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Research Article

Does biotic resistance govern forest invasions by bark and ambrosia beetles?

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The theory of biotic resistance states that community diversity promotes resistance to biological invasions. This theory has been widely explored for its ability to explain variation in habitat invasibility to non-native plant species and while the theory holds in some systems, it does not in others. In the case of invasions by herbivorous insects, invasibility could be affected by diversity of plants and/or by diversity of native insects. While only a few studies have explored biotic resistance to insect invasions, limited evidence suggests that plant diversity can actually have a positive effect on invasibility via creation of niches for herbivorous insects though other studies of insect systems indicate that plant diversity has a negative effect on invasibility by diluting the density of hosts. Almost nothing is known about how native insect diversity affects resistance to invasions by other insects. Here we analyzed a unique inventory of native and non-native Scolytinae/Platypodinae (bark and ambrosia beetles) across the conterminous USA. We assessed the correlates of geographical variation in numbers of both native and non-native species per 50 × 50 km cell. We find that native tree diversity generally has positive effects on the richness of native beetle species, while the abundance of non-native hosts promotes richness of non-native beetles. We also observed that the effect of native beetle diversity on non-native Scolytinae/Platypodinae species richness is either lacking or positive. These results indicate fundamental differences between plants and insects in the way native and non-native species interact; while interspecific competition can exert a strong influence on plant invasions, it appears less important for insects. Results thus indicate that the biotic resistance hypothesis does not explain invasion patterns of bark and ambrosia beetles.

Keywords: angiosperm, conifer, diversity, invasibility, Platypodinae, Scolytinae, species richness

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Introduction

Largely as a result of globalization, increasing numbers of insect species are expanding their ranges into new regions outside of their native ranges. Insects exhibit considerable diversity of life histories and corresponding to this are a diversity of pathways that facilitate their accidental transport and establishment (Gippet et al. 2019, Meurisse et al. 2019). While most non-native species have little known impact (Williamson and Fitter 1996), others have extremely large effects on agriculture, forestry and ecosystem functioning (Kenis et al. 2009, Bradshaw 2016).

The risk of new invasions depends both on the characteristics of the invading species as well as characteristics of the recipient habitat. Invasibility refers to the set of biotic and abiotic environmental traits that make an environment more susceptible to invasions (Lonsdale 1999). While considerable work has focused on environmental traits of invasibility to plant invasions, less is known about invasibility as it relates to insect invasions. One of the environmental traits affecting insect invasion success that has been more extensively explored is climate, though this has largely been limited to climate suitability for individual insect species (Ulrichs and Hopper 2008). Less work has focused on other environmental attributes or how climate affects invasibility to large groups of species.

A concept that dominates much of the previous work on habitat invasibility is Elton's theory of biotic resistance, which hypothesizes that more diverse communities are resistant to biological invasions (Levine and d'Antionio 1999). The theory has almost exclusively been applied to plant invasions and there is little agreement about the ubiquity of this pattern (Fridley et al. 2007). The concept has rarely been applied to insect invasions, so the role of native biodiversity in shaping ecosystem susceptibility to insect invasions remains largely unknown. A large fraction of insects are herbivores, and the availability of suitable host plants is well known to be a requirement for establishment of herbivorous insects (Guo et al. 2019). Host plant diversity is known to either promote invasions through the creation of ecological niches for insect herbivores (Liebhold et al. 2018, Bertelsmeier et al. 2024), or conversely, host plant diversity can suppress invasions; under the 'dilution effect', greater diversity of host trees can make it less likely for herbivorous insects to locate their hosts and reproduce (Jactel et al. 2021). Furthermore, greater host plant diversity could promote the diversity of predators and parasites (Jactel et al. 2021) and thereby suppress invasions. To date, evidence exists for both positive and negative effect of tree diversity on insect invasion rates with these effects varying among species or groups of insects (Ward et al. 2022).

Socioeconomic and environmental factors can also affect insect invasibility. Previous work in various insect systems indicates that local economic activity and human demographics are associated with greater travel and cargo transport which translate into increased propagule pressure (Koch et al. 2011, Epanchin-Niell et al. 2022). Human settlement also tends to be associated with plantings of diverse assemblages of plants, including non-native plants, that create ecological niches for insect herbivores and thereby facilitate invasions (Augustinus et al. 2024, Bertelsmeier et al. 2024).

Here we use the true bark and ambrosia beetles (Scolytinae and Platypodinae) as a case study for exploring landscape level drivers of habitat invasibility and biotic resistance. The true bark beetles and ambrosia beetles are not phylogenetically distinct groups, but they do represent distinct life histories; the true bark beetles generally feed on tree phloem whereas ambrosia beetles feed on mutualistic fungi which they culture in tunnels constructed in tree xylem (Kirkendall et al. 2015). More than 120 Scolytinae/Platypodinae species are known to have established outside of their native range worldwide (Lantschner et al. 2020). Many of the most damaging non-native scolytines are ambrosia beetles that are limited to colonizing dead trees in their native range but are sometimes able to colonize healthy living trees in their invaded ranges, where trees lack resistance to the pathogenic fungi that these species vector (Ploetz et al. 2013).

Here we analyze a unique, comprehensive database of the occurrence of all known native and non-native Scolytinae/Platypodinae in North America (Atkinson 2024) to investigate the drivers of invasibility in the USA. Specifically, we focus on the effects of community biodiversity, both diversity of trees and of the native bark and ambrosia beetle community, on the richness of both native and non-native Scolytinae/Platypodinae species and how effects vary between bark and ambrosia beetles and between species feeding on conifers vs. angiosperms. We hypothesize that, as is often the case for plant invasions, native biodiversity confers a level of resistance to beetle invasions. We also hypothesize that geographical variation in economic activity translates into variation in propagule pressure, leading to parallel patterns in numbers of invasions. Taken together, we anticipate that this information can provide insight into geographical variation in invasibility and ultimately guide biosecurity surveillance for new invasions in the future (Nahrung et al. 2023).

