Biodiversity and productivity in eastern US forests

Yunpeng Liu[a,b,1], J. Aaron Hogan[c] (ID), Jeremy W. Lichstein[c], Robert P. Guralnick[b,d,e] (ID), Douglas E. Soltis[b,c,d,e,1] (ID), Pamela S. Soltis[b,d,e] (ID), and Samuel M. Scheiner[f] (ID)

Despite experimental and observational studies demonstrating that biodiversity enhances primary productivity, the best metric for predicting productivity at broad geographic extents—functional trait diversity, phylogenetic diversity, or species richness—remains unknown. Using >1.8 million tree measurements from across eastern US forests, we quantified relationships among functional trait diversity, phylogenetic diversity, species richness, and productivity. Surprisingly, functional trait and phylogenetic diversity explained little variation in productivity that could not be explained by tree species richness. This result was consistent across the entire eastern United States, within eco-provinces, and within data subsets that controlled for biomass or stand age. Metrics of functional trait and phylogenetic diversity that were independent of species richness were negatively correlated with productivity. This last result suggests that processes that determine species sorting and packing are likely important for the relationships between productivity and biodiversity. This result also demonstrates the potential confusion that can arise when interdependencies among different diversity metrics are ignored. Our findings show the value of species richness as a predictive tool and highlight gaps in knowledge about linkages between functional diversity and ecosystem functioning.

biodiversity | forests | metrics | productivity | species richness

Conserving ecosystem functioning is essential for managing our planet sustainably (1–3). A fundamental component of ecosystem functioning is primary productivity, which provides the energy that sustains higher trophic levels (4), including humans (5). Primary productivity is also the basis of ecosystem carbon storage, which has offset ~25 to 30% of anthropogenic greenhouse gas emissions over recent decades (6, 7). Thus, understanding the controls of primary productivity is critical to biodiversity conservation and Earth system science.

Many experimental and observational studies have quantified relationships between biodiversity and primary productivity. Previous studies have found that the biodiversity–productivity relationship may be scale dependent, with both the form (8, 9) and strength (9, 10) of the relationship varying among ecosystems and as a function of the spatial extent of the analysis (11). Most of these studies, however, have examined relationships at small spatial extents via both experimental manipulations and studies of natural systems (12, 13). Our understanding of how different facets of biodiversity—such as species richness, phylogenetic diversity, and functional trait diversity—relate to each other, and which of these facets best predicts primary productivity (2, 14–17), remains limited, especially regarding the nature of these relationships at regional to continental extents. How best to assess relationships among biodiversity measures, productivity, and ecosystem functioning, especially at large extents, remains a key question in basic and applied biodiversity science.

The biological characteristics of species and individuals—their traits—and their interactions with each other and the environment are likely key determinants of primary productivity and other aspects of ecosystem functioning (3). Communities composed of functionally diverse groups are hypothesized to use resources more efficiently than less diverse communities (i.e., greater niche differentiation), which should lead to a positive relationship between productivity and functional diversity (1). However, a meta-analysis of the relationship between productivity and functional diversity in 78 grassland communities found that only a modest amount of the variation was explained (18). It is not clear whether the modest relationship is because productivity is only weakly determined by functional diversity or whether the relevant components of functional diversity have not been widely quantified because they have not been identified or they rely on traits that are difficult to measure at the right level (e.g., among individuals). The studies included in that meta-analysis were all conducted at small extents; at larger extents, the relationship may be even weaker due to other factors, such as differences in climate, soils, and topography, which can also affect ecosystem productivity.

Significance

Ecosystem services provided by forests—including wildlife habitat, wood, fiber, and carbon storage—depend on forest productivity, the collective biomass growth of individual trees. Forest productivity is thought to increase with tree biodiversity, but there are many ways to quantify biodiversity, with little consensus on which measures are most important. Using >1.8 million tree measurements across eastern US forests, we show that the number of species (the most widely available biodiversity measure) is as good a predictor of forest productivity as more complex biodiversity measures that consider species properties and evolutionary history. This result suggests that conservation strategies maximizing the number of species may effectively conserve ecosystem functioning.

An alternative to predicting ecosystem functioning from measured trait diversity (i.e., the component of functional diversity that can be quantified from available trait data) is to rely on phylogenetic diversity (19), which can serve as a useful proxy for functional diversity because evolutionary divergence, by definition, confers some degree of functional differentiation (20, 21). Given the rapidly increasing resolution and quality of phylogenetic trees, phylogenetic diversity could potentially provide a more useful proxy for the true functional diversity of communities than trait diversity that can be readily quantified from available databases. This may particularly be the case in studies targeting large numbers of species across broad geographic regions, given current gaps in available trait data (22, 23). Beyond serving as a proxy for functional diversity, phylogenetic diversity may capture biological mechanisms that affect ecosystem functioning but do not depend on resource partitioning (24). For example, release from herbivores, pathogens, and other natural enemies in diverse plant communities has been shown to contribute to positive diversity–productivity relationships (25). Because natural enemies are often shared among closely related plant species (26), release from these enemies should be greatest in phylogenetically diverse plant communities.

In this study, we quantify relationships among different facets of biodiversity and primary productivity across forests in the eastern United States. Our analysis leverages large, open databases of remeasured forest plots (Fig. 1), plant functional traits (27), and phylogeny (28). We addressed three questions: 1) What is the form and strength of the relationship among various facets of biodiversity? 2) What is the relationship between those facets and productivity? 3) Which facet will be of greatest practical use for conservation purposes?

Results

Diversity Patterns across Eastern US Forests. In all,188 tree species were recorded in the eastern US inventory plots (mean = 7.1, SD = 2.6, range = 3 to 20), comprising 157 angiosperm and 31 gymnosperm species. Trait values varied widely and were only weakly correlated with each other (unweighted mean trait correlations across

species ranged from –0.01 to 0.56, *SI Appendix*, Fig. S1A; basal area–weighted trait correlations across plots ranged from –0.01 to 0.55; *SI Appendix*, Fig. S1B). For the species included in our analyses, gymnosperms had lower specific leaf area (SLA), rooting depth, and leaf nitrogen (LN) content than angiosperms; wood density (WD) and maximum height did not differ between the two groups (*SI Appendix*, Figs. S1A, S2, and S3).

