A cross-scale assessment of productivity-diversity relationships

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Abstract

Biodiversity and ecosystem productivity vary across the globe and considerable effort has been made to describe their relationships. Biodiversity-ecosystem functioning research has traditionally focused on how experimentally controlled species richness affects net primary productivity (S→NPP) at small spatial grains. In contrast, the influence of productivity on richness (NPP→S) has been explored at many grains in naturally assembled communities. Mismatches in spatial scale between approaches have fostered debate about the strength and direction of biodiversity-productivity relationships. Here we examine the direction and strength of productivity's influence on diversity (NPP→S) and of diversity's influence on productivity (S→NPP), and how this varies across spatial grains using data from North American forests at grains from local (672 m^2) to coarse spatial units (median area = 35,677 km^2). We assess relationships using structural equation and Random Forest models, while accounting for variation in climate, environmental heterogeneity, management, and forest age. We show that relationships between S and NPP strengthen with spatial grain. Within each grain, S→NPP and NPP→S have similar magnitudes, meaning that processes underlying S→NPP and NPP→S either operate simultaneously, or that one of them is real and the other is an artifact. At all spatial grains, S was one of the weakest predictors of forest productivity, which was largely driven by biomass, temperature, and forest management and age. We conclude that spatial grain mediates relationships between biodiversity and productivity in real-world ecosystems and that results supporting predictions from each approach (NPP→S and S→NPP) serve as an impetus for future studies testing underlying mechanisms.

Significance statement

The relationships between diversity and productivity are central to efforts explaining global variation of biodiversity and rates of carbon sequestration. However, little is known about the relative importance of biodiversity as the driving force, or as the consequence of ecosystem-level productivity. Our analysis of a comprehensive database of North American forests reveals that biodiversity and productivity can be both cause and effect and that their relationship strengthens with spatial grain. Importantly, we show that environmental context is more important in determining biodiversity and productivity than either biodiversity or productivity alone. Productivity-diversity relationships emerge at multiple spatial grains, which should widen the focus of national and global policy and research to larger spatial grains.

Introduction

One of the most prominent questions in ecology is how to describe relationships between biodiversity and ecosystem-level productivity (1–10). Two fields of research with different motives have tried to understand causality between these variables (11). The first examines how biodiversity varies across space as a result of different levels of productivity created by environmental variation (e.g., temperature, precipitation), and has resulted in a voluminous literature on the shapes of the patterns and their potential underlying causality (1, 2, 9, 10, 12–14). The second aims to quantify changes in vital ecosystem functions such as productivity following anthropogenically-induced changes in diversity (5, 15–17). As a result of the different perspectives on the direction of causality, there remains considerable debate and confusion surrounding the relationship between diversity and productivity (18), which is exacerbated by differing spatial grains at which studies are conducted (4, 19).

Recently, there has been growing interest in assessing biodiversity ecosystem functioning (BEF) relationships in real-world, non-experimental ecosystems over large geographic extents, but likely due to logistical constraints, relationships are typically measured at local spatial grains (20–22). Results suggest that the positive effect of species richness on productivity and other ecosystem functions can be as, or more, important than abiotic environmental drivers' effects on productivity, suggesting that diversity-productivity relationships can be even stronger in real-world communities than in controlled experiments (21). However, to fully understand the influence of diversity on productivity, and vice versa, it is critical to recognize that traditional bivariate analyses may underestimate the strength of these relationships by not accounting for the effects of spatial grain, as well as those of biomass, shading, macro-climate, and management (11, 18, 23, 24).

The striking mismatch between the spatial grains of BEF experiments (cm^2 to m^2; 4), observational studies of BEF (0.04 to 1.0 ha; 20, 25), and macroecological diversity-productivity correlations (m^2 to thousands of km^2; 1, 10, 26, 27) further obscures comparisons between perspectives. However, there is a diverse array of theoretical expectations for grain dependency of the effects of productivity on diversity

(NPP→S) and of diversity on productivity (S→NPP), which predict effects to either strengthen or weaken as the spatial grain increases (Table 1). For example, spatial turnover of species that are functionally equivalent within the regional grain can offset low species richness at local grains, resulting in a strengthening of S→NPP with increasing spatial grain. The effects of NPP→S are also hypothesized to increase with spatial grain, because higher NPP is associated with greater heterogeneity at larger spatial grains, which enhances coexistence of more species at the regional grain. Moreover, other components of a community, such as biomass, can mediate relationships between productivity and diversity via their effects on competitive dominance (18). These theoretical expectations have been supported by observational data for the effects of productivity on diversity (10, 28, 29). In the case of BEF relationships (i.e. S→NPP), there is also empirical and theoretical support for grain dependence, which comes from a restricted range of small spatial grains (30–32).

Here, we aim to address the dual nature by which productivity influences diversity (NPP→S) and diversity influences on productivity (S→NPP) across spatial grains by combining structural equation models (SEM) and Random Forest models (RFs) to explicitly account for the bidirectionality of NPP→S and S→NPP. Using SEM, we propose and test hypothesis-based models (Fig. S2) that estimate the direction and strength of NPP→S and S→NPP. Next, we use RFs, an assumption-free machine learning approach (33), to quantify the relative importance of predictors of species richness and productivity. We examine both hypothesized directions of the relationship, along with a number of important covariates that influence both diversity and productivity, such as biomass, precipitation, temperature, and forest age, using a comprehensive observational dataset of North American forests at fine (area = 672 m^2; n = 46,211 plots), medium (median area = 1,386 km^2; n = 1,956 spatial units), and coarse spatial grains (median area = 35,677 km^2; 98 spatial units). We specifically ask whether the influence of productivity (and its environmental drivers) on diversity (NPP→S) played a predominant role, or whether the influence of diversity on productivity (S→NPP) was predominant, and how these relationships manifest across grains in real-world ecosystems.

Table. 1 Overview of hypotheses predicting grain dependence of relationships between net primary productivity (NPP) and species richness (S).

