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RESEARCH ARTICLE

Insect invasions track a tree invasion: Global distribution of black locust herbivores

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Abstract

Aim: Many invasive plant species benefit from enemy release resulting from the absence of insect herbivores in their invaded range. However, over time, specialized herbivores may 'catch up' with such invasive plants. Black locust is a tree species with a relatively limited native range in North America but has invaded large areas in virtually every temperate continent including North America. We hypothesize that both intra- and intercontinental spread of black locust leads to a parallel, though delayed pattern of intra- and intercontinental spread of insect herbivores.

Location: Global.

Taxon: Black locust, *Robinia pseudoacacia*, and its insect herbivores.

Methods: We compiled historical records of the occurrence of insect herbivore species associated with *R. pseudoacacia* from all world regions. Based on this list, we describe taxonomic patterns and investigate associations between environmental features and numbers of non-native specialist herbivores in the portion of North America invaded by *R. pseudoacacia*.

Results: A total of 454 herbivorous species are recorded feeding on *R. pseudoacacia* across the world, with 23 of these being specialized on *Robinia*. From this group, seven species have successfully expanded their range beyond North America. Within North America, the richness of specialists is explained by a combination of road density, *R. pseudoacacia* density, distance from the *R. pseudoacacia* native range, and climate.

Main Conclusion: Non-native herbivore species have accumulated on invasive *R. pseudoacacia* in both North America and in other continents. The steady build-up of invasions likely has diminished the enemy release that this invasive tree species has benefited from – a trend that will likely continue in the future. These findings support the hypothesis that invasive plants promote parallel though delayed invasions of specialist insect herbivores.

KEYWORDS
biological invasion, black locust, competition release, enemy release hypothesis, herbivore community, invasion disharmony, *Robinia pseudoacacia*, specialist richness, spread

1 | INTRODUCTION

Biological invasions are a major source of global change, altering a variety of ecosystem properties, functions, and processes (Ehrenfeld, 2010; Simberloff et al., 2013). Though influenced by a variety of socio-economic factors, increasing globalization in the form of international trade and travel is considered the main driver of biological invasions (Hulme, 2009; Hulme et al., 2008). There is a long history of moving plant species around the world for purposes of horticulture and agriculture; many of these species have escaped cultivation and become naturalized in non-native regions, displacing native plants and plant communities, with cascading effects on other types of organisms (Rai et al., 2022; van Kleunen et al., 2018). Resulting from this accumulation of non-native species, there is a trend of homogenization of the global flora and fauna (Seebens et al., 2015, 2017).

The enemy release hypothesis (ERH) has been advanced to explain in part why non-native plants are sometimes able to establish and become invasive in non-native regions (Blumenthal, 2005; Keane & Crawley, 2002). Under ERH, plants established outside the distributional range of their co-evolved herbivores experience lower rates of herbivory, which may result in exceptionally high growth and reproduction. For example, a cross-continental comparison of herbivore and fungal damage to *Acer platanoides* in North America vs. in its native Europe (Adams et al., 2009) and a comparison of herbivory on introduced *A. platanoides* vs. native *Acer saccharum* in North America (Cincotta et al., 2009) showed that *Acer* species experienced higher growth and lower herbivory levels in their alien habitats. Hawkes (2007) conducted a meta-analysis of published literature to demonstrate a general tendency for enemy release in non-native plants. Accelerated growth rates, due in part to the absence of co-evolved insects and plant pathogens, have been broadly exploited in agriculture and commercial forestry. For example, trees in the genera *Eucalyptus* and *Pinus* are widely planted in the southern hemisphere where they are subject to relatively low levels of herbivory, exhibiting exceptional growth rates that exceed levels seen in native tree species and in the introduced trees' native range (Hurley et al., 2016; Lombardero et al., 2008). While such enemy release may lead to higher yields of wood products, it also may contribute to the invasiveness of these species when they escape from forest cultivation (Brundu et al., 2020).

The benefits of enemy release may be short-lived as over time the probability of invasions by insect specialists increases in areas where their hosts are widely distributed (Hawkes, 2007). Hurley et al. (2016) found that there has been an increased rate of invasions by *Eucalyptus*-feeding insect species (entirely native to Australia) in areas with expansive *Eucalyptus* plantations. Herbivorous insect invasions are not limited to co-evolved specialized herbivores; the introduction of alien plants may facilitate insect invasions in general, due to increased host plant richness in the established areas. High levels of plant diversity across large spatial scales may create more ecological niches, thereby increasing the probability that an introduced insect herbivore will locate a host and establish (Guo et al., 2019; Liebhold et al., 2018). For example, invasions into North America by the spotted lanternfly *Lycorma delicatula* and the brown marmorated stink bug *Halyomorpha halys*, both native to East Asia and both considered serious pests, may have been facilitated by the presence of their preferred host *Ailanthus altissima* (Haye et al., 2015; Lee et al., 2019).

The success of invasive plants in their non-native ranges is also strongly affected by their interactions with native herbivore communities. Invasive plants affect native insects both directly, through introduction of a novel resource into ecosystems, and indirectly by altering the abundance and overall fitness of native hosts (Bezemer et al., 2014). Multiple studies have reported shifts and adaptations of native generalist and even specialist herbivores to non-native plants (Branco et al., 2015; Graves & Shapiro, 2003). However, invasive plants may sometimes possess chemical or morphological traits, which prevent successful utilization by local herbivore communities (Bezemer et al., 2014).

Black locust, *Robinia pseudoacacia*, provides a good example of a tree species with a limited native range that has been successfully introduced and spread through many parts of the Northern and Southern Hemispheres (Li et al., 2014; Martin, 2019). Before its introduction to Europe as an ornamental tree in the early 17th century (Wein, 1930), black locust was limited to its native range in the central Appalachian Mountains and the Ozark Plateau in the Eastern and Central United States (Huntley, 1990). Subsequently, its varied potential as a fast-growing source of high-quality timber and firewood, its resistance to air pollution in urban settings, and its production of nectar for use in apiculture led to its widespread planting around the world (Li et al., 2014; Martin, 2019). *Robinia pseudoacacia* performs well on disturbed sites and is considered invasive in many parts of its non-native range, with a strong negative impact on native plant species and associated communities (Martin, 2019; Vítková et al., 2017). Even in North America where it is native, *R. pseudoacacia* has greatly expanded its range, especially to the west (DeGomez & Wagner, 2001).

Though it is a member of the globally distributed Fabaceae family, the native range of the genus *Robinia* is limited to North America. Four species of *Robinia* are currently recognized: *R. pseudoacacia*, the shrubs *R. hispida* and *R. viscosa*, and *R. neomexicana* (DeGomez & Wagner, 2001). While the native range of the former three species is the eastern United States, that of the small tree-like growing *R. neomexicana* is restricted to a patchy area in the southwestern United States (Isely & Peabody, 1984; Figure 1b).

