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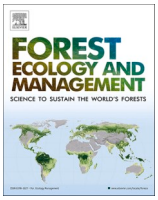

Determinants of host breadth in non-native bark and ambrosia beetles

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ABSTRACT

Most phytophagous insects are specialists, so availability of suitable host plants often may be a critical factor limiting establishment of non-native insect species. Here we investigate the extent to which established non-native tree-feeding insects utilize hosts that are native to the invaded range as well as hosts that are themselves non-native. We accomplish this by comparing host use among all native and non-native bark beetles and pinhole borers (Scolytinae and Platypodinae) established in Europe and North America reported in the literature. These groups of insects are well-known for the disparity among species in specialized behavior and development tied to host physiology. We find considerable variation in host breadth, as measured by species-level and genus-level host richness and phylogenetic diversity of hosts, among different feeding guilds (ambrosia beetles, true bark beetles, twig beetles, and others). In each region, ambrosia and twig beetles exhibit the greatest diversity of hosts. Host breadth on native plants was generally greater for native beetle species than for non-native beetle species. In contrast, host breadth of non-native beetles is generally greater on non-native plants than on plants native to the focal region. These results indicate that successful invasion of these insect herbivores is dependent on the prior introduction of their non-native host plants, or the availability of native hosts that are closely related to their ancestral host plants.

1. Introduction

When species invade new regions, they encounter habitats different from their native range that may limit their ability to establish. Key determinants to their reproduction and establishment success are the availability of essential resources, presence of natural enemies, and the suitability of the physical environment (Shea and Chesson, 2002). Together, these factors determine the ecological niche available in the novel region. While some evidence suggests that species that can exploit a wide niche are more likely to successfully invade, this is not always the case (Vázquez, 2006, MacDougall et al. 2009).

Frequently, species experience a niche shift or niche expansion following invasion of new regions (Guisan et al. 2014). Phenotypic plasticity that allows species to exploit novel niches is sometimes considered a trait that is key to invasion success (Richards et al. 2006). Most previous work comparing the ecological niche of species in their native and non-native habitat has focused on the climatic niche. However, resource utilization is another critical component of a species' niche and invading species may experience shifts or expansion of the types of resources they exploit in novel habitats (Bertheau et al. 2010). The niche breadth-range size hypothesis would predict that higher host breadth would allow a species to exist in more varied environments and therefore the geographic range size of these species would be larger (Slove and Janz, 2011, Slatyer et al. 2013).

For phytophagous insects, the availability of hosts necessary for completing the insect's life cycle plays a crucial role in invasion success. However, even insect species within the same genus often differ in the diversity of habitats and hosts they can exploit (Anacker and Strauss,

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2014). Polyphagous insect species may be more likely to find suitable hosts in novel habitats, whereas the establishment of specialized species may be more limited by host availability. In a recent study, Wang et al. (2022) concluded that non-native insect species have wider host ranges than native species and suggest that this results in generalist insect herbivores having greater invasion success. However, their analysis did not differentiate among different groups of herbivorous insects and it only evaluated host breadth across plant species native to the invaded region. Often, introduced insects feed exclusively, or in part, on non-native plant species also introduced from their native range (Crous et al. 2016) so it is important to differentiate between native and non-native plants in assessing host breadth.

Studies have shown that insects are more likely to utilize novel hosts if they are phylogenetically similar to hosts from the species' native range (Gilbert et al. 2012, Pearse and Altermatt, 2013, Mech et al. 2019). The availability of plants closely related to an invading herbivore's native hosts thus may be a crucial determinant of its establishment success. Studies that examine the details of the success of invasive insect species in new ranges in relation to their ecological niche could ultimately help predict invasions in new areas, information that would be valuable for biosecurity risk analysis (Hulme, 2011).

Here we investigate host breadth in native and non-native Scolytinae and Platypodinae (Curculionidae), the bark beetles and pinhole borers. This group is infamous for the massive impacts that some species in this group have on forest ecosystems around the world (Sun et al. 2013, Grégoire et al. 2015, Hlásny et al. 2021). Many scolytine species are well known for their highly coevolved relationships with both their tree hosts and with associated fungal species (Raffa et al. 2015). Despite these close associations, many of these species have successfully invaded novel regions (Lantschner et al. 2020, Pureswaran et al. 2022, Vilardo et al. 2022, Grégoire et al., 2023).

Given the large number of invasions (e.g., Lantschner et al. 2020, Vilardo et al. 2022, Grégoire et al., 2023) and the extensive work that has focused on insect-host interactions in this group of insects, it makes an excellent system for characterizing patterns of coevolved and novel host associations. Novel host associations may occur when a beetle invades and encounters a new tree species and when a tree species invades and encounters a new beetle (Fig. 1). Here we provide a comprehensive analysis of host breadth among all native and non-native beetles on both native and non-native hosts in both Europe and North America. By comparing species present in both regions, we are able to assess underlying patterns of host breadth. We hypothesize that host breadth varies among feeding guilds and that this variation is similar for beetles present in Europe and North America. We also hypothesize that historical filtering caused by the failure of invading species to locate hosts causes non-native beetles to exhibit greater host breadth on both native and non-native host plants. Finally, we synthesize this information to draw conclusions about how host breadth of individual bark and ambrosia beetle species affects their ability to invade.

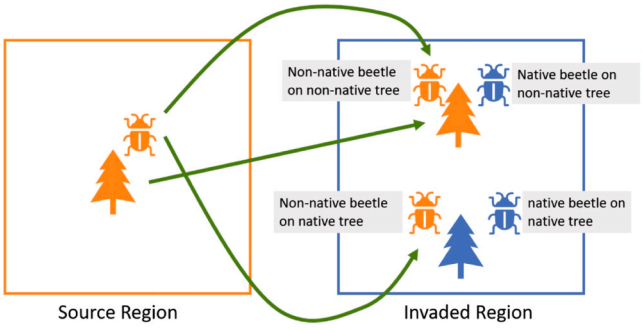

Fig. 1. Summary of coevolved and novel host associations following invasions. Beetles may be associated with their coevolved hosts either when they co-occur in their native ranges or when they both invade a new region. Novel host associations may occur when a beetle invades and encounters a tree species native to the invaded region or when a tree species invades and encounters a beetle native to the invaded region.