No.	Direction	Mechanism of grain dependence	Weakens or strengthens towards coarse grain?	Reference
I	NPP→S and S→NPP	Spatially asynchronous demographic stochasticity impacts small populations (or small grains) and averages out over large grains.	Both NPP→S and S→NPP strengthen towards coarse grains	(34)
II	NPP→S	At larger grains, higher NPP is associated with increased heterogeneity and/or dissimilarity of local patches, allowing for greater regional coexistence.	NPP→S strengthens towards coarse grains	(28, 35, 36)
III	NPP→S	A statistical interaction between NPP and grain in their effect on S emerges as a consequence of increasing occupancy with NPP.	NPP→S weakens towards coarse grains	(37)
IV	NPP→S	At very large grains (thousands of km^2 and larger), high productivity increases occupancy and population size, thus increasing the probability of reproductive isolation and speciation	NPP→S strengthens towards coarse grains	(38)
V	S→NPP	Stochastic sampling effects dominate at small grains, resource partitioning at larger grains ('spatial insurance'), and their relative magnitude determines the grain dependency.	Both strengthening or weakening possible	(39, 40)
VI	S→NPP	Functionally redundant species at the regional grain can compensate for low richness at local grains.	S→NPP strengthens towards coarse grains	(41)
VII	S→NPP	With incomplete compositional turn-over, proportional changes in larger-grain richness are always less than proportional changes in smaller-grain richness such that the explanatory power of richness on changes in functioning decreases with spatial scale.	S → NPP strengthens strengthens towards coarse grains until species richness saturates	(42)

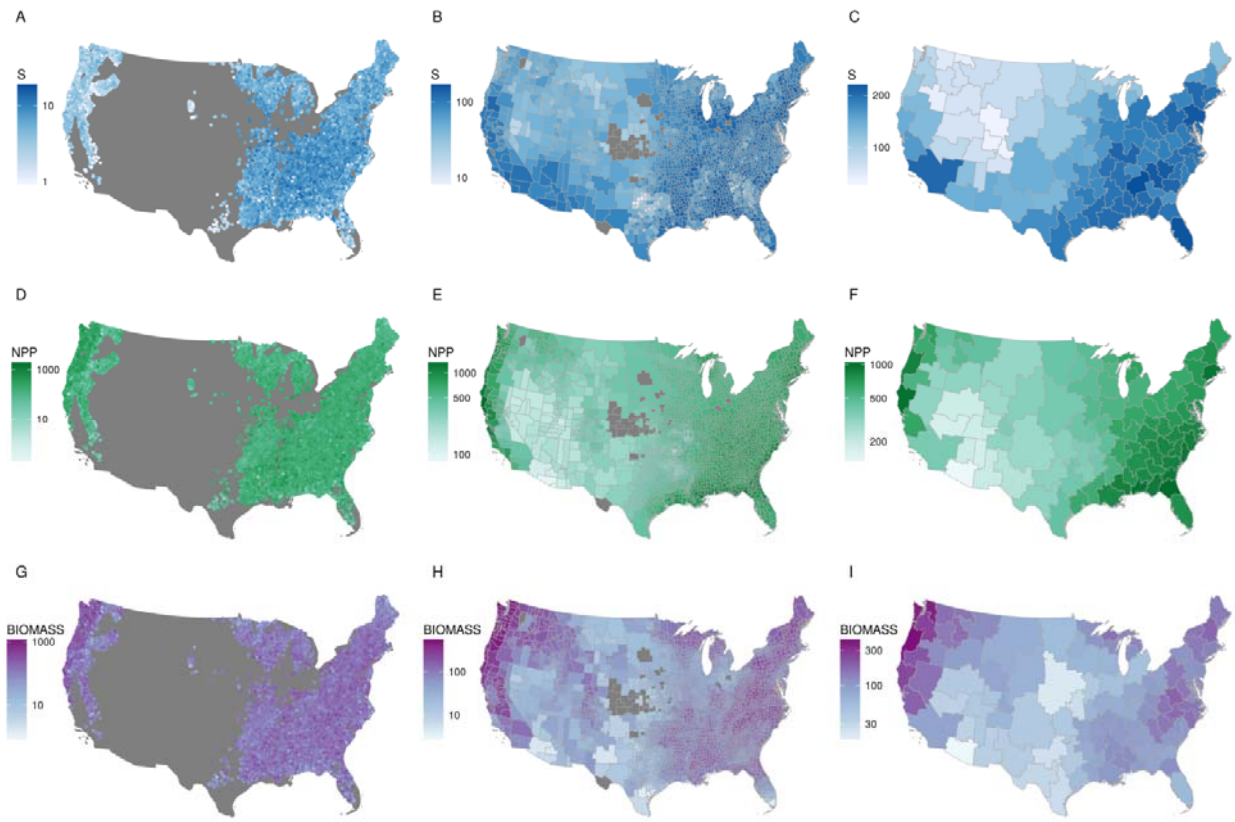

Fig.1. Maps of species richness (S), net primary productivity (NPP) [gC/m^2/year], and biomass [Mg/ha] of forests at three spatial grains across the contiguous USA. The values in all plots are on $\log_{10}$ scale.

Results

Spatial patterns in productivity (NPP) and richness (S) emerged at coarser spatial grains, with higher S and NPP usually observed in the eastern USA than in the western USA (Fig. 1). Biomass, a time-integrated measure of NPP that also influences diversity, also exhibited similar patterns (Fig. 1). Bivariate relationships among S and NPP exhibited scale dependence, with their slopes increasing with spatial grain (Fig. 2).