To quantify functional trait and phylogenetic diversity, we considered metrics that are intrinsically independent of species richness (SP)—mean pairwise trait distance weighted by basal area (MTD) and mean pairwise phylogenetic divergence (branch length) weighted by basal area (MBL). We also considered two commonly used metrics that mathematically depend strongly on species richness—functional attribute diversity (FAD) (30) and Faith's phylogenetic diversity (PD) (19). Across plots, species richness was positively correlated with FAD ($r = 0.98$) and PD ($r = 0.81$) but negatively correlated with MTD ($r = –0.69$) and MBL ($r = –0.61$) (Fig. 2 and *SI Appendix*, Fig. S4), which was also true within each ecoprovince (*SI Appendix*, Fig. S5). The strong positive relationship of FAD and PD with species richness is expected from the mathematical formulation of these indices, which are intrinsically correlated with species richness, and thus each other (*Materials and Methods, Measuring Diversity*).

To understand the negative correlation between species richness and MTD—and MBL to the extent that phylogenetic diversity reflects functional trait diversity ($r = 0.77$)—we examined how species richness related to species packing. Functional convex hull volume [functional richness, FRic (31)] measures the total volume that the species assemblages occupy in functional trait space. As expected, hull volume increased as the number of species increased (*SI Appendix*, Fig. S6A). However, as hull volume increased, MTD decreased (*SI Appendix*, Fig. S6B). Together, these patterns indicate that although increasing species richness does tend to add some additional species beyond the edges of the trait space, most species additions occur in the interior of the trait space. That is, as species richness increases, species tended to be more tightly packed in functional trait space.
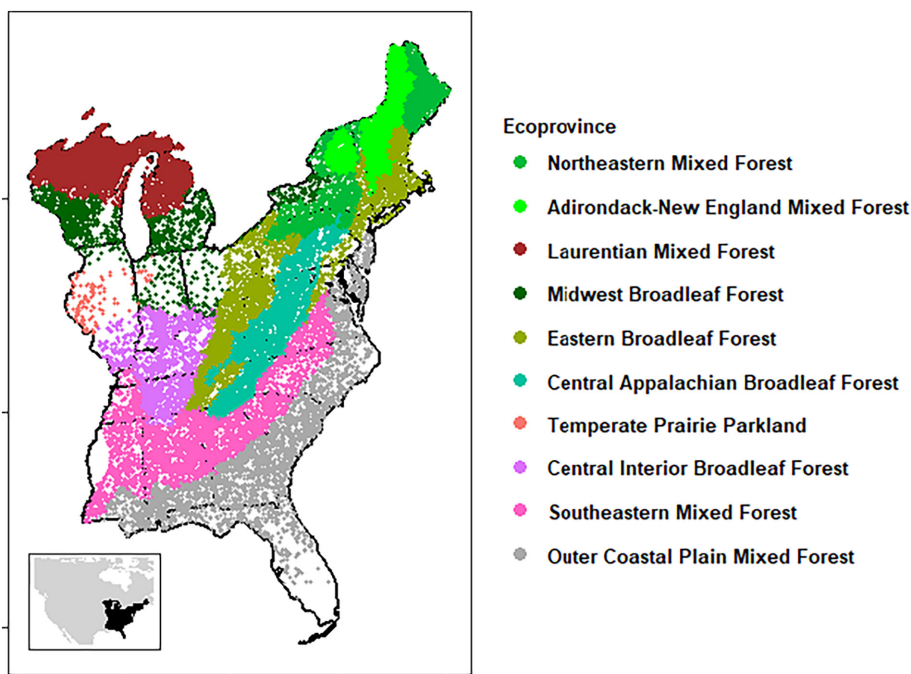
Fig. 1. Locations of the FIA plots in the eastern United States. Each dot represents a forest inventory plot. The dataset includes 23,145 plot locations with 62,698 plot measurements and 1,821,107 individual tree measurements. Colors represent different ecoprovinces (29).
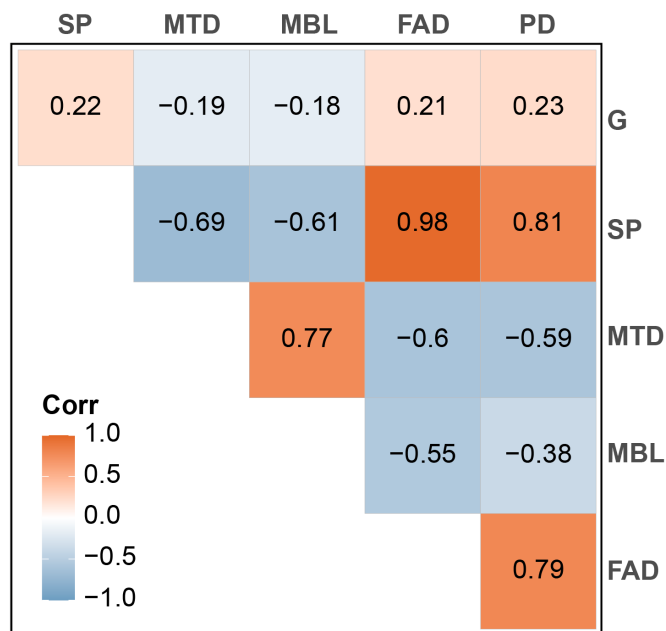
Fig. 2. Pairwise correlations between productivity and biodiversity metrics. Productivity (G) was measured as the annual growth of woody biomass (Mg/ha/y). The measures of biodiversity were: species richness (SP), MTD, MBL, FAD, and Faith's PD. All correlations were significant ($P < 0.001$).

Diversity–Productivity Relationships across Eastern US Forests. Productivity (aboveground biomass growth rate, G) increased with species richness, FAD, and PD but decreased with MTD and MBL (Fig. 2 and *SI Appendix*, Figs. S4, S5, and S7). Mixed-effects regression models explained ~21% of the variation in productivity, with diversity metrics explaining a highly significant, albeit small (up to ~1.7%), percent of the variation that could not be explained by ecoprovince, stand age, and initial biomass (partial R^2 for diversity effects, which is measured as the differences in R^2 between mixed-effects regression models including vs. not including diversity

metrics; Table 1 and *SI Appendix*, Tables S1 and S3). Although each diversity measure had statistically significant independent effects on productivity (Fig. 3, Table 2, and *SI Appendix*, Tables S2 and S4), any single measure explained nearly as much variation as when measures were combined with each other (Table 1 and *SI Appendix*, Tables S1 and S2). The low model R^2 values are characteristic of the large range in plot-level biomass growth in the inventory data (32, 33) and likely reflect multiple factors. The small size of the inventory plots (four subplots, each ~168 m², distributed over ~0.4 ha) leads to large sample variability. Furthermore, there is considerable spatial and temporal environmental heterogeneity within eastern US ecoprovinces that cannot effectively be captured by available broad-scale soil and meteorological datasets (34, 35), which constrains the explained variation in our analysis.

