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Nonnative tree invaders lead to declines in native tree species richness

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Biological invasions are profoundly altering Earth's ecosystems, but generalities about the effects of nonnative species on the diversity and productivity of native communities have been elusive. This lack of generality may reflect the limited spatial and temporal extents of most previous studies. Using >5 million tree measurements across eastern US forests from 1995 to 2023, we quantified temporal trends in tree diversity and biomass. We then analyzed community-level changes in native tree diversity and biomass in relation to nonnative tree invasion and native species colonization. Across the entire eastern United States, native tree species richness decreased over time in plots where nonnatives occurred, whereas nonnative species richness and the biomass of both natives and nonnatives increased over time. At the community scale, native richness tended to decline following nonnative invasion, whereas native biomass and richness-independent measures of trait and phylogenetic diversity tended to remain stable. These patterns can be explained by the rarity of the displaced native species and their functional and phylogenetic similarity to native species that survived nonnative invasions. In contrast, native survivors tended to be functionally distinct from nonnative invaders, suggesting an important role for niche partitioning in community dynamics. Colonization by previously absent native species was associated with an increase in native richness (beyond the addition of native colonizers), which contrasts with declines in native richness that tended to follow nonnative invasion. These results suggest a causal role for nonnative species in the native richness decline of invaded communities.

biological invasion | functional traits | functional diversity | forest dynamics | community dynamics

Nonnative species, introduced deliberately or accidentally through human-mediated processes (1), have led to significant changes in the biodiversity of native communities (2–4). Nonnative species can profoundly affect ecosystem properties (5), including nutrient cycling (6), soil composition (7, 8), fire regimes (9), and community-level traits (10). Many ecosystems contain more than one nonnative species, and the severity of their impacts and the extent to which management intervention is warranted vary widely (1, 11–13). Macroscale analyses that integrate multiple co-occurring nonnative species across wide-ranging environments can be valuable in understanding and managing the effects of invasive species (1, 10–12, 14–16). For example, invasiveness as measured by regeneration success and range size varies among species and ecoregions (15). However, many studies of the potential effects of nonnative species lack a temporal context (17) and focus on the effects of a single nonnative species even when multiple nonnative species are present in a community (11). These limitations hinder our understanding of the effects of invasion on native diversity and community assembly. Thus, we need to examine the responses of community diversity and ecosystem functioning following multiple, replicated invasions conducted over a wide regional extent that encompasses a broad range of environmental conditions.

Few generalities have emerged from studies of the effects of nonnative species on ecosystems. Plant invasions can be associated with increases or decreases in community diversity, depending on the scale of observation, interspecific dynamics, the specific make-up of the local native species pool, and the diversity metrics employed [e.g., species richness, phylogenetic diversity (PD), or trait diversity]. Some studies suggest that nonnatives are likely to result in declines in native species abundance and diversity and even local extinctions (2, 18). Proposed mechanisms of native species decline include altered habitat structure (19), reduced fitness and growth due to direct competition (14, 20), and coinvasion of novel pathogens or parasites (21). In contrast to these local interactions, nonnative invasion may lead to increased regional species richness (22–26). Further, nonnative species can alter

Significance

Biological invasions can profoundly alter ecosystems, yet the dynamics and impacts of invasions and their role in affecting different aspects of native communities—including species richness, phylogenetic and trait diversity, and biomass—remain unclear. Using >5 million tree measurements over recent decades across eastern US forests, we found that species richness of nonnatives increased, while that of natives decreased. Nonnative invasions affected species richness but not other dimensions of forest diversity or biomass. Nonnative invasions were associated with the loss of locally rare native species that were both functionally and phylogenetically similar to native species that survived. These results highlight the risk of native tree species loss due to invasion, although other aspects of ecosystem function may be less affected.

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assemblages and increase evenness in species abundances, likely due to a greater local extinction rate for rare species (27). Beyond species diversity, nonnative species may also affect other aspects of diversity. For example, the increasing abundance of nonnative species across the United States has led to shifts toward faster growing and more acquisitive strategies (e.g., greater community-weighted specific leaf area and leaf nitrogen concentration) (10). In addition to diversity, nonnative invasions can also impact productivity in potentially complex ways. One meta-analysis suggested that nonnative species increase biomass production while simultaneously resulting in native species decline (14). These diverse outcomes raise important questions about the long-term, overall impacts of nonnative species on ecosystems.

Understanding the effects of nonnative species invasions is challenging due to the many concurrent factors affecting ecosystems, such as natural and anthropogenic disturbances (28), climate change (29), and increases in productivity due to CO_2 fertilization (30) and/or nitrogen deposition (31). One approach to this complexity is to use controlled experiments to isolate the effects of nonnative invasions. However, such experiments are necessarily limited in spatial and temporal scale and may not accurately reflect the outcome of natural community-assembly processes (32). An alternative approach is to leverage large observational datasets, such as long-term plant community data (as in ref. 10) or national-scale forest inventories (as in ref. 15). One advantage of the latter approach is that "invasions" of local communities can include species that are both native to the region but not previously present in the community and others that are nonnative (i.e., introduced species new to the regional species pool). Comparing how local colonization by previously absent native vs. nonnative species may affect community dynamics could help ascertain whether nonnative species have disproportionate or unique impacts on community and ecosystem processes.

Here, we use the broad spatial and temporal coverage of the systematically sampled Forest Inventory and Analysis (FIA) database (33) to determine temporal trends in diversity (species richness, PD, and trait diversity) and biomass of native and nonnative tree species in eastern US forests. Our analyses include >5 million tree measurements from 1995 to 2023 collected under FIA's national standardized plot design (Fig. 1 and *SI Appendix*, Fig. S1). The dataset included 230 native and 28 nonnative tree species. We ask: 1) How do the diversity and abundance of native and nonnative tree species change through time? 2) Is nonnative invasion associated with changes in native tree diversity and biomass, after controlling for other differences among communities? 3) Do plots invaded by nonnative tree species differ in diversity and biomass dynamics from those colonized by previously absent native species? 4) Do local extinctions of native species (i.e., the loss of all individuals of a species that was previously recorded in a plot) depend on species rarity and/or distance in trait space from nonnative invaders and surviving natives?

Results

Broad-Scale Temporal Trends in Diversity and Abundance. Nonnative tree species are geographically widespread in the eastern United States (Fig. 1), although the number of plot measurements that included at least one nonnative tree (invaded plots, hereafter; 4,807 plot measurements in total) was much lower than those where only native trees occurred ("uninvaded plots"; 153,835 measurements in total). The terms "invaded plot" and uninvaded plot describe a plot's status at a given measurement time rather than a permanent designation. The five nonnative tree species with the greatest frequency were *Ailanthus altissima* (Mill.) Swingle
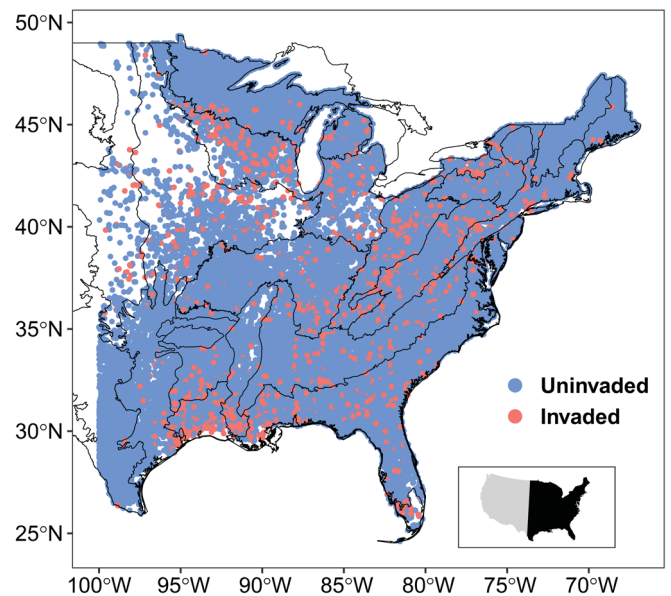

Fig. 1. Locations of FIA plots in the eastern United States. Each dot represents a forest inventory plot, and the colors represent whether at least one nonnative tree was reported in at least one inventory of a plot location (red) or not (blue). The plot measurements span the years 1995 to 2023 (see *SI Appendix*, Fig. S3 for the measurement locations by year). Most plots were measured two or more times (the mean remeasurement interval is ~5 y). The dataset includes 59,177 plot locations, 158,642 plot measurements, and 5,592,607 individual tree measurements. The study area is the contiguous United States east of 100°W longitude. Boundaries represent the ecoregions used in our analyses.