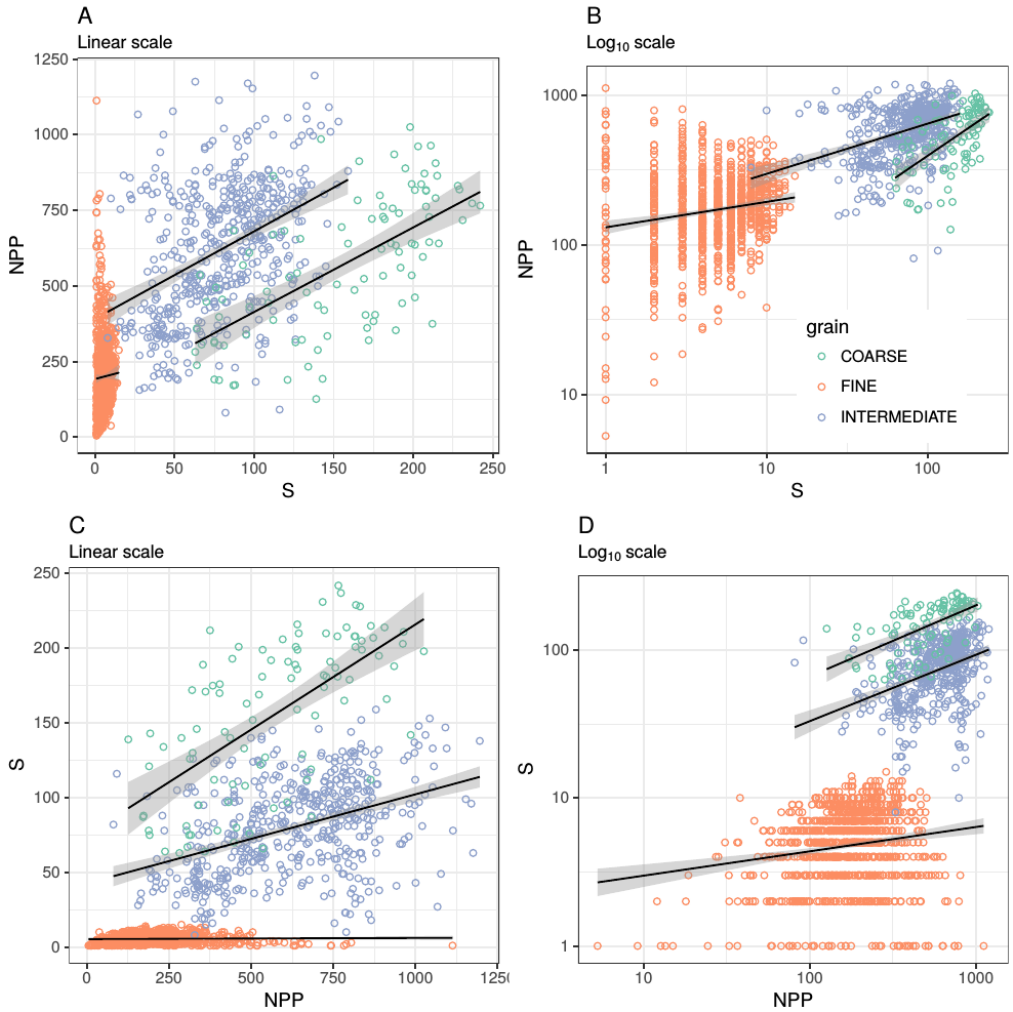

Fig. 2. Bivariate relationships between observed species richness (S) and productivity (NPP) of forests at three spatial grains across the contiguous USA, on linear (A, C) and $\log_{10}$ (B, D) scales. Panels A and B show NPP as a response to S, panels C and D show NPP as a predictor. Solid lines are least-squares linear regressions fitted at each grain, shaded areas are standard errors. Analyses were performed using stratified random samples of 1000, 500 and 98 spatial units at the fine, intermediate and coarse spatial grains, respectively.

Structural Equation Models (SEM). We examined relationships between species richness and net primary productivity (NPP) across spatial grains using two SEMs for each spatial grain: the first (S→NPP) testing the direct effect of S on NPP and the indirect effect of NPP on S (via biomass), and the second (NPP→S) testing both the direct and indirect effects of NPP on S (Fig. 3). In both SEMs, environmental variables (e.g., mean annual precipitation (MAP), mean annual temperature (MAT),

temperature seasonality, and elevation range), size of the species pool, forest age, and management were used to explain variation in S, biomass, and NPP. At the intermediate and coarse grains, we also included area (of each spatial unit) to account for variation in species richness due to the effects of area (see Methods).

