

A cross-scale assessment of productivity–diversity relationships

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Abstract

Aim: Biodiversity and ecosystem productivity vary across the globe, and considerable effort has been made to describe their relationships. Biodiversity and ecosystem functioning research has traditionally focused on how experimentally controlled species richness affects net primary productivity ($S \rightarrow NPP$) at small spatial grains. In contrast, the influence of productivity on richness ($NPP \rightarrow S$) has been explored at many grains in naturally assembled communities. Mismatches in spatial scale between approaches have fuelled debate about the strength and direction of biodiversity–productivity relationships. Here, we examine the direction and strength of the influence of productivity on diversity ($NPP \rightarrow S$) and the influence of diversity on productivity ($S \rightarrow NPP$) and how these vary across spatial grains.

Location: Contiguous USA.

Time period: 1999–2015.

Major taxa studied: Woody species (angiosperms and gymnosperms).

Methods: Using data from North American forests at grains from local (672 m^2) to coarse spatial units (median area = $35,677 \text{ km}^2$), we assess relationships between diversity and productivity using structural equation and random forest models, while accounting for variation in climate, environmental heterogeneity, management and forest age.

Results: We show that relationships between S and NPP strengthen with spatial grain. Within each grain, $S \rightarrow NPP$ and $NPP \rightarrow S$ have similar magnitudes, meaning that processes underlying $S \rightarrow NPP$ and $NPP \rightarrow S$ either operate simultaneously or that one of them is real and the other is an artefact. 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.

Main conclusions: We conclude that spatial grain mediates relationships between biodiversity and productivity in real-world ecosystems and that results supporting

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predictions from each approach ($NPP \rightarrow S$ and $S \rightarrow NPP$) serve as an impetus for future studies testing underlying mechanisms. Productivity–diversity relationships emerge at multiple spatial grains, which should widen the focus of national and global policy and research to larger spatial grains.

KEYWORDS

biodiversity–ecosystem function, biomass, climate, machine learning, more individuals hypothesis, spatial grain, species–energy relationship

1 | INTRODUCTION

One of the most prominent problems in ecology is how to describe relationships between biodiversity and ecosystem-level productivity (Adler et al., 2011; Balvanera et al., 2006; Cardinale et al., 2011, 2012; Currie, 1991; Hooper et al., 2012; Mittelbach et al., 2001; Naeem, Duffy, & Zavaleta, 2012; Rosenzweig, 1995; Tilman, Isbell, & Cowles, 2014). Two fields of research with different motives have tried to understand causality between these variables (Loreau et al., 2001). 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 (Adler et al., 2011; Connell & Orias, 1964; Currie, 1991; Fraser et al., 2015; Mittelbach et al., 2001; Rosenzweig, 1995; Waide et al., 1999). The second aims to quantify changes in vital ecosystem functions, such as productivity after anthropogenically induced changes in diversity (Cardinale et al., 2012; Isbell et al., 2017; Schulze & Mooney, 1993; Tilman, 1999). 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 (Grace et al., 2016), which is exacerbated by the differing spatial grains at which studies are conducted (Cardinale et al., 2011; Whittaker, 2010).

Recently, there has been growing interest in assessing biodiversity–ecosystem functioning (BEF) relationships in real-world, non-experimental ecosystems over large geographical extents, but probably owing to logistical constraints, relationships are typically measured at local spatial grains (Duffy, Godwin, & Cardinale, 2017; Liang et al., 2016; van der Plas, 2019). Results suggest that the positive effect of species richness on productivity and other ecosystem functions can be as important or more important than the effects of abiotic environmental drivers on productivity, suggesting that diversity–productivity relationships can be even stronger in real-world

communities than in controlled experiments (Duffy et al., 2017). However, to understand fully the influence of diversity on productivity, and vice versa, it is crucial to recognize that traditional bivariate analyses can underestimate the strength of these relationships by not accounting for the effects of spatial grain, in addition to those of biomass, shading, macroclimate and management (Cardinale, Hillebrand, Harpole, Gross, & Ptacnik, 2009; Grace et al., 2016; Loreau et al., 2001; Oberle, Grace, & Chase, 2009).

