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ORIGINAL PAPER

Variable effects of forest diversity on invasions by non-native insects and pathogens

Samuel F. Ward[1] · **Andrew M. Liebhold**[2,3] · **Songlin Fei**[4]

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Abstract

The geographical distributions of non-native forest insects and pathogens (pests) result from a multitude of interacting abiotic and biotic factors. Following arrival, the presence of suitable host trees and environmental conditions are required for pests to establish and spread, but the role of forest biodiversity in this process is not well-understood. We analyzed county-level data for 22 non-native forest pests in the conterminous United States, developing species-specific models to investigate the effects of spatial contagion, human activities, and host and non-host tree biomass or richness on the occurrence of pest species. Species-specific models indicated that (i) the spatial contagion of invasions was the most common driver of invasion incidence, (ii) facilitation effects from host biomass and richness were present in approximately half of the invasions and almost entirely observed in invasions by sap-feeding insects or pathogens, and (iii) there was substantial variation in the direction and magnitude of the effects of non-host tree biomass and richness on invasion. Our analyses highlighted the prominent role of spatially derived propagule pressure in driving intracontinental invasions whereas effects of forest biodiversity were variable and precluded broad generalizations about facilitation and dilution effects as drivers of forest pest invasions at large spatial scales.

Keywords Biodiversity · Forest insect · Habitat invasibility · Invasion · Pathogen · Species richness · Spread

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✉ Samuel F. Ward
sward@entomology.msstate.edu

[1] Department of Biochemistry, Molecular Biology, Entomology, and Plant Pathology, Mississippi State University, Mississippi State, MS 39762, USA

[2] USDA Forest Service, Northern Research Station, Morgantown, WV 26505, USA

[3] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, 165 00 Prague 6, Suchdol, Czech Republic

[4] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA

Introduction

The theory that plant diversity promotes ecosystem stability has a long history in ecology (MacArthur 1955; Elton 1958; May 1975; Tilman and Downing 1994; Naeem and Li 1997). In forest ecosystems, biodiversity is widely believed to reduce susceptibility to insect outbreaks (Brockerhoff et al. 2017; Jactel et al. 2021), with several reports indicating that tree diversity is inversely related to damage from herbivores (Jactel and Brockerhoff 2007; Guyot et al. 2016). Several mechanisms have been offered to explain this pattern, including a "dilution" effect in which tree diversity increases the complexity of chemical and physical cues through which an herbivore must navigate to procure a host (i.e., decreasing plant apparency) (Barbosa et al. 2009; Castagneyrol et al. 2013). Other explanations are that higher tree diversity supports a greater diversity and abundance of natural enemies or that tree diversity supports increasing physiological resistance of individual plants via plant-plant interactions (i.e., associational protection via defense priming) (Barbosa et al. 2009; Brockerhoff et al. 2017; Jactel et al. 2021). Most investigations of forest biodiversity-pest impact relationships, however, have focused on native herbivores and been conducted at the stand scale (Brockerhoff et al. 2017).

The diversity-stability hypothesis has also been extended to biological invasions. Several studies have found that native plant diversity increases resistance to invasions by non-native plant species (Naeem et al. 2000; Fargione and Tilman 2005; Iannone et al. 2016). However, other studies, mostly conducted at larger spatial scales, have found the opposite relationship (Levine and D'Antonio 1999; Stohlgren et al. 2003). These contradictory findings have been reconciled in the "invasion paradox" theory that posits that diversity-invasibility relationships are scale-dependent (Fridley et al. 2007; Iannone et al. 2015).