2. Methods

2.1. Data collection

We assembled a comprehensive database of hosts utilized by both native and non-native Scolytinae and Platypodinae species established in Europe and North America (north of Mexico). The Platypodinae are a much smaller group (7 species native to North America and 3 species native to Europe). but are included in this analysis because they comprise a portion of the ambrosia beetles, in addition to those in the Scolytinae. A list of all native and established non-native Scolytinae and Platypodinae species in Europe was created from the Fauna Europaea database (Knížek, 2004, De Jong et al., 2014, Alonso-Zarazaga et al. 2017) and from Wood and Bright (1992). A list of all Scolytinae and Platypodinae present in North America was extracted from the Bark and Ambrosia Beetles of the Americas Database (Atkinson, 2023). For each species, we compiled their subfamily, tribe, genus, the status of nativeness (native or non-native status in either Europe or North America) and feeding guild. Four feeding guilds were specified: true bark beetles (beetles feeding on phloem of stems and treetops), ambrosia beetles (beetles living in xylem and feeding on symbiotic fungi), twig beetles (species occurring in twigs and smaller branches, rarely on treetops), and "other" for species that did not correspond with the previous three feeding groups. This last category contains beetles that feed on herbaceous plants (including woody tissues of cacti), tree seeds, fruit, roots, and flowers, as well as the petioles of fallen leaves. We acknowledge that considerable variation in feeding life histories exist within these groups of beetles and can cause difficulty in classifying species into distinct guilds. Other systems, each with merit, exist for classifying feeding guilds in this group but we selected these four feeding categories given their previous use and ability to capture biological variation in life histories.

2.2. Genus- and species-level host breadth calculation

For each beetle species, we compiled a list of all known host genera and host families. For beetle species present in Europe, records of host genera, nativeness and feeding guild were compiled from various published sources including the Wood and Bright catalogue (Wood and Bright, 1992) and the supplementary material of Lantschner et al. (2020). A complete list of scientific literature sourced for this data compilation can be found in Appendix A.1. For each beetle species present in North America, we obtained a list of host species from the Bark and Ambrosia Beetles of the Americas Database (Atkinson, 2023). Only host records from North America were analyzed. Analyses at the host species level were only conducted for beetles present in North America because comprehensive information about host species were lacking for the European beetles.

Based on these sources, the proportion of conifer vs. angiosperm feeding beetles by beetle nativeness was evaluated. Each association between a beetle species and a host genus was assigned a status of primary or secondary. For Europe, this classification was based on the designation by Wood and Bright (1992), or elsewhere in the scientific literature listed in Appendix A.1. This literature was searched for any information about specific hosts being the main or more abundantly used hosts of the beetle species. In such cases, hosts were recorded as primary. In case where species were described in the literature as highly polyphagous species, all hosts were recorded as primary. For North America, the classification was based on host associations that were part of occurrence records in Atkinson, 2023. Using these data, a host association was considered secondary if it was reported in less than 20 % of occurrence records and was otherwise considered primary. However, in

cases where species were described as polyphagous, all hosts were recorded as primary. Only primary host genera were included in analyses to avoid including hosts that are recorded rarely or by mistake or are used by the beetle only in the absence of a truly suitable host. We acknowledge that some beetle species have been poorly studied and the lack of extensive host records may have caused us to underestimate the extent of their host breadth.

For each beetle species / host genus pair, both the beetle species and the host genus were classified as native or non-native in the focal region (Europe or North America). A host genus was classified as native to the focal region if any species in the genus was native to the region. Similarly, for each pair of beetle species and host species (these data were only available from North America) each beetle and host species were classified as native or non-native to the focal region. For each beetle species in each region, we summed the number of host genera that are native to that region and the number that are introduced. For each beetle species present in North America, we summed the number of native and non-native host species. The nativeness of each host species in North America was determined from the USDA Plant database (USDA, 2022). Throughout this manuscript when we refer to non-native hosts, we are referring to host genera or species that are not native to the focal region where beetle species are established; some of these non-native hosts may be native to the same region from which a non-native beetle species originated. That is, in the invaded range, some non-native beetle species could encounter a host with which they coevolved. The full database is made available in a public repository (Šenfeldová et al., 2024).

2.3. Phylogenetic host breadth calculation

For each beetle species we computed the phylogenetic diversity of their primary hosts (Tucker et al. 2017). We constructed a phylogenetic tree for all host genera and species that are primary hosts for the European and North American beetles using the package V.PhyloMaker (Jin and Qian, 2019) which accesses the mega-phylogeny database of seed plants from Smith and Brown (2018). Phylogenetic diversity is measured as the sum of the length of the branches in the minimal subtree containing all the taxa of the hosts (genus or species, depending on focal region) for each beetle species. The unrooted phylogenetic diversity of each beetle's primary hosts was calculated using the *pd.query* function from the R package Phylomeasures (Tsirogiannis and Sandel, 2016). For beetle species with only one primary host genus, the phylogenetic diversity was zero. For most beetle species, there were no records of feeding on non-native hosts. Given that phylogenetic diversity cannot be computed in these cases, these species were not included in the analysis. Considering this situation of insufficient data for non-native hosts, phylogenetic diversity was only analyzed for native host genera and native host species (a total of three models).

2.4. Data analysis

All statistical analyses were performed in R (R Core Team, 2021). We fit Poisson regression models to evaluate how host breadth, measured by either number of native host genera or species, or number of non-native host genera or species, varied with beetle species nativeness (native vs. non-native), feeding guild, and their interaction. Separate models were fit for numbers of host genera that were native or non-native in Europe and numbers that were native or non-native in North America (a total of four models for number of hosts). Values of native host phylogenetic diversity for each beetle species were log-transformed and analyzed with a linear model using the same predictor variables (nativeness, feeding guild and their interaction). As was the case above, separate models were computed for beetle species in Europe and North America.

For the genus- and species-level host richness models and phylogenetic diversity models, the car package (Fox and Weisberg, 2011) was used to perform ANOVAs to test the significance of predictor variables. When the beetle nativeness x feeding guild interaction term was significant ($\alpha = 0.05$), we conducted pairwise comparisons between each grouping (e.g., native ambrosia beetles vs. non-native bark beetles) using the emmeans package (Lenth et al. 2022).

In addition, we tested the correlation between numbers of native and non-native hosts (at the host genus level) for each feeding guild in Europe and in North America and for bark beetles and ambrosia beetles present in North America at the host species level.

3. Results

3.1. Description of species assemblages

A total of 829 beetle species were recorded; this included 285 species present in Europe and 544 species present in North America. A few species (13 European and 11 North American; Appendix A.2) were excluded either because host data were lacking or because their presence or nativeness in the focal region was uncertain. In both Europe and North America, the species richness of bark beetles exceeds that of the other three guilds (Fig. 2ab). In North America there are proportionally more native twig beetles than in Europe. Across all guilds, there were 36 non-native beetle species in Europe and 60 non-native species in North America. In both regions, the ambrosia beetles had the greatest number of non-native species, followed by the bark beetles.

The association of beetles with angiosperm vs. conifer hosts differed between native and non-native beetle species (Fig. 2c). In both regions, a larger proportion (54–62 %) of native beetles use conifers as hosts; a larger proportion (53–77 %) of non-native beetle species are associated with angiosperms. Among all groups, there is a small proportion of beetle species (0.5–17 %) that utilize both types of hosts.