The striking mismatch between the spatial grains of BEF experiments (from square centimetres to square metres; Cardinale et al., 2011), observational studies of BEF (from 0.04 to 1.0 ha; Chisholm et al., 2013; Liang et al., 2016) and macroecological diversity–productivity correlations (from square metres to thousands of square kilometres; Adler et al., 2011; Field et al., 2009; Hawkins et al., 2003; Mittelbach et al., 2001) further obscures comparisons between perspectives. However, there is a diverse array of theoretical expectations for grain dependence of the effects of productivity on diversity ($NPP \rightarrow S$) and of diversity on productivity ($S \rightarrow NPP$), which predict effects either to strengthen or to weaken as the spatial grain increases (Table 1; Gonzalez et al., 2020). 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 $S \rightarrow NPP$ with increasing spatial grain. The effects of $NPP \rightarrow S$ 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 (Grace et al., 2016). These theoretical expectations have been supported by observational data for the effects of productivity on diversity (Belmaker & Jetz, 2011; Chase & Leibold, 2002; Mittelbach et al., 2001). In the case of BEF relationships (i.e., $S \rightarrow NPP$), there is also empirical and theoretical support for grain dependence, which comes from a

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 \rightarrow S and $S \rightarrow$ NPP	Spatially asynchronous demographic stochasticity impacts small populations (or small grains) and averages out over large grains	Both NPP \rightarrow S and $S \rightarrow$ NPP strengthen towards coarse grains	Lande, Engen, and Saether (2003)
II	NPP \rightarrow S	At larger grains, higher NPP is associated with increased heterogeneity and/or dissimilarity of local patches, allowing for greater regional coexistence	NPP \rightarrow S strengthens towards coarse grains	Abrams (1988), Chase and Leibold (2002), Wright, Currie, and Maurer (1993)
III	NPP \rightarrow S	A statistical interaction between NPP and grain in their effect on S emerges as a consequence of increasing occupancy with NPP	NPP \rightarrow S weakens towards coarse grains	Storch et al. (2005)
IV	NPP \rightarrow S	At very large grains (thousands of square kilometres and larger), high productivity increases occupancy and population size, thus increasing the probability of reproductive isolation and speciation	NPP \rightarrow S strengthens towards coarse grains	Jetz and Fine (2012)
V	$S \rightarrow$ NPP	Stochastic sampling effects dominate at small grains, resource partitioning at larger grains ("spatial insurance"), and their relative magnitude determines the grain dependence	Both strengthening and weakening possible	Cardinale, Ives, and Inchausti (2004), Loreau, Mouquet, and Gonzalez (2003)
VI	$S \rightarrow$ NPP	Functionally redundant species at intermediate or coarse grains can compensate for low richness at local grains	$S \rightarrow$ NPP strengthens towards coarse grains	Srivastava and Vellend (2005)
VII	$S \rightarrow$ NPP	With incomplete compositional turnover, 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	$S \rightarrow$ NPP strengthens towards coarse grains until species richness saturates	Thompson, Isbell, Loreau, O'Connor, and Gonzalez (2018)

restricted range of small spatial grains (Chalcraft, 2013; Hao, Zhang, Zhao, & von Gadow, 2018; Luo, Liang, Gatti, Zhao, & Zhang, 2019).

Here, we aim to address the dual nature by which productivity influences diversity (NPP \rightarrow S) and diversity influences productivity ($S \rightarrow$ NPP) across spatial grains by combining structural equation models (SEMs) and random forest models (RFs) to account explicitly for the bidirectionality of NPP \rightarrow S and $S \rightarrow$ NPP. Using SEMs, we propose and test hypothesis-based models (Supporting Information Figure S1) that estimate the direction and strength of NPP \rightarrow S and $S \rightarrow$ NPP. Next, we use RFs, an assumption-free machine learning approach (Breiman, 2001; Hastie, Tibshirani, & Friedman, 2009), 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 m²; n = 46,211

plots), medium (median area = 1,386 km²; n = 1,956 spatial units) and coarse spatial grains (median area = 35,677 km²; 98 spatial units). We specifically ask whether the influence of productivity on diversity (NPP \rightarrow S) was stronger or weaker than the influence of diversity on productivity ($S \rightarrow$ NPP) and how these relationships manifest across grains in real-world ecosystems.

2 | METHODS

2.1 | Data

2.1.1 | Geographical extent and grain

We conducted analyses across the contiguous USA at three spatial grains (Figure 1): (a) fine grain (46,211 plots, 672 m² or 0.000672 km² each); (b) intermediate grain (1,956 units, median 1,386 km²) created

by aggregating U.S. counties to larger units based on the forested area within them (see “Spatial aggregation algorithm” below); and (c) coarse grain (95 units, median 35,677 km²) created by aggregating the intermediate-grain units further. 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 km² pixel with non-zero forest biomass, following Blackard et al. (2008).