Similarly, there are mixed results concerning the relationship between forest biodiversity and invasion by insects and pathogens (pests) (Bosso et al. 2017; Guo et al. 2019; Panzavolta et al. 2021). The effect of plant diversity on habitat invasibility can be positive (Liebhold et al. 2013, 2018; Hudgins et al. 2017), negative (Jactel et al. 2006; Haas et al. 2011), or both, differing between diversity of host vs. non-host plants (Guo et al. 2019). Tree diversity effects can also be neutral and/or dependent on spatial scale (Morin et al. 2007; Brockerhoff et al. 2017) and/or where on the biodiversity spectrum a community is located (i.e., relationships could be nonlinear) (Guo et al. 2019). At the country-level, numbers of non-native insect species were positively associated with both native and non-native plant species richness, potentially as a result of "facilitation" effects: increased plant diversity creates more niches for specialist herbivore species and these additional herbivores create more niches for insects at higher trophic levels (Liebhold et al. 2018). At a slightly smaller spatial scale (counties within the United States (US)), the number of non-native insect and pathogen species increased with overall tree diversity (Liebhold et al. 2013; Guo et al. 2019). But while host tree richness had a positive effect on the richness of non-native pests, richness of non-host trees had a negative effect (Guo et al. 2019), with the latter indicating a dilution effect of non-host plants. Thus, the diversity of hosts vs. non-hosts may disparately influence invasion success compared with overall plant community richness.

Previous analyses of invasibility to forest pests in the US have focused on the effects of tree diversity at the pest community level, such as the numbers of pest species per county (Liebhold et al. 2013; Guo et al. 2019). However, these analyses have inherent limitations as counts of pest species do not meaningfully allow for differentiation of host and non-host tree species; individual pest species have unique sets of host trees, so it is ambiguous to classify tree species as hosts when analyzing aggregate numbers of pest species. Here, we quantified the role of host and non-host tree biomass and richness on invasions of individual forest pest species across the conterminous US. Our main objective was to develop species-specific models predicting county-level occurrence of pest invasion as a function of host and non-host tree biomass and richness. This species-level approach was aimed at investigating variation in facilitation and dilution effects among pest invasions, as knowledge of these patterns could provide insight into the context in which biodiversity governs invasion dynamics (Prospero and Cleary 2017).

Material and methods

We analyzed data from the Alien Forest Pest Explorer database (Liebhold et al. 2013), which documents county-level occurrence (hereafter invasion incidence) of non-native forest insects and pathogens across the conterminous US and is limited to non-native species known to cause damage to forest trees. We selected pest species from this database for which we had approximate locations of first discovery locations (Ward et al. 2019) as well as exhaustive county-level occurrence data, as county occurrence records for several pest species are incomplete. We also excluded pests (e.g., Australian Eucalyptus longhorned beetle) that primarily attack non-native tree species. These criteria (i) narrowed-down the number of species from ~ 90 in the full Alien Forest Pest Explorer database to 13 insect and 9 pathogen species ($n = 22$ pests; Table 1) and (ii) meant that we analyzed a subset of those species evaluated by Liebhold et al. (2013) and Guo et al. (2019). For brevity, scientific names and authorities are provided in Table 1 rather than with the first mention of common names in the main text.

We linked invasion incidence for each pest with Forest Inventory and Analysis (FIA) data collected by the US Department of Agriculture—Forest Service (USDA-FS) (Bechtold and Patterson 2005), categorizing each tree species in the FIA database as a host or non-host for each insect and pathogen (Liebhold et al. 2013). The FIA program inventories forest attributes across the US, with a sampling intensity of approximately one, ~ 0.067 ha plot per ~ 2428 ha. We extracted data on biomass as total metric tons per county of live aboveground biomass for native tree species and richness as total number of native tree species occurring on plots sampled in each county. Biomass values were $\ln(x+1)$-transformed for analysis. Data from a total of 130,210 permanent fixed-area forest plots were used to obtain these estimates. A summary of diet breadth for each pest species is provided in Fig. 1, and the average host tree biomass and richness available to each pest per county is provided in Fig. 2.