Methods

Data collection

A list of georeferenced Scolytinae and Platypodinae occurrence records in the USA was extracted from the Bark and Ambrosia Beetles of the Americas Database (Atkinson 2024). This database was compiled from published occurrence records, detection records from the USDA Forest Service Early Detection Rapid Response trapping program (EDRR, Rabaglia et al. 2019), a database of specimens at the Albert J. Cook Arthropod Research Collection at Michigan State University (www.canr.msu.edu/ent/research/arthropod_research_collection/index), a database of specimens at the University of Arizona Insect Collection (https://uaic.arizona.edu/), and physical specimens examined by T. H. Atkinson from various insect collections. Only records with a verified georeference (geographic coordinates) were considered

from the original source database. The database was subset to only include specimens falling within the continental USA (Fig. 1). In total, 6558 records originated from chemically baited traps, 887 from other traps and 18 522 from other sources (direct sampling of host plants, sweep netting, other methods, and unrecorded methods). The exact number of records for individual groups is presented in Table 1.

In addition to geographical coordinates, each record included species, status of nativeness (native or non-native in the USA), principal host type (either conifer or angiosperm) and feeding guild (true bark beetles, ambrosia beetles and 'other'). The main database was subset into separate databases for native and non-native beetle species, and further divided based on host type and on feeding guild (Table 1). Using the full database and several subsets, separate analyses were conducted for native and non-native species richness to search for drivers of both native and non-native species richness.

Classification into host type was based on host association data recorded in the original database and from Šenfeldová et al. (2024). Species that do not feed on trees or shrubs were excluded from analyses of richness broken down by host type, however these species were included in the full database for analysis of total species richness and analysis of richness broken down by feeding guilds. Records of species feeding on both conifers and angiosperms were included in both host type subsets.

Three feeding guilds were considered: true bark beetles (species feeding on phloem of stems and treetops), ambrosia beetles (species living in xylem and feeding on symbiotic fungi), and 'other' for species that did not correspond with the previous groups (e.g. seed feeders such as *Coccotrypes dactyliperda*). Although a large proportion of species were classified as the feeding guild 'other', given the limited number of spatial records for these species, this group was excluded from the feeding guild analysis.

Analysis of the geographical variation in species richness was conducted across the conterminous USA (Fig. 1). The geographic coordinates of all occurrence records of individual Scolytinae/Platypodinae species were used to calculate species richness in 50 × 50 km grid cells (in cases of multiple records of the same species inside one grid cell, only one record was considered). This spatial resolution was chosen based on balancing the need to capture spatial variation in species richness, while avoiding the inflation of zero richness measurements at small scales. Cells that fell partially outside of the conterminous USA were excluded from further analyses. The final data thus consisted of 3376 cells.

The 100th meridian west was used for comparing Scolytinae/Platypodinae species richness between the eastern

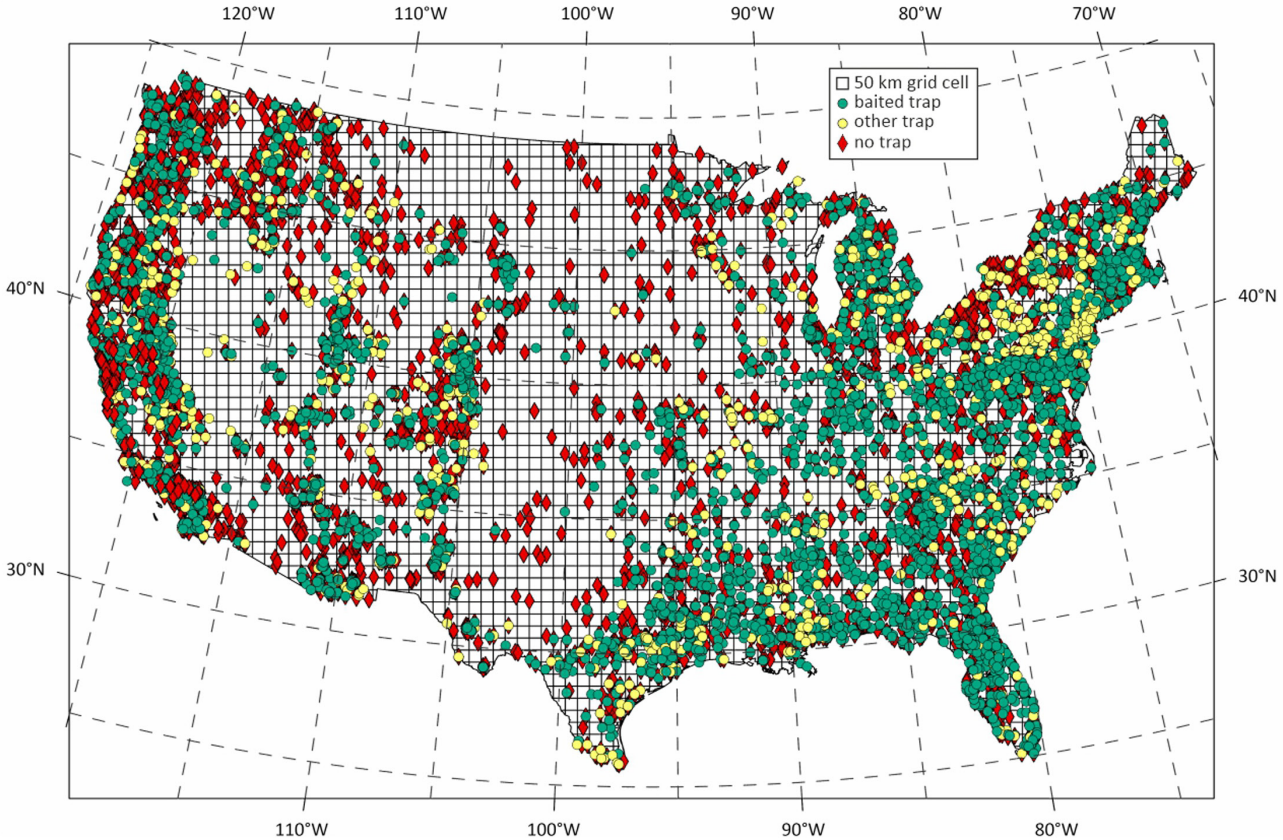

Figure 1. Location of georeferenced Scolytinae and Platypodinae occurrence records in the USA from the Bark and Ambrosia Beetles of the Americas Database (Atkinson 2024).