While the invasion success of *R. pseudoacacia* might be attributed in part to its formerly mentioned abilities to colonize disturbed sites, its escape from natural enemies in its non-native range may also have contributed. The current study set out to use the multiple independent invasions of *R. pseudoacacia* into different continents across the globe to test whether invasions of insect herbivores track the tree's invasion. Through quantitative analysis of the composition of global insect communities associated with *R. pseudoacacia* in different world regions that each have unique historical timings of the tree's invasion, we test the following hypotheses: (1) the invasion of

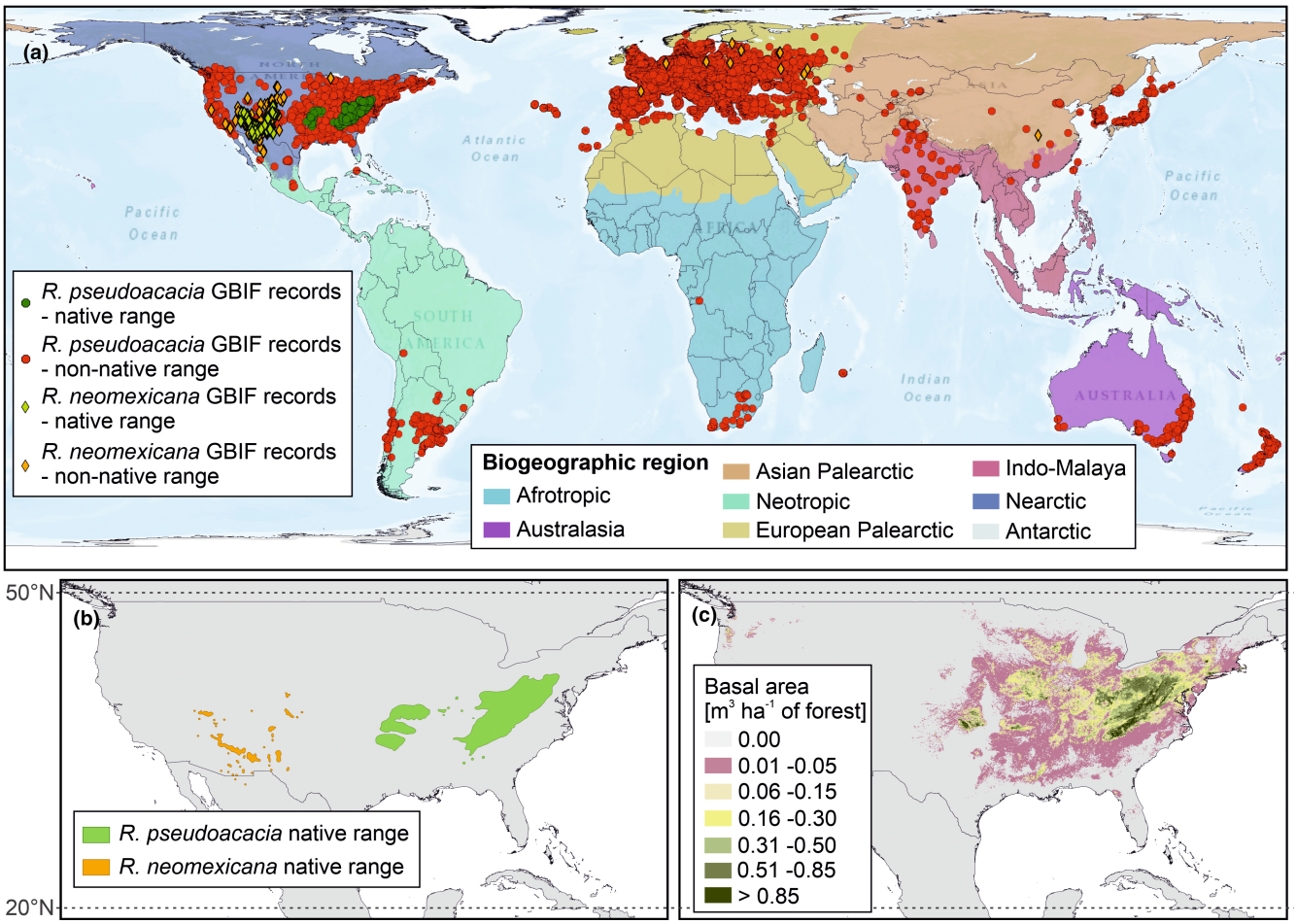

FIGURE 1 Distribution of *Robinia* spp. in North America (a) documented occurrences of *R. pseudoacacia* and *R. neomexicana* based on records from GBIF.org (2022a; 2022b) in the world; (b) native ranges of *R. pseudoacacia* and *R. neomexicana* from Little (1971); (c) basal area [m^2/ha] of *R. pseudoacacia* in forested areas of the conterminous USA from Wilson et al. (2013). Maps are based on a Behrmann cylindrical equal-area map projection.

R. pseudoacacia in seven biogeographic regions is followed by the arrival and establishment of species from the assemblage of specialist herbivores associated with this tree species in its native range; (2) the species richness of these non-native herbivore assemblages increases through time, but decreases with distance from the native range.

Only limited information is available on the community of insect herbivores of *R. pseudoacacia* in both its native (e.g., Baker, 1972; Hargrove, 1986) and non-native range (e.g., Branco et al., 2019; Kulfan, 2012). A comprehensive summary of global patterns of insect communities utilizing *R. pseudoacacia* worldwide is lacking. Here, we strive to document and quantitatively analyse (i) the composition of global insect communities associated with *R. pseudoacacia* in different world regions, (ii) the establishment and spread of *Robinia* insect specialists in their non-native ranges, and to (iii) identify the environmental and socio-economic factors that influence the geographical distribution of herbivore specialists and their spread in North America. Our intention is to focus on this model system in order to better understand the factors driving invasions of specialist herbivores from the native ranges of invasive plants. We hypothesize that both intra- and intercontinental spread of invasive plants leads to a parallel, though delayed pattern of intra and intercontinental spread of insect herbivores. Illumination of how insect invasions track intra- and intercontinental spread of invasive plants would improve our understanding of the role of plant invasions as drivers of insect invasions worldwide (Liebhold et al., 2018). The system of *Robinia* herbivores studied here represents an excellent model system due to the extensive invasion success of *R. pseudoacacia* both in North America and other temperate regions worldwide.

