand it appears to be more abundant (Fig. 4b, Table 1). In Europe *O. robiniae* spread rapidly during the late 2000s and early 2010s (Skuhravá et al. 2007, Mally et al. 2021), and in some cases the damage levels reached up to 50% (Tóth et al. 2009), but this trend seemed to subside, and currently the rates of damage caused by this species in Europe (especially in the Czech Republic) are low (Fig. 3d–4b, Table 1). This decline might be a result of parasitoid pressure by the main parasitoid of *O. robiniae*, the platygastrid wasp *Platygaster robiniae*, whose invasion closely followed the invasion of its host (Buhl and Duso 2008). However, there is uncertainty whether the widespread occurrence of *O. robiniae* at relatively high population levels in the North Island of New Zealand results from the absence of its parasitoid, or from lower interspecific competition, since all other *R. pseudoacacia* specialist insect species are absent from this region. We note that *P. robiniae* was recently found in New Zealand (Anonymous 2021).

Damage by free feeding insects was particularly high in samples from Japan (Fig 3b–4b), reaching levels comparable to those seen in the *R. pseudoacacia* native range. No free feeding *Robinia* specialists are known to have invaded Japan yet, so it is presumed that this damage was caused by native folivores that are able to use *R. pseudoacacia* as a host. The ability of native herbivores to adapt to feeding on non-native plants is known to be common, but usually is limited to very polyphagous herbivores or to herbivores that are specialized for feeding on closely related native hosts (Branco et al. 2015, Crous et al. 2016). In the case of *R. pseudoacacia*, it is possible that the high levels of free feeding damage are caused by native insects specialized for feeding on the Fabaceae. The Fabaceae is the world's third largest land plant family, and its species are native to every temperate world region (Azani et al. 2017). Therefore, there is considerable potential for native herbivore species to extend their host range to include introduced *R. pseudoacacia*.

One caveat to the interpretation of results here is that, in most regions, sampling was only conducted in one year. Populations of virtually all forest insects tend to fluctuate through time, leading to year-to-year variation in herbivory levels (Schowalter et al. 1986) and such fluctuations likely introduced 'noise' into the relationship between folivory levels and numbers of locally established folivores. In North America and the Czech Republic we did measure folivory in two successive years (not reported here) but observed relatively little interannual variation in folivory. The extreme late-summer defoliation of *R. pseudoacacia* in eastern North America (Fig. 2b) is a phenomenon that is well known to occur virtually every year (Huntley 1990).

In conclusion, data presented here from a worldwide sampling of *R. pseudoacacia* folivory confirm a global pattern of diminishing enemy release. Over the last three centuries, *R. pseudoacacia* has expanded its range in both North America and most temperate regions of other continents. Subsequent to the global spread of this invasive tree, there have been successive waves of invasions by its specialist herbivores. Herbivory levels vary considerably among world regions, reaching the highest levels in the native range of *R. pseudoacacia* and in regions in proximity to the native range. Furthermore, herbivory levels are significantly correlated with numbers of established *R. pseudoacacia* specialists, indicating that as more of these insect species establish outside of their native ranges, herbivory levels will increase. We anticipate that over the next century *R. pseudoacacia* specialists will continue to invade the *R. pseudoacacia* invaded range and enemy release will continue to deteriorate. Even though *R. pseudoacacia* is heavily defoliated in its native range (Fig. 2b), the impacts of this folivory on plant fitness has never been quantified. Consequently, it remains unclear how the demise of enemy release in invasive *R. pseudoacacia* populations will ultimately impact the invasiveness of this plant species.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8sf7m0cww (Medzihorský et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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