Table 1. Number of occurrence records for different groups of Scolytinae/Platypodinae species sampled using different methods.

Group	Chemical-baited trap	Other trap	No trap
Total native Scolytinae/Platypodinae species richness	10 947	2197	17 848
Total non-native Scolytinae/Platypodinae species richness	4343	715	2339
Conifer feeding - native	6311	792	11 688
Angiosperm feeding - native	4626	1371	6006
Conifer feeding - non-native	778	92	250
Angiosperm feeding- non-native	3531	623	1926
Ambrosia beetles - native	4076	972	3617
True bark beetles - native	5846	791	10 240
Ambrosia beetles - non-native	3606	481	1176
True bark beetles - non-native	712	96	837

and the western USA. An independent samples *t*-test was used to evaluate the differences in mean richness between the two regions.

Species richness analysis

Geographical variation in Scolytinae/Platypodinae species richness was explored by evaluating associations with a set of candidate environmental and socio-economic predictor variables (Supporting information): 1) average annual mean temperature [°C] (Fick and Hijmans 2017); 2) annual precipitation total [mm] (Fick and Hijmans 2017); 3) human population density [no. inhabitants per cell] (Schiavina et al. 2019; 4) average income per capita ; 5) total length of roads [km] (CEC 2010); 6) total forest area [km^2] (Dewitz 2023); 7) basal area of native angiosperms [m^2]; 8) basal area of non-native angiosperms [m^2]; 9) basal area of native conifers [m^2]; 10) basal area of non-native conifers [m^2]; 11) number of native angiosperm species; 12) number of non-native angiosperm species; 13) number of native conifer species; 14) number of non-native conifer species. Basal area and species richness (number of species) were derived from a raster database of the live tree species basal area interpolated for each species in the contiguous USA from forest inventory plots (Wilson et al. 2012), this database contains data only for woody plants, excluding other plant species. Basal area was calculated as a total sum of basal areas of all tree species in a given group (e.g. native conifers) in each grid cell and number of species was calculated as the sum of all species with basal area > 0 in each cell. Additionally, (xv) number of traps in a grid cell (sum of categories 'baited trap' and 'other trap' used in Table 1) was included as a predictor with the expectation that this variable accounts for spatial variation in sampling (Beck et al. 2014). Socioeconomic variables (human density and per capita income) were also included, in part to account for variation in sampling intensity, but also to account for the role of human activities in promoting the transport and establishment of both non-native species and native species which may establish outside of their original ranges.

For each model of non-native beetle richness, the corresponding subset of native richness was also included as a predictor (e.g. native angiosperm feeding richness was used as a predictor in the model predicting non-native angiosperm feeding richness).

For each of the 10 species groups shown in Table 1, separate models predicting species richness were fit. All predictors and response variables were log-transformed prior to model fitting. All candidate predictors were first checked for collinearity by calculating pairwise Pearson's correlation coefficients (Supporting information). In situations in which two or more predictor variables were collinear ($|r| > 0.7$), separate general linear models using each of the collinear variables were fitted for each of the 10 species richness groups and the model with the best performance (lowest AIC score) was selected. For each of the 10 selected linear models, the moran.test function from the spdep package (Bivand 2022) was used to check residuals for spatial autocorrelation. Using resultant correlograms, the errorsarlm function from the package spdep (Bivand 2022) was used to refit each model based on maximum likelihood estimation of spatial simultaneous autoregressive error models. This method accounted for spatial autocorrelation among residuals.

Results

Geographical variation in native species richness

There were a total of 30 992 records corresponding to 471 native Scolytinae/Platypodinae species (Fig. 2a). Across the conterminous USA, at least one Scolytinae/Platypodinae species was recorded in 56% of the 50 × 50 km cells and 18% of the grid cells had more than 10 species recorded (Fig. 2b). Total native Scolytinae/Platypodinae species richness was higher in the eastern North American forest regions (Table 2).

There were a total of 12 003 records of 170 species of native angiosperm-feeding Scolytinae/Platypodinae (Fig. 2a). Over 62% of cells have zero records of native angiosperm feeding species and only 6% of grid cells had more than 10 species recorded (Fig. 2c). Occurrence records indicated a higher number of species in the eastern region of the USA compared to the west (Table 2, Fig. 2c). There were 18 791 occurrence records corresponding to 287 native conifer-feeding species (Fig. 2a, d), with 53% of cells having zero recorded species and 13% having more than 10 species recorded. As in the case for previous groups, conifer-feeding species richness was on average significantly higher in the eastern regions of the USA (Table 3, Fig. 2d).