To evaluate the effects of tree biomass and richness on invasion incidence, we needed to also incorporate (i) the propensity of pests to invade counties closer to their point of initial discovery and (ii) human activities that could facilitate the establishment and spread of pests in new areas into models. To account for spread, we estimated a term, spatial proximity, by taking the inverse of the distance of each county centroid to the first discovery location of each pest. Thus, larger values indicated a given county was closer to the discovery location. The variable for spatial proximity was $\ln(x)$-transformed for analysis. To account for human activities, such as the spread of infested materials and any potential detection biases, a variable for human population density per county in 2010 was obtained from the US Census Bureau (US Census Bureau 2010) and $\ln(x+1)$-transformed for analysis.

Previous analyses of forest pest invasions in the US have focused on patterns of pest diversity per county (i.e., a community-level approach) and indicated that tree species

Table 1 Common names, scientific names, and feeding guilds for non-native forest insects and pathogens in the United States. Exhaustive, reliable records of county-level occurrence were available for these species

n	Common name	Scientific name	Feeding guild
1	Emerald ash borer	*Agrilus planipennis* Fairmaire	Borers
2	Japanese cedar longhorned beetle	*Callidiellum rufipenne* (Motschulsky)	Borers
3	Mediterranean pine engraver	*Orthotomicus erosus* (Wollaston)	Borers
4	Pine shoot beetle	*Tomicus piniperda* (Linnaeus)	Borers
5	Sirex woodwasp	*Sirex noctilio* Fabricius	Borers
6	Browntail moth	*Euproctis chrysorrhoea* (Linnaeus)	Foliage-feeders
7	Spongy moth	*Lymantria dispar* (Linnaeus)	Foliage-feeders
8	Winter moth	*Operophtera brumata* (Linnaeus)	Foliage-feeders
9	Balsam woolly adelgid	*Adelges piceae* (Ratzeburg)	Sap-feeders
10	Circular hemlock scale	*Nuculaspis tsugae* (Marlatt)	Sap-feeders
11	Hemlock woolly adelgid	*Adelges tsugae* (Annand)	Sap-feeders
12	Pine bast scale	*Matsucoccus matsumurae* (Kuwana)	Sap-feeders
13	Spruce aphid	*Elatobium abietinum* (Walker)	Sap-feeders
14	Beech bark disease[a]	*Nectria faginata* (Lohman, Watson & Ayres) Cast. & Rossman	Pathogens
		Nectria ditissima (Tul. & C. Tul.) Samuels & Rossman	Pathogens
	Beech scale insect	*Cryptococcus fagisuga* Lindinger	(Sap-feeders)
15	Butternut canker	*Ophiognomonia clavigignenti-juglandacearum* (Nair, Kostichka, & Kuntz) Broders & Boland	Pathogens
16	Dogwood anthracnose	*Discula destructiva* (Fr.) Munk ex H. Kern	Pathogens
17	European larch canker	*Lachnellula willkommii* (Hartig) Dennis	Pathogens
18	Laurel wilt[a]	*Harringtonia lauricola* (T.C. Harr. et al.) Z.W. de Beer & M. Procter	Pathogens
	Redbay ambrosia beetle	*Xyleborus glabratus* Eichhoff	(Borers)
19	Oak wilt	*Bretziella fagacearum* (Bretz) Z.W. de Beer, S. Marincowitz, T.A. Duong & M.J. Wingfield	Pathogens
20	Port-Orford-cedar root disease	*Phytophthora lateralis* (Tucker & Milbrath)	Pathogens
21	Sudden oak death	*Phytophthora ramorum* (Werres, De Cock & Man in't Veld)	Pathogens
22	White pine blister rust	*Cronartium ribicola* J.C. Fisch.	Pathogens