2 | MATERIALS AND METHODS

2.1 | Global database of *Robinia pseudoacacia* herbivore communities

We compiled a comprehensive database of known records of insect herbivore species feeding on *R. pseudoacacia* drawing from the scientific literature, online databases, and personal observations (see Appendix S1 for a complete list of sources). To examine the interregional

patterns of herbivore communities, species occurrence data were summarized for each biogeographic region sensu Wallace (1876). The Palearctic region was further subdivided into its Asian and European portions with the Ural Mountains, the Caspian Sea, and the Zagros Mountains marking the division line. Each recorded herbivore species was classified into one of six feeding guilds: folivores (feeding on leaf tissue), gall-makers, sap-feeders, wood-borers, root-feeders, and frugivores (feeding on fruit). Furthermore, herbivores were classified according to levels of host specificity consisting of monophages (feeding only on the genus *Robinia*), oligophages (feeding on *Robinia* and other Fabaceae genera), and polyphages (hosts spanning multiple plant families). Differences in proportions of species in these categories among biogeographical regions were tested for statistical significance based on Chi-squared statistics using the *chisq.test* function in the R statistical software v4.0.0 (R Core Team, 2020).

Species identified as monophagous (referred to as '*Robinia* specialists' below) were chosen for further analysis of spatial and temporal patterns in their distributions. For this purpose, geo-referenced occurrence records including the year of observation of these species were compiled from the scientific literature as well as from the online databases GBIF (https://www.gbif.org), iNaturalist (https://www.inaturalist.org) and BAMONA (https://www.butterfliesandmoths.org). Appendix S2, Table S2.1 provides DOI links to the GBIF occurrence dataset for each specialist species. Furthermore, the occurrence records of *Robinia* specialist species that we assembled from the literature and databases other than GBIF were uploaded to GBIF as occurrence datasets for each species (Medzihorský et al., 2023). For records where source publications did not include specific geographical locations, the occurrence of species was defined as a geometric centroid of the region (county, municipal district, city, etc.) listed in the source material using GeoHack (https://www.mediawiki.org/wiki/GeoHack).

2.2 | Spatio-temporal analysis of *Robinia* specialists

The geographic coordinates of all occurrence records were aggregated into 50 × 50 km cells prior to analysing the spatial and temporal distribution of *Robinia* specialists. Each grid cell contained a presence–absence value for each species and the total number of specialist species (based on occurrence records from 1800 to 2022) was summed for each cell. In cases of multiple records of the same species inside one grid cell, only the first (oldest) record was considered to analyse the temporal pattern of spread of *Robinia* monophages established outside the native range of *R. pseudoacacia*, using the cumulative number of invaded grid cells through time. We acknowledge that the lack of records for a species from a cell does not prove its absence, but sample species richness is statistically associated with underlying true species richness. Based on the resulting geodatabase, spatial analyses were conducted using ESRI ArcGIS 10.8. (ESRI, 2019).

In addition, a detailed evaluation of the geographical variation in the richness of monophagous species was conducted for the Nearctic region. For this analysis, occurrence records were limited to those located inside the Nearctic region between latitudes 20° N (Central Mexico) and 50° N (Southern Canada), broadly corresponding with the current distribution of *R. pseudoacacia* in North America (see Appendix S3, Figure S3.1). As in the global analysis, counts of species richness were made for each 50 × 50 km cell.

To explore possible mechanisms explaining current specialist species richness, we evaluated associations with a set of candidate socio-economic and environmental variables (Appendix S3, Figure S3.1): (i) average basal area of *R. pseudoacacia* [m^2/ha] (Wilson et al., 2013) available only from USA forest land (density of trees in urban areas were not estimated in these data); (ii) number of GBIF records of *R. pseudoacacia* (GBIF.org, 2022a) and *R. neomexicana* (GBIF.org, 2022b); (iii) average annual mean temperature [°C], (iv) annual precipitation total [mm], (v) temperature seasonality [standard deviation 100], (vi) precipitation seasonality [coefficient of variation] (Fick & Hijmans, 2017); (vii) population density [no. inhabitants km^{-2}] (Schiavina et al., 2019); (viii) total length of railroads [km] (CEC, 2010a); (ix) total length of roads [km] (CEC, 2010b), and (x) distance [km] from the native range of *Robinia* calculated as the nearest planar distance between the geometrical centroid of a given grid cell and the border of the native range. We performed two versions of our analysis. In the first analysis, we fit a mixed-effects model using the above predictor variables (i–x), and including only numbers of *R. pseudoacacia* GBIF records and distance from its native range, that is, without GBIF records of *R. neomexicana*. In the second analysis, we fit the same model but using numbers of GBIF records for both *R. pseudoacacia* and *R. neomexicana* and the distance from the native range calculated from the merged native ranges of both *Robinia* species. Our logic here was that *R. neomexicana* may be an ancestral native host for these *Robinia* specialists and therefore partly explain their successful establishment in new areas. Native ranges of both *Robinia* species were based on digitized versions of maps published by Little (1971) (Thompson et al., 1999).

All variables were first checked for collinearity by calculating pairwise Pearson's correlation coefficients (Appendix S3, Table S3.2) and any collinear variables with $|r| > 0.7$ were eliminated from the analysis, based on their relative performance in the model (comparing Z-values).

Given the over-dispersion of source data, with the conditional variance greatly exceeding the conditional mean, a negative binomial regression model (McCullagh & Nelder, 1989) was used to estimate the effect of the candidate socio-economic and environmental variables on specialist richness (No. of species) in the Nearctic region. Data were analysed using the R statistical software 4.0.0 (R Core Team, 2020) using the *glm.nb* function from the MASS package (Venables & Ripley, 2002).

3 | RESULTS

3.1 | Herbivore community composition

The current distribution of *R. pseudoacacia* includes seven biogeographic regions: the Nearctic (where the native range is located), the European and Asian Palearctic, the Neotropic, Indo-Malaya,

the Afrotropic and Australasia (Figure 1a). Worldwide, 454 insect herbivorous species are documented feeding on *R. pseudoacacia*. The Nearctic has the highest number of species recorded feeding on *Robinia* (225 species), followed by the European Palearctic with 111 recorded species (Figure 2a; Appendix S4). Most of the herbivores utilizing *R. pseudoacacia* are known from these two regions. The Afrotropic region and especially Australasia exhibit very few records of *Robinia* herbivores, with nine and three species, respectively (Figure 2a; Appendix S4). Non-native species represent up to 33% (in Australasia) of the total *Robinia* herbivore communities in the regions, with the highest number recorded in the European Palearctic (24 species). The total numbers of herbivore species in each biogeographical region are negatively correlated with the year of *R. pseudoacacia* establishment (Appendix S5). Proportions of native and non-native species differ significantly among biogeographical regions ($X^2 = 21.02$, df = 6, $p < 0.01$).