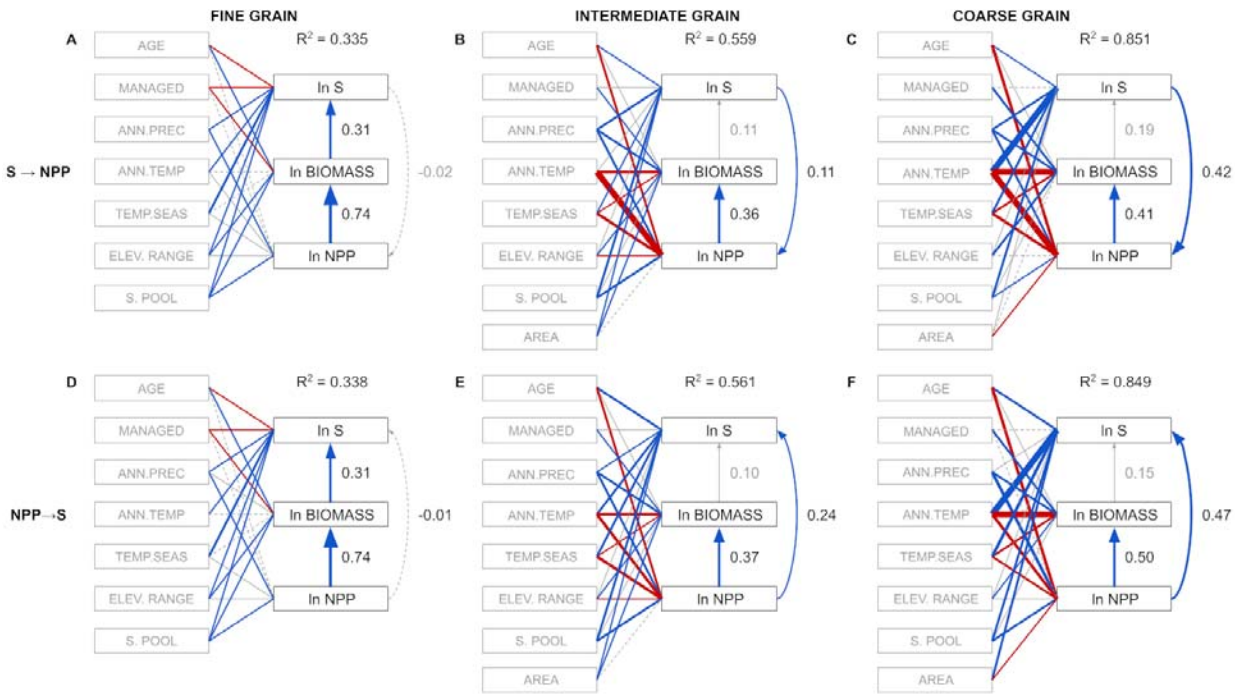

Fig. 3. Structural equation models (SEM) testing the influence of diversity (S) on productivity (NPP)('S → NPP'; A, B, C) and that of NPP on S ('NPP → S'; D, E, F), once controlling for environmental variables (e.g., mean annual precipitation, mean annual temperature, temperature seasonality, and elevation range), size of the species pool, forest age, and management, in forests across the contiguous USA at three spatial grains. Both models fit the data well at all spatial grains (P-value of the Chi-square test > 0.1; Table S1). Boxes represent measured variables and arrows represent relationships among variables. Solid blue and red arrows represent significant (P< 0.05) positive and negative standardized path coefficients, respectively, and their width is scaled by the corresponding standardized path coefficient. Solid and dashed gray arrows represent non-significant (P>0.05) positive and negative standardized path coefficients, respectively. AGE is forest age, MANAGED is forest management, ANN.PREC is mean annual precipitation, ANN.TEMP is mean annual temperature, TEMP.SEAS is temperature seasonality, ELEV.RANGE is elevation range, S.POOL is the regional species pool, and AREA is area. S, BIOMASS, NPP, and AREA were natural log transformed prior to analysis.

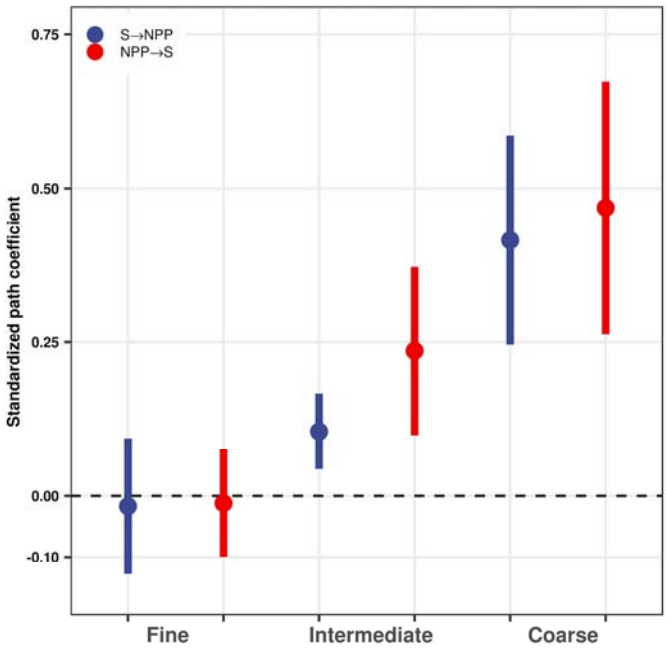

Fig. 4. Direct effects of diversity on productivity (S → NPP) and productivity on diversity (NPP → S) estimated with structural equation models (SEM) in forests across the contiguous USA at three spatial grains. Points are standardized path coefficients and solid lines are 95% confidence intervals.

Both models fit the data well for all spatial grains (P-value of the Chi-square test > 0.1; Table S1). At each spatial grain, both SEMs had similar R^2 values averaged over S, biomass and NPP, indicating a similar fit of the model to the data. R^2 values for both SEMs increased with spatial grain, from 0.34 at the fine grain, to 0.56 at the intermediate grain and 0.85 at the coarse grain. Generally, the strength of effects of S → NPP and NPP → S were similar within each spatial grain, but both increased in strength with increasing spatial grain (Fig. 3 & 4). At the fine spatial grain, we found a weak direct effect of S → NPP (Fig. 3A) and NPP → S (Fig. 3D), but an indirect effect of NPP on S via biomass (standardized path coefficient of indirect effect = 0.23; Fig. 3D). At the intermediate spatial grain, we found a similarly strong direct effect of S on NPP (standardized path coefficient of direct effect = 0.11, Fig. 3B and 4) as NPP on S (standardized path coefficient of direct effect = 0.24; Fig. 3E and 4) and weak indirect effects of NPP on S (standardized path coefficient of indirect effect = 0.04; Fig. 3E). Similarly at the coarse spatial grain, we found strong direct effects of S on NPP (0.42, Fig. 3C and 4) and of NPP on S (0.47, Fig.

3F and 4) and weak indirect effects of NPP on S (standardized path coefficient of indirect effect = 0.08; Fig. 3F).

Overall, the SEMs show that the productivity-diversity relationship increases in strength with spatial grain, and both relationships (S→NPP and NPP→S) explain similar amounts of variation, albeit with some differences in the direct and indirect effects. At fine spatial grains, our SEMs show greater support for a strong indirect effect of NPP on S via biomass, but do not support the inverse effect of S on NPP. Towards coarser spatial grains, our SEMs do not conclusively show stronger support for one direction of causality over the other. These patterns were robust to the direction of paths between S and biomass (Fig. S3A, B, and C; Table S1) and between biomass and NPP (Fig. S3D, E, and F; Table S1).