[a] Pest-disease complexes, recorded as pathogens for analyses

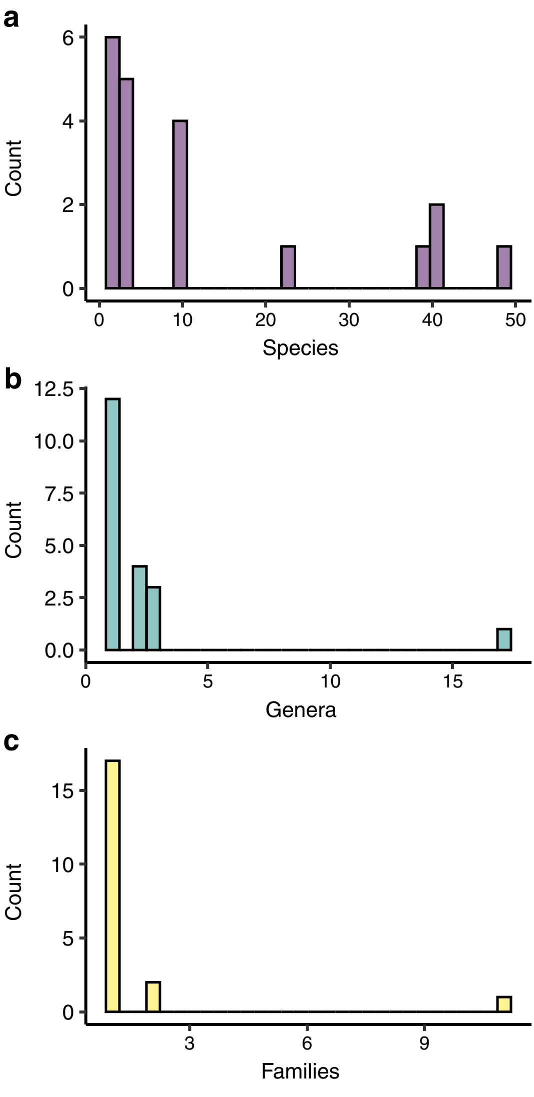

Fig. 1 Number of tree **a** species, **b** genera, and **c** families fed on by 20 non-native forest insects and pathogens in the US. Two extreme generalists, spongy moth (feeds on 480 species, 154 genera, 58 families) and winter moth (143, 13, 9) are not depicted

biomass and richness have similar effects on invasion (Guo et al. 2019). To assess the robustness of that conclusion, we developed two models predicting invasion incidence of each pest as a function of spatial proximity, human population density, and then a combination of either (i) host and non-host biomass (biomass models) or (ii) host and non-host richness (richness models). Thus, we developed two logistic regression models for each species (22 species × two modeling frameworks for 44 total models). We did not fit models that included biomass and richness together because of collinearity, for which we adopted a threshold of $|r| > 0.7$ (Dormann et al. 2013), between host biomass and host richness. Collinearity between predictors in each of the 44 models was assessed using pairwise correlations and, when collinearity between any pair of predictors surpassed our chosen threshold, the pest was removed from the corresponding analysis. This meant that three and five pests were removed from the biomass and richness analyses, respectively (Online Appendix 1).

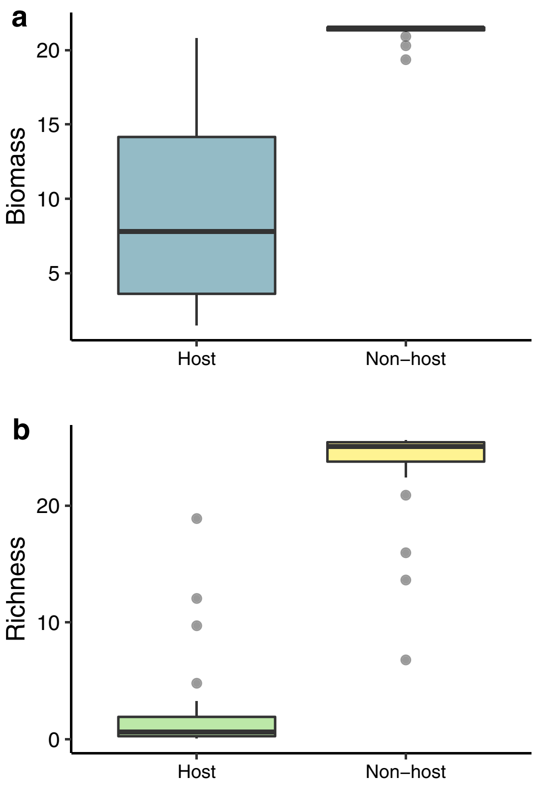

Fig. 2 Average host and non-host tree biomass (ln(metric tons + 1)) and richness across all counties per species for 22 non-native forest insects and pathogens established in the conterminous US. Tree data are from the USDA Forest Service—Forest Inventory and Analysis program

