Tree diversity regulates forest pest invasion

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Edited by Rodolfo Dirzo, Department of Biology, Stanford University, Stanford, CA, and approved March 5, 2019 (received for review December 10, 2018)

Nonnative pests often cause cascading ecological impacts, leading to detrimental socioeconomic consequences; however, how plant diversity may influence insect and disease invasions remains unclear. High species diversity in host communities may promote pest invasions by providing more niches (i.e., facilitation), but it can also diminish invasion success because low host dominance may make it more difficult for pests to establish (i.e., dilution). Most studies to date have focused on small-scale, experimental, or individual pest/disease species, while large-scale empirical studies, especially in natural ecosystems, are extremely rare. Using subcontinental-level data, we examined the role of tree diversity on pest invasion across the conterminous United States and found that the tree-pest diversity relationships are hump-shaped. Pest diversity increases with tree diversity at low tree diversity (because of facilitation or amplification) and is reduced at higher tree diversity (as a result of dilution). Thus, tree diversity likely regulates forest pest invasion through both facilitation and dilution that operate simultaneously, but their relative strengths vary with overall diversity. Our findings suggest the role of native species diversity in regulating nonnative pest invasions.

biotic resistance | constraint envelope | facilitation | dilution | host vs. nonhost

Biological invasions often lead to novel, and sometimes complex, species interactions within and among trophic levels (1–3). These novel cross-trophic interactions can have serious socioeconomic consequences, such as the emergence of new human diseases and outbreaks of agricultural and forest pests (4, 5). To date, numerous studies have separately examined how host species diversity may promote or diminish parasite/disease diversity (6, 7). While small-scale and experimental research (especially on a single parasite) has provided empirical and theoretical evidence of facilitation, dilution, or both (8), corresponding patterns in natural ecosystems are largely unknown, especially over regional or continental scales. More importantly, the role of overall community diversity (i.e., hosts plus nonhosts in the entire assemblages) in multipest invasion remains elusive (9–12).

The relationship between tree diversity and susceptibility to pest invasions is central to invasion biology and has implications in ecosystem management (13). Theory predicts that high diversity (defined here as species richness) is generally associated with lower average abundance for each component species (14). When considering cross-trophic aspects of the invasion processes (e.g., host-parasite, plant-pest), facilitation assumes that more host species provide more niches for herbivores/pathogens, especially for specialists (e.g., the "host diversity begets parasite diversity" hypothesis) (15–19). In contrast, dilution assumes that the amount and accessibility of hosts are reduced in more diverse communities, making it difficult for pests to establish (i.e., dilution effects) (20, 21).

Although broadly applied to parasites, the facilitation and dilution effects could also be applied to plant-pest interactions (13). Whether a plant species is colonized by pests depends on what the neighboring plants are and on how many of them there are (e.g., host vs. nonhosts and their relative proportions), as well as on the direct and indirect interactions among neighboring species (6, 13). Here we hypothesized that both facilitation and dilution can occur within the same forest community at the same time, although their relative strengths may vary. To test this hypothesis, we used a large dataset encompassing 130,210 forest plots established by the United States Department of Agriculture Forest Service's Forest Inventory and Analysis Program (FIA; https://www.fia.fs.fed.us/) and a county-level pest occurrence dataset covering the conterminous United States (48 states and 2,098 counties) (https://www.nrs.fs.fed.us/tools/afpe) (22) to examine the possible effects of native host and nonhost tree diversity on nonnative pest/disease invasions.

Results

Generalized linear model (GLM) regression analysis revealed that the relationship between the total number of pest species and tree species diversity (host and nonhost tree species combined) was hump-shaped or unimodal (a near-symmetric curve; Fig. 1*A*). That is, pest diversity was the highest when county tree diversity was approximately 30–35 species (second-order regression, $R^2 = 0.17$, $F = 298.39$, $P < 0.0001$) (Fig. 1*A*). Furthermore, the data formed an envelope (a data cloud); that is, the relationship was better described or constrained by the hump-shaped boundary. Plots with either low or high tree

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Significance

Understanding the relationship between tree diversity and pest invasions is of critical importance both to the theoretical understanding of invasion ecology and to the development of effective pest management practices to mitigate the enormous damages caused by nonnative pests. However, evidence of facilitation and dilution remains elusive, especially in natural ecosystems at large scales. Using a unique large dataset encompassing 130,210 forest plots with county-level pest occurrence dataset across the United States, we show that tree-pest diversity relationships are hump-shaped. Both facilitation and dilution appear to coexist, but their relative strength varies with overall native tree diversity. Our findings provide insight into the interaction between facilitation and dilution, which are critical for understanding the invasions of forests by nonnative pests.