3.2. Genus-level host breadth

The number of hosts varied considerably across all analyzed groups (Figs. 3 and 4). The species with the highest number of native host genera (32) was the native North American twig beetle *Hypothenemus eruditus*. For Europe, the beetle with the highest number of hosts (24) was the native ambrosia beetle *Anisandrus dispar*. The ambrosia beetle *Xyleborus perforans* is non-native in Europe where it has more non-native host genera (36) than any other beetle species analyzed in Europe. For North America, the species with the greatest number of non-native host genera (13) was the native ambrosia beetle *Coptoborus ricini*. On average, both native and non-native beetle species in each region feed on more native host genera than non-native genera. However, non-native beetle species in each region have a larger proportion of non-native hosts.

There is a consistent difference in host breadth among feeding guilds, measured by both numbers of host genera and by host phylogenetic diversity (Figs. 3 and 4, Tables 1 and 2). Ambrosia beetles and twig beetles feed on the most host genera while bark beetles and species in the "other" category feed on the fewest. This pattern is true for both native and non-native host genera. Similar patterns of variation in host breadth among feeding guilds are evident when comparing host phylogenetic diversity among these same guilds (Figs. 3 and 4). Species present in North America generally share a similar pattern in host breadth among feeding guilds as seen among species present in Europe.

Differences in host breadth when considering the nativeness of both beetles and hosts were more complex. In Europe, non-native beetle species fed on more non-native hosts compared with native beetle species (Figs. 3 and 4, Tables 1 and 2). However, beetle nativeness was not statistically associated with the numbers of non-native host genera in North America, nor did it affect the phylogenetic diversity of hosts of beetles in North America.

In both regions and for both native and non-native hosts, there is a significant interaction between the nativeness of beetles and their feeding guild ($p < 0.004$), indicating that the association between number of hosts and beetle nativeness varies among feeding guilds. For

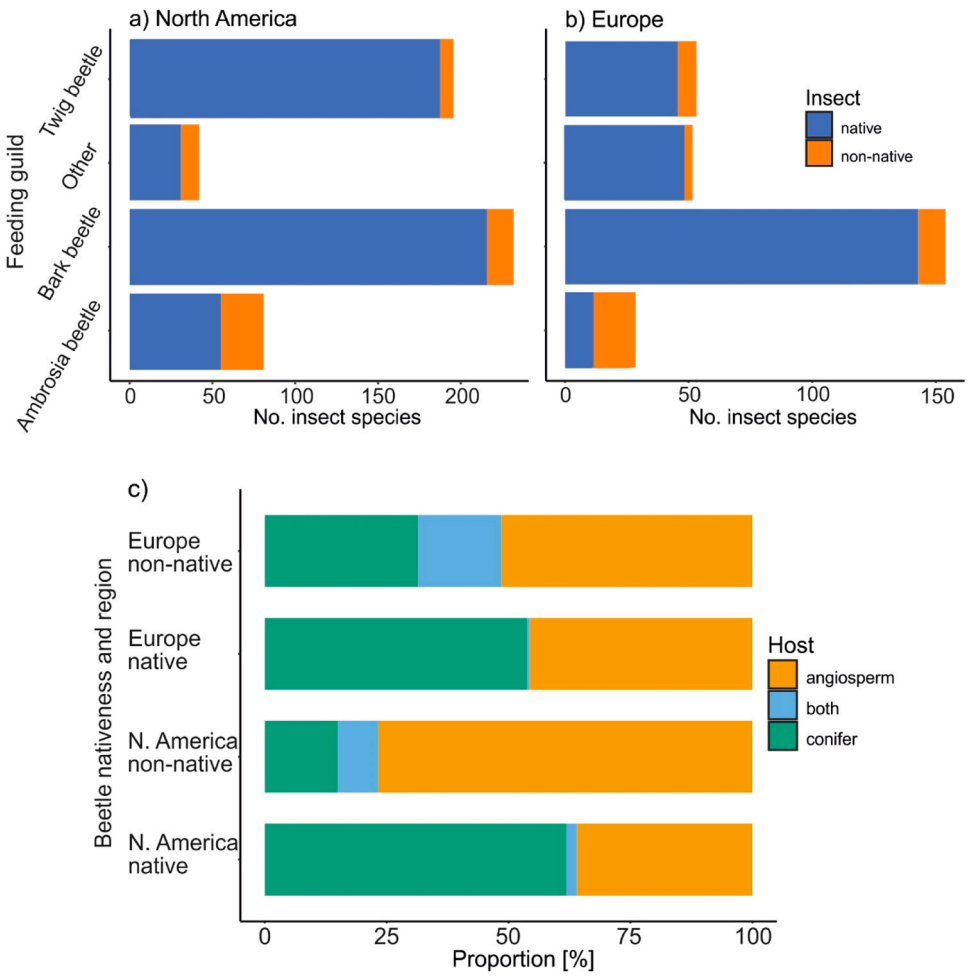

Fig. 2. Distribution of Scolytinae and Platypodinae beetle species among guilds and host groups. a) Distribution of numbers of native and non-native species among feeding guilds in North America and b) Distribution of numbers of native and non-native species among feeding guilds in Europe. c) Proportions of native and non-native beetle species feeding on angiosperms, conifers or both types of hosts in Europe and North America.

example, host breadth generally differed more between native and non-native twig beetles than between native and non-native ambrosia beetles (Figs. 2 and 3). The interaction between beetle nativeness and feeding guild was also significant for phylogenetic diversity ($p < 0.006$). In both Europe and North America, non-native twig beetles feed on more host genera (native and non-native hosts) than native twig beetles. The same pattern of higher host breadth can be seen in the ambrosia beetle guild, but this result was significant only for European region ($p < 0.0001$). In addition, the opposite situation can be seen for bark beetles, where their non-native host breadth is higher for introduced host species, but this result was only significant for North America ($p = 0.0007$); (Tables 1 and 2).

3.3. Host phylogenetic diversity

A phylogenetic tree was built for all host genera and species of the Scolytinae and Platypodinae species present in Europe and North America. Phylogenetic diversity of hosts showed considerable variation among beetle species. The species with the highest native host phylogenetic diversity was the North American native twig beetle *Hypothenemus eruditus*. Also native to North America, the congeneric *H. seriatus* had the second highest native host phylogenetic diversity. In the case of non-native host genera, the highest host phylogenetic diversity was in the introduced species *Hypothenemus crudiae* followed by native *Coptoborus ricini*. The highest phylogenetic diversity among native hosts in Europe is found in the ambrosia beetle feeding guild with native *Anisandrus dispar* having the most phylogenetically diverse hosts and non-native *Xylosandrus germanus* with the second most diverse native hosts. The beetles with the highest non-native host phylogenetic diversity were *Xyleborus perforans* and *Euplatypus parallelus*, both not native in the European region. Overall, *Hypothenemus, Xyleborus*, and *Xylosandrus* were the genera that demonstrated the highest host phylogenetic diversity. The bark beetle species *Hypothenemus eruditus* is uniquely polyphagous and the range of its hosts is disproportionately large compared to other species. It should be noted however that analysis of global genetic variation within this species by Kambestad et al. (2017) indicates that it is likely comprised of several smaller species.