(Simaroubaceae, 1,447 plot measurements), *Triadica sebifera* (L.) Small (Euphorbiaceae, 1,222 measurements), *Melia azedarach* L. (Meliaceae, 403 measurements), *Paulownia tomentosa* (Thunb.) Steud. (Paulowniaceae, 377 measurements), and *Morus alba* L. (Moraceae, 323 measurements) (see *SI Appendix*, Figs. S1 and S2 for the geographic and temporal distribution patterns of nonnative tree species).

Averaged across all plots from 2000 through 2021 (the years with complete geographic coverage for all the ecoregions in the eastern United States; *SI Appendix*, Fig. S3), nonnative live tree density [number of trees per hectare (TPHA)], species richness, and biomass increased ($P < 0.01$; *SI Appendix*, Fig. S4 and Table S2). The percentages of plot-level density, richness, and biomass that include nonnative tree species also increased over time ($P < 0.01$; *SI Appendix*, Fig. S4 and Table S2). Compared with the uninvaded plots, native species in the invaded plots generally exhibited higher species richness but lower tree density and lower biomass (Fig. 2).

Considering only invaded plots (i.e., plot measurements with at least one nonnative live tallied tree), nonnative species richness increased ($P < 0.01$), whereas native species richness decreased ($P = 0.04$; Fig. 2 and *SI Appendix*, Table S3). There were no significant trends in nonnative or native tree densities in invaded plots, but the biomass of both nonnatives and natives increased significantly over time in invaded plots (Fig. 2 and *SI Appendix*, Table S3). Considering only uninvaded plots, there was no significant trend in native species richness (Fig. 2 and *SI Appendix*, Table S3). Native tree density decreased over time in uninvaded plots ($P = 0.01$), whereas native biomass increased ($P < 0.01$; Fig. 2 and *SI Appendix*, Table S3).

For native species, we considered two additional facets of biodiversity—PD and trait diversity—each assessed by two metrics: For PD, we used Faith's PD and mean phylogenetic branch length (MBL); for trait diversity, we used functional attribute diversity (FAD) and mean trait distance (MTD). Both PD and FAD were
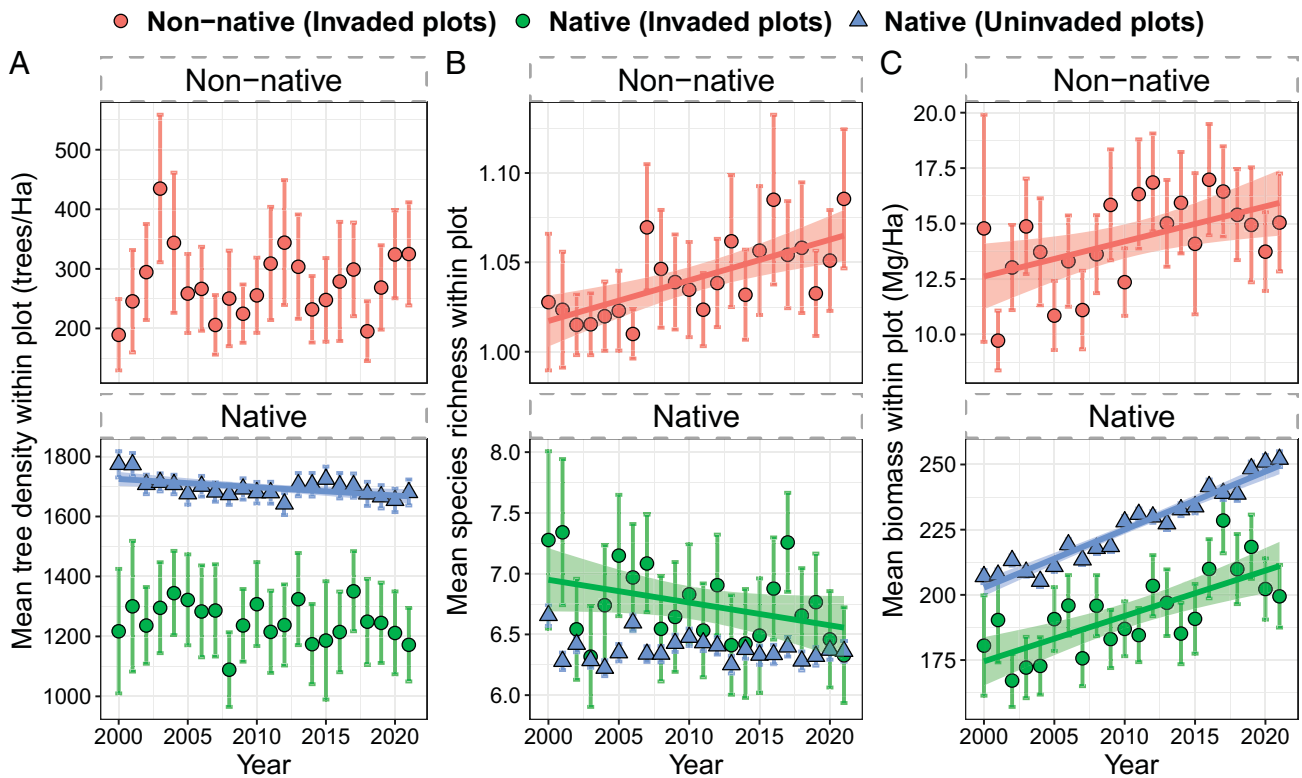
Fig. 2. Trends in (*A*) tree density, (*B*) species richness, and (*C*) biomass in invaded and uninvaded forest plots from 2000 to 2021. Density, species richness, and biomass values (mean ± 1.96 SE of plot-level values for locations measured in a given year) were based on live trees and were calculated separately for invaded (at least one nonnative tree present at the time of measurement) and uninvaded plots. Thus, nonnative density, richness, and biomass values are means of invaded plots, rather than means of all eastern US plots (see *SI Appendix*, Fig. S4 for corresponding nonnative trends across all eastern US plots). Trend lines are shown only for cases that are statistically significant (*P* < 0.05). For detailed statistical results, see *SI Appendix*, Table S2.

measured as the sum of the total phylogenetic or trait distances, respectively, of all measured native trees in each plot; these metrics are strongly correlated with species richness (34). Both MBL and MTD were measured as the mean value of the pairwise distances; these metrics are not inherently correlated with species richness (34). Trait distance was measured in the five-dimensional space defined by five species-level traits: wood density (WD, g/cm^3), leaf nitrogen content (LN, mg/g), plant maximum height (H$_{max}$, m), specific leaf area (SLA, mm^2/mg), and maximum rooting depth (R$_{max}$, m). FAD of native species decreased over time in invaded plots (*P* = 0.02). Otherwise, there were no significant temporal trends in phylogenetic or functional diversity (*SI Appendix*, Fig. S5 and Table S3).