Model results were visualized graphically and Bonferroni corrected values (i.e., $|Z| \geq 2.99$, indicating $p = 0.05/(36 \text{ models})$), used to identify statistically clear relationships between invasion incidence and predictors, were overlaid on graphs to account for developing multiple models. We also visually assessed the role of pest feeding guild (borer, foliage-feeder, sap-feeder, or pathogens) by coloring points by guild. The data that support findings of this study are available in the supplementary material (Online Appendix 2).

Results

Across all the individual species models except one (the richness model for sudden oak death), the spatial proximity predictor was strongly, positively correlated with invasion incidence, indicating that, as expected, counties located closer to the initial discovery location were more likely to be invaded (Fig. 3). The effects of human population density on invasion incidence varied in both modeling frameworks, with invasions by about half of the pests exhibiting a non-significant ($|Z| < 2.99$) relationship (Fig. 3).

There was support for the facilitation hypothesis, as invasions by approximately half of the pests were positively associated with biomass (11 pests) or richness (9 pests) of host trees (Fig. 3). Of the invasions that did exhibit a significant, positive association with host biomass (Fig. 3a) and richness (Fig. 3b), all were either by sap-feeding insects or pathogens except for the invasion by pine shoot beetle. Analyses of pine shoot beetle provided

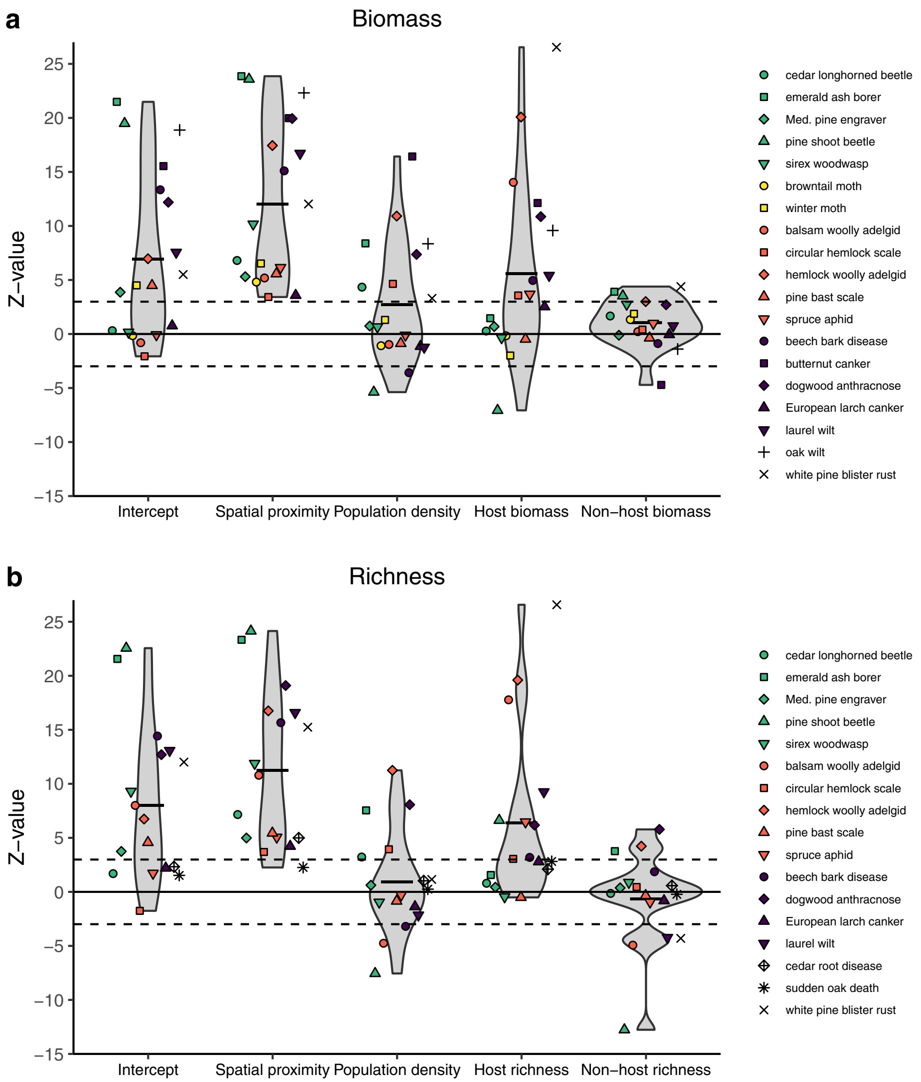

Fig. 3 Summary of logistic regression models (one model per pest per panel) predicting county-level occurrence of 19 (panel **a**) and 17 (panel **b**) forest insects and pathogens in the conterminous US fit as a function of four predictors (*x*-axes, with each panel indicating a modeling framework). The solid black line indicates zero whereas the dashed lines indicate *Z*-values corresponding to Bonferroni-corrected *p*-values to account for fitting multiple models. Points are jittered in the *x*-direction to reduce overlap and colored by guild (green = borers, yellow = foliage-feeders, red = sap-feeders, purple = pathogens). Thicker horizontal bars indicate mean *Z*-values for each predictor across all models

contradictory evidence for facilitation-dilution effects, as invasion by this pest was negatively correlated with host biomass but positively correlated with host richness.