2.1.2 | 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 might be better predictors of net primary productivity (Cadotte, 2015; Paquette & Messier, 2011; Venail et al., 2015). We extracted S at the fine spatial grain from the Forest Inventory and Analysis National Program (FIA) database v.1.7.0 (USDA Forest Service, 2017). We restricted our analysis to plots on forested land that were sampled using the national FIA design (plot design code 1; Burrill et al., 2018). All plots were surveyed between 1998 and 2016, each consisting of four circular 168 m² subplots with a total area of 672 m² in which all individuals larger than 12.7 cm diameter at 1.3 m were recorded and

identified to species level. For each plot, we pooled data from all subplots to estimate S. In total, our final dataset included 344 woody species and 93,771 plots. We estimated S at the intermediate and coarse spatial grains by counting the number of unique woody species in each spatial unit using data for the contiguous USA provided in The Biota of North America Program's (BONAP) North American Plant Atlas (Kartesz, 2015).

2.1.3 | Taxonomic harmonization of species names

We cleaned scientific names from the FIA and BONAP datasets and harmonized them to accepted species based on The Plant List (2013) and the Taxonomic Name Resolution Service (2018), following the protocol described by Meyer, Weigelt, and Kreft (2016). We included hybrid forms but excluded any names that could not be resolved to the species level.

2.1.4 | Filtering of species occurrences

We restricted our analyses to tree species that are likely to occur in forests. At the fine spatial grain, we included native and alien species. At the intermediate and coarse spatial grains, however, we

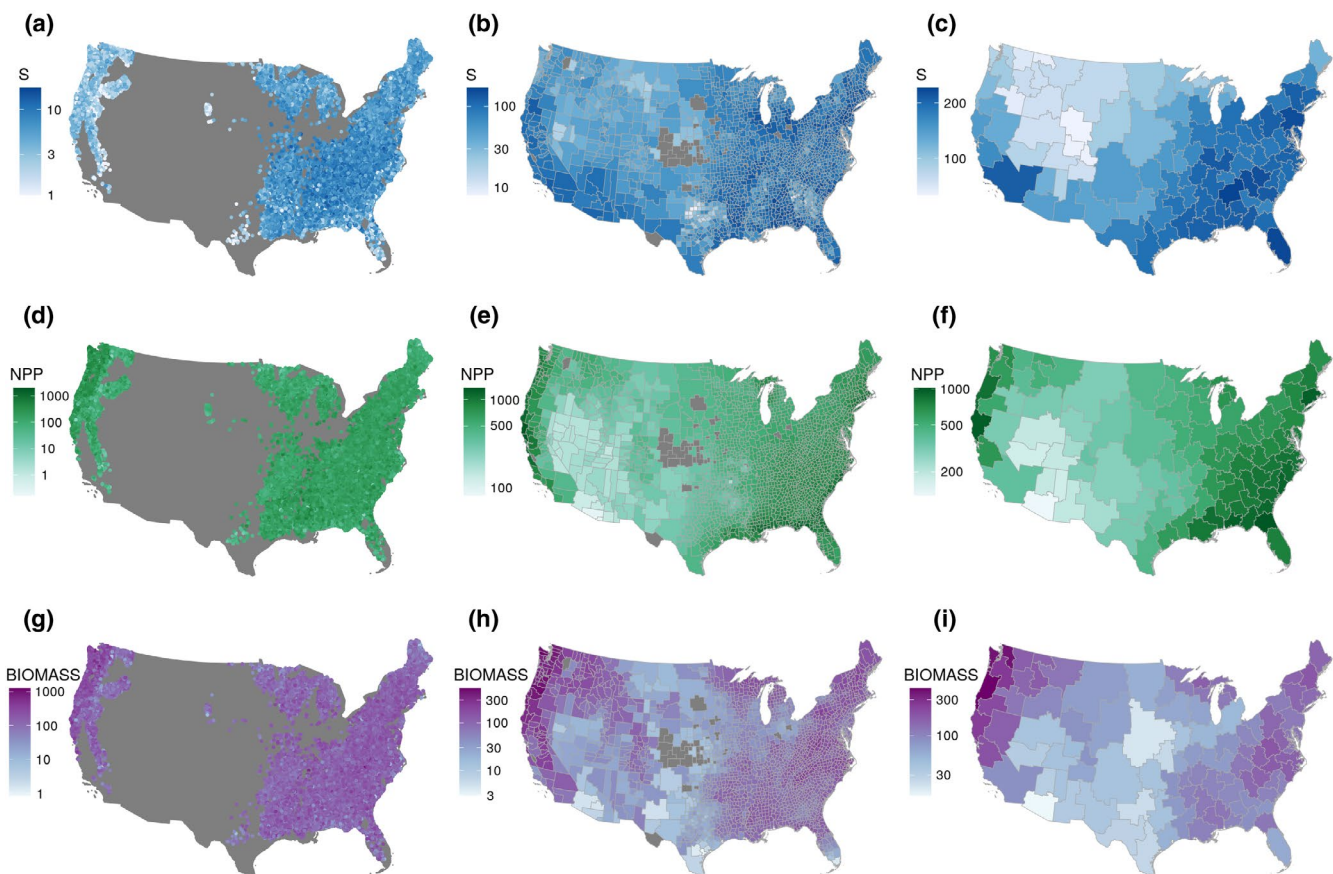


FIGURE 1 Maps of species richness (S), MODIS-derived net primary productivity (NPP; in grams of carbon per square metre per year) and biomass (in megagrams per hectare) of forests at three spatial grains across the contiguous USA. The values in all plots are on a log₁₀ scale [Colour figure can be viewed at wileyonlinelibrary.com]