While productivity always had a positive relationship with species richness, the relationship of productivity to functional trait and phylogenetic diversity depended on the metric and the model (Fig. 3 and Table 2). For phylogenetic diversity, PD always had a positive relationship, and MBL always had a negative relationship regardless of the model. For functional trait diversity, MTD always had a negative relationship. In contrast, FAD had a positive relationship when considered singly or combined with PD, but a negative relationship when combined with species richness. This discrepancy highlights the importance of considering mathematical relationships between diversity metrics and species richness, which can influence the magnitude and sign of correlations between a given biodiversity measure and ecosystem functioning.

Variation in Diversity–Productivity Relationships in Relation to Stand Age, Initial Biomass, Ecoprovince, and Species Richness. Stand age, initial plot biomass (at the beginning of the interval during which productivity was measured), and ecoprovince explained a substantial portion of the variation in productivity (Table 1). This is unsurprising given the large range in plot stand ages and initial biomass (*SI Appendix*, Fig. S8) and the broad environmental differences among eastern US ecoprovinces (29). It also raises the issue of whether the general trends concerning

Table 1. Linear mixed models of productivity (aboveground biomass growth rate, G) in forest inventory plots

Model	Diversity metrics in model	AIC	Fixed-effect R^2 (%)	Total R^2 (%)	Partial R^2 (%)
3 diversity metrics	SP, PD, and FAD	90,080	15.87	21.04	1.61
	SP, MTD, and MBL	90,038	15.94	21.37	1.68
2 diversity metrics	SP and MBL	90,056	15.86	21.35	1.60
	SP and MTD	90,044	15.90	21.25	1.64
	MTD and MBL	90,041	15.72	21.29	1.46
	SP and PD	90,106	15.82	20.84	1.56
	SP and FAD	90,092	15.72	21.17	1.46
	PD and FAD	90,117	15.73	20.71	1.47
1 diversity metric	SP	90,124	15.64	20.96	1.38
	PD	90,112	15.67	20.65	1.41
	FAD	90,163	15.40	20.76	1.14
	MBL	90,084	15.38	21.19	1.12
	MTD	90,052	15.64	21.15	1.38
SP, MBL, and single trait	H_{max}	90,029	15.85	21.45	1.59
	WD	90,062	15.71	21.37	1.45
	LN	90,063	15.82	21.34	1.56
	SLA	90,063	15.90	21.34	1.64

Each model included one or more diversity metrics—species richness (SP), phylogenetic diversity (PD or MBL), and trait diversity (FAD or MTD)—or the basal area-weighted SD of a single trait. Trait diversity metrics were calculated without R_{max}. All models included stand age and initial biomass as fixed factors and ecoprovince as a random factor. The fixed-effects R^2 represents the amount of variation explained by all fixed effects combined (without the ecoprovince random effect). The total R^2 is the amount of variation explained by the entire model, including both fixed and random effects. The partial R^2 is the difference in the fixed-effects R^2 between models with and without the relevant diversity metric(s). See Table 2 for the coefficients and their significance in each model. The sampling unit of analysis is a forest inventory plot location (n = 23,145).
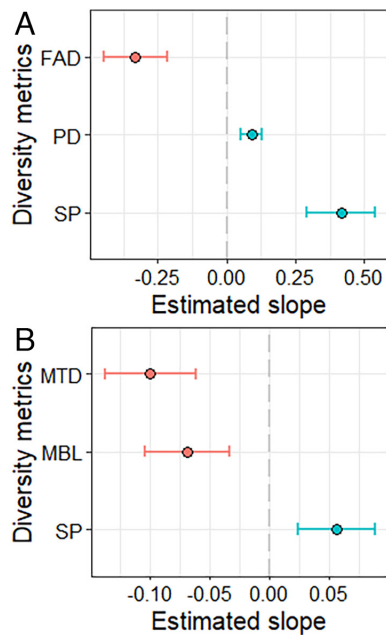
Fig. 3. Relationships of diversity measures with biomass productivity (G) in mixed-effects models. The models included either (*A*) FAD and PD, or (*B*) MTD and MBL, along with species richness, stand age, and initial biomass as fixed effects and ecoprovince as a random effect. Slopes represent the partial effect of each diversity metric, controlling for all other effects.

the various biodiversity metrics interacted with these factors. Therefore, we conducted additional analyses that grouped plots by stand age and initial biomass bins and by ecoprovince.

Within stand age bins [subsets of FIA (Forest Inventory and Analysis) plots with similar stand age], the models explained from 17 to 29% of the variation in productivity (G). Species richness was negatively related to productivity in young stands (<30 y) and

positively related in older stands (>50 y, *SI Appendix,* Fig. S8*A* and Table S6). The overall positive relationship for the entire dataset (Fig. 3) likely occurs because most of the stands (67.0%) are in the older group. In contrast, the effect of MTD was always negative or not significantly different from zero. For MBL, the effect was not different from zero for all but one age class (80 to 90 y), where it was negative.

Within initial biomass bins (subsets of FIA plots with similar initial biomass), the models explained 14 to 21% of the variation in productivity (G). The effect of biodiversity was the strongest in plots with the lowest initial biomass (<50 Mg, partial R^2 = 6.8%, *SI Appendix*, Fig. S8*B* and Table S7). Within each initial biomass bin, the sign of biodiversity effects was consistent with the results based on all plots (Fig. 3). The effects of species richness were always positive or not different from zero. In contrast, the effects of MTD and MBL were always negative or did not differ from zero. There were no obvious trends in the sign or magnitude of diversity effects across initial biomass bins (*SI Appendix,* Fig. S8*B*).