Random Forest models (RFs). To assess the relative importance of each predictor of species richness and NPP, and to provide an assumption-free alternative to the SEMs, we fitted two random forest models for each of the three spatial grains: one with NPP and the other with S as response variables. We found that NPP was an important predictor of S at the fine and intermediate spatial grains (Fig. 5A), with unimodal and linear effects respectively (Fig. 5), but was less important relative to other predictors at the coarse spatial grain. For S, we found that species pool, MAT, MAP, and forest age were the best predictors at all spatial grains (Fig. 5). In line with the SEM analyses, the overall explained variation of S increased towards coarse spatial grains, from 0.38 at the fine grain to 0.51 at the intermediate and 0.85 at coarse grains. For NPP, we found that species richness was one of the weakest predictors relative to other predictors at all spatial grains (Fig. 5B), with management, forest age, MAP, and especially biomass being the most important predictors (Fig. 5B). The overall explained variation of NPP also increased towards coarse spatial grains, from 0.62 at the fine spatial, to 0.82 at the intermediate spatial grain and 0.83 at the coarse spatial grain.

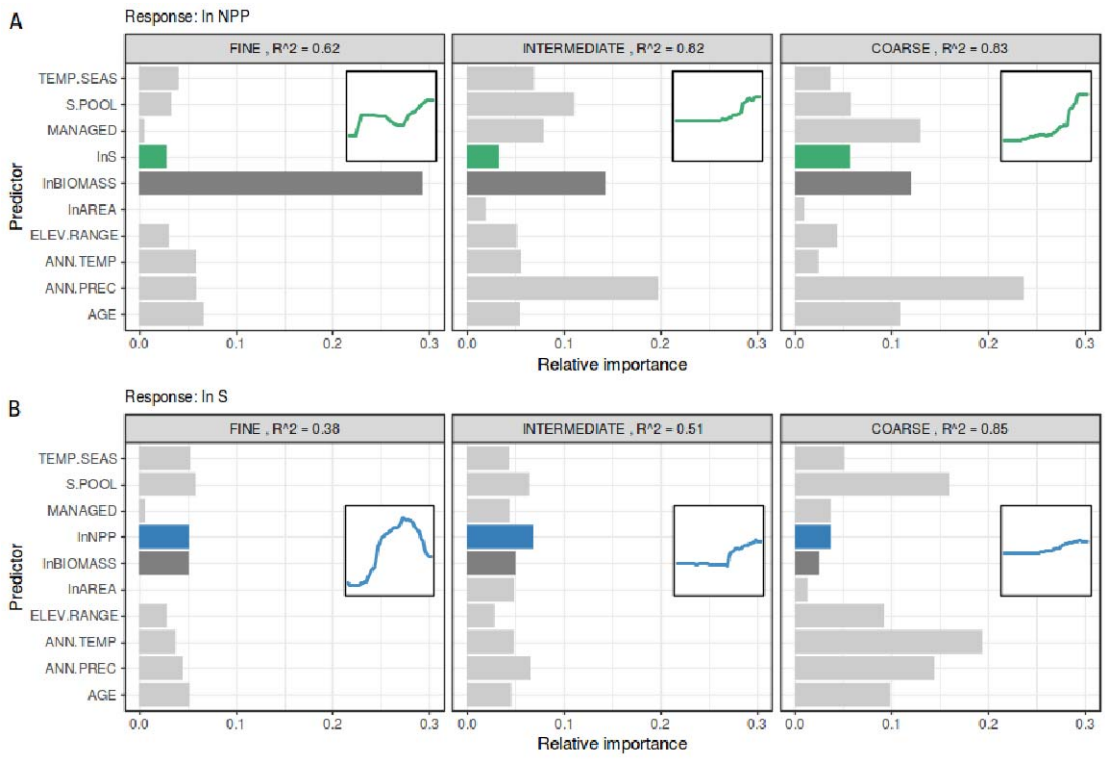

Fig. 5. Relative variable importance from random forest models explaining NPP and species richness (S) and NPP at three spatial grains, which is the mean decrease in squared error caused by each of the variables, rescaled such that it sums up to the total pseudo R^2. The curves in the insets show shapes of the partial response of ln NPP or ln S (after accounting for all of the covariates); all of the insets have the same span of the y-axis. For complete responses with axis scales and tick-marks see Fig. S5.

Discussion

The first important result is the similar magnitude of the S→NPP (18) and NPP→S (10, 26, 43) relationships at all grains. This reflects, in part, that both productivity and species richness have many environmental and geographical drivers in common (44), which complicates distinguishing correlation from causation, even when using SEMs (45, 46). There are two possible interpretations of this result: (i) it may indicate that diversity's causal effects on productivity and productivity's causal effects on diversity operate simultaneously, which was suggested by (18), but never demonstrated on observational data from large spatial grains. Alternatively (ii), if only one direction of the diversity-productivity relationship is real and causal, it may be possible to fit another model assuming the opposite direction because of multicollinearity in the data or non-identifiability of the causal direction (47). Without large-grain

experiments that manipulate diversity in ways that mimic biodiversity change (i.e. species gains and losses) in real-world ecosystems (11, 48–50), we see little hope for resolving this with contemporary data and approaches.

Our second important result is that both S→NPP and NPP→S strengthen from the fine to the intermediate grain, and in the case of the SEM both relationships continue strengthening towards the coarsest grain. While grain-dependent shifts are often expected (Table 1), this had not been shown previously with empirical data for S→NPP using spatial grains coarser than several hectares (25, 31, 32). If the S→NPP direction is the real causal one, then our results from SEM and RF analyses support several theoretical expectations (Table 1) and give further impetus to efforts quantifying biodiversity effects in naturally assembled ecosystems at broad spatial scales (51). If the NPP→S direction is the real causal one, then our results are in line with (27, 35), but are in contrast with (29, 37), particularly when upscaling from the fine grain to intermediate grain, where both the SEM and RF analyses give congruent results. Intriguingly, a third possibility is that both NPP→S and S→NPP are real and that they operate simultaneously, as suggested by our SEM results. In this case, we are unaware of any theory that considers how this reciprocal relationship would be expected to change with increasing spatial grain. The one caveat applicable to interpreting any direction of diversity-productivity relationships is that of demographic stochasticity (mechanism I in Table1), which may weaken both NPP→S and S→NPP, or their synergistic interplay, at fine spatial grains. In our study, the strong local effect of demographic stochasticity appears plausible given the small area of the forest plots (0.067 ha) and small population sizes (12.24 ± 0.02 trees per plot; range = 1- 157 trees per plot) therein. This would suggest that temporal changes in local scale biodiversity (52, 53) may have under-appreciated effects on ecosystem function (54).