Author contributions: Q.G. designed research; Q.G., S.F., K.M.P., and A.M.L. performed research; A.M.L. contributed new reagents/analytic tools; Q.G., S.F., K.M.P., and J.W. analyzed data; and Q.G., S.F., K.M.P., and A.M.L. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Data deposition: The data used in this study are available at the Purdue University Research Repository (https://doi.org/10.4231/MM0B-JT53).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1821039116/-/DCSupplemental.

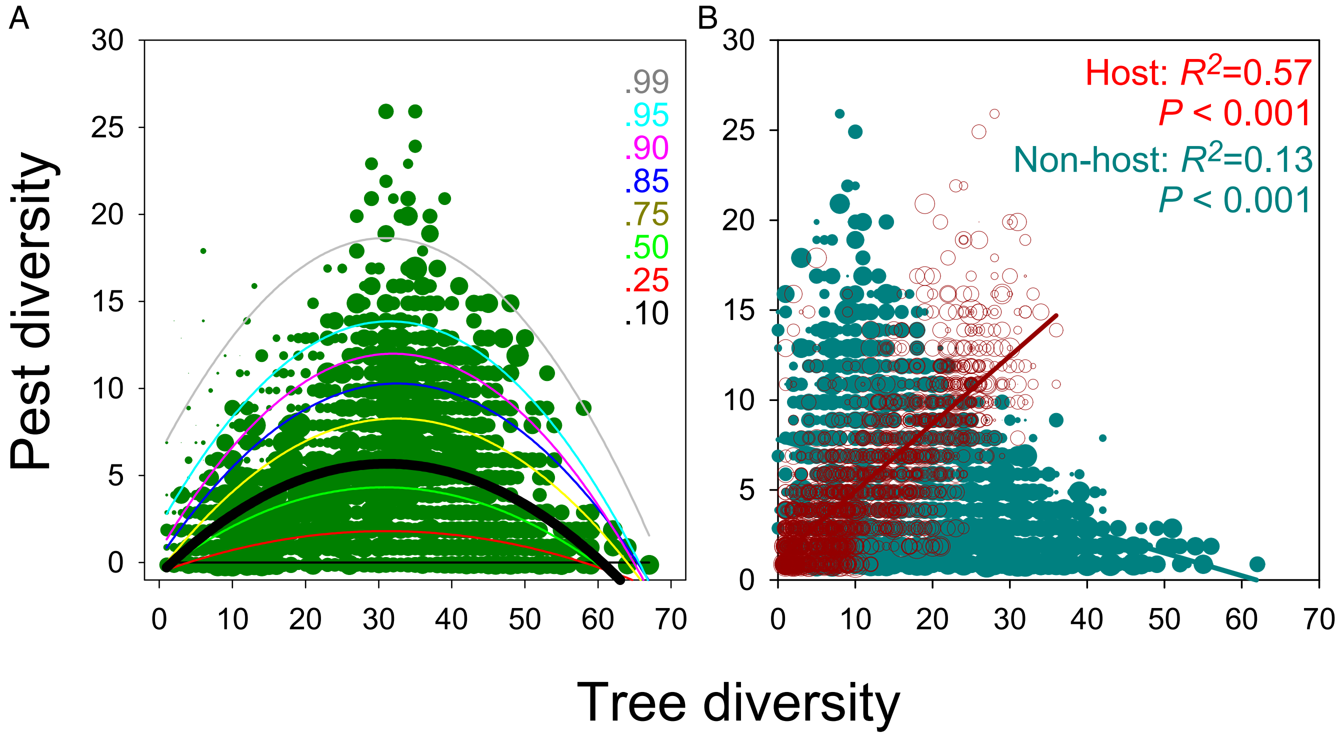

Fig. 1. The relationships between native tree species diversity (host plus nonhost) and pest diversity across the conterminous United States (n = 2,098 counties; symbol size reflects the relative forest area in each county). (*A*) Results based on second-order quantile regression for each quantile and polynomial regression for all data (i.e., data in all quantiles combined). The thinner hump-shaped regression curves were based on quantile thresholds of 0.1, 0.25, 0.5, 0.75, 0.85, 0.9, 0.95, and 0.99 from bottom to top, respectively. The corresponding equations and significance for each quantile are given in *SI Appendix*, Table S1. The thicker black curve represents the second-order polynomial regression with all data (counties) considered (R^2 = 0.17; P < 0.001). In all cases, the pattern switched from positive to negative. (*B*) The opposite relationships between host tree species diversity and pest diversity, and between nonhost tree diversity and pest diversity, across the conterminous United States.

diversity always had low pest diversity, but plots with moderate tree diversity ranged from high to low pest diversity.