excluded alien species because we could not be certain whether they occurred in forests because many are cultivated, particularly in urban ecosystems (Kowarik, 2008; Pearse et al., 2018). We therefore filtered the BONAP data to native species classified as “trees” in the BONAP taxonomic query database (Kartesz, 2015). We further filtered out 70 county-level occurrences of five non-woody species from the BONAP dataset. Species woodiness was inferred from woodiness data (Zanne et al., 2014) and species lists of trees, shrubs and subshrubs (USDA NRCS, 2018), except for 37 species without such data, for which we inferred woodiness from online searches or assumed resemblance among congeneric species. We also filtered out eight FIA plot-level species occurrences and 1,595 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 26 September 2016; <https://doi.org/10.15468/dl.mka2y5>; Supporting Information Supplementary Note 1). 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.

2.1.5 | Net primary productivity (NPP)

At all spatial grains, we calculated NPP using MODIS-derived estimates, which we supplemented further with plot-derived estimates at the fine spatial grain. Briefly, we calculated NPP using the MODIS-derived MOD17 A3 product (Zhao, Heinsch, Nemani, & Running, 2005; Zhao & Running, 2010), which gives annual values of NPP as grams of carbon per square metre per year in 30 arc-s pixels (c. 1 km² 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, then averaged these across the intermediate and coarse grains. We use MODIS-derived NPP in the analyses presented in the main text to ensure comparability across spatial grains.

At the fine spatial grain, we also estimated NPP using plot-derived data. For a large subset of plots in the FIA database that have been measured at least twice between 1999 and 2015 ($n = 46,211$, on average plots re-measured every 5.8 years), we calculated net annual net aboveground carbon change (in grams of carbon per square metre per year). This was measured as the net change in aboveground tree carbon between two measurements as the sum of aboveground carbon growth of living trees, ingrowth by recruitment and loss from tree mortality (NPP_{mort}; Chen & Luo, 2015). Tree-level carbon was estimated by multiplying tree-level biomass (see next subsection) by .48, but we recognize that

gymnosperms might have higher carbon content than angiosperms (Thomas & Martin, 2012). For plots with more than two inventories, tree productivity was calculated for each period and then averaged. NPP_{mort} was weakly correlated with MODIS-derived NPP at the fine spatial grain ($r = .19$), suggesting that it might capture different processes. Therefore, we provide the analyses using the plot-derived NPP at the fine spatial grain in the Supporting Information. Results concerning the strength of the S–NPP relationship were qualitatively similar for both NPP measures.

2.1.6 | Biomass (BIOMASS)

At all spatial grains, we derived biomass values using a map of aboveground forest biomass of the USA, which is derived by modelling FIA plot biomass as a function of geospatial predictor variables (Blackard et al., 2008). This data layer had a grain of 250 m × 250 m² therefore, the average within each of the intermediate- and coarse-grain spatial units was taken.

For analyses using plot-derived NPP, we estimated tree-level biomass at the fine spatial grain using generalized biomass equations developed for North American tree species (Chojnacky, Heath, & Jenkins, 2013). For each FIA plot, we calculated aboveground biomass (in megagrams per hectare) as the sum of the individual biomass of living trees per hectare.

2.1.7 | Number of trees (N)

At the fine scale, we estimated the number of trees directly from each FIA plot. For the intermediate and coarse spatial grains, we estimated the number of trees using a global map of tree density (Crowther et al., 2015). Given that the grain of the data layer was 1 km × 1 km, average tree density was calculated within each spatial unit at the intermediate and coarse spatial grains.

2.1.8 | Forest age (AGE) and management (MANAGED)

For each plot in the fine-scale dataset, we extracted forest age and management history from the FIA dataset. Forest age was estimated using dendrochronological records (Burrill et al., 2018). Management regimen 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 km² resolution layer (Pan et al., 2012). Management regimen 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.