The phylogenetic diversity of native hosts differed significantly between native and non-native beetle species for both twig beetles ($p < 0.0001$) and the 'other' category ($p = 0.0112$) for beetles in North America (Fig. 3) and for ambrosia ($p = 0.0359$) and twig beetles ($p = 0.0004$) in Europe (Fig. 4). In general, introduced beetle species had higher phylogenetic diversity of native hosts than their native counterparts (Tables 1 and 2). Phylogenetic diversity for the non-native beetle species in the 'other' feeding guild in Europe did not have sufficient numbers of species (N = 3) to meaningfully test for differences between native and non-native beetles.

3.4. Species-level host breadth

Analysis at the host species level for beetles in North America indicated that both native bark beetles and native ambrosia beetles had

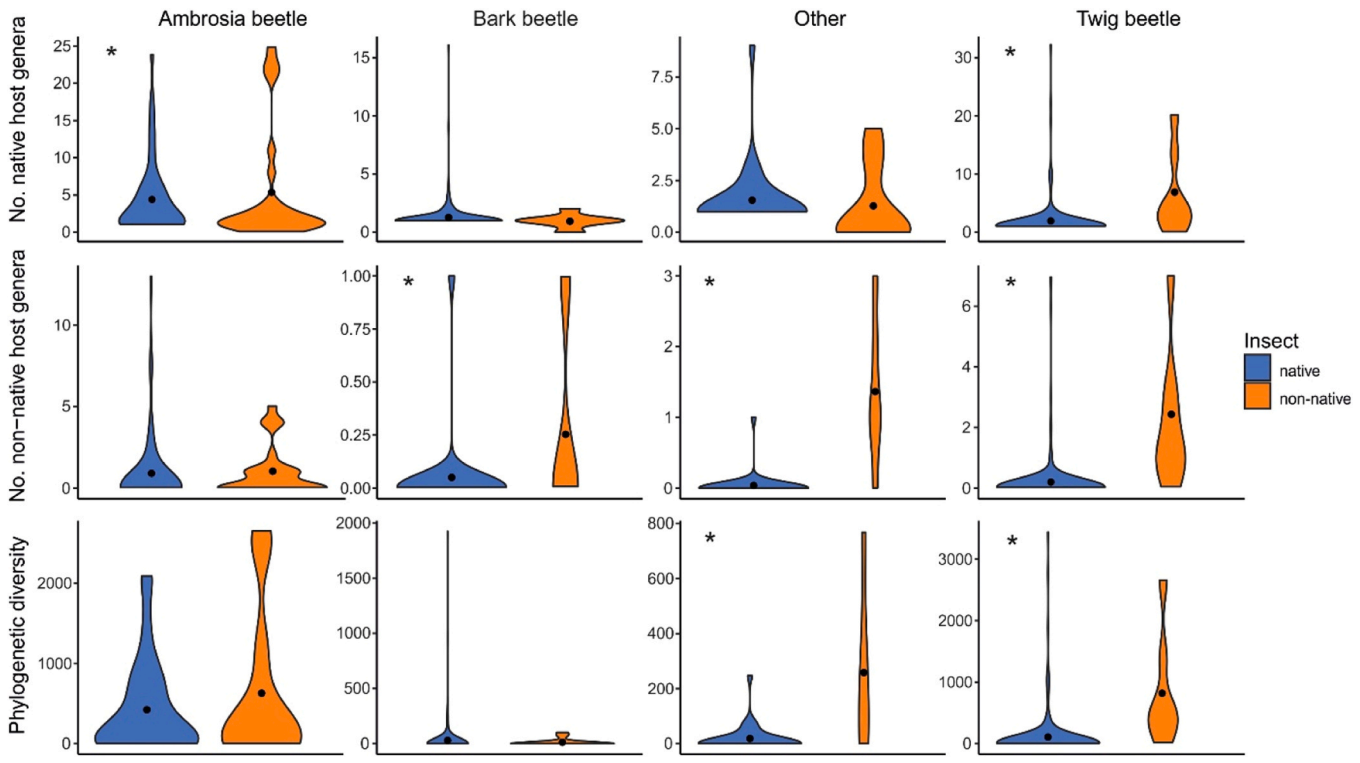

Fig. 3. The distribution of host richness (represented by number of host genera) and phylogenetic diversity for beetle species present in North America. The width of each curve corresponds with the number of beetle species for each host genus richness or phylogenetic diversity value. The first two rows show the distribution of number of host genera (native hosts in the first row and non-native hosts in the second row) among insect feeding guilds. The third row shows phylogenetic diversity of native host genera among feeding guilds. Differences between native (blue) and non-native (orange) beetle species are evident. The black point represents the mean value. Asterisks indicate significant differences ($P < 0.05$) between native and non-native beetles in each feeding guild based on ANOVA. Each row of panels was analyzed with a single modelling framework. Note that panels have different y-axes scales.

more native hosts than non-native beetles (Fig. 5). Conversely, in these same beetle groups, non-native beetles had more non-native host species than native beetles. However, for both feeding guilds, the phylogenetic diversity of native hosts was not significantly different between native and non-native beetles ($p = 0.5$ and $p = 0.08$). Overall, there is a trend of native beetles in the North America feeding mostly on native host species, and conversely, introduced bark beetles feeding mostly on non-native hosts (Table 3).

3.5. Correlation in numbers of native and non-native hosts

Among beetle species, numbers of native hosts are generally correlated with numbers of non-native hosts (Fig. 6). At the host genus level, the correlation in numbers of native and non-native hosts among all North American beetle species was $r = 0.528$ ($p < 0.0001$) and the correlation for beetles in Europe was $r = 0.241$, ($p < 0.0001$). At the host species level, numbers of native and non-native hosts were significantly correlated among North American ambrosia beetles ($r = 0.452$, $p < 0.0001$), but the correlation was not significant for North American bark beetles ($r = 0.0818$, $p = 0.2258$).

3.6. Host associations of reciprocal beetle invasions between Europe and North America

We focused on 15 beetle species native to Europe that have invaded North America and 8 species native to North America that have invaded Europe (Table 4). For these species, we had information both about their ancestral hosts (at the genus level) in their native and invaded ranges. We lacked information about hosts in the native range of beetle species originating from other regions (i.e., Asia, Africa etc.) so they were not included in this table. For species shown in Table 4, we found that host breadth, expressed by mean number of host genera per beetle species, is generally greater in these beetles' indigenous region than in their invaded region. Furthermore, when beetles invade a new region, most species (21 out of 23) feed on host genera that are native to both their native range and the invaded region; however, about 1/3 of non-native beetles feed on host genera that are not native to the invaded region.