On further testing of the robustness of the above result, quantile regressions also revealed hump-shaped relationships between native tree species diversity and nonnative pest diversity (Fig. 1*A*). The relationships transitioned from positive to negative at intermediate levels of tree diversity. The hump-shaped curves were observed for all the quantiles analyzed (*SI Appendix*, Table S1). Similarly, randomly drawn subsets of samples (counties) (n = 50, 100, 500, and 1,000) from the 2,098 total counties included in the analysis yielded similar results as patterns using data from all counties (*SI Appendix*, Fig. S1).

The diversity of nonnative invasive pests increased significantly with host tree diversity but decreased with nonhost tree diversity across the conterminous United States (Fig. 1*B*). The specialist and generalist nonnative invasive pests showed both similarities and differences in their relationships with host and nonhost tree diversity, respectively (Fig. 2). The diversity of both specialist and generalist invasive pests increased with host tree diversity, indicating the occurrence of facilitation, but this effect was stronger for specialists than for generalists (Fig. 2*A*). In contrast to their relationships with host tree diversity, both generalists and specialists exhibited a hump-shaped relationship with nonhost tree diversity; that is, pest diversity first increases when nonhost diversity is low and then decreases when nonhost diversity becomes very high (Fig. 2*B*).

The structural equation model (SEM) that included selected physical and human factors explained 40% of the variation in pest diversity. We found a significant positive correlation between pest diversity and human population density, a proxy for pest propagule pressure (23–26) and host tree diversity (Fig. 3). Annual mean temperature was negatively related to pest diversity, while precipitation had a positive effect. However, forest area and spatial autocorrelation had little effect on the general patterns, as shown by randomly drawn county subsamples with smaller sample sizes and thus with greater physical isolation among themselves (*SI Appendix*, Fig. S1). Spatial autoregression (SAR) and ordinary least squares (OLS) regression analyses also showed similar associations between pest diversity and various biological, environmental, and human factors (*SI Appendix*, Table S2). Despite the influence of this broad spectrum of external factors (detected either separately from tree diversity by GLM regression or OLS/SAR or jointly by SEM with native tree diversity also considered), tree diversity imposes significant effects on pest invasions.

Discussion

Our results, especially the hump-shaped patterns, suggest that facilitation and dilution can simultaneously influence pest invasion in the same forest ecosystems (27) (Fig. 1). Both the diversity and biomass of the host trees showed significant positive correlation with pest diversity, indicating the facilitation effect; in contrast, pest diversity was negatively related to the diversity and biomass of nonhost trees, suggesting a dilution effect in all these models (Figs. 1*B*, 2, and 3 and *SI Appendix*, Table S2). Although in general the relative strengths vary with the overall host community diversity (and the relative proportion of host vs. nonhost species), the threshold (the peak of the hump-shaped cloud in Fig. 1) could change with other factors, such as climate, resource availability, spatial scale, and habitat fragmentation related to human disturbances (27–29).