2.1.9 | Climatic variables

For all grains, we used WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) bioclimatic variables at 30 s resolution. Many of the WorldClim variables are strongly collinear with one another or with other variables in the analysis (Supporting Information Table S1; Figure S1). Thus, only three variables that captured different aspects of the climate were selected: mean annual temperature (BIO1; ANN.TEMP), mean precipitation (BIO12; ANN.PREC) and temperature seasonality (BIO4; TEMP.SEAS). At the fine scale, for each FIA plot we extracted the values of the 30 s pixel in which the plot was found. For the intermediate and coarse grains, we averaged the values across all pixels within each spatial unit.

2.1.10 | Elevation range (ELEV.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 (Stein, Gerstner, & Kreft, 2014). The USGS SRTM1 dataset (USGS, 2009) with 1 s (c. 30 m × 30 m) 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 s SRTM pixels within the buffer. At the intermediate and coarse scales, elevation range was calculated as the difference between the minimum and maximum elevation points within each spatial unit.

2.1.11 | Species pools (S.POOL)

We calculated regional species pools for each spatial grain as probabilistic dispersal pools (Karger et al., 2016). For each intermediate-grain spatial unit and each species in our dataset, we first estimated the probability of the species being part of the species pool in the unit as the joint probabilities that dispersal might happen between that unit and any of the intermediate-grain occurrences of the species within the contiguous USA. Owing to insufficient data on the dispersal abilities of species, we assumed that dispersal probability between focal units and occurrences of species would decay with great-circle distance between the centroids of the respective regions. We explored five alternative exponential distance-decay functions, with scaling coefficients that determined the probability that a species occurring in neighbouring units would disperse to the focal unit of .975, .95, .90, .80 and .60. We chose the function with $p = .8$, which exhibited the strongest correlation between species pool and species richness at all spatial grains (Supporting Information Figure S2). Finally, we calculated species pools for each spatial unit as the sum of the individual probabilities for all species of dispersal from any of their respective occurrences. For each coarse-grain unit, we summed the joint probabilities of the species 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 the Supporting Information (Table S1) and visualized in the Supporting Information (Figure S1).

2.1.12 | Spatial aggregation algorithm

Given that U.S. counties vary dramatically in their area (Supporting Information Figure S3), from Falls Church (VA) at 5.1 km² to San Bernardino (CA) at 52,109 km², it is difficult to assign one categorical grain size to county-level data. Thus, we aggregated county data for species richness to create new spatial units, with the goal of minimizing variation in forested area (A) between spatial units. We achieved this using a greedy algorithm that worked as follows:

1. Calculate variance (V_1) of forested area (A) across all counties.
2. Randomly select a focal county with a probability proportional to $1/\sqrt{A+1}$, which will most probably select counties with small A.
3. Randomly choose a county adjacent to the focal county and merge it with the focal county.
4. Update the variance (V_2) of forested area across all spatial units in the USA and compare it with the original variance V_1 .

If the $V_2 < V_1$, the algorithm accepts the merged unit and returns to step one. If the variance does not decrease, the algorithm repeats step 3 until $V_2 < V_1$, with a 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 returns to step one. The algorithm started with 3,107 counties, and we first terminated it when 1,956 merged spatial units were created. We classified these spatial units as the intermediate spatial grain (Figure 1). We then allowed the algorithm to continue until it reached 98 merged spatial units, which we classified as the coarse spatial grain (Figure 1). Although the algorithm substantially reduced variation in area within both spatial grains (Supporting Information Figure S3), it did not eliminate the variation entirely. For this reason, we used area as a covariate in the statistical analyses at the intermediate and coarse spatial grains.

2.1.13 | Stratified random sampling

Large areas of the contiguous USA are environmentally homogeneous, whereas other parts are environmentally unique and small. We used stratified random sampling (Cochran, 1977) for the fine and intermediate spatial grains in order to (a) enhance environmental representativeness of the data, (b) prevent excessive statistical leverage of the large number of data points from homogeneous areas, and (c) reduce spatial pseudoreplication (autocorrelation) by increasing the geographical 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 (Figure 1). We then took a random and proportionally sized sample of spatial units from each of the strata (fine grain, $n = 1,000$; intermediate grain, $n = 500$). We did not use stratified random sampling at the coarse spatial grain because of the small number of spatial units ($n = 98$). The spatial locations of the stratified samples are in the Supporting Information (Figure S4). All the analyses presented here, in addition to our main conclusions, are based on these stratified subsamples of the data.

2.1.14 | Data transformation and standardization

Before analysis, species richness, biomass, N , NPP and area were natural log-transformed to meet normality assumptions of the standardized major-axis regressions and SEMs.

2.2 | Data analyses

We quantified simple bivariate relationships between diversity and productivity for each spatial grain using standardized major-axis regression with the “sma” function in the R package “smatr” (Warton, Duursma, Falster, & Taskinen, 2012). We then used two

complementary statistical approaches to assess the impacts of diversity and productivity and vice versa while simultaneously accounting for covariates that influence both.