4. Discussion

When a herbivorous insect species arrives in a novel habitat, the presence of suitable host plants is a critical determinant of its establishment success. As a consequence, the native and invaded ranges of herbivorous insects and plant pathogens are limited by the geographic ranges of host plants suitable for their reproduction (Gougherty and Davies, 2022, Gohli and Jordal, 2017). Upon arrival of an insect in a new area, its hosts from the native range may not be present, so its invasion success may depend upon being able to use plants related to those on which it evolved. This situation can be considered an example of "ecological fitting" which is the process whereby organisms can only colonize novel environments by forming novel (not coevolved) associations with other species (in this case plants) that have specific traits (Janzen, 1985, Agosta, 2006).

In the case of herbivorous insects and plant pathogens utilizing novel hosts in their invaded ranges, there is considerable evidence that the suitability of novel hosts is strongly related to their phylogenetic similarity to native hosts. Several studies have documented a strong phylogenetic signal, driving host associations of both insects (Pearse and Hipp, 2009, Pearse and Altermatt, 2013, Mech et al. 2019) and plant pathogens (Bufford et al. 2016).

Given the critical nature of host availability to the establishment success of invading insect herbivores, it can be expected that

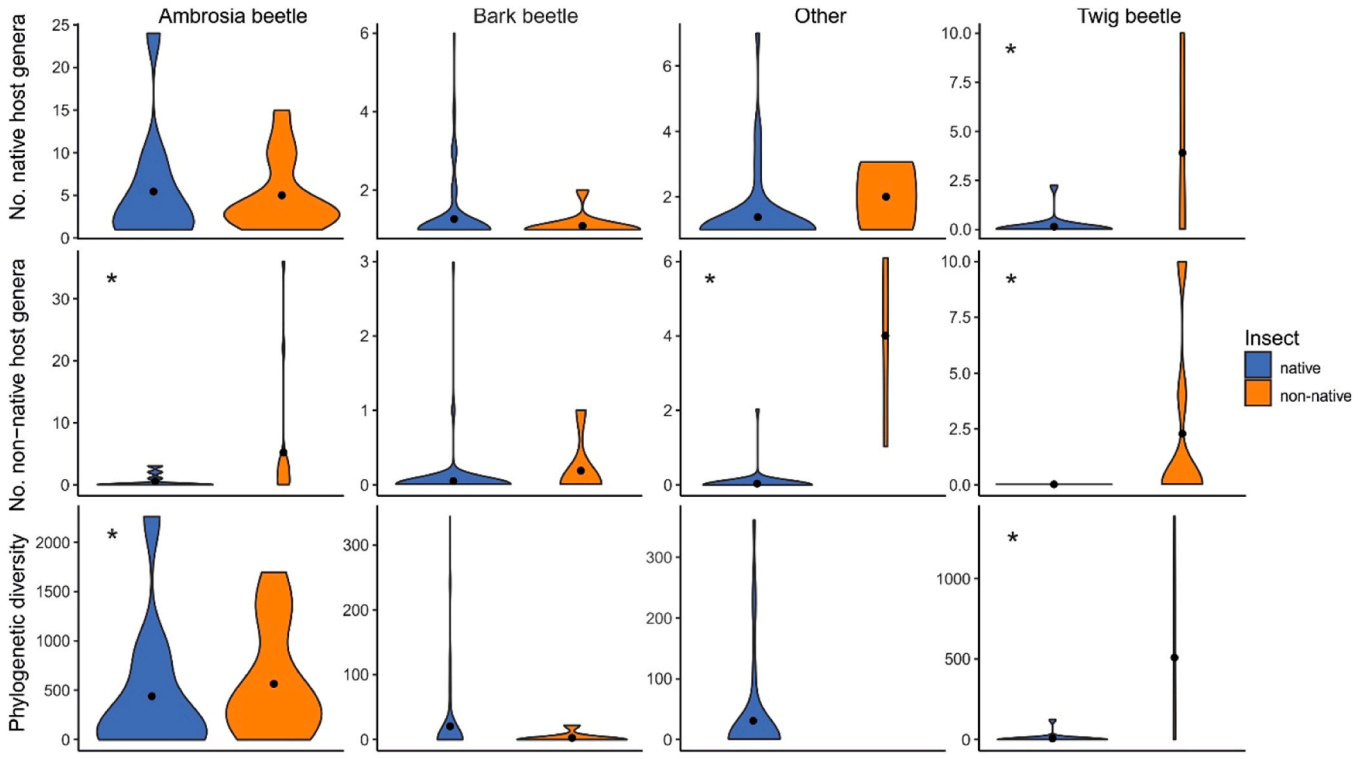

Fig. 4. The distribution of host richness (represented by number of host genera) and phylogenetic diversity for beetle species present in the European region. The width of each curve corresponds with the number of beetle species for each host genus richness or phylogenetic diversity value. The first two rows show the distribution of numbers of host genera (native hosts in the first row and non-native hosts in the second row) for beetles in the four feeding guilds. The third row shows phylogenetic diversity of native host genera for beetles in the four feeding guilds. Differences between native (blue) and non-native (orange) beetle species are evident. The black point corresponds to the mean. Asterisks indicate significant differences ($P < 0.05$) between native and non-native beetles within a given feeding guild based on ANOVA. Each row of panels was analyzed with a single modelling framework. Note that panels have different y-axes scales.

Table 1
ANOVA table showing the significance of factors affecting host breadth of beetles in North America. Factors include nativeness (native vs non-native beetles), feeding guild (bark beetle, ambrosia beetle, twig beetle, other) and their interactions. Results are presented for numbers of native host genera, numbers of non-native host genera and phylogenetic diversity (PD) of native host genera. The second part of the table shows the significance of pairwise comparisons in host breadth between native and non-native beetles for different feeding guilds, illustrating the nativeness*guild interaction. Note that results for host richness were calculated using a Poisson model, but the analysis of phylogenetic diversity was based on a linear model of log transformed data.

	Native hosts		Non-native hosts		Native hosts PD		
	LR Chisq	Pr(>Chisq)	LR Chisq	Pr(>Chisq)	Sum Sq	F value	Pr(>F)
intercept					627.13	130.19	5.03E-27
nativeness	4.43	0.0353	0.48	0.4880	0.03	0.01	0.9357
feeding guild	156.58	1.00E-33	105.07	1.26E-22	352.82	24.41	8.84E-15
nativeness*feeding guild	37.85	3.05E-08	47.51	2.71E-10	117.62	8.14	2.65E-05
Contrast between native and non-native beetles within feeding guilds							
	Estimate	p value	Estimate	p value	Estimate	p value	
Ambrosia beetle	-0.23	0.0337	-0.17	0.4847	-0.04	0.9357	
Bark beetle	0.31	0.2621	-2.05	0.0011	-0.15	0.8167	
Twig beetle	-1.20	9E-16	-2.53	3.47E-17	-4.51	1.41E-07	
Other	0.19	0.5417	-3.71	0.0003	-2.70	0.0112	

polyphagous herbivores might be more widely represented among successful invaders than host specialists (Vázquez, 2006). Gougherty and Davies (2021) found that plant communities more closely related to a pest's native hosts may be more invasible. Further, Gougherty and Davies (2022) and Wang et al. (2022) found that successfully established pests of trees tend to have greater host tree breadth than native pests. However, these studies only considered hosts that are native to invaded region, even though non-native hosts may be widely abundant due to planting or to their own invasiveness. In our results from both Europe and North America, we found that non-native twig beetles had higher native host breadth but in other guilds there was no difference between native and non-native host breadth at the host genus level (Figs. 3 and 4). In contrast, genus-level non-native host breath was greater for non-native beetle species than for native species in several guilds. Furthermore, analysis at the host species level indicated that native host breadth is greater for native beetles than for non-native beetles but that host breadth on non-native hosts is greater for non-native beetles than for native beetles (Fig. 5).