Invasions by most pests were not clearly associated with biomass or richness of non-host trees, but there was some mixed evidence of both facilitation and dilution effects from non-hosts. Invasions by emerald ash borer, pine shoot beetle, and white pine blister rust were positively associated with non-host biomass (Fig. 3a) and invasions by emerald ash borer, hemlock wooly adelgid, and dogwood anthracnose were positively associated with non-host richness (Fig. 3b), indicating facilitation effects. However, invasions by pine shoot beetle and white pine blister rust provided contradictory evidence, indicating dilution effects by exhibiting negative correlations with non-host richness. There was additional evidence of dilution effects in invasions by three other species: invasion by butternut canker was negatively associated with non-host biomass whereas invasions by balsam wooly adelgid and laurel wilt were negatively associated with non-host richness.

Discussion

The density of both host (Morin et al. 2009; Hudgins et al. 2017; Ward et al. 2020; Mally et al. 2021) and non-host (Rigot et al. 2014) trees can be key determinants in the spread of invading insects and pathogens. Overall, our results indicate that facilitation effects, acting through both host species biomass and richness, often mediate landscape-scale invasion dynamics (Guo et al. 2019). However, it appears that the facilitative role of host trees (Fig. 3a, b) is highly idiosyncratic, varying substantially among species (Fig. 3): invasions by about half of the pests were not clearly associated with host biomass (Fig. 3a) and/or richness (Fig. 3b). Effects of non-host trees were rarer, but there was weak evidence of both facilitation and dilution effects driving some invasions (Fig. 3).

Across most models, spatial proximity was the strongest predictor of invasion, highlighting the importance of spread from the point of introduction compared with host and non-host biomass or richness in non-urban forest areas, as our tree data did not include urban plantings. This accords well with the widely-recognized importance of propagule pressure as a driver of biological invasions (Simberloff 2009). The availability and density of urban forests, which were not directly measured here but could be correlated with human population density, may play a more important role than our findings suggest (Colunga-Garcia et al. 2009, 2010; Koch et al. 2018; Branco et al. 2019).