The proportion of species in each order also differs significantly among biogeographic regions ($X^2 = 184.2$, df = 42, $p < 0.01$). Except for Indo-Malaya, Lepidoptera (moths and butterflies) are the dominant group of *Robinia*-feeding insects in all biogeographic regions, contributing 35%–100% to the total species pool, though Hemiptera (true bugs, aphids, scale insects, cicadas) have the highest fraction of species recorded feeding on *R. pseudoacacia* in the native Nearctic region (Figure 2b; Appendix S4). Coleoptera (beetles) are dominant in Indo-Malaya, accounting for almost 50% of the species in this region (Figure 2b; Appendix S4).

The folivore-feeding guild comprises the majority of black locust herbivore species globally (Figure 2c; Appendix S4); the sap-feeding guild (represented by the Hemiptera) is most prevalent in the Nearctic region (Figure 2c; Appendix S4; $X^2 = 120.1$, df = 40, $p < 0.01$).

Most of the herbivore community can be considered polyphagous, ranging from 70% to 90% of species recorded in the various

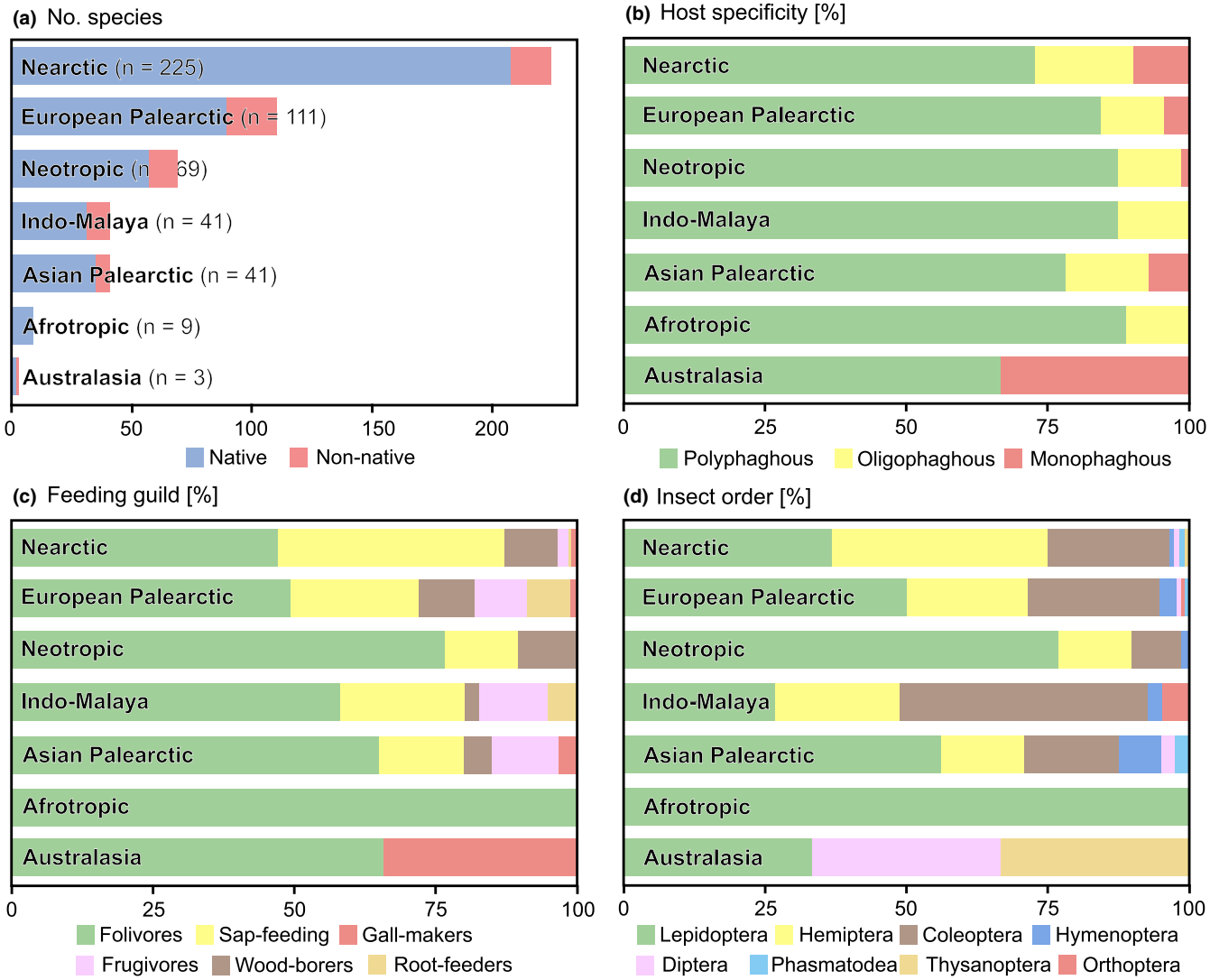

FIGURE 2 Summary of globally recorded insect herbivores of *Robinia pseudoacacia* (see Figure 1a for locations of biogeographical regions) (a) Total numbers of species in biogeographic regions where *R. pseudoacacia* is present; (b) proportion of classes of host specificity in each biogeographic region; (c) proportion of feeding guilds in each biogeographic region; (d) proportion of insect orders in each biogeographic region.

biogeographic regions; however, there is no difference among biogeographic regions ($X^2 = 17.7$, df = 12, $p = 0.13$; Figure 2d). In total, 23 of the 454 globally recorded species feeding on black locust can be considered monophages.

3.2 | Temporal intra-regional patterns in spread of *Robinia* specialists

To date, six species of *Robinia* specialists have invaded biogeographic regions outside of their native Nearctic region: the aphid *Appendiseta robiniae*, the sawfly *Euura tibialis*, the gall midge *Obolodiplosis robiniae*, and the three gracillariid leafminers *Chrysaster ostensackenella*, *Macrosaccus robiniella*, and *Parectopa robiniella* (Figure 3a–f; Appendix S6, Figure S6.3). Of these six species established outside of the Nearctic region, the gall midge *O. robiniae* is the most successful, with the largest invaded area in the Asian and European Palearctic, while also exhibiting the most rapid spread in the short time after its original discovery in Europe in the early 2000s (Figure 3e); it is also the one of the six *Robinia* specialists that are established in Australasia (New Zealand). The other five species spread less rapidly in non-native areas (Figures 3a–d,f). Of the three gracillariid leafminers, *M. robiniella* (Figure 3d) and *P. robiniella* (Figure 3f) became established in the European Palearctic in the second half of the 20th century, and both are steadily spreading throughout the region. *Chrysaster ostensackenella* has only been discovered outside of the Nearctic in the Asian Palearctic region in the early 2010s (Figure 3c; but see Huemer & Mayr, 2022). The sawfly *E. tibialis* was the first species to be recorded outside of the Nearctic, and it is documented from the European Palearctic region since the early 19th century (Figure 3b) and recently in the Asian Palearctic region. The aphid *A. robiniae* is the only specialist that is recorded from the Neotropic region (Figure 3a).