Community-Level Changes in Native Diversity and Biomass Associated with Nonnative Invasions. Beyond the broad-scale trends described above, we further examined the dynamics of native diversity and biomass using sequences of three consecutive plot measurements ("remeasurement sequences"). Specifically, we modeled native diversity and biomass in relation to the biomass of three types of species: nonnative colonizers, native colonizers, and nonnative survivors (definitions in Fig. 3). (Native survivors were included in the response variables.) We examined the potential effects of the biomass nonnative invaders (colonizers and survivors) and native colonizers at t_2 on the subsequent annualized rates of change in native diversity and biomass from t_2 to t_3 (i.e., the change divided by the number of years from t_2 to t_3). The response variables (changes in native diversity and biomass) were defined to exclude native colonizers and thus represent changes in the community of native species already present at t_1 plus native species present only at t_3 (i.e., those that arrived after the colonizers, where applicable). To increase the likelihood that

our analysis identified fundamental differences in the effects of nonnative invaders vs. native colonizers on native community, we controlled for potentially confounding variables in our statistical
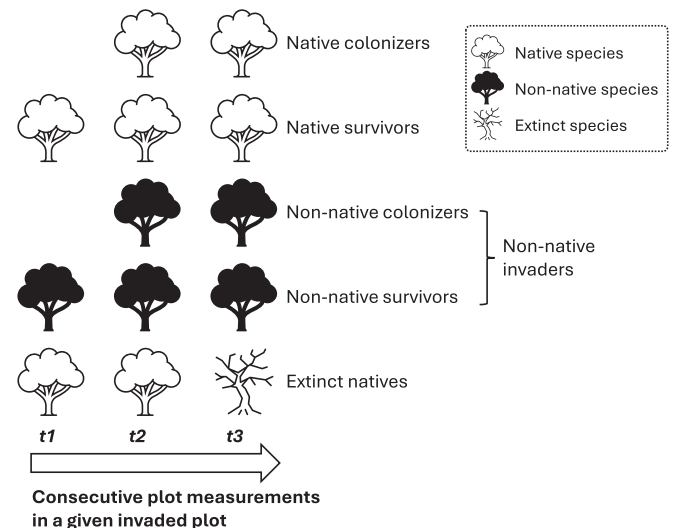

Fig. 3. Classification of species in plot remeasurement sequences. The species categories used in our analyses are illustrated with tree icons. Each icon represents a species in a sequence of three consecutive measurements of plot location (remeasurement sequence). "Colonizers" are species that were absent (i.e., no live trees tallied) at the first measurement (t_1) but present (at least one live tree tallied) at both the second (t_2) and third (t_3) measurements. "Survivors" are species that were present at all three measurements. "Nonnative invaders" includes nonnative colonizers and survivors. "Extinct natives" are native species that were present at t_1 and went locally extinct between t_2 and t_3 (i.e., following nonnative invasion). Species that were absent at t_1, present at t_2, and absent at t_3 were considered unsuccessful colonizers and were not assigned to any species group.

models, including stand age (successional stage), initial native biomass and diversity, and ecoregion (broad-scale differences in climate and soil, *SI Appendix*, Fig. S6).

Changes in native diversity and biomass associated with non-native invasion differed from those associated with native colonization (Fig. 4 and *SI Appendix,* Table S4). Changes in native species richness, PD, and FAD were negatively related to the biomass of both nonnative colonizers and nonnative survivors ($P \le 0.05$ in all cases; *SI Appendix*, Table S4). In contrast, changes in native species richness, PD, and FAD were positively associated with the biomass of native colonizers ($P < 0.01$ in all cases). These contrasting responses are consistent with patterns in the raw data. In the 16,277 remeasurement sequences with at least one native colonizer and no nonnative invaders, the mean change in native richness from t_2 to t_3 (excluding native colonizers) was 0.14 species/y. In contrast, in the 720 sequences with at least one nonnative invader (colonizers and/or survivors) and without native colonizers, the mean change in native richness was –0.01 species/y, which is significantly lower than sequences with only native colonizers (t test $P < 0.01$). Although the sign of native richness change is consistent in the raw data and statistical models, the magnitude of change inferred from models controlling for multiple covariates is larger. At the mean biomass in invaded plots of nonnative colonizers (3.1 Mg/ha; z-score = 3.6) and survivors (8.1 Mg/ha; z-score = 3.0), the model implies losses of 0.03 and 0.02 native species/y, respectively.

Changes in the richness-independent metrics of native diversity (MBL and MTD) were not associated with the biomass of nonnative invaders, but MBL was positively associated with the biomass of native colonizers, and MTD was negatively associated

with the biomass of native colonizers (Fig. 4 and *SI Appendix,* Table S4). Native biomass change was neither associated with nonnative invaders nor with native colonizers (Fig. 4 and *SI Appendix,* Table S4).

The contrasting relationships of nonnative invasion with plot-level native species richness (which declined following nonnative invasion) and native species biomass (which appeared unaffected) may be explained in part by a disproportionate loss of locally rare native species. The native species that went locally extinct tended to be rare in terms of both density and biomass compared to native survivors (Fig. 5A), which helps explain why declining native species richness was not associated with declining native biomass. The disproportionate loss of locally rare native species was mirrored at a broader geographic scale (Fig. 5B).

The contrasting relationships of nonnative invasion with different facets of native diversity—declines in species richness, PD, and FAD but no change in richness-independent diversity metrics (MBL and MTD; Fig. 4)—indicate that local extinctions of native species had little effect on the mean abundance-weighted distances among native species in phylogenetic and functional trait space. In contrast, when MBL and MTD were measured without abundance weightings, they were negatively associated with the biomass of nonnative invaders (*SI Appendix*, Fig. S7). Also, phylogenetic and functional redundancy between locally extinct and surviving native species may contribute to the insensitivity of MBL and MTD to native species loss. Mean phylogenetic and trait distances between locally extinct and surviving native species were similar to those between different native survivors (Fig. 6 and *SI Appendix,* Figs. S8–S10), suggesting that locally lost and surviving native
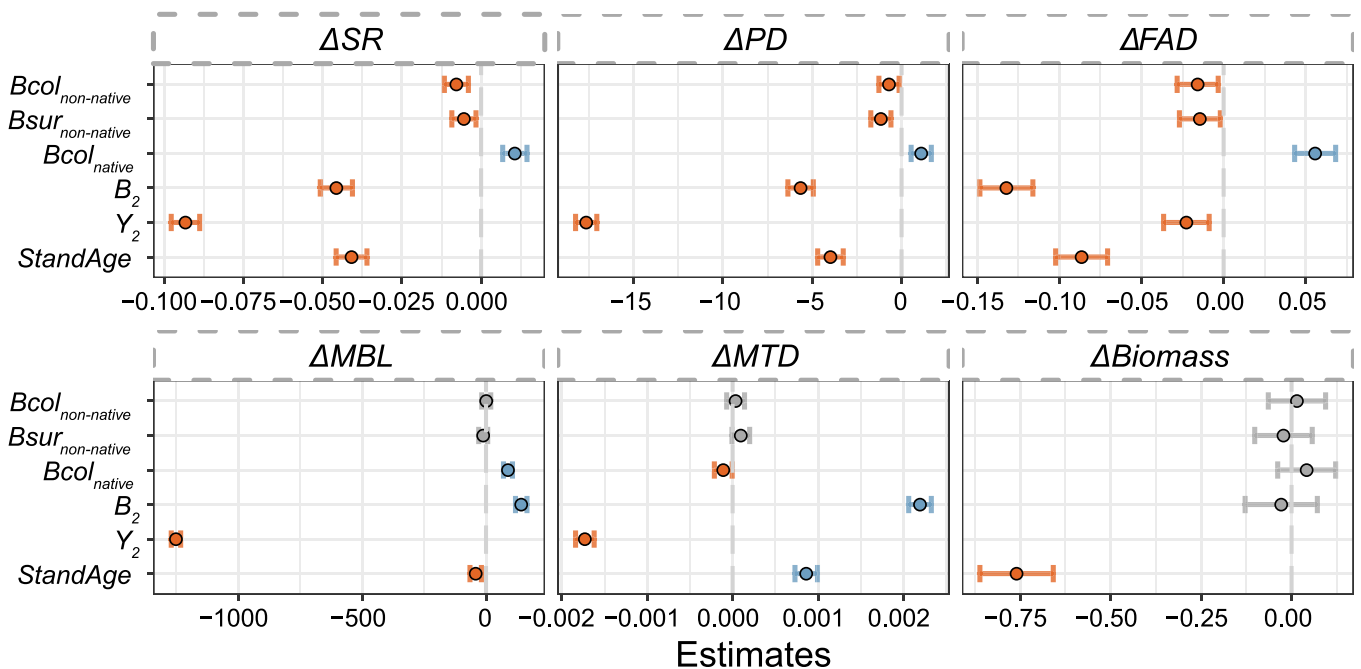