When the plots were divided by ecoprovince, the direction of effects of biodiversity on productivity (G) varied (*SI Appendix,* Fig. S9*A* and Table S8). Overall, the models explained 9 to 27% of the variation in productivity (G). While the results were generally similar to the broad-scale analysis that spanned the entire eastern United States (Fig. 3), some differences were found. Results for species richness and MBL were mostly consistent between the broad-scale and ecoprovince-scale analyses. Within ecoprovinces, species richness and MBL effects were typically opposite one another, being positive for richness and negative for MBL (as in the broad-scale analysis) or not different from zero. The one exception was the Southern Mixed Forest, where the relationships were reversed—negative for species richness and positive for MBL. Results for MTD were less consistent between the broad-scale and ecoprovince-scale analyses. Effects of MTD on productivity (G) were significantly negative in three ecoprovinces and significantly

Table 2. The coefficients and their significance from linear mixed models of the effect on productivity (G) of fixed factors—stand age (STD), initial biomass (IniBio), and different combinations of diversity metrics—with ecoprovince as a random effect

Model	Diversity metrics in model	Diversity metric(s)			IniBio	STD
		SP	Phylo	Trait		
3 diversity metrics	SP, PD, and FAD	0.42***	0.09***	−0.33***	0.75***	−0.67***
	SP, MTD, and MBL	0.06***	−0.07***	−0.10***	0.74***	−0.68***
2 diversity metrics	SP and MBL	0.09***	−0.13***	-	0.74***	−0.68***
	SP and MTD	0.06***	-	−0.15***	0.74***	−0.68***
	MTD and MBL	-	−0.08***	−0.13***	0.74***	−0.68***
	SP and PD	0.08***	0.10***	-	0.75***	−0.67***
	SP and FAD	0.52***	-	−0.36***	0.74***	−0.68***
	PD and FAD	-	0.14***	0.0	0.76***	−0.67***
1 diversity metric	SP	0.16***	-	-	0.75***	−0.68***
	PD	-	0.16***	-	0.76***	−0.67***
	FAD	-	-	0.14***	0.76***	−0.68***
	MBL	-	−0.17***	-	0.74***	−0.68***
	MTD	-	-	−0.18***	0.74***	−0.68***
SP, MBL, and single trait	SP, MBL, and H_{max}	0.13***	−0.12***	−0.08***	0.72***	−0.68***
	SP, MBL, and WD	0.09***	−0.12***	0.02	0.73***	−0.68***
	SP, MBL, and LN	0.08***	−0.13***	0.02	0.74***	−0.68***
	SP, MBL, and SLA	0.10***	−0.12***	−0.02	0.74***	−0.68***

Values in this table are for models presented in Table 1 (four functional traits). All the models include one or more diversity metrics: species richness (SP), phylogenetic diversity (Phylo, including PD and MBL), and trait diversity (Trait: FAD, MTD, or the SD of single traits). The traits were WD, LN content, SLA, and species maximum height (Hmax). Statistical significance is indicated as *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

positive in two, which contrasts with the negative MTD effects in the broad-scale analysis (Fig. 3*B*). The inconsistent signs of MTD effects across ecoprovinces may reflect differences in community assembly processes, which may warrant additional exploration.

Finally, although SP has no intrinsic correlation with MTD and MBL, the variances of MTD and MBL tend to decrease as SP increases [see *Materials and Methods* and an analogous result in Fig. 2*E* of Laliberté and Legendre (36)]. To evaluate the potential effects of this heteroskedasticity on our results, we repeated our regression analysis within groups of FIA plots separated into SP bins, which constrains the SP range and thus the degree of heteroskedasticity (each bin was roughly three species wide; see *SI Appendix*, Table S9). The positive dependence of productivity on SP and the negative dependence of productivity on MTD and MBL, as observed in the analysis of all FIA plots combined (Fig. 3*B*), were also observed within most SP bins (*SI Appendix*, Fig. S9*B* and Table S9). Eight of the 15 diversity effects (three metrics in five SP bins) were nonsignificant (*SI Appendix*, Table S9), which may be due to the limited sample size and limited range of diversity (especially for SP) within each bin. To further evaluate the potential effects of heteroskedasticity, we translated the observed MTD and MBL in each FIA plot to standardized effect size (SES) values relative to a null model, and we repeated our regression analysis with these SES values substituted for the original MTD and MBL values. In this null model–adjusted analysis, productivity had a significant positive dependence on SP and a nonsignificant negative dependence on MTD and MBL (*SI Appendix*, Fig. S10). Together, these analyses suggest limited issues with heteroskedasticity, a robust positive dependence of productivity on SP, and a negative or nonsignificant dependence of productivity on MTD and MBL (Fig. 3*B* and *SI Appendix*, Figs. S9*B* and S10).

Tests of Effects of Missing Data. Species with missing trait data generally accounted for a small proportion within any given FIA plot (less than 5% of the species or less than 6% of the total basal area in a plot, *SI Appendix*, Table S10). Even for this well-studied flora and set of ecologically important traits, we were missing about 20% of all species-trait combinations, albeit mostly for rare species. The effect of missing data on functional trait diversity was further reduced for the metrics weighted by basal area as missing values were mostly associated with less abundant species (Eq. **2**). The exception was rooting depth (R_{max}), which was missing for approximately 29% of all species or 23% of the total basal area. Due to this large percentage of missing data, we did not include R_{max} when calculating trait diversity (MTD and FAD) in our primary analyses presented above. To evaluate the potential effects of excluding an important trait, we repeated the analyses with R_{max} included (with weights in Eq. **1** set to 0 for missing data). The results with R_{max} included (*SI Appendix*, Tables S1 and S2) were generally the same as the results without R_{max} (Tables 1 and 2). Finally, to evaluate the effect of variation in the number of traits used for distance measures of different species on estimates of species distances in trait space, we imputed missing values (*Materials and Methods, Missing Data*). The results with imputation (*SI Appendix*, Tables S3 and S4) were generally the same as the results without imputation (Tables 1 and 2). Because both sets of additional analyses were nearly identical, we conclude that our results are robust to missing data.