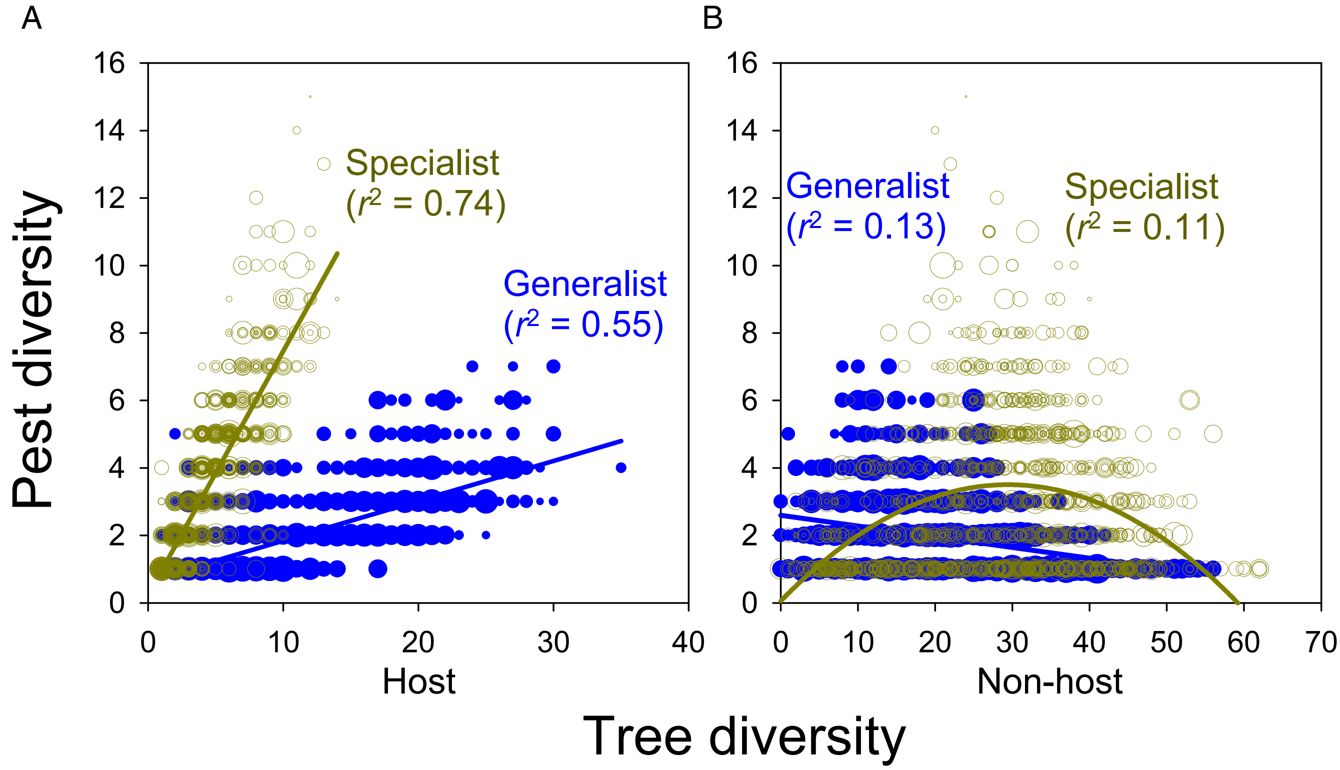

Fig. 2. The relationships between native host/nonhost diversity and the diversity of specialist and generalist nonnative invasive pests in forest ecosystems across the conterminous United States (n = 2,098 counties; symbol size reflects the relative forest area in each county). (*A*) Specialists showed a steeper increase with host tree diversity compared with generalists ($P < 0.0001$ in both cases). (*B*) Both specialists and generalists showed hump-shaped relationships with nonhost tree diversity ($P < 0.0001$ in both cases). The hump-shaped relationship was slightly better than the first-order regression for generalists [corrected Akaike information criterion (AICc) = 10,479.58 vs. 10,485.72] but much stronger than the first-order regression for specialists (AICc = 6,179.14 vs. 6,329.92).

One likely explanation for the positive host-pest relationship is that as the number of hosts increases, the total number of niches to support pests also increases (partly through the increased overall niche diversity) (Fig. 1*B*), especially for specialists, a relationship consistent with the host diversity begets parasite diversity hypothesis (13, 16). However, the dilution effect could also occur at the entire host community level and/or among host species alone (30). In those cases, dilution suppresses pest invasions when the diversity in the entire host community becomes high enough (Fig. 1 *A* and *B*) (6, 15, 31, 32). This is because, first, at the whole community level, the mean abundance of each tree species declines with increasing tree diversity (*SI Appendix*, Fig. S2) even as total tree biomass increases, leading to a dilution effect. Facilitation by host species is increasingly diluted by the presence of more coexisting nonhost species as shown by the negative relationship between nonhost biomass and pest diversity (*SI Appendix*, Fig. S3 and Table S2) (6). Second, in a diverse host community, host individuals are more likely isolated from one another due to the presence of nonhost species (Fig. 1*B*), and therefore pests need to search larger areas to locate their resources (33, 34). Third, diverse plant communities may support more natural enemies for potential nonnative pests and diseases (35).