Fig. 4. Community-scale associations of changes in native diversity and biomass with nonnative invasion and native colonization. Each panel shows the standardized coefficients from a multiple regression model whose response variable is indicated in the panel title. The response variables are community-level changes in native tree species richness (*ΔSR*), phylogenetic diversity (*ΔPD*), functional attribute diversity (*ΔFAD*), mean phylogenetic branch length (*ΔMBL*), mean trait distance (*ΔMTD*), or biomass (*ΔBiomass*). The response variables measure annualized rates of change in the diversity and biomass of the native tree community between the second and third of three consecutive plot measurements (t_1, t_2, and t_3). The fixed effects include the t_2 biomass of nonnative colonizers (*Bcol_nonnative*), the t_2 biomass of nonnative survivors (*Bsur_nonnative*), and the t_2 biomass of native colonizers (*Bcol_native*), as well as other variables intended to control for potentially confounding factors (all measured at t_2): plot biomass (B_2), native species diversity (Y_2; the t_2 value of the diversity metric corresponding to the response variable), and stand age. Native colonizers were excluded when calculating all response and explanatory variables except for *Bcol_native*. Ecoregion was treated as a random effect to account for broad-scale differences in climate, soil, and potential natural vegetation communities (*SI Appendix,* Fig. S6). Estimates (with 1.96 SE) represent the partial effect of each explanatory variable, controlling for all other variables. Explanatory variables were standardized to a common scale. Symbols in blue indicate significant positive relationships, symbols in red indicate significant negative relationships, and symbols in gray indicate nonsignificant relationships. For detailed statistical results, see *SI Appendix, Table S4*.
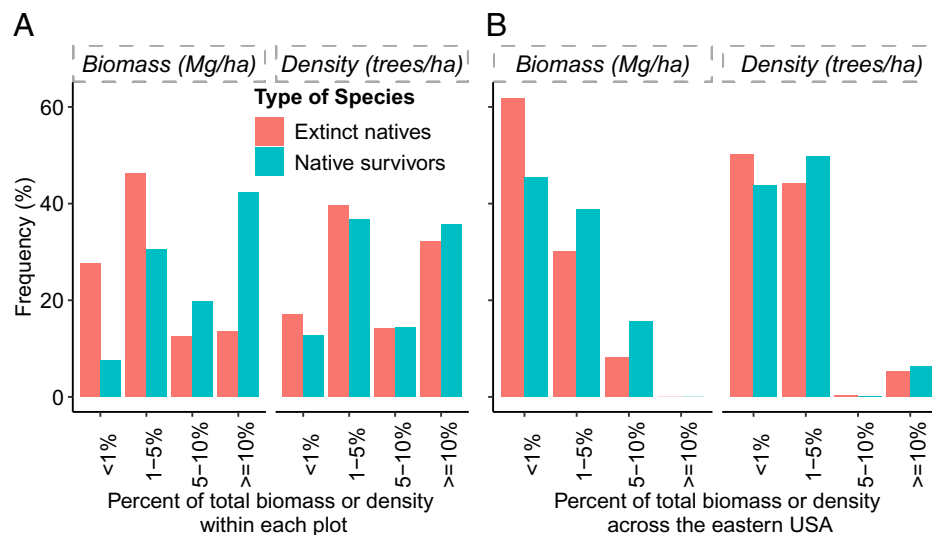
Fig. 5. Relative abundance of native tree species that went locally extinct following nonnative invasion vs. native species that survived invasion. Extinct natives tended to be rare (overrepresented in the "<1%" abundance category) relative to native survivors. Relative abundance (percent of total biomass or density) was calculated (A) within each community (FIA plot) or (B) at the scale of the entire eastern United States. In both (A and B), the y-axis is the percentage of cases in a given abundance category; within each species type (extinct or native survivors), the bar heights sum to 100%. A given species may be represented by multiple cases of extinction and/or survival. The community-scale analysis is based on all plot remeasurement sequences that included at least one nonnative invader and at least one extinct native species (see Fig. 3 for definitions; n = 1,024 sequences). The analysis at the scale of the entire eastern United States is based on the same set of extinction and survival cases as the community-scale analysis, but each relative abundance is a species' percent biomass or density relative to the total biomass or density across all plot measurements in the eastern US dataset (Fig. 1). Thus, extinct natives tended to be rare at both local (A) and eastern US (B) scales. Total abundance (biomass or density) includes both native and nonnative species in panels (A and B).

trees tended to occupy nondistinct regions of trait and phylogenetic space.

Phylogenetic and trait-space distances between different species groups may also help explain why certain native species survived nonnative invasion while others went locally extinct. The phylogenetic and MTDs between nonnative invaders and native survivors were relatively large (indicating separation in both phylogenetic relatedness and trait space) compared to the mean phylogenetic and trait distances between nonnative invaders and locally extinct natives (Fig. 6 and *SI Appendix*, Figs. S8–S10).

Discussion

Using recent systematic forest inventories from across the eastern United States, we investigated temporal trends in diversity and biomass of native and nonnative trees and changes in community dynamics associated with nonnative tree invasions. Across all plots, nonnative tree species increased in density, biomass, and diversity. For plots with nonnative species, species richness of nonnatives increased over time, while native species richness declined. At the community scale, invasion by nonnative tree species was associated with declines in native species richness. Native species that went locally extinct following nonnative invasion tended to be rare (at both community and eastern US scales) and functionally and phylogenetically similar to the new nonnative invaders. In contrast, the surviving native species tended to be functionally and phylogenetically distinct from the nonnative invaders. A decline in species richness of the resident native community is not an inevitable result of species addition. In stark contrast, communities that were colonized by previously absent native species, native richness tended to further increase. Given the above evidence, along with our effort to control for successional stage, forest attributes, and environmental factors (stand age, initial native biomass and diversity, and ecoregion), the most plausible explanation for the loss of native species following nonnative invasion is competitive displacement of native species by functionally similar nonnative species. However, given the limitations of observational

studies in determining causality (see "Caveats" section below), we refer to "potential effects" of nonnative species.