3.3 | *Robinia* specialist richness in the Nearctic region

Robinia pseudoacacia has widely expanded its native range in North America (Appendix S3, Figure S3.1a). While the data shown in Figure 4b are limited to forest (non-urban) settings in the conterminous USA, GBIF records indicate that it has a rather limited distribution in the neighbouring countries of Canada and Mexico (Appendix S3, Figure S3.1a). Overall, 22 insect species in North America were identified as *Robinia* specialists (Figure 4c; Appendix S2, Table S2.1; Appendix S7, Table S7.4); one species (*Euura hispidae*) was omitted from the further analysis as this species had a limited number of documented records (less than 10). Almost all these species have apparently expanded their North American ranges at least 500 km beyond the native range of *R. pseudoacacia* (Figure 4a,c). In the region beyond 600 km from the native range, specialist richness generally declines, and there are only sporadic records of individual species even though the invaded range of *R. pseudoacacia* extends to at least 3000 km (Figure 4). The distribution of the locust borer, *Megacyllene robiniae*, is the most well-documented, both in the literature and public databases (Appendix S2, Table S2.1; Medzihorský et al., 2023; Appendix S7, Table S7.4k); the species is continuously documented at distances up to 2700 km from the black locust native range (Figure 4c).

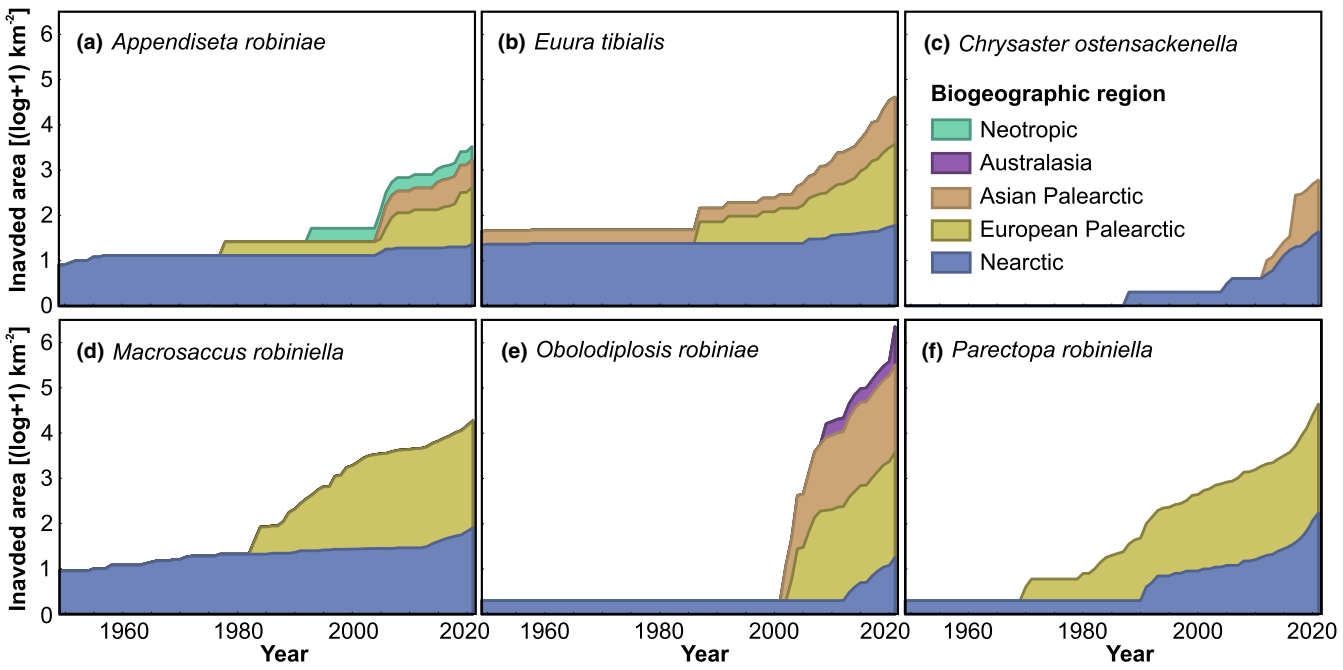

FIGURE 3 Cumulative area (expressed as $\log(a+1)$ km^2) invaded over time for *Robinia* specialist insect species that have established outside of the Nearctic region: (a) *Appendiseta robiniae*; (b) *Euura tibialis*; (c) *Chrysaster ostensackenella*; (d) *Macrosaccus robiniella*; (e) *Obolodiplosis robiniae*; (f) *Parectopa robiniella*.

3.4 | Effects of socio-economic and environmental variables on *Robinia* specialist richness

Results of the negative binomial regression including only *R. pseudoacacia* variables are shown in Appendix S3, Table S3.4, and Appendix S3, Table S3.3 shows the results of the full model. Population density, total length of railroads, and temperature seasonality were removed due to collinearity with other variables (Appendix S3, Table S3.2). The final model with significant effects includes total length of roads, basal area of *R. pseudoacacia*, number of GBIF records of *R. pseudoacacia*, distance from the native range of *R. pseudoacacia*, annual precipitation total, precipitation seasonality, and annual mean temperature. The total length of roads has the highest predictive power and most positive effect ($Z = 27.0$; Appendix S3, Table S3.4a) on the number of recorded specialists. The second highest scoring predictor is basal area of *R. pseudoacacia*, followed by distance from the native range of *R. pseudoacacia*, where a shorter distance is associated with a higher number of recorded specialists. Colder mean temperatures and lower variability in precipitation seasonality are found to have a positive influence on specialist richness. The number of GBIF records of *R. pseudoacacia* has the least predictive power on specialist richness among the set of investigated variables. The model that included the numbers of GBIF records for both *R. neomexicana and R. pseudoacacia* along with distance from the merged native ranges of the two *Robinia* species (Appendix S3, Table S3.4b) showed very similar patterns, with the total length of roads again having the highest predictive power ($Z = 25.6$), followed by the number of GBIF records of *Robinia* ($Z = 15.4$) and distance from the merged native ranges ($Z = -10.5$; Appendix S3, Table S3.4b). Both versions of the model performed nearly equally, showing both the same significance of the independent variables and the positivity or negativity of relationships with the species richness, with the exception of annual total precipitation, which does not have a significant effect on specialist richness in Model 1.