The third key result is that other predictors, such as temperature and biomass, were particularly influential in all our analyses. That is, the grain dependence of the relationship between S and NPP was coupled with a clear increase in the effect of annual temperature (but not precipitation) on both S and NPP towards coarse grains, which supports the notion that either temperature-dependent diversification (55, 56) or

ecological limits (43) shape diversity at these spatial grains. The consistently weak effect of precipitation is expected since we focus on forests, which only grow above certain precipitation thresholds (57). Second, we found a positive, indirect effect of NPP on species richness via forest biomass at the fine spatial grain, which supports multiple hypotheses (Table 1) such as the view that higher ecosystem productivity enhances species diversity by enabling larger numbers of individuals per species to persist due to lower extinction rates (35, 37, 58), particularly at fine grains where stochastic extinctions occur (34). The clear importance of temperature, biomass, and other predictors such as forest age, seasonality, or species pool (Figs. 3, 4) highlights that even when the NPP→S relationship holds across grains, other drivers are considerably more important in predicting both (e.g., 59). Hence, integrating the environmental context surrounding ecological communities into modeling diversity-productivity relationships is a necessary step towards making robust predictions of either biodiversity or ecosystem functioning at any spatial grain.

Our results reveal that mechanisms associated with one direction of diversity-productivity relationships may provide insight to observed patterns of either direction, despite being initially formulated at a different spatial grain. For example, the positive, indirect effect of NPP on species richness via forest biomass at the fine spatial grain provides support for the more individuals hypothesis (37), although it is typically tested at regional to continental spatial scales. Increasingly, macroecological mechanisms such as speciation gradients (60) and water-energy variables are being examined in small-grain experimental grasslands to explore their role in mediating niche-based processes (61) and biodiversity effects (62), respectively. Similarly, efforts to upscale biodiversity effects on productivity - developed initially to identify local scale mechanisms such as complementarity and selection effects (63, 64) - may emerge as a crucial mechanism in determining spatial variation in ecosystem functioning at large spatial scales. Rather than uniquely focusing on the direction and strength of S-NPP once accounting for other factors, our results show that mechanisms associated with S→NPP and NPP→S likely underpin the context dependency of diversity-productivity relationships across spatial grains (Table 1). These recent

developments in BEF research and macroecology suggest that conceptual integration between these two disciplines is just beginning (65), yet further efforts to bridge disciplinary gaps are essential to deepen current understanding of mechanisms that underpin the shifts in diversity-productivity relationships across spatial scales.

To conclude, we show that the relationship between diversity and productivity strengthens toward coarse grains. This result is in line with expectations from both BEF theory, and some (but not all) expectations from macroecological studies on NPP→S, and highlights the potential of demographic stochasticity to distort diversity-productivity relationships at fine grains. Moreover, we find similar support for both directions of diversity-productivity relationships across spatial grains, revealing that biodiversity and productivity can be both cause and effect. Future research on this relationship needs to move from fine-grain experiments and observational studies to coarse grains in order to fully understand and predict the impacts of anthropogenic biodiversity change on ecosystem function.

Methods

Data

Geographic extent and grain. We conducted analyses across the contiguous USA at three spatial grains (Fig. 1): (1) fine grain (46,211 plots, 672 m^2 or 0.000672 km^2 each), (2) intermediate grain (1956 units, median 1,386 km^2) created by aggregating US counties to larger units based on the forested area within them (see 'spatial aggregation algorithm' below), and (3) coarse grain (95 units, median 35,677 km^2) created by further aggregating the intermediate grain units. We restricted our analyses to forested areas to make comparisons within and among spatial grains in similar ecosystems. For the intermediate and coarse grains, we defined an area as forested if it fell into a 1 km^2 pixel with non-zero forest biomass following (66).

Spatial aggregation algorithm. To minimize variation in species diversity (defined below) due to differences in area between spatial units within the intermediate and coarse spatial grains, we created an

algorithm that minimized variation of forested area at each spatial grain. The algorithm worked in an iterative process as follows: (1) Calculate variance of area across all counties. (2) Randomly select a focal county with a probability proportional to 1/sqrt(forest area+1), which will more likely select small rather than large counties. This was because small counties can be merged to approach the grain of the large counties, thus decreasing variation in area. (3) Select a random adjacent county and merge it with the focal county. (4) Updated the variance of area across all spatial units in the USA and compare it to the original variance. If the new variance is lower than the original variance, the algorithm accepts the merged unit and returns to step one. If the variance does not decrease, the algorithm repeats step 3 until it decreases, with the maximum number of attempts of 1,000. If the variance still does not decrease even after 1,000 attempts, the algorithm rejects the merge, and returned to step one. The algorithm started with 3,107 US counties, and we first terminated it when 1,956 merged spatial units were created (intermediate grain dataset) and then after it reached 98 merged spatial units (coarse grain dataset) (Fig. 1). Although the algorithm substantially reduced variation in area within both spatial grains (Fig. S9), it did not eliminate the variation entirely, and thus we still used area as a covariate in the statistical analyses at the intermediate and coarse spatial grains.

Species richness (S). For all spatial grains, we estimated diversity as species richness (S) because it is the most commonly used and best understood metric of biodiversity, although other measures of diversity may be better predictors of net primary productivity (67–69). We extracted S at the fine spatial grain from the Forest Inventory and Analysis National Program (FIA) database v. 1.7.0 (70). We restricted our analysis to plots on forested land that were sampled using the national FIA design (plot design code 1) (71). All plots were surveyed between 1998 and 2016 and contain four circular 168 m^2 sub-plots with a total area of 0.067 ha in which all individuals larger than 12.7 cm diameter at 1.3 m were recorded and identified to species level. In total, our final dataset included 344 woody species and 93,771 plots. To estimate S at the intermediate and coarse spatial grains, we used data on the extant native species of trees for the contiguous USA provided in The Biota of North America Program's (BONAP) North American

Plant Atlas (72).