Discussion

Our study is one of the largest analyses of the productivity–biodiversity relationship in natural forests to date and explores the effects of how different metrics of phylogenetic and functional trait diversity might alter our perception of that relationship. Although both functional trait and phylogenetic diversity hold promise for advancing our understanding of the determinants and predictors of ecosystem functioning, few studies have quantified how these two facets of biodiversity relate to each other, to species richness, and to primary productivity. Our results show that the number of species in a community (i.e., species richness), despite its simplicity as a metric, has as much or more explanatory power as functional trait or phylogenetic diversity, likely because species richness is determined, in part, by assembly processes that act on the functional and phylogenetic diversity of the available species pool (37). This result was consistent across different datasets and analyses: the entire eastern United States; within ecoprovinces; within data subsets of similar stand age, initial biomass, or species richness; and in a null model that accounted for heteroskedasticity.

The most surprising result was the negative relationship between functional trait diversity and productivity. This relationship is opposite of that predicted based on the theory that species with different functional traits will either use a wider variety of resources or respond in different ways to temporal heterogeneity, leading to greater total productivity (38). The associated negative relationship of MTD (which is the primary metric of functional diversity in our study) with both productivity and species richness is neither expected a priori from its mathematical formulation nor consistently observed in other studies (15, 16). We have four hypotheses for this seeming contradiction. We emphasize that these hypotheses are not mutually exclusive; all these mechanisms may play a role.

First, the theory linking functional traits to productivity may be correct, but data limitations may obscure the positive diversity–productivity relationship in some empirical analyses. If functional trait data do not include all relevant traits, as species richness increases, "true" functional trait diversity may also increase, but in unmeasured dimensions. Species richness may thus be a better proxy for true, unmeasured functional diversity than any functional diversity metric itself. Over the past few decades, the scientific community has made remarkable progress in assembling open, global trait databases [e.g., TRY (27) and BIEN (https://bien.nceas.ucsb.edu/bien/)] that can facilitate studies of functional diversity and its ecosystem consequences. For example, an analysis of data from >46,000 plant species identified the "global spectrum of plant form and function" (39), which explains the majority of variation in six key plant traits with just two main axes: plant size and the leaf economics spectrum, the latter ranging from short-lived leaves with fast photosynthetic returns on investment to long-lived leaves with high lifetime returns (40). Although relevant traits (e.g., adult stature and leaf mass per area) have been measured for only a small fraction of the global flora (41), these traits are already available for many taxa in some regions of the world (e.g., woody plants in North America and Europe), and it is conceivable that these traits could be measured for most of the global flora in the foreseeable future. Even so, clear gaps, especially in belowground traits, are still pernicious and will require concerted community effort to close them.

Second, the theory may be correct, but only up to a limit. One way that greater functional diversity can lead to greater productivity is through a reduction in year-to-year variation in productivity by species that compensate for one another in their responses to environmental variation. A simulation model of the effects of diversity on temporal stability in a community found that the greatest negative covariance among species (i.e., greater community stability) was at intermediate values of niche separation (see figure 1C in ref. 36). It may be that greater functional trait diversity does lead to higher productivity, but only up to a point. After that, it may be that higher functional redundancy (42) leads to greater ecosystem functioning. A large value of MTD indicates little redundancy because all the

species are very different from each other. Thus, it may be that the mean difference in trait values is not the best metric of functional diversity, despite its common usage, most typically as functional dispersion [FDis; (36)].

Third, it may be that the theory is wrong, and it is the addition of redundant species into a community that provides ecological buffering. This hypothesis is a combination of the previous two: Different species with similar trait values may still have differences in their responses to environmental variation because of other differences in their physiology or morphology. The result would be a positive correlation of species richness with productivity and a negative correlation with MTD.

Finally, it may be that other processes affect the relationship between functional trait diversity and productivity. For example, an increase in functional redundancy may reduce the impacts of natural enemies because each species occurs at lower density (25). Such negative density dependence would result in a positive dependence of productivity on species richness and functional redundancy, but a negative dependence of productivity on functional trait diversity. Alternatively, it may be that environmental stress and competition are linked to species richness. Low species richness may be due to greater environmental stress, and it is hypothesized that greater stress results in more competition (43). As environmental stress decreases, species numbers increase, competition decreases, and productivity increases. The decreased competition could allow the additional species in the community to be more similar in their trait values, resulting in a smaller mean difference among the species—a lower MTD. In sum, more research is needed to understand how various facets of functional diversity relate to community assembly processes and ecosystem functioning.

Previous studies that have quantified relationships among ecosystem functioning and various facets of biodiversity (functional trait, phylogenetic, and species richness) typically have been restricted in geographic scope, limited in the number of communities sampled, or used metrics of functional and phylogenetic diversity that are confounded with species richness (15, 44, 45). A recent study, spanning much of China, overcame these limitations and showed that a composite measure of ecosystem functioning was positively related to plant functional diversity, but negatively related to phylogenetic diversity and species richness (16). Their results differ from ours, but a direct comparison is difficult because the two studies used different measures of ecosystem functioning. We also found that the performance of species richness in predicting productivity varied among ecoprovinces. Therefore, the generality of our results for other regions and their implications for primary productivity are unknown. Standardizing metrics of ecosystem functioning and biodiversity may facilitate reaching more general conclusions.

There is broad consensus in the scientific community that protecting both biodiversity and ecosystem functioning should be high priorities (46), but the contributions of different facets of biodiversity to ecosystem functioning (14, 15, 17), as well as the feedbacks and causal links between them (2), are complicated. While our study does not attempt to resolve questions about feedbacks or causality, we show—using a large dataset spanning a broad geographic region—that functional trait and phylogenetic diversity explained very little of the variation in the productivity of eastern US forests that could not be explained by tree species richness alone. Furthermore, when considered across the entire eastern United States, measures of functional trait and phylogenetic diversity that are formulated to be independent of species richness were negatively correlated with productivity, whereas the effects of species richness on productivity were consistently positive in all analyses. This result demonstrates the potential

confusion that can arise when interdependencies among different diversity metrics are ignored.