When generalists and specialists of nonnative pests are considered separately in terms of their relationships with host trees (Fig. 2*A*), specialists show a stronger host-pest relationship (i.e., steeper positive slope) than generalists (36). The likely reason for this is that specialists have fewer host species, and therefore specialists should accumulate more quickly when more hosts are available compared with generalists, which do not rely on a single host (37). In contrast, the relationships of generalists and specialists of nonnative pests with nonhost trees are also hump-shaped (Fig. 2*B*). The increasing phase (similar to the left side of Fig. 1*A*) could also be due to the facilitation effect when overall tree diversity is low and both host and nonhost trees are positively related to each other, such as in harsh environments or early succession (14). In addition, the slope of the increasing phase could be partially influenced by the method of how hosts were defined; that is, tree species were classified for each county as hosts only for pest species present in the county, but not for pests that have yet to invade the county. In contrast, the decreasing phase (an indication of the dilution effect) becomes apparent only when nonhost tree diversity reaches a certain level (>15 species for generalists and >25 species for specialists; Fig. 2*B*). This result could be due to the large difference in their diversity levels (41 specialist pests vs. 25 generalist and oligophagous pests).

Successful establishment of nonnative pest populations arriving at a particular level of tree diversity can be simultaneously influenced by many other factors, such as propagule pressure, host condition (e.g., age, individual host susceptibility), the abiotic environment, the presence of other pests, and stochastic events (14, 19, 28). Moreover, given the typical lags between arrival and impact and between impact and recognition of impact, these observed invasion patterns are likely to vary over time (i.e., the time lag effect) (5, 38). To better understand pest invasions and impacts on forest ecosystems, the role of native tree diversity needs to be examined within broad anthropogenic and environmental contexts (39). To this end, although SEM reveals significant direct/indirect effects of other selected

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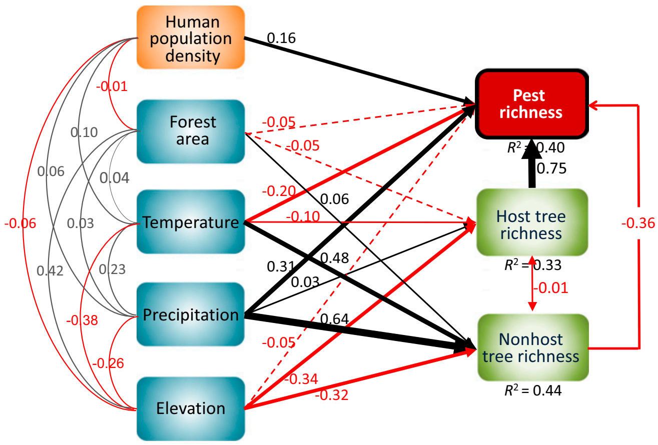

Fig. 3. Estimated structural equation model showing the effects of selected physical and human factors on pest diversity across the conterminous United States (n = 2,098 counties). It also shows the effects of these factors on host and nonhost tree diversity. Black lines indicate positive effects; red lines, negative effects. The thickness of the lines indicates significance levels. Dashed lines indicate that the effects are nonsignificant. R^2 represents the relative amount of variance explained for each dependent variable by the model. Values on the left are correlations among selected physical and social variables. The remaining values indicate the standard path coefficients. Standardized root mean square residual = 0.049; goodness-of-fit index = 0.965; root mean square error of approximation = 0.221; McDonald centrality = 0.979; Bentler comparative fit index = 0.953; AIC = 377.121. Temperature and precipitation are annual means (*SI Appendix*, Table S2). Note that the fit of models that include host and nonhost biomass is rather poor; thus, those models are not presented.

variables, such as human population density, precipitation, temperature, and elevation, none of these had greater effects on pest diversity than host and nonhost tree diversity (i.e., the generally low R^2 values in Fig. 1*B* vs. Fig. 3), further suggesting the key role of native tree diversity in facilitating and resisting pest invasions.

In short, our findings suggest the possible role of native tree diversity in the facilitation and dilution of nonnative pest invasions, and thus have important implications for guiding surveillance for new invasive species. Our observations also suggest that concurrent facilitation and dilution by host and nonhost trees drive geographical variation in pest invasions along with influences from anthropogenic and physical habitat characteristics. The relative proportion of component tree species (hosts vs. nonhosts) plays a key role in determining pest invasions (40), as indicated by our evidence that host diversity may promote pest diversity while neighboring nonhost species could enhance the associational resistance of host species to nonnative pest invasions (6). However, it is important to point out that our conclusions are based on field observations in natural ecosystems, their ultimate confirmation will require experimental manipulation, although the design and implementation of such an experiment across large spatial scales will be challenging. Recent analyses indicate that pest species continue to be introduced and spread around the globe (3). Under climate and land use changes, many tree species could expand, contract, or undergo latitudinal/elevational shifts in their geographical ranges (38, 41). It is crucial to examine how such changes over time and the associated geographical variation in plant diversity and habitat invasibility might affect future pest distributions and invasions.