Potential Effects of Nonnative Species on Native Forest Communities. The potential effect of invasion on native species richness (loss of 0.01 native species per year per invaded forest plot) may seem minor but is nevertheless biologically meaningful. The turnover rate of canopy trees in temperate forests is about 1%/y (35, 36), which is equivalent to a turnover time of 100 y. A loss of 0.01 species per year thus implies a loss of one native species per community turnover. Alternatively, a loss of 0.01 species per year implies that over one decade, one out of 10 forest plots would lose one native species, which is substantial given that the mean native richness in these plots is 6.2 species. These potential effects are likely conservative; our models imply a loss in the average plot of 0.02 to 0.03 native species/y.

Our competition-based explanation is consistent with ecological theory (20). Given the similarity in phylogenetic relatedness
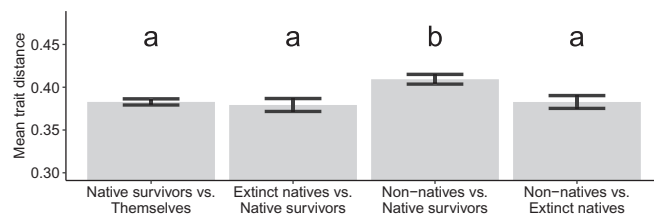
Fig. 6. Distance in trait space between species groups. Trait distance between species in different groups, averaged across plot remeasurement sequences that included at least one nonnative invader and at least one extinct native (see Fig. 3 for definitions; n = 1,024 remeasurement sequences, which we refer to here as "plots" for brevity). Error bars are 95% CI, estimated as mean ± 1.96 SE across the 1,024 plots. "Native survivors vs. themselves" is the mean distance among native species in a given plot that survived invasion. Extinct natives are native species that went locally extinct following nonnative invasion. "Nonnatives" includes nonnative colonizers and survivors. Mean functional distances were measured within each plot and then averaged across plots. Plot-level mean distances were compared to each other using paired *t* tests (bars labeled with different letters indicate that the mean distances differed significantly, with *P* < 0.05).

and trait values between nonnative invaders and locally extinct native species (Fig. 6 and *SI Appendix,* Figs. S8–S10), strong resource competition (i.e., niche overlap) is expected, although other mechanisms of community assembly may sometimes dominate. For example, nonnative plants in a riparian community subject to severe flooding were functionally similar to co-occurring natives due to environmental filtering (37). In addition to outcompeting some native species (14), nonnative species may replace closely related natives (38) through alterations in biotic interactions [e.g., nonnatives attract pollinators or seed dispersers of the native plants (39)], and heterospecific pollen interference (40), or inhibit native regeneration through cocolonization of new pathogens (18, 41). Locally rare native trees were especially likely to be lost (Fig. 5*A*). Beyond the inherent vulnerability of small populations to extirpation, local rarity may indicate poor competitive capacity in a given environment (18), which may increase the likelihood of displacement. Native species that went locally extinct also tended to be rare at the scale of the entire eastern United States (Fig. 5*B*), suggesting that these species may be vulnerable to adverse impacts of nonnative invasions at broad geographic scales.

Despite the decline in native species richness, richness-independent metrics of phylogenetic and functional diversity (MBL and MTD, respectively) appear robust to invasion. The insensitivity of the abundance-weighted metrics of MBL and MTD to invasion likely reflects both the rarity of the displaced native species and their locations in phylogenetic and trait space (i.e., their phylogenetic and functional similarity to surviving native species; Fig. 6 and *SI Appendix,* Figs. S8 and S9). However, we cannot generally conclude that trait diversity is unaffected by nonnative invasions. Our analysis was limited to five widely available functional traits, which likely provide an incomplete view of the true functional diversity of plant communities and focused only on native tree species; we did not quantify the direct effects of nonnative invasion on the diversity of the entire community.

Native community biomass also appeared robust to the loss of native species. This insensitivity of native community biomass to local species loss again may reflect the rarity of the displaced native species (Fig. 5*A*), as well as compensatory growth by functionally similar surviving natives. This interpretation is consistent with the "insurance" hypothesis (42), which posits that ecosystem function can be resilient to biodiversity loss due to functional redundancy in species assemblages. Some native species might even benefit from the addition of nonnatives (22, 23). However, although native rare species might be functionally similar to dominant species along some trait dimensions, they may differ in their responses to environmental stresses or disturbances, thereby conferring community resilience under changing biotic and abiotic conditions (43, 44). Thus, although apparently robust in the short time frame of our study (~5-y postinvasion period), this result does not necessarily imply long-term biomass stability. The continued loss of rare species could eventually lead to ecosystem vulnerability if dominant species decline or are lost without functionally equivalent rare species replacing them (43). Furthermore, the loss of rare species is likely to change community structure and biological interactions (45), as well as contribute to floristic homogenization (46), which may reduce resistance of ecosystems to abiotic global change drivers (e.g., drought) and increasing human activity (47, 48).

The Broad-Scale Invasion Status of Eastern US Forests. In our study, forest plots that were invaded by nonnative trees generally had higher native species richness than those that were not invaded (Fig. 2), consistent with previous findings that hotspots of native plant diversity are more heavily invaded than areas of low plant diversity (16, 49). Regions with higher native diversity may provide more resources and/or have a higher species turnover rate, allowing for more invasion (49, 50). We further found that the plots invaded by nonnatives had lower tree density and total biomass compared to uninvaded plots (Fig. 2). Communities with low density and biomass (e.g., due to recent disturbance) may offer low resistance to invasion (51).

Over the past two decades, nonnative species have increased in diversity, density, and biomass across eastern US forests (*SI Appendix,* Fig. S4), consistent with previous findings that nonnative trees are undergoing range expansions in the United States (52). These temporal trends may reflect land use change (53) and the subsequent spread of nonnatives after establishment (54). The two most frequent nonnative tree species in our study (*A. altissima* and *T. sebifera*), as well as others that are widely established (e.g., *M. alba, Ulmus pumila, Acer platanoides, M. azedarach,* and *Picea abies*), were previously identified as highly invasive (15).

The biomass of native trees increased over time in both invaded and uninvaded communities, suggesting that these trends are unrelated to invasions. The increasing biomass of eastern US forests has been well documented and is likely related to forest recovery from previous nonforest land use (48, 55) and growth enhancement due to rising atmospheric CO_2 concentrations (48, 56) and nitrogen deposition (57). Given that most eastern US forests are still free of nonnative tree species and that nonnatives account for only a small fraction of the biomass increase (Fig. 2), invasions have likely played only a minor role, if any, in eastern US biomass trends. As discussed above, the effects of nonnative invasion on biomass or other ecosystem properties may become more apparent if nonnatives continue to spread and native diversity continues to decline.

Caveats. Three key aspects of our modeling approach and results suggest that the association between nonnative invasion and native richness decline reflects a causal effect of nonnatives: i) our control of potentially confounding variables (stand age, initial stand diversity, initial stand biomass, and ecoregion); ii) trait distributions of nonnative invaders, displaced native species, and native survivors that are consistent with a direct role of competition in invasion dynamics; and iii) the observed increase in native species richness following colonization by previously absent native species, which contrasts with the native richness decline observed in communities invaded by nonnative species. Despite these multiple lines of evidence, macroscale observational studies such as ours cannot definitively establish causality and are complementary to site-scale controlled experiments (58–60). Other mechanisms unaccounted for in our models may also contribute to the patterns we report. For example, interactions with multiple groups of organisms (e.g., herbivores, pollinators, soil microbes, pathogens) may affect the diversity and/or productivity of native trees (61, 62) and associations with nonnative trees (63–65).