These results support the concept that the presence of non-native plants plays an important role in facilitating insect invasions. In a global analysis of non-native insect species richness, Liebhold et al. (2018) found that the number of naturalized invasive plants in a region was the strongest driver of the number of non-native insects in that region. Other studies have found similar associations between tree

Table 2
ANOVA table showing the significance of factors affecting host breadth of beetles in Europe. Factors include nativeness (native vs non-native beetles), feeding guild (bark beetle, ambrosia beetle, twig beetle, other) and their interactions. Results are presented for numbers of native host genera, numbers of non-native host genera and phylogenetic diversity (PD) of native host genera. The second part of the table shows the significance of pairwise comparisons in host breadth between native and non-native beetles in different feeding guilds illustrating the nativeness*guild interaction. Note that results for host richness were calculated using a Poisson model, but the analysis of phylogenetic diversity was based on a linear model of log transformed data.

	Native hosts		Non-native hosts		Native hosts PD		
	LR Chisq	Pr(>Chisq)	LR Chisq	Pr(>Chisq)	Sum Sq	F value	Pr(>F)
intercept					131.21	36.99	5.48E-09
nativeness	0.53	0.4684	53.69	2.35E-13	15.81	4.46	0.0359
feeding guild	77.76	9.26E-17	21.83	7.08E-05	92.50	13.04	4.57E-06
nativeness*feeding guild	23.57	3.07E-05	18.70	0.0003	29.06	4.10	0.0180
Contrast between native and non-native beetles within feeding guilds							
	Estimate	p value	Estimate	p value	Estimate	p value	
Ambrosia beetle	0.13	0.4671	-2.25	9.93E-08	-1.58	0.035927	
Bark beetle	0.15	0.6234	-1.50	0.0655	0.26	0.719643	
Twig beetle	-1.30	5.50E-08	-19.00	9.83E-01	-2.73	4.63E-04	
Other	-0.35	0.4155	-4.46	6.75E-09			

richness and numbers of non-native insect species (Guo et al. 2019, Ward et al. 2022) as a result of the "facilitation effect". A higher diversity of trees creates more ecological niches for invading insects and thus increases the chances that arriving insect herbivores will find hosts. Our results support the hypothesis that non-native plants are an important resource for invading insect species.

A good example of how non-native insects utilize hosts from their native range are the set of 23 scolytine species that have reciprocally invaded between Europe and North America (Table 4). In their invaded range, most of these species feed on host genera that are native in their native range, including genera that are native in both their native and invaded ranges and genera that are exclusively native to their native range and introduced in their invaded range. The generally high host specificity of most of these beetles indicates that the presence of these hosts was crucial to the success of their establishment.

Forister et al. (2015) found that most insect species are specialists, though there is some variation in specialization across insect feeding guilds. Bark- and wood-boring insects exhibit moderate levels of host specialization somewhere between high specialization in leaf-miners and lower specialization in free-feeding folivores. Our results generally support the conclusions of Forister et al. (2015) as we found skewed distributions of both numbers of host genera and numbers of host species as well as of host phylogenetic diversity (Figs. 3, 4 and 5).

Previous studies have reported that ambrosia beetles tend to be more polyphagous than other Scolytinae (Hulcr et al. 2007, Kirkendall et al. 2015). Our analysis confirmed the polyphagous nature of ambrosia beetles at both the host genus (Figs. 3 and 4) and species levels (Fig. 5) though host breadth also was high for twig beetles. Although both of these guilds were mostly polyphagous, they differed in how nativeness affected their associations with native vs. non-native hosts at the host genus level. Among twig beetles, non-native beetles tended to be associated with a higher proportion of non-native hosts and native beetles tended to be associated with a higher proportion of native hosts but use of native and non-native host genera did not differ among native and non-native ambrosia beetles (Figs. 3 and 4).

The biology of ambrosia beetles is unique. In contrast to phloem-feeding by other groups, ambrosia beetles excavate tunnels in xylem where they cultivate fungi that their larvae feed on (Beaver, 1989, Hulcr and Stelinski, 2017). The wide host breadth of ambrosia beetles is therefore explained in part by the wide host breadth of the fungi on which they feed. Whereas bark beetles must contend with the strong defensive reaction of live or freshly weakened trees to their attacks, ambrosia beetles mostly colonize dying or dead trees, and do not feed on the tree itself, so host defense is less acute. Larvae of many twig beetles also feed on fungi, and this may explain their wide host tree breadth as well (Kirkendall et al. 2015). Overcoming host defenses may require specialization and therefore bark beetles are more specialized on hosts than ambrosia beetles (Raffa and Berryman, 1987, Raffa et al. 2015). Given the wider breadth of hosts of ambrosia beetles, their host range is less limited and their potential to invade new areas may be higher thus, explaining their dominant representation in non-native assemblages (Atkinson et al. 1990, Sauvard, 2007, Kirkendall and Faccoli, 2010, Lantschner et al. 2020, Grégoire et al., 2023); (Fig. 2a).

Across both regions and beetle groups there is at least a weak tendency for species with the greatest breadth of native hosts to also exhibit greater breadth of non-native hosts (Fig. 6); this pattern is present in both native and non-native beetles at both the host species and genus level. A similar correlation between host breadth on native and novel hosts was reported for Lepidoptera by Jahner et al. (2011). Such correlations may reflect a physiological capacity of generalist insect species to tolerate varying host defenses on both native and non-native plants.

Variation in host breadth among beetle guilds and between native and non-native beetle species was generally similar between Europe and North America (Figs. 3 and 4, Tables 1 and 2). Though comparison of absolute levels of host breadth between Europe and North America was not an objective of this study, we note that among all guilds, host breadth was generally higher for native beetles in North America than for native beetles in Europe (Fig. 2a, b). This pattern can be at least partially explained by the higher overall tree species richness in North America compared to Europe (Svenning and Skov, 2007).

It should be pointed out that there are inherent limits to almost all databases of insect-host plant associations. First, there is a tendency for such lists of host species to be more completely described for more common or damaging insects that receive more attention; such errors have the potential to introduce consistent bias in certain analyses though we have no reason to expect that was a major problem in our study. Second, an observation of an insect on a plant or record of attraction of an insect to a plant does not necessarily mean that the insect is capable of feeding on the plant and surviving to reproduce (Ward, 1988, Cunningham and Zalucki, 2014). Finally, there are instances of extremely rare host associations that have limited biological meaning. We attempted to remove such rare associations in compiling the data here, but we acknowledge that despite these attempts, some errors may persist.