Taxonomic harmonization of species names. We cleaned scientific names from the FIA data and the BONAP data and harmonized them to accepted species based on The Plant List (73) and the Taxonomic Name Resolution Service (TNRS)(74), following the protocol described in (75). We included hybrid forms but excluded any names that could not be resolved to the species level.

Filtering of species occurrences. We restricted our analyses to woody species occurring in forest. To this end, we initially filtered the BONAP data to species classified as 'trees' in BONAP's taxonomic query database (72). We further filtered out 70 county-level occurrences of 5 non-woody species from the BONAP dataset. Species woodiness was inferred from woodiness data (76) and species lists of trees, shrubs and subshrubs (77), except for 37 species without such data for which we instead inferred woodiness from online searches or assumed resemblance among congeneric species. We also filtered out 8 FIA plot-level species occurrences and 1595 BONAP county-level species occurrences that we deemed unlikely to be forest occurrences, as inferred from independent species occurrences within forested pixels recorded in FIA plots and Global Biodiversity Information Facility (GBIF) point-occurrence records (Downloaded via https://www.gbif.org/ on 26th September 2016; doi:10.15468/dl.mka2y5; Supplementary Note). To make species richness data internally consistent across the different spatial grains, we added a further 6,593 quality-vetted county-level forest occurrences of woody species from FIA plot records to the 282,991 occurrences in the taxonomically harmonized BONAP dataset.

Net primary productivity (NPP). For a large subset of plots in the FIA database that have been measured at least twice (n = 46,211, on average plots remeasured every 5.8 years), we calculated tree productivity. This was measured as the change in tree C over time due to growth (gC m^{-2} y^{-1}), and is the sum of aboveground C increment of living trees between two measurements and conservatively excludes recruits and dead trees (67). Tree-level carbon was estimated by multiplying tree-level biomass (see below) by 0.48, but recognize that gymnosperms may have higher carbon content than that of

angiosperms (78). For plots with more than two inventories, tree productivity was calculated for each period and then averaged.

At intermediate and coarse spatial grains, we calculated NPP using the MODIS-derived MOD17 A3 product (79, 80), which gives annual values of NPP as gC m^{-2} yr^{-1} in 30 arc-sec pixels (roughly 1 km^2 around the equator). Here, NPP is defined as the annual sum of daily net photosynthesis minus the cost of growth and maintenance of living cells in permanent woody tissue. We averaged the annual values from 2000 to 2015 for each pixel, and then averaged these across the intermediate and coarse grains.

Biomass. At the fine scale, we estimated tree-level biomass using generalized biomass equations developed for North American tree species (81). For each plot we calculated aboveground biomass (Mg ha^{-1}) as the sum of individual biomass of living trees per hectare.

For the intermediate and coarse spatial grains we derived biomass values using a map of aboveground forest biomass of the USA, which is derived by modeling FIA plot biomass as a function of geospatial predictor variables (66). This data layer had a grain of 250 x 250 m^2, therefore, the average within each of the intermediate- and coarse-grain spatial units was taken.

Forest age and management. For each plot in the fine-scale dataset, we extracted forest age and management history from the FIA data set. Forest age is estimated using dendrochronological records (71). Management regime was a binary variable that indicated whether any forest management activity, e.g. harvest, thinning, tree planting, had been observed in any inventory or not.

At the intermediate and coarse grain, forest age was calculated as the average forest age from NASA NACP 1 km^2 resolution layer (82). Management regime at the intermediate and coarse grains was calculated as the proportion of managed FIA plots within all FIA plots that were within each spatial unit.

Climatic variables. For all grains, we used WorldClim (83) bioclimatic variables at 30 sec resolution. Many of the WorldClim variables are strongly collinear with one another, or with other variables in the

analysis (Table 1). Thus, only three variables that captured different aspects of the climate were selected; mean annual temperature (BIO1), mean precipitation (BIO12), and temperature seasonality (BIO4). At the fine scale, for each FIA plot we extracted the values of the 30 sec pixel in which the plot was found. For the intermediate and coarse grains, we averaged the values across all pixels within each spatial unit.

Elevation range. We used elevation range as a proxy for topographic and habitat heterogeneity, a variable that has been shown to be a good predictor of species richness (84). The USGS SRTM1 dataset (85) with 1 sec (approx. 30 x 30 m^2) resolution was used for all spatial grains. At the fine-scale, we calculated a 250 m diameter buffer around each FIA plot and calculated the elevation range using all 1 sec SRTM pixels within the buffer. At the intermediate and coarse scale, elevation range was calculated as the difference between the minimum and maximum elevation points within each spatial unit.

Species pools. We calculated regional species pools for each spatial grain as probabilistic dispersal pools (86). For each intermediate-grain spatial unit and each species in our data set, we first estimated the species' probability of being part of the unit's species pool as the joint probabilities that dispersal might happen between that unit and any of the species' intermediate-grain occurrences within the contiguous US. Due to insufficient data on species' dispersal abilities, we assumed that dispersal probability between focal units and species' occurrences would decay with great-circle distance between the respective regions' centroids. We explored five alternative exponential distance-decay functions, with scaling coefficients that determined the probability of a species occurring in neighboring units would disperse to the focal unit of 0.975, 0.95, 0.90, 0.80, and 0.60. We chose the function whose resulting species pool estimate most strongly correlated with species richness. Finally, we calculated species pools for each spatial unit as the sum of all species' individual probabilities of dispersal from any of their respective occurrences. For each coarse-grain unit, we summed the species' joint probabilities of dispersal between any of their intermediate-grain occurrences and any of the intermediate-grain units nested within the coarse unit. For fine-grain units, we assumed that their species pools would equal those of the intermediate-grain spatial units in which they were nested.

All of the variables used in our analyses are listed and summarized in Table 2.

Table 2. Overview of all variables used in the SEM and RFs.