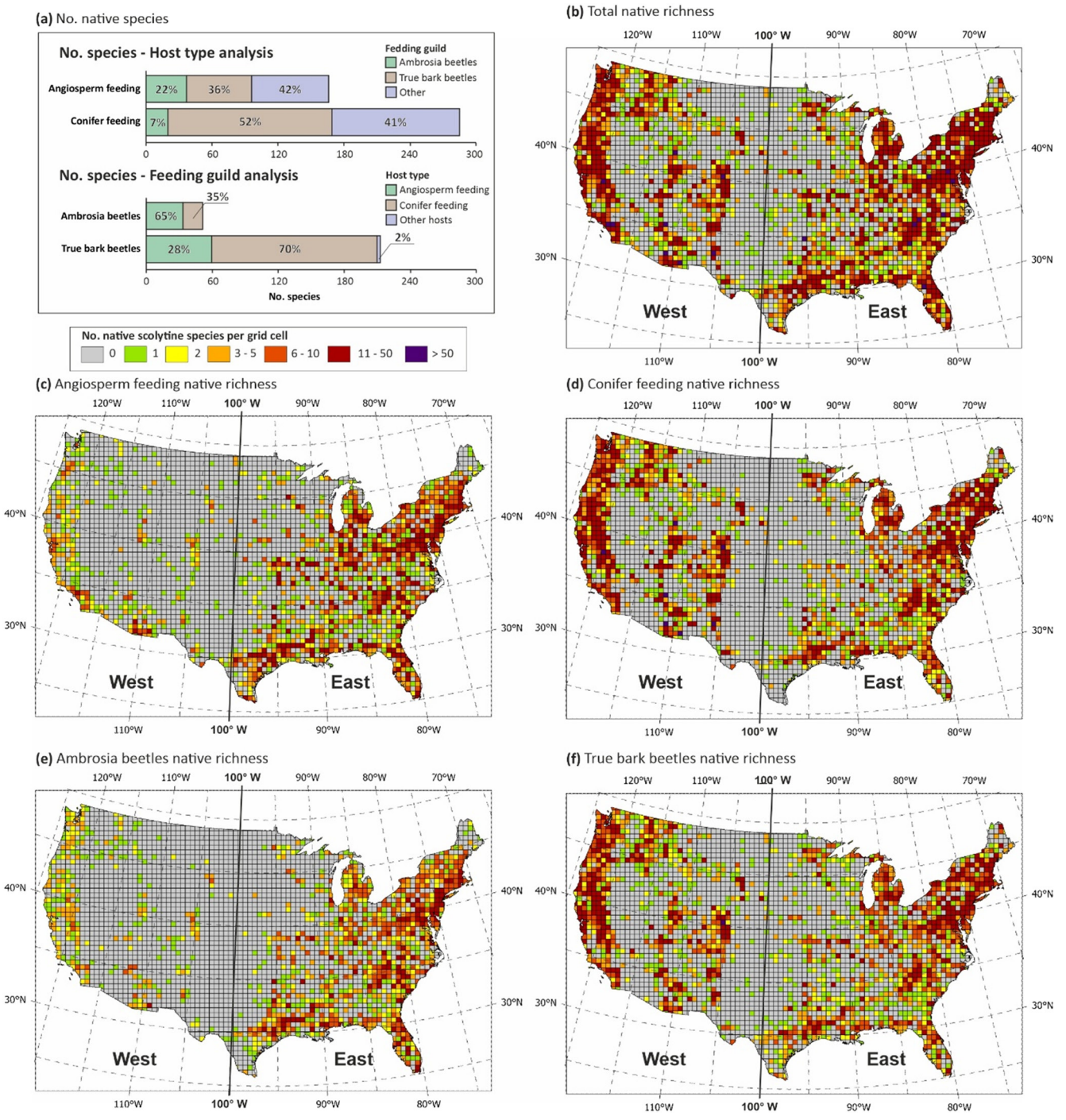

Figure 2. Native Scolytinae/Platypodinae species richness in 50 × 50 km grid cells across the conterminous USA (a) richness of species grouped by host type (angiosperm or conifer) or guild (bark beetle or ambrosia beetle); (b) richness of all native species; (c) richness of angiosperm feeding native species; (d) richness of conifer feeding native species; (e) richness of native ambrosia beetles and (f) richness of native true bark beetle species

Similar patterns were observed among feeding guilds. Native ambrosia beetles had 8665 records of 54 species (Fig. 3a, e) and 67% of cells had zero recorded species and only 3% had more than 10 species. The vast majority of Scolytinae/Platypodinae native angiosperm-feeding records were in the eastern portion of the US (Table 3, Fig. 2e). There were 16 877 native true bark beetle records representing 211 species (Fig. 2a); 50% of grid cells had zero species recorded and 11% of cells had more than 10 species (Fig. 2f). No significant difference in native true bark beetle species richness was found between western and eastern regions (Table 3).

Table 2. Independent samples *t*-tests comparing numbers of native Scolytinae/Platypodinae species in the western versus eastern parts of the conterminous USA (delineated by the 100th meridian).

Group	West AVG ± SD	East AVG ± SD	t-value	p
Total native richness	4.62 ± 9.67	6.74 ± 10.4	−6.09	< 0.001
Native angiosperm feeding richness	0.56 ± 1.63	3.57 ± 6.14	−18.85	< 0.001
Native conifer feeding richness	4.02 ± 8.53	3.14 ± 5.05	3.68	< 0.001
Native ambrosia beetle richnesss	0.42 ± 1.13	2.41 ± 3.88	−19.60	< 0.001
Native true bark beetle richnesss	3.20 ± 6.55	3.15 ± 4.93	0.23	0.82

Model of native species richness

Given the number of collinear predictors in the analysis of native Scolytinae/Platypodinae richness, a total of 304 (76 iterations for each group) models with unique combinations of predictors were analyzed. Results for all models are shown in the Supporting information. Table 3 shows results of the best performing model for each group.

Number of traps was the strongest positive predictor in all iterations of the models in all five models of native beetle species richness (Table 3, Supporting information). Both climatic variables were also positive predictors with average precipitation having the bigger effect in models for total, conifer feeding, ambrosia beetle and true bark beetle native richness, only being outperformed by annual mean temperature in the angiosperm feeding model (Table 3).

Socioeconomic variables had uniformly positive effects. Out of this subset of predictors, human population density had the strongest effect in all models of native Scolytinae/

Table 3. Final (best fit) spatial simultaneous autoregressive error models of native beetle species richness. Models for each beetle species richness response variable are shown in unique columns. Values represent estimates for candidate predictors and *p* values. Bold values indicate significant variables with p < 0.001, grey values indicate p > 0.05. The symbol '—' represents collinear predictors not included in the best performing model. Superscript letters indicate collinear predictors. Footnotes a–g highlights the covariate predictors e.g. not used in the same model.