First, we fitted SEMs, which allow the assessment of indirect effects, including feedback loops, address causality and take into account potential collinearity among covariates (Grace, Anderson, Olf, & Scheiner, 2010; Shipley, 2016). The paths in our candidate SEMs were based on previous evidence of causal links between S , biomass and NPP (Figure 2; Grace et al., 2016). Second, to gain a better understanding of the relative importance of each variable in explaining variation in the response variables within models, we fitted random forest models (RFs) (Hastie et al., 2009). The results from SEMs provide insight into differences among models (i.e., between the two causal pathways per spatial grain, and among spatial grains), whereas results from RFs provide additional insights into the relative importance of different predictor variables within models.

2.2.1 | Structural equation modelling

To test the relative importance of $S \rightarrow \text{NPP}$ and $\text{NPP} \rightarrow S$, we fitted two SEMs per spatial grain. For each SEM, we started with a “saturated” model, which included the relationships between S , NPP

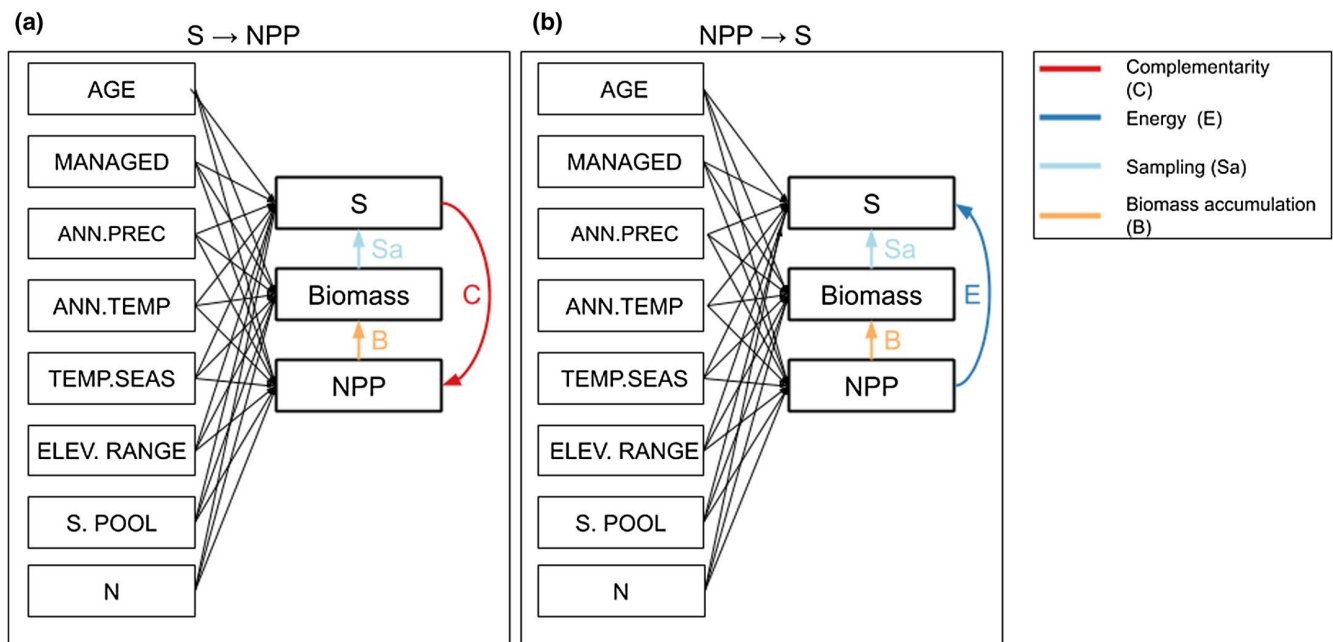


FIGURE 2 Hypothetical causal models for structural equation models (SEMs) testing the relative importance of species richness (S) on net primary productivity (NPP; $S \rightarrow \text{NPP}$; a) and NPP on S ($\text{NPP} \rightarrow S$; b) in forests across the contiguous USA at three spatial grains. Paths in colour represent possible ecological mechanisms influencing the direction of the relationship; red paths represent complementarity effects (c), dark blue paths represent “species–energy” relationships (e), light blue paths represent sampling (or niche) effects (Sa) and orange paths represent biomass accumulation (B). Black paths are relationships of additional covariates with S , NPP and BIOMASS and are not hypothesized to occur in a particular direction. AGE is forest age, ANN.PREC is mean annual precipitation, ANN.TEMP is mean annual temperature, ELEV.RANGE is elevation range, MANAGED is forest management, N is the number of individuals, S.POOL is the regional species pool, and TEMP.SEAS is temperature seasonality. At the intermediate and coarse spatial grains, we added AREA to the SEMs to account for differences in the area of spatial units. S , BIOMASS, NPP and AREA were natural logarithmically transformed before analysis [Colour figure can be viewed at wileyonlinelibrary.com]