Our study points to the potential value of species richness alone as a predictive tool for biodiversity science. Maximizing species richness was also shown in a recent case study to be an optimal reserve-design strategy, as it successfully captured phylogenetic and functional trait diversity (47). Thus, focusing conservation efforts on species richness may be a simple, yet powerful, conservation strategy (48–51). However, our results may not be universal. Although species richness is relatively easy to estimate, and phylogenetic diversity is increasingly so given the rapidly expanding availability of open phylogenetic data [e.g., Open Tree of Life (52, 53)], our understanding of functional diversity is far from complete (27). The easiest-to-measure functional traits are only available for a small fraction of the world's biota, and data for more difficult-to-measure traits [e.g., belowground (54) and hydraulic traits (55)] are even scarcer. Mechanistic ecophysiological studies linking traits to the functioning of individuals and ecosystems are critical to developing a process-based understanding of global biogeochemical cycles (56) and to designing reserves (57), but making such connections remains a major challenge.

Given the limitations of the available trait data, our capacity to directly quantify functional trait diversity across broad geographic scales will likely be constrained for the foreseeable future. Advances in understanding the effects of functional trait diversity on ecosystem functioning will rely on detailed site-level studies, as well as indirect insights that can be gleaned from broader-scale studies of species richness and phylogenetic diversity, which may serve as useful proxies for functional trait diversity. Although functional trait diversity has been found to be sensitive to gaps in trait data (58), the conclusions here are based on a temperate forest system in eastern North America, where such data are relatively comprehensive compared to most other biomes in the world, especially the species-rich tropics (41). Still, we were missing on average up to 4% of trait-species combinations in each plot for well-studied aboveground traits and 29% for a belowground trait (Table S10). Although our results appear robust to missing data (compare Tables 1 and 2 and *SI Appendix*, Tables S1–S4), the effect, in general, of missing data on trait diversity estimation and predicting ecosystem productivity is unclear. Thus, an important remaining challenge is to understand under what conditions (e.g., community assembly processes or geographic regions) phylogenetic and functional trait diversity provide additional critical information, beyond that provided by species richness. Furthermore, our study focuses on productivity, which is only one aspect of ecosystem functioning. The various facets of biodiversity may have different relationships with other ecosystem functions, such as litter decomposition and carbon sequestration (59), pest and pathogen control, and cultural services (60). Studies of other ecosystem functions besides productivity are limited, especially in natural forest communities. Further exploration is needed into the relationships among different facets of biodiversity and various aspects of ecosystem functioning (61, 62).

Materials and Methods

Data Overview. We quantified relationships among forest productivity, functional trait diversity, PD, and species richness in nonplantation forests of the eastern United States. Our analysis is based on 1,821,107 individual tree measurements in 23,145 systematically sampled forest inventory plots that were measured and remeasured from ~2000 to 2020 (Fig. 1). These forest inventory data were combined with publicly available trait data and a phylogeny derived from the Open Tree of Life. As an index of productivity, we calculated the rate of aboveground biomass production (Mg/ha/y) from plot remeasurements; this

biomass growth rate (G) comprises ~40% of total net primary production in temperate forests (63) and accounts for ~70% of changes in total ecosystem carbon stocks in US forests over recent decades (64). We detail the assembly of these data products below.

FIA Data and Plot Filtering. Our analyses used national-scale, systematically sampled forest inventory data from the FIA program of the United States Department of Agriculture Forest Service. Because eastern US forests are considerably more diverse both functionally and phylogenetically than western US forests (65), and because FIA remeasurement intervals are longer in the western United States (~10 y) than in the eastern United States (~5 y), we restricted our analyses to plots from the eastern United States (Fig. 1). 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 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, aboveground biomass, and other tree-level variables (66).

We used FIA database version 9.0, downloaded in November 2022 from https://www.fia.fs.usda.gov/. We restricted our analyses to plot locations that were measured at least twice (i.e., at least one remeasurement) using the current national standardized annual sampling design (67), which was implemented in most US states beginning around 2000. We further restricted our analyses to plot measurements on accessible forest lands that were classified into a single condition (e.g., stand age and soil type) and not classified as artificially regenerated plantations. We did not include plots incapable of supporting at least 1.40 m^3/ha/y of wood volume growth (which excludes plots assigned to the lowest of FIA's seven site productivity classes) or plots that lost more than 20% of their standing biomass stock to natural mortality or timber harvest between measurements (see *SI Appendix*, Table S5 for details). The dataset we analyzed included 62,698 surveys at 23,145 plot locations. Each plot location was assigned to an ecoprovince by aggregating the ecological subsection codes reported by FIA to the province level (29). Each ecoprovince (Fig. 1) represents an area of similar geology, soil type, and climate that supports a similar potential natural vegetation type.

Measuring Biomass Growth Rate. For each plot, we calculated the plot-level aboveground biomass growth rate (G; Mg/ha/y) of trees with DBH ≥ 2.54 using a mass balance approach, described in detail below. In our dataset, 11,114 plots were measured twice (resulting in one G estimate), 8,143 plots were measured three times (two G estimates), 3,399 plots were measured four times (three G estimates), and 489 plots were measured five times (four G estimates). For plots with multiple G estimates, we used the mean value in subsequent analyses so that each plot was represented just once in each analysis.

To estimate G, we first calculated the plot-level live aboveground biomass stock (B_t; Mg/ha) of trees with DBH ≥ 2.54 for each plot at each time t by summing the product of individual tree aboveground biomass estimates (b_i for tree i) and their expansion factors (TPHA$_i$, the number of trees per hectare that a tallied tree represents) for all trees ($i = 1$ to n) alive at time t: $B_t = \sum_{i=1}^{n} (b_i \times \text{TPHA}_i)$. Data on b_i and TPHA$_i$ are in the FIA Tree table for all trees with DBH ≥ 2.54(66), where b_i (DRYBIO_AG from the FIA Tree table) is estimated by combining DBH measurements with allometries and the component-ratio-method (66, 68), and TPHA$_i$ is calculated as the inverse of the tree's sampling area. In our analysis, b_i is converted from pounds to metric tons (Mg), and the TPHA values are a constant (2.47 acre/ha) times the "trees per acre unadjusted" values reported in the FIA Tree table. We then estimated G based on the biomass dynamics of a plot between times t and $t+\Delta t$: $B_{t+\Delta t} - B_t = \Delta t \cdot G - M_t - C_t$, where M_t and C_t, respectively, are the time-t biomass stocks of trees that died or were cut (harvested) between times t and $t+\Delta t$ (69). Rearranging yields the estimate of G over the interval t to $t+\Delta t$: $G = (B_{t+\Delta t} - B_t + M_t + C_t)/\Delta t$.