4 | DISCUSSION

Based on the global analysis reported here, we confirm our hypothesis that both intra- and intercontinental spread of invasive *R. pseudoacacia* leads to a parallel, though delayed pattern of intra and intercontinental spread of insect herbivores that feed on it. Specifically, we find that the richness of established specialist herbivores feeding on *R. pseudoacacia* in seven biogeographic regions is positively related to the length of time since the tree species has been introduced (Appendix S5, Table S5.4). Furthermore, in regions of North America outside the native range of *R. pseudoacacia*, the numbers of established herbivore species steadily increase with time, and richness is inversely related to distance from the *R. pseudoacacia* native range (Appendix S3, Table S3.4; Figure 4).

Herbivory levels and herbivore community composition associated with alien plants such as *Eucalyptus* or *Prunus serotina* have been shown to increase over time after the introduction of a non-native plant species (Hawkes, 2007; Hurley et al., 2016; Schilthuizen et al., 2016), and patterns of global diversity of *Robinia* herbivores are consistent with these observations. A meta-analysis of 62 studies showed that herbivory on invasive plants tends to increase over time since naturalization, supporting the concept of declining enemy release (Hawkes, 2007). The Nearctic region, in and around the native black locust range, supports the most diverse herbivore community, followed by the European Palearctic (Figure 2a). The latter region also harbours most of the globally recorded non-native *Robinia* herbivores, likely due to the long-established trans-Atlantic trade and respective pathways for insect spread (Wilson et al., 2009). Furthermore, black locust has been established in Europe longer than in any other alien region, with its introduction in the first half of the 17th century (Wein, 1930), whereas it was introduced in other world regions around the turn of the 19th century (e.g., Guo et al., 2022; Martin, 2019; Owen, 1996). Herbivore specialists from *Robinia*'s native range had comparatively more time in Europe to 'catch up' with their invading host plant than in the other regions (sensu Hawkes, 2007). In comparison, the Afrotropic and especially Australasian regions report very few herbivores feeding on black locust. Much of this may reflect generally low rates of species reporting (Rocha-Ortega et al., 2021). However, *R. pseudoacacia* was introduced to South Africa only in the late 19th century, and its distribution on the continent is largely restricted to this country (Figure 1a; Martin, 2019); in China, it is reported naturalized since 1878 (Guo et al., 2022); in Australia, the first known trees were planted before 1850 (Martin, 2019), and in New Zealand, it was naturalized in 1870 (Owen, 1996). The negative correlation between the year of the first known *R. pseudoacacia* establishment and the number of recorded herbivorous species observed in each biogeographic region (Appendix S5) supports the theory of increasing herbivore species richness on non-native plants. Though we did not collect data on herbivory levels, temporal patterns of increasing numbers of invasions by specialist herbivores observed in our results (Figure 3; Appendix S5) suggest that invasive *R. pseudoacacia* may face decreasing enemy release over time. Furthermore, these results support our hypothesis that global patterns of herbivore invasions follow a parallel, though delayed pattern of intra- and intercontinental spread.

In addition to being affected by invasions by specialist herbivores from their native range, non-native plants may also be affected by resident polyphagous insects that can utilize them as hosts. As the majority of insect herbivores are specialists on a narrow group of related plant species (Forister et al., 2015), a key determinant of the ability of any insect herbivore to utilize an introduced plant as a host is the plant's phylogenetic similarity to native host plants (Grandez-Rios et al., 2015; Harvey et al., 2012; Pearse & Altermatt, 2013). This phylogenetic trend may help explain the proportionally more frequent oligophagous species observed in the Asian Palearctic (Figure 2), where closely related native leguminous trees occur (e.g., *Styphnolobium japonicum*, *Maackia amurensis*), whereas such hosts are less common or absent in other biogeographic regions. To date,