and biomass, and relationships of all additional covariates on S , NPP and biomass (except for area at the fine spatial grain) (Figure 2). The $S \rightarrow$ NPP model evaluated how S directly affects NPP and how NPP indirectly affects S via biomass and, therefore, included a feedback loop. The NPP \rightarrow S model tested the direct effect of NPP on richness and, unlike the $S \rightarrow$ NPP model, did not include a feedback loop. This way, we tested the direct effect of S on NPP ($S \rightarrow$ NPP model), the direct effect of NPP on S (NPP \rightarrow S) and the indirect effect of NPP on S (included in both models).

Model fit can be tested only 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. Given that SEMs had an 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 fits to the data were still accepted (chi-square test; $p > .05$). This indicates that the models are identifiable and their results robust. Therefore, we did not reduce the model further, and models maintained the same number of paths within each scale. Given that models at the fine spatial grain including the number of individuals (N) did not fit the data well ($p < .05$), we excluded this variable. Models at the intermediate and coarse spatial grains including N fitted the data well ($p > .05$), but we present models without N for consistency with the fine spatial grain and because the sampling effects captured by N are also captured by area.

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 (Rosseel, 2012).

2.2.2 | Random forest models

To assess the relative importance of each variable in predicting the response variables within models, we used RFs (Breiman, 2001; Hastie et al., 2009; Liaw & Wiener, 2002). We used the "randomForest" function in the R package "randomForest", with all RFs 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 five.

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 RFs (including biomass). To quantify the relative importance of each predictor, we calculated the mean decrease of squared error across all 500 trees using the "importance" function. The importance values were then scaled between zero and one, with one 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.

2.2.3 | Nonlinear responses and spatial autocorrelation

Structural equation models offer the advantage of modelling complex, causal relationships (Grace et al., 2010; Shipley, 2016), but they can be difficult to fit to data with nonlinear responses or spatial pseudoreplication. Although it is possible to model nonlinearity in SEMs (e.g., using polynomials; Grace et al., 2010; Shipley, 2016), this often comes at the cost of interpretability. A similar problem applies when it comes to another prevalent problem of observational geographical data: spatial autocorrelation, which statistical models have so far addressed by modelling it either in residuals or in the response (Dormann et al., 2007). However, because of the causal loop in the SEMs (Figure 2), the key response variables are also predictors, which prevented us from estimating spatial autocorrelation. In our analyses, we account for these issues in the following manner:

1. In the SEM analyses, we keep the relationships linear, given the approximately linear pairwise relationships between the raw NPP, S and biomass data (Supporting Information Figures S5–S7).
2. In the SEM analyses, we do not model spatial autocorrelation directly.
3. We address spatial autocorrelation in the random forest analysis by allowing the algorithm to model smooth geographical trends in the response (by including the X and Y spatial coordinates as predictors), and we measure spatial autocorrelation in the response and in residuals.
4. We allow the random forest analysis to detect nonlinear responses.

2.2.4 | Reproducibility

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

3 | 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 (Figure 1). Biomass, a time-integrated measure of NPP that also influences diversity, also exhibited similar patterns (Figure 1). Bivariate relationships between S and NPP exhibited scale dependence (Figure 3). Although not significantly correlated at the fine spatial grain (standardized major-axis regression: $R^2 = .00$, $p = .73$), S and NPP were significantly correlated at the intermediate (standardized major-axis regression: $R^2 = .15$, $p < .001$) and coarse (standardized major axis-regression: $R^2 = .35$, $p < .001$) spatial grains. The slope of S -NPP increased from 0.86 (95% confidence intervals: 0.80, 0.94) at the intermediate spatial