Furthermore, not all correlations observed in our study necessarily imply causal relationships. For example, although it is possible that the positive association between native colonization and native species richness reflects a causal, facilitative effect, a concurrent temporal change in the environment (e.g., shifts in soil microbial communities, climate, or disturbance) could create the same positive relationship. As well, the aggregate positive relationship may mask variation in the effects of different native species. For example, *Robinia pseudoacacia* is native to the eastern United States but has recently expanded its range both within and beyond the United States (66). In its nonnative range, it has a negative impact on biodiversity (67); a species-level analysis might reveal similar negative effects on native tree diversity within the United States.

We only considered a single aspect of ecosystem functioning (live biomass of native trees, which is related to productivity and represents a substantial fraction of forest carbon storage). Many other components of ecosystem functioning were not considered. Although some of these are correlated with live tree biomass (68), explicitly quantifying the impact of nonnative tree invasions on these multiple components of ecosystem functioning would be valuable.

Finally, although the FIA dataset provides a large, unbiased sample of US forests, the information collected at any one location is limited due to the small plot size, the lack of individual-level data for trees with a diameter smaller than 2.54 cm, and the lack of data for nontree vegetation. In terms of interactions between native and nonnative trees, we expect that these data limitations would lead to noise but not systematically bias our results. Nonnative tree species whose rates of recruitment, growth, and survival are insufficient to be included in an FIA plot sample are unlikely to exert a strong, direct influence on forest community dynamics. However, given the strong effects of nonnative grasses, herbs, and shrubs on ecosystem properties and tree recruitment (69, 70), because our analysis is limited to trees, it may underestimate the total impact of nonnative plants on native forest communities.

Conclusions

Invasion of nonnative tree species in eastern US forests has accelerated over the past two decades and is associated with a decline in native tree species richness (and richness-dependent metrics of trait diversity) but not with richness-independent diversity metrics or changes in native community biomass, which may be due to differences in the responses of rare and common native species to niche-based competition. These findings call for early detection and a rapid response (71) to nonnative tree species, even if they are not yet considered invasive, given their potential negative effects on native tree diversity. Additionally, our findings suggest different responses of diversity and biomass of native communities following the invasion of nonnative species. Mitigating the negative effects of nonnative tree invasions on native tree diversity should be a conservation priority relative to aspects of ecosystem functioning, such as biomass, that appear robust to invasion. Nevertheless, the resilience of forest biomass to invasion could be temporary, as the ongoing loss of native species may alter community structure and reduce ecosystem resistance to environmental stressors over time. Therefore, long-term monitoring of multiple facets of biodiversity and ecosystem functioning will be critical for detecting the long-term effects of nonnative invasions.

Methods

Overview. We quantified temporal trends in diversity and abundance for native and nonnative trees in nonplantation forests at the scale of the eastern United States and within ecoregions, and we performed more detailed analysis of plot remeasurement sequences to further evaluate potential effects of nonnative species on native communities. Our analysis included 59,177 systematically sampled forest inventory plot locations, including 158,642 plot measurements and 5,592,607 individual tree measurements from 1995 to 2023 (Fig. 1 and *SI Appendix*, Fig. S3). The dataset included 258 tree species, including 28 nonnative species. Species were defined as "nonnative" if they were recorded in the Global Register of Introduced and Invasive Species–United States (Contiguous) (GRIIS ver. 2.0, 2022) as "widespread invasive (category E)" or "invasive (category D2)" (72). We verified the native status of the species examined here using United States Department of Agriculture (USDA) Plants (plants.usda.gov), Biota of North America Program (BONAP, bonap.net), and Plants of the World Online (POWO,

powo.science.kew.org). Of the 230 native species in this study, 207 were recorded as "native" in BONAP and all the species were recorded as native in USDA Plants and POWO. Six species were listed as nonnative but not invasive in GRIIS, USDA Plants, BONAP, and POWO: *Ginkgo biloba* L., *Cordia sebestena* L., *Tilia cordata* Mill., *Castanea mollissima* Blume, *Citrus trifoliata* L., and *Quercus acutissima* Carruth. These species only accounted for 25 individual tree measurements in nine plot locations (out of 59,177). We excluded those nine plots from all of our analyses. Integrating these systematically sampled forest inventory data with publicly available data on plant functional traits and phylogeny, we analyzed the association of nonnative species with different aspects of native communities: biomass and multiple facets of diversity.

Forest Inventory Data. The forest inventory data were obtained from the FIA program of the USDA Forest Service (FIA database version 9.2, downloaded in April 2024 from fia.fs.usda.gov). For consistency, we restricted our analyses to plots measured using FIA's national standardized sampling design (33), which was implemented in most regions of the United States starting in the late 1990s or early 2000s. We further restricted our analyses to the eastern United States (coterminous United States east of 100°W longitude; Fig. 1) because few plot locations in the western United States have been measured three or more times, as required by our analysis of community dynamics (see below). Furthermore, the dominant life forms of nonnative plants are better sampled by FIA in the eastern than in the western United States. In the western United States–where grasslands and shrublands are widespread–the dominant nonnative plants are grasses and forbs (73). In contrast, in the eastern United States, forests are widespread, and nonnative trees and shrubs are common (74). Recent studies have found that nonnative trees are more common in forests of the eastern United States than those of the western United States (15, 75–77). For example, nonnative trees are almost entirely absent from the Rocky Mountain states, and only one or two nonnatives occur in the ecoregions along the Pacific Coast from California to Washington; in contrast, no fewer than eight nonnative tree species were found in the Mid-Atlantic states and the southeastern United States (see figures 2 and 3 in ref. 15). Our analysis is restricted to areas classified by FIA as nonplantation forests and to tree species included in the individual-level data reported in the FIA Tree table. We further restricted our analysis to plots dominated by a single condition (e.g., stand age and soil type) to minimize within-plot heterogeneity (see *SI Appendix*, Table S1 for details of plot filtering).

Eastern US FIA plots are measured (i.e., inventoried) roughly every 5 y. Each plot consists of four 7.32-m-radius subplots, one centrally located and the other three spaced 36.6 m apart in a triangular arrangement. Within each plot, trees with a diameter at breast height (DBH) greater than 12.7 cm are inventoried. Trees with a DBH of 2.54 to 12.7 cm are inventoried in 2.07-m-radius microplots (one per subplot). Data reported for each inventoried individual include DBH, height, species identity, allometry-based estimates of aboveground and belowground biomass, and other tree-level variables (78). In our analyses, the biomass of each individual was calculated as the sum of aboveground and belowground wood biomass estimates reported by FIA. Biomass per unit area (Mg/ha) for each plot measurement (all species combined or individual species) was estimated as a weighted sum of the individual biomass values, weighting by the number of TPHA in the FIA sample (reported as trees per acre, TPA_UNADJ, in the FIA database). Densities of nonnative and native species (trees/ha) for each plot measurement were estimated as the sum of TPHA values. The belowground biomass of 42 tree individuals in eight uninvaded plots was missing, and we removed those plots from our analysis.

Each FIA plot was assigned to an ecoregion based on its ecological subsection code aggregated at the ecoprovince level (79) (*SI Appendix*, Fig. S6). Each ecoregion represents an area of similar geology, soil type, and climate that supports a similar potential natural vegetation type.

Each FIA plot measurement represents a sample of trees with DBH ≥ 2.54 cm in a community, rather than a complete inventory of all individuals in an area. Therefore, it is likely that many FIA plot measurements provide incomplete data on species occurrences. For clarity, our text often refers to species or individuals that are "tallied" (which means that the species or individual was included in the reported data); this is implied throughout our paper even when not stated explicitly. Tree species whose rates of recruitment, growth, and survival were insufficient to be included in the set of tallied individuals are unlikely to exert a strong, direct influence on forest community dynamics. We therefore assume that limitations of FIA tree sampling introduce noise but no systematic bias in our analysis.