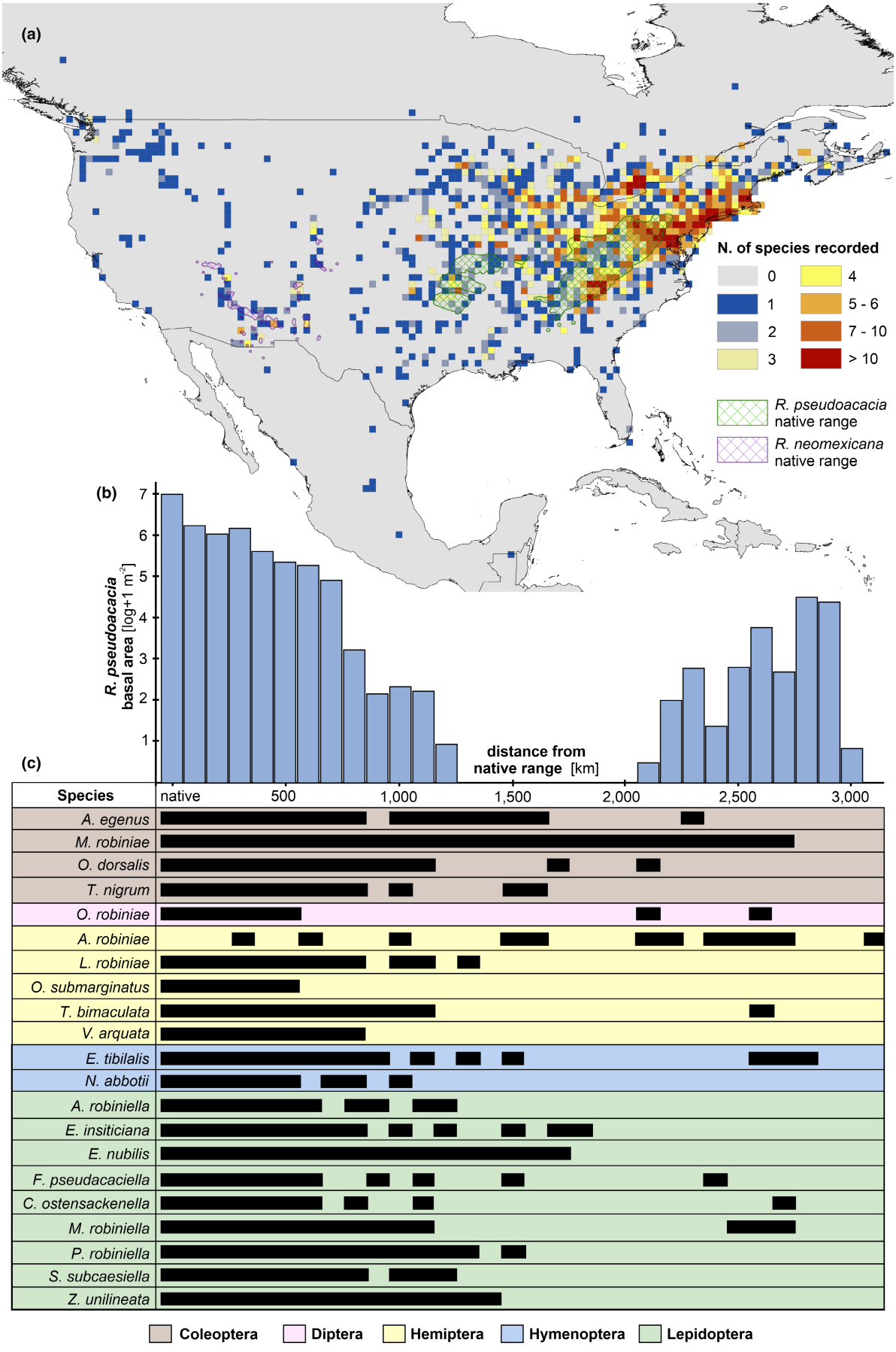

FIGURE 4 Spatial distribution of *Robinia pseudoacacia* specialist insect species in North America. (a) Map of the Nearctic region, showing numbers of species recorded in 50 × 50 km grid cells. Map created using a Behrmann cylindrical equal-area map projection; (b) sum of *R. pseudoacacia* basal area (log $x + 1\,m^2$) in the native range ('native' on x-axis) and in 100 km buffer zones around the tree's native range; (c) spatial records of *Robinia* specialists in 100 km buffer zones around the native range of *R. pseudoacacia*. Figure 4b,c share a common x-axis.

six North American *Robinia* specialists have managed to establish in other biogeographic regions of the world. Among these, the locust gall midge *Obolodiplosis robiniae* appears to be the most successful species, with the largest invaded area despite being the second-most recent invader (Figure 3e). The species' success is likely attributable to factors such as its expressed multivoltinism with up to six generations per year (Shang et al., 2015), a high average spread rate of 128 km per year in Europe, and its (potentially human-mediated) ability to quickly spread over long distances (Mally et al., 2021).

The sawfly *Euura tibialis* has been established for the longest time in a biogeographic region other than the Nearctic (Figure 3b). It is present in Europe at least since 1825 (Rasplus et al., 2010), and has recently also been reported from Japan (Ichikawa, 2015; Shinohara & Hara, 2020). In Europe, this parthenogenetic species feeds on *R. pseudoacacia* and *R. viscosa*. In its native North American range, it was also reported to feed on *R. hispida* and the honey locust, *Gleditsia triacanthos* (Darling & Smith, 1985; Raizenne, 1957). The report of Raizenne (1957) of honey locust as a food plant is suspicious, and we suppose that the author might have misidentified *R. pseudoacacia* as *G. triacanthos*. *Euura tibialis* might be confused with a related species, *E. hispidae*, which also feeds on *Robinia*; so far, the latter species is only known from the USA (Darling & Smith, 1985; Taeger et al., 2018).

Appendiseta robiniae is the only one of the six *Robinia* specialists that has established in South America (Pagnone et al., 1993). In favourable conditions, the species produces up to 11 generations per year; development is however strongly temperature-dependent, with an optimum below 30°C (Borowiak-Sobkowiak & Durak, 2012). Being such a strongly reproducing species and adapted to temperate climates, *A. robiniae* is likely to spread to other regions where its host is found in abundance, such as New Zealand and South Africa.

The leafminer family Gracillariidae is the most successful group, with three *Robinia* specialist species established in other regions of the world: *Parectopa robiniella* and *Macrosaccus robiniella* have invaded the European Palearctic in the 1970s and 1980s and since then have successfully spread across large parts (Mally et al., 2021), while *Chrysaster ostensackenella* has established in the Asian Palearctic only very recently, where it is reported from East China and South Korea (Koo et al., 2019; Liu et al., 2015). Even more recently, Huemer and Mayr (2022) reported a single specimen of *Ch. ostensackenella* from Central Italy as a first record for Europe, and they suspect the species to be already established in that region but confirmation of this is needed.

In addition to the six North American *Robinia*-feeding insect species that have invaded other biogeographic regions (Figure 3), there appears to be a seventh species. The phytophagous chalcidoid wasp *Bruchophagus robiniae*, feeding on the seeds of *R. pseudoacacia* and *R. viscosa*, was described in 1970 from Ukraine (Zerova, 1970). As the species has only been recorded from *Robinia* and not from other Fabaceae native to the Palearctic (Zerova, 1970; Zerova et al., 2017), it appears unlikely that it is native to that region. However, to our knowledge, *B. robiniae* has not been recorded from its presumably native North American range (see Appendix S6, Figure S6.3b). It may be that the fauna associated with *R. pseudoacacia* in its rather limited native range is incompletely characterized. Interestingly, *B. robiniae* is not the only *Robinia* specialist that was first scientifically described from its (presumably) non-native range: *Appendiseta robiniae* was described from Denver, Colorado (Gillette, 1907), and *Euura tibialis* from the English Isle of Wight (Newman, 1837), but both have subsequently been recorded from the native range of *R. pseudoacacia*.

North America supports the highest diversity of *Robinia* specialists. The range of most specialists is found at least 500 km beyond *R. pseudoacacia*'s native range, indicating that, like their host, they have expanded their North American ranges. The locust borer, *Megacyllene robiniae*, appears to be the most successful species in extending its range, as it is present in all 100 km zones from black locust's native range up to 2700 km beyond, reaching the North American West coast and Central Mexico. *Megacyllene robiniae* is a large beetle in the Cerambycidae family with a colourful appearance, which likely contributed to the species' extensive occurrence data over a large range. The locust borer is also the species with the largest impact on black locust (DeGomez & Wagner, 2001). The sawfly *Nematus abbotii*, the plant bug *Orthotylus submarginatus*, and the treehoppers *Thelia bimaculata* and *Vanduzea arquata* have not been found further than 500 km from the *R. pseudoacacia* native range, although this may in part reflect a lack of reporting of these species. A similar sampling bias may be responsible for the sparsity of records for *Appendiseta robiniae* and *Obolodiplosis robiniae* across the non-native North American range. This is especially pronounced in the case of *O. robiniae*, where the few North American records are outnumbered by more than 1000 records from other parts of the world, where the species has a large (mostly aesthetic) impact on black locust. In its native range, however, *O. robiniae* appears to be present only in low numbers, or under-sampled. However, in the case of *A. robiniae*, this species was collected in the southwestern USA, within the range of *R. neomexicana* (Miller et al., 2016), so *R. neomexicana* may be its ancestral host.

Within North America, there are several Chrysomelid beetles that have specialized on *Robinia*, and most of these have expanded their North American range, although none of them has ever invaded another world region. Among these, *Odontota dorsalis* often reaches epidemic densities, causing extensive defoliation of its host (Ford & Cavey, 1985). Despite its extreme abundance, this species appears to be a poor invader. It has never invaded another biogeographic region and only has a limited area in North America where black locust is abundant (Appendix S7, Figure S7.4n).