Kirkendall et al. (2015) reported that worldwide, most (82 %) scolytine genera feed predominantly on angiosperms. However, this statistic may be strongly influenced by the high scolytine diversity in the tropics since we found that among native species in both Europe and North America, 50 % or more (54–62 %) native species predominantly feed on conifers (Fig. 2b). However, among non-native species in North America, >75 % of species predominantly feed on angiosperms. This may reflect either the dominance of angiosperm-feeding species

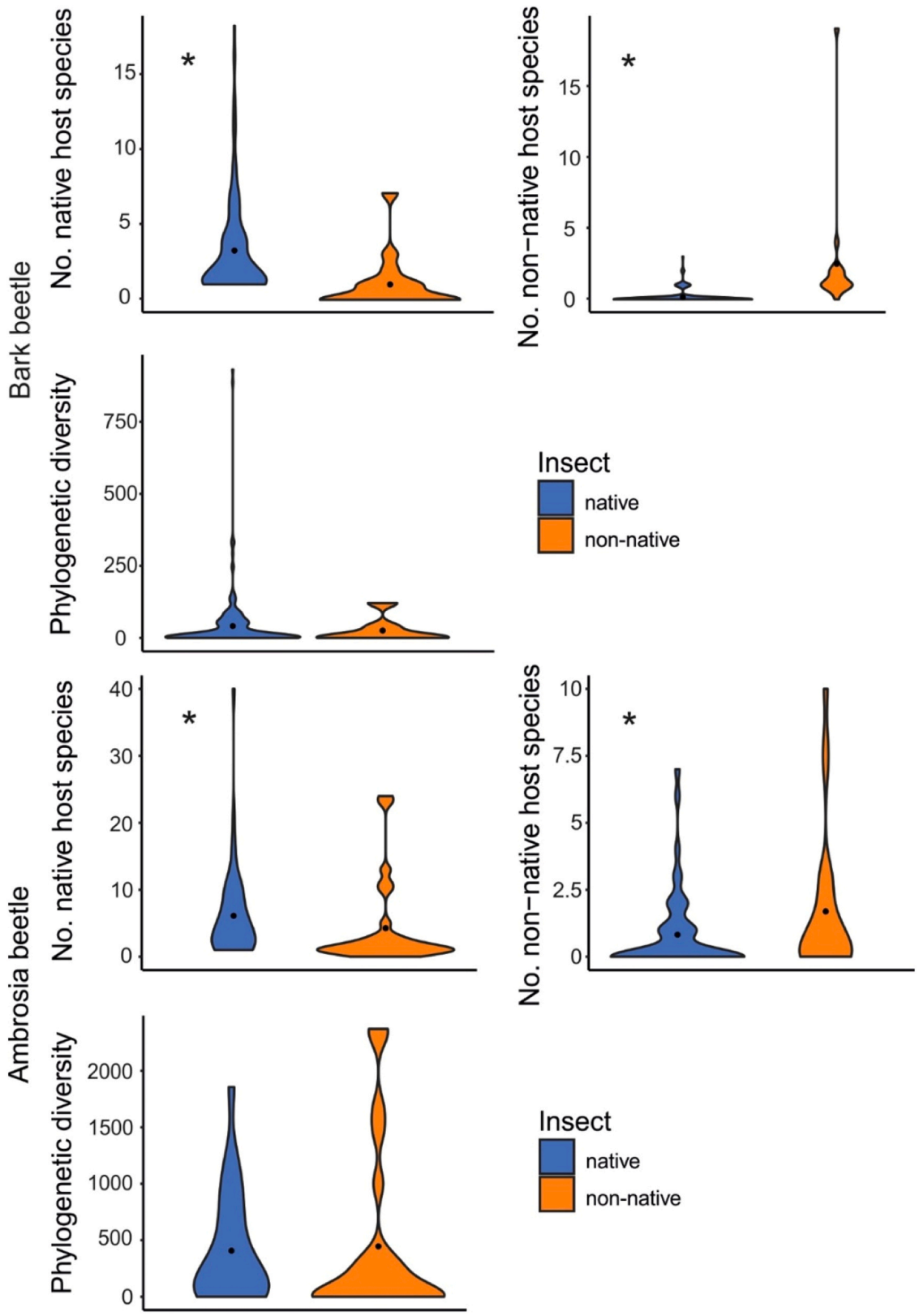

Fig. 5. Host breadth on native tree species in North America for native and non-native true bark beetles expressed as number of native host species and phylogenetic diversity of native host species. The width of each curve corresponds with the number of beetle species for each host species richness or phylogenetic diversity value. The third and fourth lines show results for American ambrosia beetles. Data on host breadth on non-native hosts is unavailable (too few observations for meaningful summarization). Black points represent mean values. Asterisks indicate significant differences ($P < 0.05$) between native and non-native beetle species based on ANOVA. Each row of panels was analyzed with a single modelling framework. Note, that panels have different y-axis scales.

Table 3
ANOVA table showing the significance of nativeness (native vs non-native beetles) on host breadth of bark and ambrosia beetles in North America at the host species level. Results are presented for numbers of native host species, numbers of non-native host species and phylogenetic diversity (PD) of native host species.

Bark beetles of the North America										
	Native host species			Non-native host species			Native hosts PD			
	LR Chisq	Pr(>Chisq)	Estimate	LR Chisq	Pr(>Chisq)	Estimate	Sum Sq	F value	Pr(>F)	Estimate
Intercept			1.18			-1.86	947.58	249.09	1.12E-37	2.13
nativeness	28.19	1.10E-07	-1.11	112.42	2.89E-26	2.79	1.71	0.45	0.50	-0.50
Ambrosia beetles of the North America										
	Native host species			Non-native host species			Native hosts PD			
	LR Chisq	Pr(>Chisq)	Estimate	LR Chisq	Pr(>Chisq)	Estimate	Sum Sq	F value	Pr(>F)	Estimate
Intercept			1.81			-0.23	948.21	111.77	2.67E-16	4.31
nativeness	10.87	9.79E-04	-0.36	11.67	6.36E-04	0.75	26.20	3.09	0.0831	-1.29