	Total native richness		Angiosperm feeding richness		Conifer feeding richness		Ambrosia beetle richnesss		True bark beetle richnesss	
Predictor	Z-value	p	Z-value	p	Z-value	p	Z-value	p	Z-value	p
Average annual mean temperature	0.21	0.84	**3.64**	**< 0.001**	−0.27	0.79	3.16	< 0.05	−0.60	0.55
Average precipitation totals [a]	**11.54**	**< 0.001**	1.47	0.14	**12.88**	**< 0.001**	**5.40**	**< 0.001**	**13.61**	**< 0.001**
Human population density [b]	**15.63**	**< 0.001**	**8.73**	**< 0.001**	**13.45**	**< 0.001**	**5.14**	**< 0.001**	**14.33**	**< 0.001**
Average income per capita	1.49	0.14	**5.00**	**< 0.001**	0.35	0.73	2.80	< 0.05	1.29	0.20
Total length of roads [b]	—	—	—	—	—	—	—	—	—	—
Total forest area [c]	**6.11**	**< 0.001**	2.57	< 0.05	**6.10**	**< 0.001**	—	—	**5.26**	**< 0.001**
Basal area of native angiosperms [a, c]	—	—	—	—	—	—	—	—	—	—
Basal area of native conifers [c, d]	—	—	—	—	—	—	**5.67**	**< 0.001**	—	—
Basal area of non-native angiosperms [e]	—	—	2.91	< 0.05	—	—	2.20	< 0.05	—	—
Basal area of non-native conifers [f]	0.83	0.41	—	—	—	—	3.03	< 0.05	—	—
Number of native angiosperm species [a, g]	—	—	—	—	—	—	—	—	—	—
Number of native conifer species [d]	**5.52**	**< 0.001**	−2.26	< 0.05	**9.68**	**< 0.001**	—	—	**5.47**	**< 0.001**
Number of non-native angiosperm species [e, g]	**−6.02**	**< 0.001**	—	—	**−7.82**	**< 0.001**	—	—	**−6.88**	**< 0.001**
Number of non-native conifer species [f]	—	—	**3.35**	**< 0.001**	−1.33	0.18	—	—	1.49	0.13
Number of traps	**49.70**	**< 0.001**	**55.96**	**< 0.001**	**44.17**	**< 0.001**	**63.18**	**< 0.001**	**47.55**	**< 0.001**

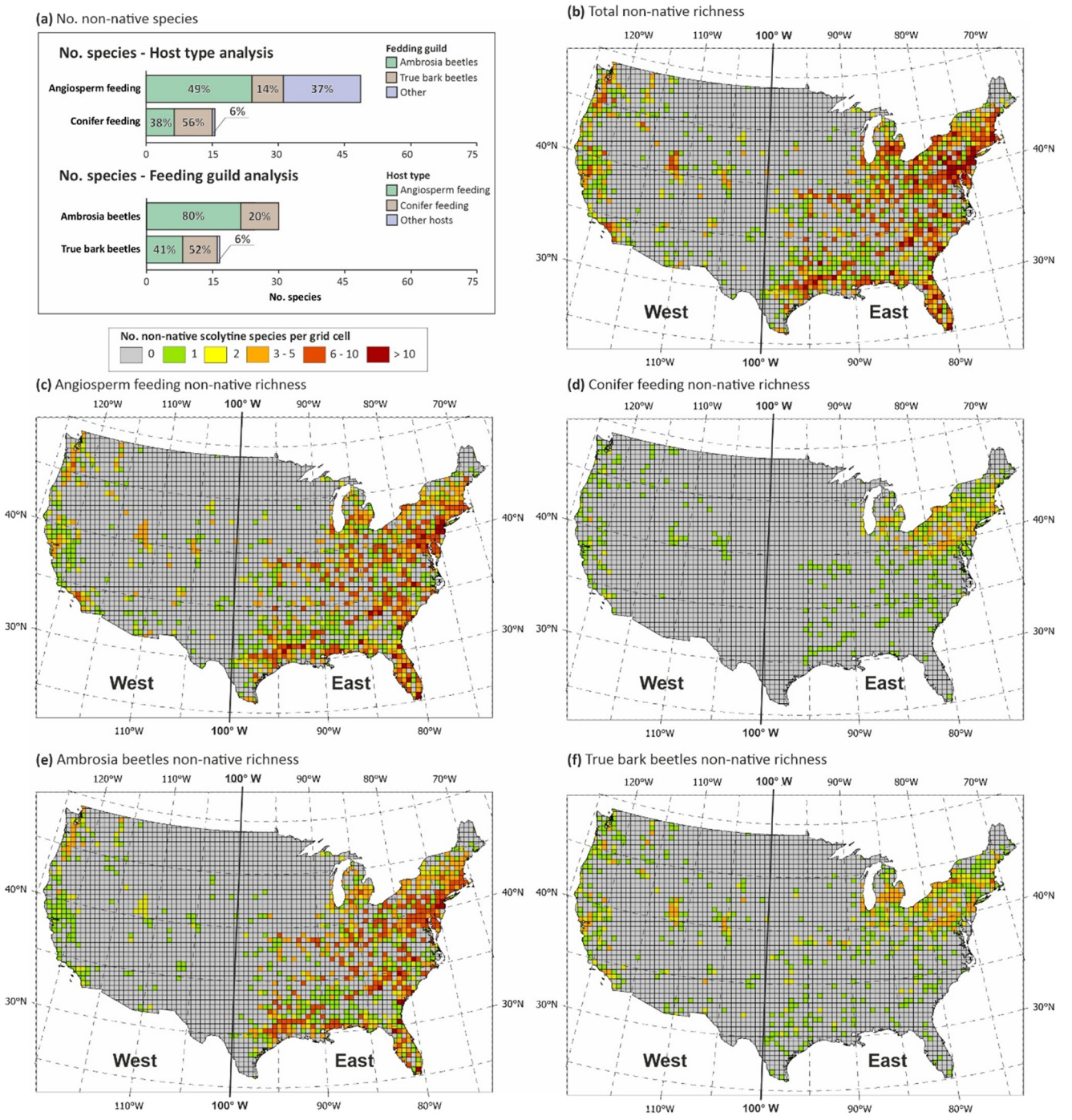

Figure 3. Non-native Scolytinae/Platypodinae species richness in 50 × 50 km grid cells across the conterminous USA: (a) total richness of species grouped by host type (angiosperm or conifer) or guild (bark beetle or ambrosia beetle); (b) richness of all non-native species; (c) richness of angiosperm feeding non-native species; (d) richness of conifer feeding non-native species; (e) richness of non-native ambrosia beetles and (f) richness of non-native true bark beetle species.