Liebhold et al. (2021) found Chrysomelidae to be slightly under-represented among non-native assemblages around the world, suggesting that there may be some unknown characteristics of beetles in this family that lessen their likelihood of successful establishment in non-native regions.

Variation among herbivore species in the extent of both their intra- and intercontinental invasion success most likely coincides with the phenomenon of 'invasion disharmony', where certain groups of insects are over-represented among non-natives, while others are under-represented. This phenomenon has previously been demonstrated for worldwide Coleoptera (Liebhold et al., 2021) and Lepidoptera (Mally et al., 2022) invasions. Among the North American native *Robinia* specialists, *Megacyllene robiniae* has spread the furthest beyond the black locust native range in the Nearctic, while it has not spread to any other biogeographic region. In contrast, *Obolodiplosis robiniae* is among the least successful spreaders in North America in terms of distance from black locust native range but has successfully spread to the European and Asian Palearctic as well as to New Zealand. Such patterns of invasion disharmony have been hypothesized to result from biological traits that affect either their likelihood of transport in invasion pathways or their probability of establishment upon arrival, thereby filtering which species are successful invaders. Taken together, these factors result in interspecific variation in invasion success and invasion disharmony (Liebhold et al., 2021).

Within North America, there was considerable variation in the species richness of *Robinia* specialists (Figure 4a). Some of the areas with the greatest richness fell slightly outside of the native range of *R. pseudoacacia*. This reflects not only the spread of these species within North America, but also a likely greater search/reporting effort in the mid-Atlantic region. Road density has the highest predictive power on specialist richness, and significantly contributed to explaining the species richness in our final model (Appendix S3, Table S3.4a). Historically, *R. pseudoacacia* has frequently been used for soil erosion control (Keresztesi, 1980; Vítková et al., 2017) and in afforestation efforts in heavily disturbed areas (Zeleznik & Skousen, 1996) such as mining lands and along transport corridors (Bettosini, 2014; Kolbek et al., 2004). Such large-scale changes in landscape elements promote the movement of herbivorous species by altering the abundance of host plant species, by improving the structural connectivity of favourable habitats (Bezemer et al., 2014), and by increasing the overall risk of invasion in urban-influenced areas (Branco et al., 2019; Paap et al., 2017; Ward et al., 2019). *Robinia* density (both basal area and number of GBIF records) was also a significant predictor of species richness, most likely reflecting the positive effect of host abundance on population growth and spread (Liebhold & Tobin, 2008). Similarly, Mally et al. (2021) found that *Robinia* density facilitated the spread of three non-native *Robinia* specialists in Europe. Moving farther from the black locust native range, specialist herbivore richness generally declined in areas beyond 500 km from the native range (Figure 4c), and distance was the third most significant predictor of richness in our model (Appendix S3, Table S3.4a). For most insects, climatic suitability is a critical factor that influences their invasiveness and potential spread rate (Bacon et al., 2014; Ward & Masters, 2007). The negative effect of annual mean temperature and precipitation seasonality on species richness observed in our results may initially seem perplexing; however, it probably reflects the mostly northward expansion of *R. pseudoacacia* in North America (Appendix S3, Figure S3.1a) toward higher latitudes and colder climates (Appendix S3, Figure S3.1e), and a similar pattern was reported by Mally et al. (2021) for Europe.

Given its extensive distribution in North America and elsewhere in the world, black locust can be considered a massively successful invasive species (Martin, 2019; Vítková et al., 2017). Successful plant invasions may be attributable to different factors, such as changes in the plant's genetic composition following its introduction, the plant's phenotypic plasticity, as well as escape from herbivores and pathogens (Hawkes, 2007). Numerous studies have investigated these different aspects, but it remains difficult to clearly distinguish between the effects of these factors on the success of this particular plant. Black locust exhibits a high genetic diversity in its native range (Mebrahtu & Hanover, 1989; Surles et al., 1989) as well as in China (Guo et al., 2022), but studies directly comparing the genetic composition between native and non-native populations are still lacking. Bouteiller et al. (2021) found differences in the phenotypic plasticity between native and non-native (European) populations of black locust, with an increased germination rate in the European populations. Furthermore, numerous other studies investigated black locust in its non-native range and found a generally high degree of phenotypic plasticity, also in comparison with other trees (e.g., Granata et al., 2020; Guo et al., 2018; Luo et al., 2016; Mantovani et al., 2014; Su et al., 2021; Xu et al., 2009). Within North America and elsewhere, the success of black locust can be attributed to its ability to thrive in disturbed habitats (Boring & Swank, 1984). Its traits of nitrogen fixation and indeterminant growth allow the species to grow quickly in sites with poor soil conditions. Human activities such as agricultural clearing, road building, etc. have no doubt promoted the spread of this species. However, the role of enemy release in the success of black locust remains uncertain. The species often suffers from very high levels of herbivory in its native range (Hargrove et al., 1984), but similar levels of herbivory are not reported from other biogeographic regions. Here we document markedly lower diversity of *Robinia*-feeding herbivores in its invaded range. To clarify the role and impact of insect herbivory in the success of black locust as an invasive plant, it would be useful to carry out studies in North America (both in the native and invaded ranges) as well as in invaded areas in other continents. In North America, the complete native herbivore assemblage appears to be tracking the spread of black locust beyond its native range (Figure 4a,c) while herbivore assemblages in other continents remain incomplete; this pattern may facilitate future studies to distinguish between the effects of 'enemy release' and those of 'competition release' (Keane & Crawley, 2002) in black locust.

Results presented here demonstrate a more general pattern in which the global spread and local dominance of invasive plants promote invasions of specialist herbivores. Widely distributed invasive plants provide ecological niches for non-native herbivores, and their presence increases the likelihood of successful herbivore

establishment following arrival. The global proliferation of invasive plants thus explains the global association between plant and insect invasions (Liebhold et al., 2018). Furthermore, the steady accumulation of specialist herbivores over time contributes to a decline in the beneficial release of invasive plants from natural enemies.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GBIF as occurrence records dataset at https://doi.org/10.15468/zt8g2r.

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BIOSKETCH

Our research team specializes in reconstructing global insect invasion dynamics as part of the larger project 'EVA4.0–Advanced research supporting the forestry and wood processing sector's adaptation to global change and the 4th industrial revolution' at the Czech University of Life Sciences. Our current focus is on the global distribution, diversity, systematics, biogeographic patterns, and host specificity of non-native insect species feeding on *Robinia pseudoacacia*.

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SUPPORTING INFORMATION

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

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