Methods

The geographical distributions of 91 species of nonnative forest insect herbivores and forest pathogens known to cause damage in the United States are recorded at the county level in the Alien Forest Pest Explorer database (https://www.nrs.fs.fed.us/tools/afpe) (24). For ecological relevance, we analyzed distribution data for only the 66 pest species (51 insects and 15 pathogens) that primarily utilize native tree species (*SI Appendix*, I). These species of insects and pathogens are limited to herbivorous species that feed on foliage, sap, phloem, or wood and exclude predators, pollinators, and detritivores. Note that the majority of nonnative insects, which are not known to cause noticeable damage, are not included in this database due to lack of information about their distributions and impacts. In this study, we also excluded pests primarily of horticultural trees and crops, along with a parasitic plant species (European mistletoe; *Viscum album* L.).

Data on forest tree species composition were collected through FIA (42). FIA uses a quasi-systematic design as part of a consistent national sampling protocol to inventory forest attributes across all ownerships, with a sampling intensity of approximately one plot per 2,428 ha of land (42). The data in this analysis encompass 130,210 permanent fixed-area forest plots (each approximately 0.067 ha) located in 2,098 counties in which both host and nonhost trees were identified across the conterminous United States. We used plot-level data to record the native tree diversity (total number of native tree species occurring on plots in each county) and the total native tree live aboveground biomass (total amount of biomass occurring on plots in the county). In addition, we downloaded the FIA's remote-sensing derived estimates of forest cover area for each county.

We used a comprehensive list of invasive pests (66 species; see above), including species with strict host specialization and many generalists to avoid potential bias in terms of species selection, not a subset of species as in many previous studies. The determination of host specialization and host ranges of pest species followed Liebhold et al. (24) (*SI Appendix*, Table S2), who compiled a list of the primary tree species used as hosts by each pest summarized from the scientific literature, regulatory reports, and university extension service bulletins and related materials (*SI Appendix*, I). Each tree species was categorized as a host or nonhost for each county based on whether it was a host for any of the 66 damaging invasive forest pests present in the county. To examine the possible presence of facilitation due to the addition of host species and to test whether dilution is truly occurring but not because of the absence of host species, we classified the 66 pest species as specialist (n = 41), generalist (n = 15), or oligophagous (feeding on two or more genera from the same family or from closely related families; n = 10) agent. For this analysis, the oligophagous agents were combined with the generalists. We then conducted additional analyses separately on generalists and specialists by accounting for the presence of suitable host species.

Geographical variation in numbers of established pests may reflect variation in propagule pressure and climate conditions, as well as variation in habitat invasibility, and is likely to be scale-dependent (43). Because the effects of tree diversity on pest invasion are expected to be mediated by associated factors (see above) with high collinearity, we used SEM to tease apart these effects and to account for the codependence among the responsible variables (44). To examine the possible contribution of spatial autocorrelation, we applied SAR and OLS regression.

The examined anthropogenic and environmental variables included human population density, native host and nonhost tree diversity and biomass, forest area, mean annual temperature and precipitation, and elevation. Population data were compiled from https://www.census.gov/2010census; climate and elevation data were compiled from https://www.ncdc.noaa.gov/. To specifically examine the role of tree community diversity (defined here as richness) on the number of nonnative pests, we first analyzed the relationships between all native tree species (host and nonhost tree species combined) and nonnative forest pests within each county. We performed regression and quantile regression analysis (45) by binning the county-level data into eight groups based on relative pest diversity—i.e., ≤0.1, 0.11–0.25, 0.26–0.5, 0.51–0.75, 0.76–0.85, 0.86–0.9, 0.91–0.95, and 0.96–0.99—to test the possible presence of facilitation and dilution effects.

ACKNOWLEDGMENTS. We thank C. Oswalt and many individuals of the US Department of Agriculture Forest Service's Forest Inventory and Analysis Program for providing the forest plot data and J. Canavin for downloading and processing the county-level occurrence data for each pest and pathogen species. We also thank M. Carrig (Duke University) for suggestions on structural equation modeling. This study was supported in part by the National Science Foundation (Macrosystems Biology Grants DEB-1241932 and DEB-1638702) and by the Czech Operational Programme Research, Development, and Education (EVA4.0; no. CZ.02.1.01/0.0/0.0/16_019/0000803).

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