Platypodinae richness (Table 3). Average income per capita had lower predictive value and was statistically significant only in the native angiosperm feeding species richness and ambrosia beetle richness models. Total length of roads had positive effects in the models where the predictor was included (Supporting information) but it did not appear in the best performing model.

For the models predicting total, angiosperm feeding, conifer feeding and true bark beetle native richness, forest area was the best forest density predictor, while basal area of

native conifers performed better in the ambrosia beetle richness model (Table 3). Native ambrosia beetle richness and native angiosperm feeding richness were also positively associated with basal area of non-native trees (Table 3). Basal area and number of native angiosperm species had positive effects in the models where these predictors were included (Supporting information), but they were not part of any of the best performing models. Basal area and numbers of non-native angiosperm and conifer species had positive effects on native angiosperm feeding species richness and ambrosia beetle native richness. In contrast, numbers of non-native angiosperm species had negative impacts on total, conifer feeding and true bark beetle native Scolytinae/Platypodinae richness (Table 3).

Geographical variation in non-native species richness

There were 7397 records of 60 non-native Scolytinae/Platypotinae species (Fig. 3a). Across the USA, 31% of grid cells recorded at least one non-native species and 20% of the cells had more than one species recorded. Higher total non-native species richness was recorded in the eastern portion of the USA compared to the west (Table 4, Fig. 3b).

There were 6080 records of 47 non-native angiosperm feeding beetle species (Fig. 3a). More than 71% of grid cells had zero records of non-native angiosperm feeding beetles and only 19% of grid cells had more than two species recorded. As was the case with total non-native richness, higher numbers of non-native species were recorded in the eastern region (Table 4, Fig. 3c). There were 1120 individual records of 16 species of non-native conifer feeding species (Fig. 3a). Almost 88% of cells had zero recorded non-native conifer feeding species and only 3% of grid cells had more than two species recorded. Numbers of non-native conifer feeding species were higher in eastern North American (Table 4, Fig. 3c).

Patterns for individual feeding guilds were again very similar to patterns seen for each host type subset. For non-native ambrosia beetles, there were 5263 records of 25 species (Fig. 3a); 76% of cells had zero recorded species and 14% of cells had more than 10 species. Non-native ambrosia beetle richness was greater in the eastern region (Table 4, Fig. 3d). There were only 1008 records of 17 species of non-native true bark beetles (Fig. 3a), with 83% of cells having zero species recorded and 5% of cells with more than two species (Fig. 3f). Significantly higher richness was again found in the eastern regions (Table 4), although the east versus west difference for non-native true bark beetle species richness was much lower compared to other groups (Table 4, Fig. 3f).

Model of non-native species richness

With the high number of collinear predictors in the analysis of non-native Scolytinae/Platypodinae richness, a total of 912 models (152 each for total, conifer feeding and true bark beetle non-native richness; 228 each for angiosperm feeding and ambrosia beetles non-native richness) with unique combinations of predictors were analyzed. Results for all models are shown in the Supporting information. Table 5 shows results of the best performing model for each group.

As in case of native Scolytinae/Platypodinae richness, number of traps was the strongest positive predictor in all iterations of the models in all five models of native beetle species richness (Table 5, Supporting information). Total and group native Scolytinae/Platypodinae species richness, had the biggest positive effect in the model iterations where these predictors were included (Supporting information), but models where they were replaced by number of traps always outperformed models that included them (Table 5).

Both climatic variables had positive effects on total non-native Scolytinae/Platypodinae richness, however these variables were less significant in the individual group models (Table 5). Average per capita income was a positive predictor of non-native richness in all five models (Table 5). Similarly, human population density had a positive effect on total, angiosperm feeding and true bark beetle non-native richness, while having a negative effect on conifer feeding non-native richness (Table 5). Total length of roads did not perform well in any model.

Forest area and basal area of native conifers and angiosperms had negative effects on the non-native richness, however the basal areas of non-native trees had a significant positive effect in all models. Basal area of non-native angiosperms was positively associated with total, angiosperm feeding and ambrosia beetles non-native richness, while basal area of non-native conifers was a strong predictor in conifer feeding and true bark beetle models (Table 5).

Tree diversity predictors did not perform well in most models. The only significant predictors in the group were native conifer species richness which had a positive effect on non-native ambrosia beetle richness and non-native angiosperm feeding species richness in the best performing models (Table 5).

Table 4. Independent samples *t*-test of number of non-native Scolytinae/Platypodinae species in the western versus eastern parts of the conterminous USA (delineated by the 100th meridian).

	West	East		
Group	AVG ± STD	AVG ± STD	t-value	p
Total non-native richness	0.38 ± 1.09	1.95 ± 3.27	−18.19	< 0.001
Non-native angiosperm feeding richness	0.27 ± 0.83	1.64 ± 2.78	−18.76	< 0.001
Non-native conifer feeding richness	0.08 ± 0.3	0.27 ± 0.69	−10.33	< 0.001
Non-native ambrosia beetle richnesss	0.15 ± 0.51	1.42 ± 2.55	−19.60	< 0.001
Non-native true bark beetle richnesss	0.21 ± 0.65	0.37 ± 0.89	−5.92	< 0.001

Table 5. Final (best fit) spatial simultaneous autoregressive error models of non-native Scolytinae/Platypodinae species richness. Models for each beetle species richness response variable are shown in unique columns. Values represent estimates for candidate predictors and p values. Values in bold indicate significant variables with $p < 0.001$, greyed values indicate $p > 0.05$, and the symbol '—' represents collinear predictors not included in the best performing model, superscript letters indicate collinear predictors. Footnotes a–g highlights the covariate predictors e.g. not used in the same model.