Invasion incidence was, surprisingly, negatively correlated with host biomass for one pest, pine shoot beetle (Fig. 3a), the opposite of what would be expected to result from a facilitation effect. The negative host biomass-invasion relationship might be attributable to the arrival of this pest in Ohio (Haack 2020) in an area with relatively low abundances of pine. Nonetheless, it is likely that climatic effects have inhibited the invasions of this and other pests into regions with suitable hosts, potentially obscuring or strengthening some facilitation and dilution effects.

Both modeling frameworks (i.e., biomass models and richness models) elucidated the positive effects that host trees can have on invasions by forest pests (Fig. 3), which could simply reflect the increased potential of finding a host and/or the increased potential that a preferred or optimal host occurs in a community. Insects can experience mismatches between host preference and insect performance (Gripenberg et al. 2010), and the likelihood a preferred host that also maximizes insect fitness will be encountered increases with forest diversity. The negative association of invasion by some species with non-host richness but neutral or positive effects of non-host biomass (Fig. 3; e.g., pine shoot beetle) could indicate that dilution effects sometimes arise from the increased probability that a highly disruptive, non-host occurs in the community. That is, if a rare, non-host tree species is attractive to an herbivore for oviposition but not suitable for its development, it could serve as a population sink (i.e., an attractive sink) (Delibes et al. 2001); higher non-host richness would increase the chance that such hosts occur in a given county.

The spatial and/or temporal scale of our analysis could have influenced results, as we were only able to evaluate the spatial configuration of trees at the county-level—the resolution of our pest data—potentially overlooking the influences of tree distributions on pest invasions at the subcounty level. For example, our richness metric would treat a county with two spatially isolated monocultures of different tree species numerically equivalent to a county containing a single forest with a mixture of two tree species. There is good evidence that the configuration of hosts across the landscape and within a stand could influence both herbivore and/or invasion dynamics (Rigot et al. 2014). Moreover, we quantified variation in pest occurrence (presence/absence), but forest diversity can also influence impacts (e.g., annual host mortality rates or infection rates) caused by a given pest (Rottstock et al. 2014). Indeed, community wide prevalence of a pest might decrease with increasing forest diversity, but tree-level pest abundance may remain high (Rosenthal et al. 2021).

Our analysis generally provides stronger support for the facilitation effect than the dilution effect, although results are highly variable among species, potentially because the invaded ranges analyzed here were likely constrained by factors not captured by our explanatory variables. As noted above, ranges of many forest pests are well known to be affected by climate (Srivastava et al. 2021; Koch 2021). Additionally, our data were a recent snapshot of human population density and forest composition and may not reflect the historical conditions some pests encountered as they were invading decades ago. It may also be that facilitation-dilution effects are stronger along the leading edge of invasions, yet temporal invasion data for most non-native forest pests in the US are not available at a high enough resolution to detect such effects. Even within a site, associational resistance can change through time, as host plants can become more apparent to herbivores by exhibiting faster growth rates than other members of the community (Castagneyrol et al. 2020). Another aspect of variability not considered was that of plant health or chemical defense (e.g., as mediated by site quality or plant functional group), which could influence pest population growth (Becerra 2015; Richards et al. 2015) and consequently establishment.

Lastly, we caution that our analyses were limited to pests that can cause significant economic or ecological damage, and results may not hold for invading species that are less impactful and/or abundant. As more high-resolution spatial data become available, future investigations of facilitation and dilution effects on pest invasion would benefit from a more explicit consideration of spatial scale, including sub-county patterns of host density and dispersion. Understanding the influences of plant diversity at finer scales might inform the design of more pest resistant landscapes (Riley et al. 2022), of particular importance in urban environments that are a frequent point of establishment and initial spread for invading tree pests.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-022-02443-4.

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Author contributions All authors contributed to the study conception, data curation, and analyses. The first draft of the manuscript was written by SFW and all authors provided substantial input on subsequent versions. All authors read and approved the final manuscript.

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Data availability The data supporting findings of this study are available in the supplementary material (Online Appendix 2).

Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.

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