Phylogeny and Trait Data. The phylogenetic framework used here was obtained from Park et al. (80), which was based on 12 commonly used molecular loci (plastid: *atpB*, *atpB-rbcL*, *matK*, *ndhF*, *rbcL*, *rps4*, and *trnL-trnF*; mitochondrial: *atp1*, *atpA*, *matR*, and *rps3*; nuclear: ITS) and includes 10,147 vascular plant species in North America. Comparison of this phylogenetic tree with the FIA plot data identified 35 species that were missing from the phylogeny; we added each missing species to its respective genus in the phylogeny as part of a polytomy, using add.species.to.genus in phytools version 2.1.1 (81).

We selected five functional traits for analysis that were available for most eastern US tree species, following Liu et al. (34), but with updated datasets. Four of the traits–WD (g/cm^3), LN (mg/g), H_{max} (m), and SLA (mm^2/mg)–were included in the global spectrum of plant form and function (82). We added a fifth trait, R_{max} (m), due to its important role in belowground resource acquisition and competition (83, 84). LN, SLA, and R_{max} values were obtained from the TRY database (85) (accessed in March 2024) and the BIEN database version 4.2 (86) (accessed in March 2024). R_{max} values were supplemented with data from Tumber-Dávila et al. (87) and Guerrero-Ramírez et al. (88). For WD, we used the wood specific gravity (dry mass per green volume) values reported by FIA. H_{max} was estimated as the 99th percentile of individual heights reported by FIA for each species. We used species-level trait values to assign trait values to individuals; intraspecific trait variation in eastern US forests has little effect on trait diversity estimates (34). The numbers of species lacking data for LN, SLA, and R_{max} were 4, 4, and 71 species, respectively. To fill in these missing data, phylogenetic-based imputation was conducted using the phylopars function in Rphylopars version 0.3.10 (89), assuming Brownian motion of the trait in the phylogeny. Distances in trait space among species occurring in the same plot were calculated following Liu et al. (34).

Before integrating the FIA plot data with phylogenetic and trait data, species names from all databases were standardized using the Taxonomic Name Resolution Service V5.0 (tnrs.biendata.org/, accessed March 2024), following World Flora Online (http://www.worldfloraonline.org).

Measuring Diversity. We calculated three types of diversity metrics for each plot measurement: species richness, PD, and trait diversity. Species richness was the number of species tallied. For PD, we used two common metrics: Faith's PD (90), the sum of all branch lengths [in million years (Ma)], and mean pairwise phylogenetic distance (MBL). For trait diversity, we also used two metrics: FAD (43), the sum of pairwise species distances in trait space, and MTD. Because both PD and FAD are sums of branch lengths or trait distances, they inherently contain species richness as a component, whereas MBL and MTD do not intrinsically depend on species richness (34). For conciseness, we refer to MBL and MTD as "richness-independent" measures of diversity, although correlations between these metrics and species richness may arise due to community assembly processes (34). Both MBL and MTD were calculated using a basal area-weighted approach. The weight for each individual was its DBH^2 multiplied by its TPHA value, which is equivalent to weighting each tree by its basal area. All diversity metrics were calculated following Liu et al. (34).

Statistical Analyses. Unless stated otherwise, estimates of diversity and abundance were restricted to trees that were alive at a given measurement time.

Broad-scale temporal trends in diversity and abundance. Trends were estimated using data only from 2000 to 2021, because years prior to 2000 and after 2021 had limited geographic coverage in the FIA dataset (*SI Appendix*, Fig. S3). This limited coverage could bias the trends if the regions with available data in the low-coverage years were not representative of the entire eastern United States. Temporal trends were analyzed using linear regression, where the explanatory variable was the FIA plot measurement year, and the response variable was the mean value (across plots measured each year) of diversity (species richness, PD, FAD, MBL, or MTD) or abundance [density (trees/ha) or biomass (Mg/ha)]. We averaged data across plots within each year before fitting the regressions so that each year was weighted equally; i.e., for all trend analyses, the sampling unit was the mean of FIA plots measured each year (2000 to 2021; $n = 22$). For comparison, we also repeated the regressions using the plot-level diversity and abundance values (not averaging across plots within years). Those analyses led to qualitatively identical results; for simplicity, we only report trends based on plot averages by year.

Trend analyses were performed for the following cases at the scale of the entire eastern United States (mean across all plot measurements): nonnative trees in all plots; nonnative trees in invaded plots (plots with ≥1 live tallied nonnative tree); native trees in invaded plots; and native trees in uninvaded plots (plots with no live tallied nonnative trees). The terms "invaded plots" and "uninvaded plots"

describe a plot's status at a given measurement time, rather than a permanent designation. Trends in phylogenetic and trait diversity were quantified only for native trees.

Community-level changes in native diversity and biomass associated with nonnative invasions. We used sequences of three consecutive FIA plot measurements (denoted t_1, t_2, and t_3) to quantify the potential effects of nonnative invasions on native communities. The sampling unit for this analysis was a remeasurement sequence (t_1, t_2, and t_3). The analysis included all remeasurement sequences in which all three consecutive plot measurements met our filtering criteria (*SI Appendix*, Table S1). The data that met these requirements spanned the years 1995 to 2023; i.e., the earliest year for t_1 was 1995, and the latest year for t_3 was 2023. Unlike the trend analysis described above, the plot-level analysis of community change included all available data years, because we sought to maximize the sample size of remeasurement sequences. We do not expect differences in regional coverage (*SI Appendix*, Fig. S3) to bias our analysis of community change, but any such bias should be accounted for by the ecoregion random effect in the models (see Eq. **1** and details below). A given plot location could be included in the analysis more than once if it was measured more than three times. The analysis included 27,500 unique plot locations. Of these, 12,014 plots were represented in the analysis once; 11,462 plots were represented twice; 3,882 plots were represented three times; and 142 plots were represented four times. Thus, the sample size for this analysis was $n = 47,152$ remeasurement sequences. To account for the multiple observations at some plots, we included a plot-level random effect in our analysis (see below).

Our statistical models were designed to quantify the potential effects of nonnative invaders on native community dynamics (annualized rates of change). For comparison with nonnative invaders, we also considered the potential effects of native colonizers (i.e., native species that were previously unrecorded in a remeasurement sequence). We considered the potential effects of two types of nonnative invaders: Nonnative colonizers were defined as individuals of nonnative species that were absent (no live trees tallied) at t_1 but present (at least one live tree tallied) at both t_2 and t_3; nonnative survivors were defined as individuals of nonnative species that were present at all three measurements (t_1, t_2, and t_3). Nonnative species records that did not fit either of these definitions (e.g., a nonnative species present in a given plot at t_1 but absent at t_2 or t_3) were considered unsuccessful invasions at the plot level (either because of natural mortality or intentional removal) and were not included in the models. Native colonizers were defined in a similar manner as nonnative colonizers. We did not consider the potential effects of native survivors, because these species were included in our response variables.