	Total non-native richness		Angiosperm feeding richness		Conifer feeding richness		Ambrosia beetle richnesss		True bark beetle richnesss	
Predictor	Z-value	p	Z-value	p	Z-value	p	Z-value	p	Z-value	p
Total native Scolytinae/Platypodinae species richness [a]	—	—	—	—	—	—	—	—	—	—
Group native Scolytinae/Platypodinae species richness [a]	—	—	—	—	**6.93**	**< 0.001**	—	—	**11.55**	**< 0.001**
Average annual mean temperature	**3.97**	**< 0.001**	**3.93**	**< 0.001**	0.58	0.56	2.92	< 0.05	2.48	< 0.05
Average precipitation totals [b]	**4.14**	**< 0.001**	—	—	2.88	< 0.05	1.83	0.07	1.81	0.07
Human population density [c]	**9.22**	**< 0.001**	**8.45**	**< 0.001**	−2.03	< 0.05	—	—	**7.26**	**< 0.001**
Average income per capita	**5.71**	**< 0.001**	**5.53**	**< 0.001**	**4.68**	**< 0.001**	2.49	< 0.05	**5.07**	**< 0.001**
Total length of roads [c]	—	—	—	—	—	—	1.11	0.27	—	—
Total forest area [d]	−3.17	< 0.05	—	—	—	—	−3.29	< 0.05	—	—
Basal area of native angiosperms [b, d]	—	—	−2.92	< 0.05	—	—	—	—	—	—
Basal area of native conifers [d, e]	—	—	—	—	**−6.16**	**< 0.001**	—	—	**−6.25**	**< 0.001**
Basal area of non-native angiosperms [f]	**4.02**	**< 0.001**	**4.56**	**< 0.001**	—	—	**7.26**	**< 0.001**	−1.19	0.23
Basal area of non-native conifers [g]	**5.69**	**< 0.001**	—	—	**14.08**	**< 0.001**	0.62	0.54	**13.09**	**< 0.001**
Number of native angiosperm species [b, h]	—	—	—	—	—	—	—	—	—	—
Number of native conifer species [e]	0.47	0.63	1.22	0.22	—	—	2.15	< 0.05	—	—
Number of non-native angiosperm species [f, h]	—	—	—	—	2.88	< 0.05	—	—	—	—
Number of non-native conifer species [g]	—	—	0.93	0.35	—	—	—	—	—	—
Number of traps [a]	**75.35**	**< 0.001**	**74.03**	**< 0.001**	**30.98**	**< 0.001**	**78.85**	**< 0.001**	**17.38**	**< 0.001**

Discussion

Elton's theory of biotic resistance posits that more diverse communities are resistant to biological invasions (Levine and d'Antionio 1999). The theory has been more widely applied to plant invasions though, even for plants, the pattern is not entirely consistent and is more common at small spatial scales (Fridley et al. 2007). The concept has rarely been applied to insect invasions, but analyses reported here do not provide good support for it. Tree species richness had either no effect or a positive effect on the richness of non-native Scolytinae/Platypodinae (Table 5). Furthermore, the richness of native Scolytinae/Platypodinae had either no effect or a positive effect on non-native richness, opposite of what would be expected under the biotic resistance hypothesis.

The failure of either tree diversity or native Scolytine/Platypodinae diversity to confer biotic resistance to beetle invasions suggests that resistance to insect invasions is fundamentally different from resistance to plant invasions which provides most of the empirical evidence for the biotic resistance hypothesis. While direct competition is known to play an important role in the community ecology of plants and is important during the establishment phase of non-native plants (Gioria et al. 2023), direct interspecific competition appears to be less important for insects (Kaplan and Denno 2007). Instead, much of the evidence points towards the availability of hosts as a key determinant of invasion success by insects. Indeed, many lines of evidence indicate that both native and non-native plant diversity creates ecological niches for herbivorous insects and in this way, plant diversity facilitates invasions (Liebhold et al. 2018, Bertelsmeier et al. 2024).

This concept that the availability of non-native hosts supports non-native insect establishment is in part supported by our results that generally indicate a positive effect of non-native tree basal area on non-native Scolytinae/Platypodinae

richness (Table 5). Basal area of non-native angiosperms had a positive effect on the richness of non-native angiosperm feeding beetle species and basal area of non-native conifers had a positive effect on the richness of non-native conifer feeding Scolytinae/Platypodinae species. These positive effects can be considered an example of the 'facilitation effect' (Bruno et al. 2003). In the context of biological invasions by phytophagous insects, the facilitation effect functions via host plants creating resources for specialist herbivores, thereby facilitating their establishment. Guo et al. (2019) analyzed the county level distribution of 91 species of damaging non-native forest insects and diseases and found that abundance of host tree species had a positive effect on the invasion of a county by a pest species. Conversely, they found that the abundance of non-hosts had a negative effect on pest invasion. They concluded that the negative effect of non-hosts was an example of the 'dilution effect' in which the presence of non-hosts adversely affects host finding or population growth. The dilution effect has been implicated as a primary mechanism for the negative effect of biodiversity on parasitism in host-parasite systems (Civitello et al. 2015). Ward et al. (2022) re-analyzed the data from Guo et al. (2019) and found that while there was a significant facilitation effect in most pest species, dilution effects were rarely detected. In the analysis reported here, we found some evidence for a dilution effect. Native conifer basal area negatively affected non-native conifer-feeding beetle richness and native angiosperm basal area negatively affected non-native angiosperm feeding beetle richness (Table 5). The positive effects of non-native tree basal area contrasts with the negative effects of native tree basal area and likely reflects the opposing effects of facilitation vs. dilution on insect establishment (Guo et al. 2019). It should be pointed out that non-native tree density is relatively low across the conterminous USA (Lugo et al. 2022) and this may partially explain the lack of a stronger effect of non-native tree richness on beetle richness.