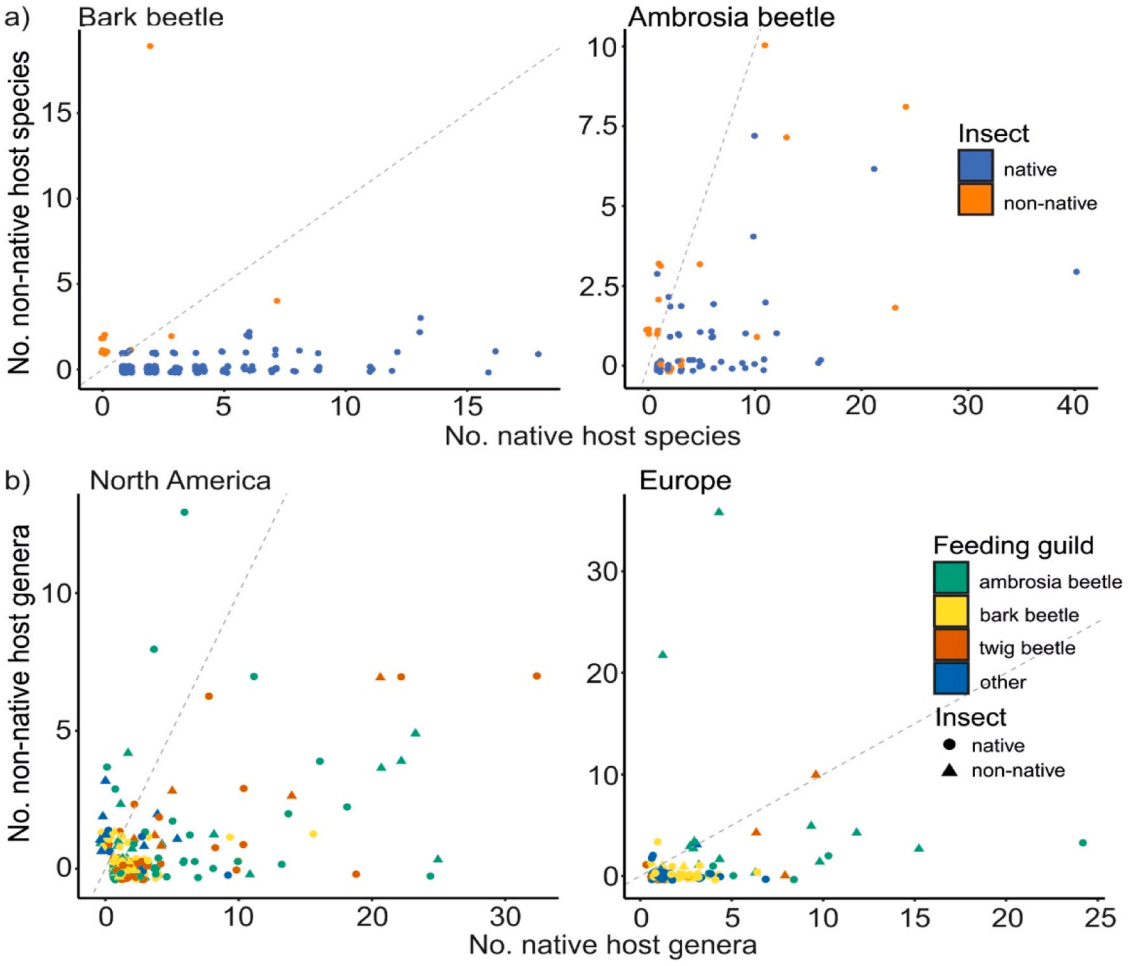

Fig. 6. Correlation between numbers of native and non-native hosts for both native and non-native Scolytinae and Platypodinae species. A) data for bark and ambrosia beetles present in North America with number of hosts measured at the species level. B) data for different guilds in north America and Europe with numbers of hosts measured at the genus level. Dashed line corresponds to equal numbers of native and non-native hosts. Note, that axis scales are not the same for each plot. Also note that points have been "jittered" to facilitate visualization.

worldwide or the high diversity of angiosperms in eastern North America where invasions of forest insects has been most frequent (Liebhold et al. 2013). Ohmart (1989) noted that broadleaf trees lack the constitutive defense system that conifers use to defend against tree-killing bark beetle attacks which provides a partial explanation for the overall greater diversity on angiosperms.

5. Conclusions

We report a pattern in which host breadth on native plants is greater for native beetle species than for non-native species. Conversely, host breadth of non-native beetles tends to be greater on non-native plants. This latter pattern indicates that insect herbivore invasion success is promoted by the presence of ancestral host plants that have previously invaded from the beetle's native range. These results contribute to explaining the macroecological pattern of insect invasions being correlated with plant invasions through space and time (Liebhold et al. 2018, Bonnamour et al. 2023).

Table 4
Number of host genera used by North American Scolytinae and Platypodinae species introduced to Europe and vice versa, showing mean numbers of host genera in various categories.

Species	Native to	Hosts in beetle native range	Hosts in beetle invaded range				
			All hosts	Hosts native to invaded range		Hosts not native to invaded range	
		Hosts native to beetle native range		Hosts native to beetle native range	Hosts not native to beetle native range	Hosts native to beetle native range	Hosts not native to beetle native range
Gnathotrichus materiarius	North America	1	6	4	0	2	0
Monarthrum mali	North America	6	3	3	0	0	0
Pityophthorus juglandis	North America	1	1	1	0	0	0
Pityophthorus solus	North America	1	1	1	0	0	0
Hypothenemus eruditus	North America	32	20	8	2	2	8
Dryocoetes affaber	North America	1	1	1	0	0	0
Phloeotribus liminaris	North America	1	1	1	0	0	0
Xyleborus affinis	North America	16	1	1	0	0	0
Hylastes opacus	Europe	1	1	1	0	0	0
Hylurgops palliatus	Europe	1	2	2	0	0	0
Hylastinus obscurus	Europe	4	2	1	0	1	0
Hylurgus ligniperda	Europe	1	1	1	0	0	0
Tomicus piniperda	Europe	1	1	1	0	0	0
Phloeotribus scarabaeoides	Europe	1	1	0	0	1	0
Scolytus mali	Europe	3	1	1	0	0	0
Scolytus multistriatus	Europe	1	1	1	0	0	0
Scolytus rugulosus	Europe	6	2	2	0	0	0
Orthotomicus erosus	Europe	1	1	1	0	0	0
Pityogenes bidentatus	Europe	1	1	1	0	0	0
Dactylotrypes longicollis	Europe	2	1	0	0	0	1
Crypturgus pusillus	Europe	1	1	1	0	0	0
Trypodendron domesticum	Europe	10	1	1	0	0	0
Xyleborus monographus	Europe	1	1	1	0	0	0
Mean number of genera		4.04	2.26	1.52	0.09	0.26	0.39

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CRediT authorship contribution statement

Samuel F. Ward: Writing – review & editing, Formal analysis. **Andrew M. Liebhold**: Writing – original draft, Supervision, Formal analysis, Conceptualization. **Marek Turčáni**: Writing – review & editing, Project administration, Funding acquisition. **Soňa Šenfeldová**: Writing – original draft, Formal analysis, Data curation, Conceptualization. **Miloš Knížek**: Writing – review & editing, Data curation. **Thomas H. Atkinson**: Writing – review & editing, Data curation. **Nathan P. Havill**: Writing – review & editing, Formal analysis. **Robert J. Rabaglia**: Writing – review & editing, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data compiled and analyzed here can be freely downloaded from the Zenodo repository: https://zenodo.org/records/10927845.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121908.

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