We used linear mixed models that controlled for stand age, stand biomass, and broad-scale edaphic-climatic factors (represented by ecoregion) as follows:

$$\Delta Y_{23} \sim Bcol_{nonnative} + Bsur_{nonnative} + Bcol_{native} + B_2 + Y_2 + StandAge + \alpha eco,$$
[**1**]

where ΔY_{23} was the annualized rate of change for native species from t_2 to t_3 in one of the response variables (ΔSR, ΔPD, ΔFAD, ΔMBL, ΔMTD, or $\Delta Biomass$), measured as the difference between the t_3 and t_2 values divided by the number of years from t_2 to t_3. Native colonizers were represented by the explanatory variable $Bcol_{native}$ (see details below) and were not included in the response variables (ΔY_{23}). Specifically, the ΔY_{23} calculations included live native trees belonging to the following species: At t_2, ΔY_{23} included native species tallied at both t_1 and t_2, thus excluding native colonizers and native species tallied at only t_2, i.e., failed native colonizers that did not survive to t_3). At t_3, ΔY_{23} included all tallied native species except for native colonizers (these t_3 species include native species that survived from t_1 to t_3, native species tallied at t_1 and t_3 but not t_2, and native species tallied only at t_3). $Bcol_{nonnative}$ and $Bsur_{nonnative}$ were the t_2 live biomass (Mg/ha) of nonnative colonizers and survivors, respectively. $Bcol_{native}$ was the t_2 live biomass (Mg/ha) of native colonizers. B_2 was the t_2 plot live biomass (Mg/ha) of native trees, excluding native colonizers. Y_2 was the t_2 value of the diversity variable corresponding to ΔY_{23} (e.g., if ΔY_{23} was the rate of change in species richness from t_2 to t_3, then Y_2 was species richness at t_2). This variable was not included in the $\Delta Biomass$ model, because B_2 was already included in all models and thus not relevant for the $\Delta Biomass$ model. $StandAge$ was the stand age at t_2 reported by FIA [mean age of trees in the dominant size class (91); αeco was an additive random effect (intercept) for ecoregion, controlling for the broad-scale edaphic-climatic differences in the mean responses not explained by the fixed effects. We did not include ecoregion-level random slopes because the available data were insufficient to constrain the slopes in some ecoregions;

the number of remeasurement sequences with nonnative species ranged from 2 to 9,438 across ecoregions and there are nine ecoregions with fewer than 1,000 remeasurement sequences. All explanatory variables were standardized to unit variance so that effect sizes could be compared on a common scale.

To explore the robustness of the results, we considered two alternative model forms. First, eastern US FIA plots are remeasured roughly every 5 y on average, with a range of 3 to 10 y. Variation in remeasurement intervals was accounted for in the response variables described above by annualizing rates of change, and we expect this variation to introduce noise into our analysis but no systematic bias. To explore this issue, we repeated the regression analyses while also including as covariates the time intervals from t_1 to t_2 and from t_2 to t_3. Second, some plot locations were represented in the analysis by more than one remeasurement sequence. To account for this nonindependence, we added a plot-level random effect (intercept) to Eq. **1**, in addition to the ecoregion random effect. Both of these alternative model forms yielded nearly identical results as Eq. **1**; for simplicity we only report results based on Eq. **1**.

Quantifying the abundance distribution of extinct natives and native survivors. We estimated the relative abundance–both live biomass (Mg/ha) and live tree density (trees/ha)–of native species that went locally extinct following nonnative invasion (extinct natives) and native species that survived these invasions ("native survivors"). This analysis was based on the set of FIA plot remeasurement sequences (t_1, t_2, and t_3) with at least one nonnative invader (colonizer and/or survivor as defined above) and at least one native species that went locally extinct between t_2 and t_3 (i.e., at least one live tallied tree at t_1 and t_2 and none at t_3). There were 1,024 plot remeasurement sequences (912 different plot locations) that met these criteria.

To quantify relative abundance at the plot (community) scale, relative biomass (%) was measured as 100 times a species' t_2 live biomass (the sum of TPHA × biomass for all live tallied trees of a given species) divided by the t_2 total plot live biomass (the corresponding sum over all species in the plot). Similarly, relative density (%) was measured as 100 times a species' t_2 live density (the sum of TPHA for all live tallied trees of a given species) divided by the t_2 total plot live density (the corresponding sum over all species). These plot-scale measures of relative abundance may vary across plots for a given species. Plot-scale relative-abundance distributions (Fig. 5A) are the percentage of extinction and survival cases (each "case" is an instance of plot-level species extinction or survival) in different plot-scale relative-abundance categories.

To quantify relative abundance at the scale of the eastern United States, we first calculated the relative biomass and density of each species across all FIA plot measurements in the entire eastern US dataset (Fig. 1). For relative biomass (%), this was 100 times a species' total live biomass in the dataset (the sum of TPHA × biomass for all live tree records of a given species in the entire dataset) divided by the total live biomass of all species combined. For relative density (%), this was 100 times a species' total live density in the dataset (the sum of TPHA for all live tree records of a given species in the entire dataset) divided by the total live density of all species combined. These measures of relative abundance at the scale of the eastern United States do not depend on plot-scale abundances. These relative abundance distributions (Fig. 5B) are the percent of extinction and survival cases (the same cases considered in Fig. 5A) in different relative abundance categories.

Quantifying distances between species groups in trait and phylogenetic space. To explore the potential role of traits and phylogeny in explaining patterns in community dynamics, we compared mean trait and phylogenetic distances between different species groups. For example, consider the first two bars in Fig. 6 and *SI Appendix*, Figs. S8–S10, labeled "native survivors vs. themselves" and "extinct natives vs. native survivors." The height of the first bar represents the mean distance in trait space between pairs of native species that survived nonnative invasions (community-level invasions recorded in FIA plot remeasurement sequences). The height of the second bar represents the mean distance in trait space between i) native species that went locally extinct following nonnative invasions and ii) native species that survived the invasions. The similar heights of the bars indicate that extinct natives were, on average, no more different from native survivors than native survivors were from each other, which implies that extinct natives and native survivors have similar distributions in the trait space.

For each FIA plot remeasurement sequence (t_1, t_2, and t_3), the mean distance between two groups of species, which we label here as "group A" and "group B" (to represent the *x*-axis labels in Fig. 6 and *SI Appendix*, Figs. S8–S10), was calculated as follows. First, we measured the distance (d_{ij}) from each species i in group A to each species j in group B. The phylogenetic distance was measured as the distance (in Ma) of species i and j in the phylogeny. The trait distance was measured following equation (1) in ref. 34, which is 1 minus the Gower similarity index (92) based on the space defined by the five traits included in our analysis. In the case of native survivors vs. themselves, groups A and B are the same, and d_{ij} was measured from each native survivor to all other native survivors. Then, following equation (4) in ref. 93, we calculated the mean distance from each species i to all species j as $D_i = \sum_j w_j d_{ij} / \sum_j w_j$, where the weights ($w_j$) were the t_2 basal areas of each species j. Finally, these values were averaged across species in group A as $D = \sum_i w_i D_i / \sum_i w_i$, where the weights ($w_i$) were the t_2 basal areas of each species i. This method yields the identical mean distance (D) for a remeasurement sequence irrespective of how groups A and B are labeled, e.g., the mean distance from "extinct natives to native survivors" is equal to the mean distance from "native survivors to extinct natives."

We repeated this analysis with two different sets of FIA plot remeasurement sequences. Fig. 6 shows trait distance results for all remeasurement sequences that include at least one extinct native and at least one nonnative colonizer or survivor ($n = 1,024$ remeasurement sequences; 912 different plot locations). *SI Appendix*, Fig. S8 shows trait distance results for all remeasurement sequences that include at least one extinct native and at least one nonnative colonizer (nonnative survivors may or may not be present, $n = 247$ remeasurement sequences; 199 different plot locations). *SI Appendix*, Figs. S9 and S10 are the phylogenetic analogs of the trait-based analyses.

Data, Materials, and Software Availability. All data used in this manuscript are from public databases. All code needed to evaluate the conclusions in the paper and the data on phylogeny and functional traits can be found at Zenodo (https://zenodo.org/records/14968893). Previously published data were used for this work (33).

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