Variable	Abbreviation	Units	The grain at which data are used	Source, reference, or link	Layer resolution, if applicable
Species richness	S	# of species	fine	FIA	
			intermediate, coarse	BONAP	
Net Primary Productivity	NPP	$gC/m^2/year$	fine	FIA	
			intermediate, coarse	MODIS (79)	1 km^2
Biomass	BIOMASS	Mg/ha	fine	FIA	
			intermediate, coarse	(66)	1 km^2
Forest age	AGE	years	fine	FIA	
		years	intermediate, coarse	NACP (81)	1 km^2
Management regime	MGMT	managed or not	fine	FIA	
		proportion of managed FIA plots	intermediate, coarse	FIA	
Mean annual precipitation	MAP	average mm/y	all grains	WorldClim	1 km^2
Mean annual temperature	MAT	average □/y	all grains	WorldClim	1 km^2
Temperature seasonality	TEMP.SEAS	standard deviation of monthly □ * 100	all grains	WorldClim	1 km^2
Elevation range (altitudinal span)	ELEV.RANGE	m	all grains	SRTM v 2.1	30 arc-sec
Size of species pool	S.POOL	# of species	all grains	FIA, GBIF, BONAP	

Stratified random sampling. Large areas of the contiguous US are environmentally homogeneous, while other parts are environmentally unique and small. We employed stratified random sampling (87) for the fine and intermediate spatial grains in order to (1) enhance environmental representativeness of the data, (2) prevent excessive statistical leverage of the large number of data points from homogeneous areas and

(3) reduce spatial pseudoreplication (autocorrelation) by increasing the geographic distance between data points. We first identified 11 strata at the fine and intermediate grains respectively, using multivariate regression trees with S, NPP and biomass as response variables and all covariates as predictors (Fig. 1). We then took a random and proportionally sized sample of spatial units from each strata (fine grain, N = 1,000; intermediate grain, N = 500). We did not use stratified random sampling at the coarse spatial grain because the number of spatial units was small (N = 98) and spatial autocorrelation was low. The spatial locations of the stratified samples are in Fig. S1. All of the analyses presented here, as well as our main conclusions, are based on these stratified sub-samples of the data.

Data transformation and standardization. Prior to analysis, species richness, biomass, NPP, and area were natural-log transformed.

Data Analyses

Two complementary statistical approaches were used. First, we fitted structural equation models (SEMs), which allow the assessment of indirect effects including feedback loops, address causality, and take into account potential collinearity among covariates (45, 46). The paths in our candidate SEMs were based on previous evidence of causal links between S, biomass, and NPP (Figure S2; 18). Second, to better understand the relative importance of each variable in explaining variation in the response variables within models, we fitted Random Forest models (RFs) (33). The results from SEMs provide insight into differences among models (i.e. between the two causal pathways per spatial grain, and among spatial grains), while results from RFs provide additional insights into the relative importance of different predictors variables within models.

Structural Equation Modelling (SEM). To test the relative importance of S on NPP ('S→NPP') and NPP on S ('NPP→S') we fitted two SEMs per spatial grain. For each SEM, we started with a 'saturated' model, which included the relationships between S, NPP, and biomass, and relationships of all additional covariates on S, NPP, and biomass (except for area at the fine spatial grain) (Figure S2). An effect of area

on NPP and biomass was included because in many models this proved necessary to obtain an accepted model. The S→NPP model evaluated how S directly affects NPP and how NPP indirectly affects S via biomass and, therefore, included a feedback loop. The NPP→S model tested the direct effect of NPP on richness and, unlike the S→NPP model, did not include a feedback loop. This way, we tested the direct effect of S on NPP (S→NPP model), the direct effect of NPP on S (NPP→S), and the indirect effect of NPP on S (included in both models).

To test the sensitivity of the relative importance of S on NPP to the direction of the relationships between S and biomass ('S → Biomass') or biomass and NPP ('Biomass → NPP', we fitted two additional SEMs per spatial grain as described above. The S → Biomass model evaluated how S directly affects NPP and biomass and how S indirectly affects biomass via NPP. The Biomass → NPP model tested the direct effect of S on NPP and the direct effect of biomass on S. Neither Biomass → NPP or S → Biomass models includes an indirect effect of NPP on S, as was the case for the S → NPP or NPP → models.

Model fit can only be tested on unsaturated models, i.e. those that have at least one missing path. Therefore, we removed the path with the lowest standardized path coefficient from the model. As SEMs had equal number of paths, we could compare model fit across all models within each spatial grain using their unadjusted R^2 values. After excluding the additional paths, path coefficients of S, NPP, and biomass remained qualitatively the same, and model fit to the data were still accepted (Chi-square test; $P>0.05$). This indicates that the models are identifiable and their results are robust. Therefore, we did not further reduce the model, and models maintained the same number of paths within each scale.

To assess the differences among scales in the relationships between S, NPP and biomass for each model, we compared the standardized regression coefficients using their 95% confidence intervals. All SEMs were fitted using the 'sem' function of the 'lavaan' package in R (88).

Random Forest models (RFs). To assess the relative importance of each variable in predicting the response variables within models, we used Random Forest models (RFs) (33, 89, 90). We used the

'randomForest' function in the R package 'randomForest', with all RF models produced using the default settings: 500 trees, one third of predictors sampled in each tree, sampling with replacement of the entire dataset, and terminal node size of 5.

At each of the three spatial grains we fitted two RFs, one with S as a response variable and the other with NPP as a response variable. All predictors that were used in the SEMs were used in the RF models (including biomass). To quantify the relative importance of each predictor, we calculated the mean decrease of squared error across all 500 trees using the function 'importance'. The importances were then scaled between 0 and 1, with 1 being the most important predictor. Using the function 'partialPlot', we extracted the partial responses of S and NPP to visualize the relationship between the two variables after accounting for all other covariates.

Reproducibility. All data on species richness, biomass, NPP, covariates, and R code used for the data processing and analyses are available on Figshare (DOI: 10.6084/m9.figshare.5948155) under a CC-BY license.

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Author contributions

Conceived project and designed research: DC, MvdS, KBM, JMB, JC, KG, DG, JH, FM, CM, PK.

Compiled data: DC, KG, CM, FM, PK. Analyzed data: MvdS, PK. Wrote the paper: All authors.

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