Trait Data. We selected five functional traits for analysis that were available for most eastern US tree species. Four of the traits–WD (g/cm^3), LN (mg/g), plant maximum height (H$_{max}$, m), and SLA (mm^2/mg)–are included in the global spectrum of plant form and function (39). For supplementary analyses, we also included a fifth trait, maximum rooting depth (R$_{max}$, m); greater variability in rooting depth among species is expected to increase the efficiency of belowground resource uptake [e.g., shallow vs. deep-soil water and nutrients (70)]. WD, LN, and SLA values were obtained from the TRY database (27) (accessed in May 2022). R$_{max}$

values also were obtained from TRY and augmented using the latest data from Tumber-Dávila et al. (71) and Guerrero-Ramírez et al. (72). WD values were augmented using data reported by FIA (WOOD_SPGR_GREENVOL_DRYWT in the FIA REF_SPECIES table). H$_{max}$ was estimated for each species using individual tree heights reported by FIA. Specifically, we defined H$_{max}$ as the 95th and 99th percentile of heights [HT in the FIA Tree table (66)] reported for a given species. The H$_{max}$ values based on the 95th and 99th percentiles were highly correlated with each other ($r = 0.98$); thus, only the 99th percentile of heights was used in measuring H$_{max}$ in further analyses. Because not all species had measurements of all traits, we evaluated the impact of missing data by performing additional analyses (see below).

The trait values of a species vary in space, which may bias trait distance measurements in each FIA plot. To account for variation in traits within species among plots, we used a geographical buffer prior to calculating trait distances among species in each FIA plot, making use of the fact that multiple measures of georeferenced trait values existed in the data sources that we used. Specifically, we set a circular spatial buffer (moving window) for each FIA plot location, using the "st_buffer" function in the *sf* R package (73), and then intersected the FIA plot locations (using the approximate coordinates reported in the public FIA data) with the georeferenced trait records using the "st_intersection" function. The geographical coordinates of trait records were obtained from FIA plots (for H$_{max}$) and the TRY database (for the other four traits). The trait value of a species in a plot was assigned the mean value of all trait records located within the buffer. The diameter of the buffer ranged from 100 to 900 km. The buffer size varied by trait and was determined by maximizing trait coverage (i.e., at least 1 georeferenced trait record located within the buffer of a plot) for all FIA plots at the finest possible geographic scale. Specifically, WD of a species in a given plot was assigned the mean value of WD of this species in all plots within a 900-km diameter buffer; the buffers for LN, SLA, R$_{max}$, and H$_{max}$ were 600 km, 400 km, 500 km, and 100 km, respectively. After the buffer process, some trait data of a certain species may be missing in a FIA plot because the trait data are outside the buffer of the FIA plot. In these instances, we replaced missing values with the mean values of all available trait data for the species. Distances in trait space among species coexisting in the same plot were calculated following Gower (74):

$$D_{ij} = 1 - \frac{\sum_{k=1}^{n} w_{kij}\left(1 - \frac{|x_{kj} - x_{ki}|}{x_{k.max} - x_{k.min}}\right)}{\sum_{k=1}^{n} w_{kij}}, \quad [\mathbf{1}]$$

where D_{ij} is the trait distance between species i and j, and x_{ki} and x_{kj} are the values of trait k of species i and j, respectively. $x_{k.max}$ and $x_{k.min}$ are the maximum and minimum values of trait k, respectively, and w_{kij} is the weight of trait k for the species i-j pair, which is 1 if both species have values for trait k and 0 if trait k is missing in either species i or j.

Measuring Diversity. Phylogenetic trees for the species in FIA plots (*SI Appendix*, Fig. S3) were extracted from the ALLMB tree presented by Smith & Brown (28), which uses GenBank data and the Open Tree of Life (52, 53) with a phylogenetic backbone provided by Magallón et al. (75). Prior to calculating diversity metrics, species names from FIA plots, trait databases, and the phylogeny were standardized using the Taxonomic Name Resolution Service V5.0 (https://tnrs.biendata.org/, accessed: 6 April 2022), following Tropicos (https://www.tropicos.org/) and World Flora Online (http://www.worldfloraonline.org). Pairwise branch distances were then calculated.

Because site productivity is the sum of the productivity of each individual (1, 76), functional trait diversity and phylogenetic diversity were both calculated using a basal area-weighted approach, where the weight for each tree was its DBH^2 multiplied by its TPHA value (see above); this is equivalent to weighting each tree by its basal area. MTD and MBL were calculated as:

$$X = \frac{\sum_{i=1}^{S} \sum_{j \neq i}^{S} d_{ij} n_i n_j}{S(S - 1)N^2}, \quad [\mathbf{2}]$$

where X is either MTD or MBL, d_{ij} is either the pairwise phylogenetic distance (branch length) or trait distance (Eq. **1**) between species i and j, n_i is the total basal area of species i, N is the total basal area of all species, and S is species richness.

We also calculated two commonly used metrics, Faith's PD (19), the sum of all branch lengths [in million years (Ma)]:

$$PD = \sum_{i}^{S} \sum_{\in b(S_i)} L_{ib}, \qquad [\mathbf{3}]$$

where L_{ib} is the length of the bth branch segment of the ith species on the phylogenetic tree, and FAD (30), the sum of the pairwise trait distances:

$$FAD = \sum_{i=1}^{S} \sum_{j \neq i}^{S} d_{ij}. \qquad [\mathbf{4}]$$

Because both PD and FAD are sums of branch lengths or trait distances, they inherently contain species richness as a component.