With the exception of Borges et al. (2006), few studies have investigated how native insect diversity confers resistance to invasions by non-native insects, but our results are in part consistent with Borges et al. (2006) finding that native diversity is positively related to insect invasions. Native conifer feeding beetle richness had a positive effect on non-native conifer feeding beetle richness and native angiosperm feeding beetle richness had a positive effect on non-native angiosperm feeding beetle richness (Table 5). As mentioned in the Results, total native beetle richness was highly collinear with numbers of traps so it did not appear in any of the final models that included numbers of traps, but in all of the models that included total native beetle richness, it always had a significant positive effect on non-native beetle richness. Analyzing variation in numbers of Scolytine species present in each US state and in each European country, Marini et al. (2011) also found a positive association between numbers of native and non-native beetle species. Higher native insect diversity may be indicative of the general availability of more resources and ecological niches that might support the establishment of novel insect species.

The geographical distribution of total native Scolytinae/Platypodinae richness appears approximately uniform across forested regions of the USA (Fig. 2b) and closely mirrors the geographical distribution of forest area (Supporting information). Total native species richness was slightly higher in the eastern USA compared to the west (Table 2) and forest area was a significant factor affecting species richness in each 50 × 50 cell (Table 3). In contrast, native angiosperm feeding Scolytinae/Platypodinae species richness was more strongly concentrated in forested regions of the eastern USA compared to western regions (Fig. 2c) as was the case for native ambrosia beetle species richness (Fig. 2e). This pattern can be explained by the greater angiosperm species richness in eastern forests compared to western forests (Supporting information) given that the majority of native ambrosia beetles feed on angiosperms (Fig. 2a). A larger fraction of true bark beetles feed on conifers (Fig. 2a) so it is not surprising that the richness of both conifer feeding native Scolytinae/Platypodinae and native true bark beetles were both significantly associated with native conifer richness (Table 3).

Similar to native beetle species, the richness of non-native Scolytinae/Platypodnae species was slightly greater in the eastern portion of the USA (Fig. 3b, Table 4). A stronger spatial trend of higher richness in the east was seen in both angiosperm-feeding non-native species (Fig. 3c) and non-native ambrosia beetles (Fig. 3e). Though native Scolytinae/Platypodinae are dominated by conifer-feeding species and true bark beetles (Fig. 2a), non-native species are dominated by angiosperm feeding species and ambrosia beetles (Fig. 3a). Given the greater diversity of angiosperms in the eastern USA (Supporting information), it is not surprising that angiosperm feeding non-native species richness and non-native ambrosia beetle richness is greater in the east (Table 4). Surprisingly, the richness of non-native conifer feeding species and non-native true bark beetles is greatest in the northeastern USA, even though conifer richness is generally greater in the southeastern and western USA (Supporting information). This geographical pattern mirrors the richness of total non-native pest species (insects and pathogens) observed by Liebhold et al. (2013) and Ward et al. (2019), who suggested that this pattern may result, in part, from the longer history of European colonization and commerce in the northeastern USA; these processes may also explain the pattern seen in non-native conifer feeding species and true bark beetles.

Most models indicated a positive effect of both precipitation and temperature on richness of native and non-native Scolytinae/Platypodinae (Table 3, 5). These results are generally consistent with similar analyses by Marini et al. (2011) and Rassati et al. (2016). While these climatic associations may indicate direct effects of climate on beetle performance and establishment, they may also reflect indirect effects. Forests in regions growing in areas with higher temperatures and precipitation generally achieve higher levels of biomass (Lieth 1975) and this greater biomass might provide more ecological niches for scolytines and platypodines and thereby support more native and non-native beetle species.

Species occurrence data often exhibit spatial bias (Beck et al. 2014, Rocha-Ortega et al. 2021). Species are more likely to be sampled and recorded in areas with greater human population density. A large fraction of the data analyzed here was collected as part of the USDA Forest Service Early Detection-Rapid Response Program (Rabaglia et al. 2019). In this program, traps are preferentially located in wooded areas near high-risk locations such as transportation hubs and warehouses, in fragmented forests, and in urban forests and parks. It can be expected that occurrence records that originate from sampling without using traps also may be preferentially located in more accessible locations. We attempted to address this bias by including numbers of traps and human population density as term in all beetle species richness models. Indeed, numbers of traps and human population density were significantly positive predictors for all the models of native and non-native Scolytinae/Platypodinae richness (Table 3, 5) except human population density was not a positive predictor in two of the non-native Scolytinae/Platypodinae richness models (Table 3).

In addition to accounting for variation in sampling effort, the socio-economic variables of human population density and per capita income most likely reflect variation in propagule pressure and thereby influence non-native beetle richness. Among these, per capita income consistently had a positive effect on all groups of non-native beetle species (Table 5) reflecting the positive effect of economic activity on invasions.

The database analyzed here is unique in its spatial and taxonomic extent. There are few insect taxa for which a comprehensive compilation exists of all native and non-native species across a large region. However, with the trend of growing spatially referenced biodiversity databases, such data may increasingly become available. The availability of such data will allow application of similar analyses which may or may not confirm general conclusions regarding whether insects conform to the biotic resistance hypothesis.

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Author contributions

Jiří Trombik: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Soňa Šenfeldová**: Data curation (equal); Formal analysis (equal); Investigation (equal). **Samuel F. Ward**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Thomas H. Atkinson**: Data curation (equal); Methodology (equal); Supervision (equal); Validation (equal); Writing – original draft (equal). **Andrew M. Liebhold**: Conceptualization (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cjsxksnm8 (Trombik et al. 2025).

Supporting information

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

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