Statistical Analyses. Unless stated otherwise, the sampling unit in all analyses was an inventory plot location. All variables were calculated for each plot remeasurement and then averaged across all remeasurements at each location, as described above for G. For example, for a plot measured three times (t_1, t_2, and t_3), all diversity metrics and other covariates were calculated at t_2 and t_3 and then averaged. Thus, each plot location occurred once in each analysis. First, we calculated pairwise correlations among growth and the diversity metrics and among the SD of the five traits weighted by basal area. Then, we explored the association between growth and the diversity metrics using linear mixed-effects models. To control for stand history and broad edaphic-climatic factors, each model included a random intercept term for ecoprovince (ECO) and fixed effects for stand age (STD), initial biomass (IniBio), and between one and three diversity components: species richness (SP), phylogenetic diversity (PD or MBL), and functional trait diversity (MTD or FAD), or the basal area-weighted SD of a single trait. For the single-trait models, the basal area-weighted SD was determined for each trait in each plot as the square root of the basal area-weighted variance, which was calculated using the "wtd.var" function in the Hmisc package version 5.1-0 (77) in R, with basal area weights as described above. All numeric variables (i.e., all variables except ecoprovince) were standardized to zero mean and unit variance prior to fitting the models so that the model coefficients (slopes) are standardized to a common, unitless scale. We compared model fits using R^2 and AIC. We recognize that biodiversity–productivity relationships often are not linear over their entire range (78). We used linear model forms, however, because they can easily accommodate random effects and are straightforward to interpret in terms of the sign and magnitude of effects and because preliminary analyses using generalized additive (nonlinear) models yielded qualitatively similar inferences. The robustness of our results to linear vs. nonlinear forms likely indicates that most FIA plots fall within the linear portion of the biodiversity–productivity relationships.

For additional exploration of the effects of stand age, the initial biomass of the plots, and environmental heterogeneity as captured by ecoprovince, we divided the plots into groups of different stand ages (10-y intervals) or initial biomass (50-Mg intervals). We then repeated linear mixed-effects models for each group. For each group of stand ages, biodiversity metrics (i.e., SP, MBL, and MTD) and initial biomass are fixed factors, and ecoprovinces are random factors; for each group of initial biomass, biodiversity metrics and stand age are fixed factors, and ecoprovinces are random factors. We also explored biodiversity–productivity relationships within each ecoprovince. For each ecoprovince, we conducted ordinary least squares regressions, with species richness (SP), phylogenetic diversity (MBL), trait diversity (MTD), stand age (STD), and IniBio included as independent variables.

Missing Data. To account for missing data, we did three sets of analyses: 1) excluding the trait with substantial missing information, R_{max}, 2) including R_{max} because it is known to be important for productivity in trees, and 3) excluding R_{max} but imputing missing values for the other four traits. We imputed the missing values for LN and SLA using the "phylopars" function in Rphylopars version 0.3.9 (79). The missing values were replaced by restricted maximum likelihood values that were estimated based on the trait values of other species and the phylogeny under a Brownian evolution model. The results of the first set are reported in the main text (Tables 1 and 2). The other two sets (*SI Appendix*, Tables S1–S4) provide tests of the robustness of our conclusions by either including a potentially important functional trait or by estimating missing values so that all pairwise measures of trait distances are based on the complete set of traits. The number of species with missing values (no data for a given trait), out of the 188 species, was 0 for WD, 54 for LN, 21 for SLA, 108 for maximum rooting depth (R_{max}), and 0 for maximum height (H_{max}). For each trait, we measured the average percent of species without data and the average percent of basal area (m^2/ha) of these species across FIA plots. The average

percentage across plots for each trait was calculated as the average percentage among species within each plot and then averaged across all plot locations.

Relationships between Species Richness and Other Diversity Metrics. The form of Eq. **2**, a mean value, ensures that the MBL and MTD metrics that we used for phylogenetic and functional trait diversity, respectively, have no intrinsic correlation with species richness (SP). Thus, any correlations that arise in any given empirical dataset will be due to processes affecting community assembly.

An additional issue is heteroskedasticity in the relationships between species SP and other diversity metrics. If all species in the regional species pool are present at a single site, SP takes on its maximum possible value, and both MBL and MTD metrics become highly constrained as the only variance is due to differences in species abundances. Conversely, as the number of species in a site declines, the range of possible values increases for both MBL and MTD [see results for a related metric, FDis, in Fig. 2*E* of Laliberté and Legendre (36)]. This heteroskedasticity might affect our conclusions, depending on the amount of heteroskedasticity over the observed range of SP. In our data, SP values for single inventories of FIA plots ranged from 3 to 21, out of a total of 188 species in the eastern US FIA dataset. Because all variables, including SP, were averaged over multiple inventories of each FIA plot to calculate means for subsequent statistical analyses, the SP values used in our analysis were often not integers and ranged from 3.0 to 19.5.

To explore the potential effects of heteroskedasticity on our results, we conducted two analyses. The first analysis involved implementing the mixed-effects model reported in Fig. 3*B* for groups of FIA plots that were separated into the following SP bins: (3, 4.5), (4.5, 7.5), (7.5,10.5), (10.5,13.5), and (13.5,19.5), with the last bin being wider due to the small number of FIA plots with SP > 13.5 (see sample sizes in *SI Appendix*, Table S9). The mixed-effects model reported in Fig. 3*B* was fit separately to the FIA plots in each bin so that the SP range and potential heteroskedasticity were constrained. The second analysis involved translating the observed MBL and MTD values into SES values using a null model and then using the SES values in place of the observed MBL and MTD as explanatory variables in the mixed-effects model reported in Fig. 3*B*. The null model was based on simulated communities following the methods of Laliberté and Legendre (36). Specifically, we created 10,000 simulated communities for each observed SP value from 3 to 21 as follows: In each simulated community, each species identity was randomly assigned from the pool of 188 species, and each abundance was randomly drawn from a lognormal distribution; the log-scale parameters were mean 0 and SD 1, but the results are insensitive to the lognormal parameter values because numeric variables were standardized prior to fitting the mixed-effects model. We then paired each FIA plot with the set of simulated communities whose SP level matched the rounded (nearest integer) SP value of the FIA plot, and we calculated the FIA plot's SES for MTD as (observed MTD value − mean of simulated MTD values)/(SD of simulated MTD values). We calculated SES values for MBL in the analogous way. Finally, we fit the same mixed-effects model reported in Fig. 3*B*, except using the SES values for each FIA plot as explanatory variables instead of the observed MTD and MBL values.

Author affiliations: [a]Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory of Earth Surface Processes of Ministry of Education, Peking University, Beijing 100871, China; [b]Florida Museum of Natural History, University of Florida, Gainesville, FL 32611; [c]Department of Biology, University of Florida, Gainesville, FL 32611; [d]Genetics Institute, University of Florida, Gainesville, FL 32610; [e]Biodiversity Institute, University of Florida, Gainesville, FL 32611; and [f]Division of Environmental Biology, NSF, Alexandria, VA 22314

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