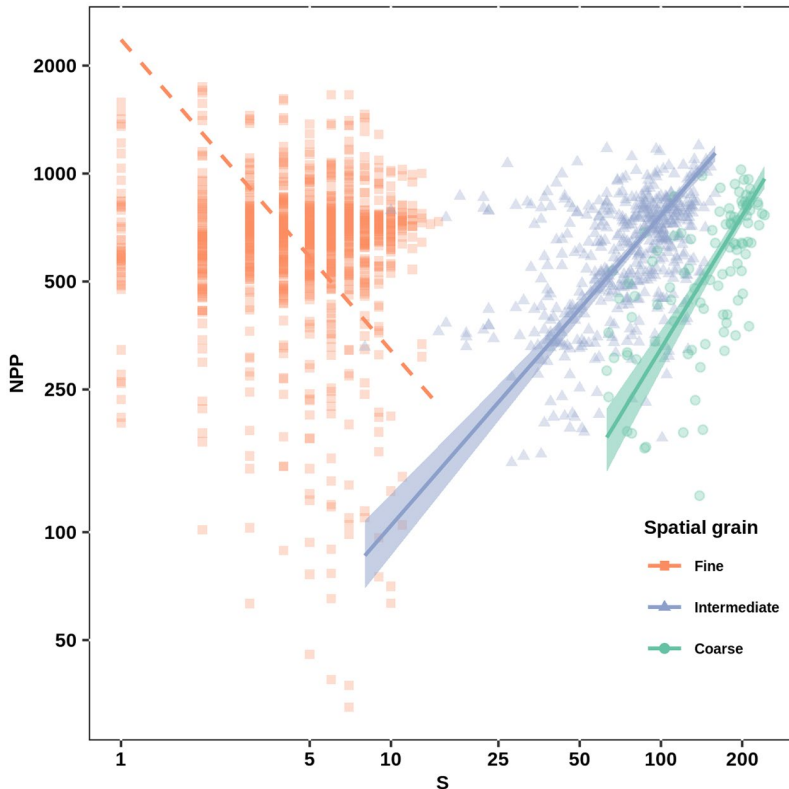


FIGURE 3 Bivariate relationships between observed species richness (S) and net primary productivity (NPP) of forests at three spatial grains across the contiguous USA. Continuous lines are standardized major-axis regressions fitted at each spatial grain with statistically significant slopes ($p < .05$), and dashed lines are standardized major-axis regressions with non-significant slopes ($p > .05$). Shaded areas are 95% confidence intervals. NPP is MODIS derived at all spatial grains. Note that axes are on the natural logarithmic scale. Analyses were performed using stratified random samples of 1,000, 500 and 98 spatial units at the fine, intermediate and coarse spatial grains, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

grain to 1.23 (95% confidence intervals: 1.05, 1.45) at the coarse spatial grain. Similar patterns were observed when using plot-derived estimates of NPP at the fine spatial grain (Supporting Information Figure S8).

3.1 | Structural equation models

We examined relationships between species richness and NPP across spatial grains using two SEMs for each spatial grain: the first ($S \rightarrow \text{NPP}$) testing the direct effect of S on NPP and the indirect effect of NPP on S (via biomass), and the second ($\text{NPP} \rightarrow S$) testing both the direct and indirect effects of NPP on S (Figure 4). In both SEMs, environmental variables (e.g., mean annual precipitation, mean annual temperature, 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 the area (of each spatial unit) to account for variation in species richness attributable to sampling effects.

Both models fitted the data well for all spatial grains (p -value of the chi-square test $> .1$; Supporting Information Table S2). 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. The R^2 values for both SEMs increased with spatial grain, from .21 at the fine grain to .56 at the intermediate grain and 0.85 at the

coarse grain. Generally, the strengths of effects of $S \rightarrow \text{NPP}$ and $\text{NPP} \rightarrow S$ were similar within each spatial grain, but both increased in strength with increasing spatial grain (Figures 4 and 5). At the fine spatial grain, we did not find a detectable direct effect of $S \rightarrow \text{NPP}$ (Figure 4a) or $\text{NPP} \rightarrow S$ (Figure 4d), and found effectively a null indirect effect of NPP on S via biomass (standardized path coefficient of indirect effect = -0.002 ; Figure 4a). At the intermediate spatial grain, we found a direct effect of S on NPP (standardized path coefficient of direct effect = 0.11, Figures 4b and 5) of similar strength to NPP on S (standardized path coefficient of direct effect = 0.24; Figures 4e and 5) and weak indirect effects of NPP on S via biomass (standardized path coefficient of indirect effect = 0.04; Figure 4b). Likewise, at the coarse spatial grain we found strong direct effects of S on NPP (0.42; Figures 4c and 5) and of NPP on S (0.47; Figures 4f and 5) and weak indirect effects of NPP on S via biomass (standardized path coefficient of indirect effect = 0.08; Figure 4c).

Overall, the SEMs suggest that the productivity–diversity relationship increases in strength with spatial grain, and both relationships ($S \rightarrow \text{NPP}$ and $\text{NPP} \rightarrow S$) explain similar amounts of variation. At all spatial grains, our SEMs do not conclusively show stronger support for one direction of causality over the other. Similar patterns were observed when using plot-derived estimates of NPP (Supporting Information Figure S9; Table S2), except for the direction of direct effects of S on NPP and NPP on S , which was negative.

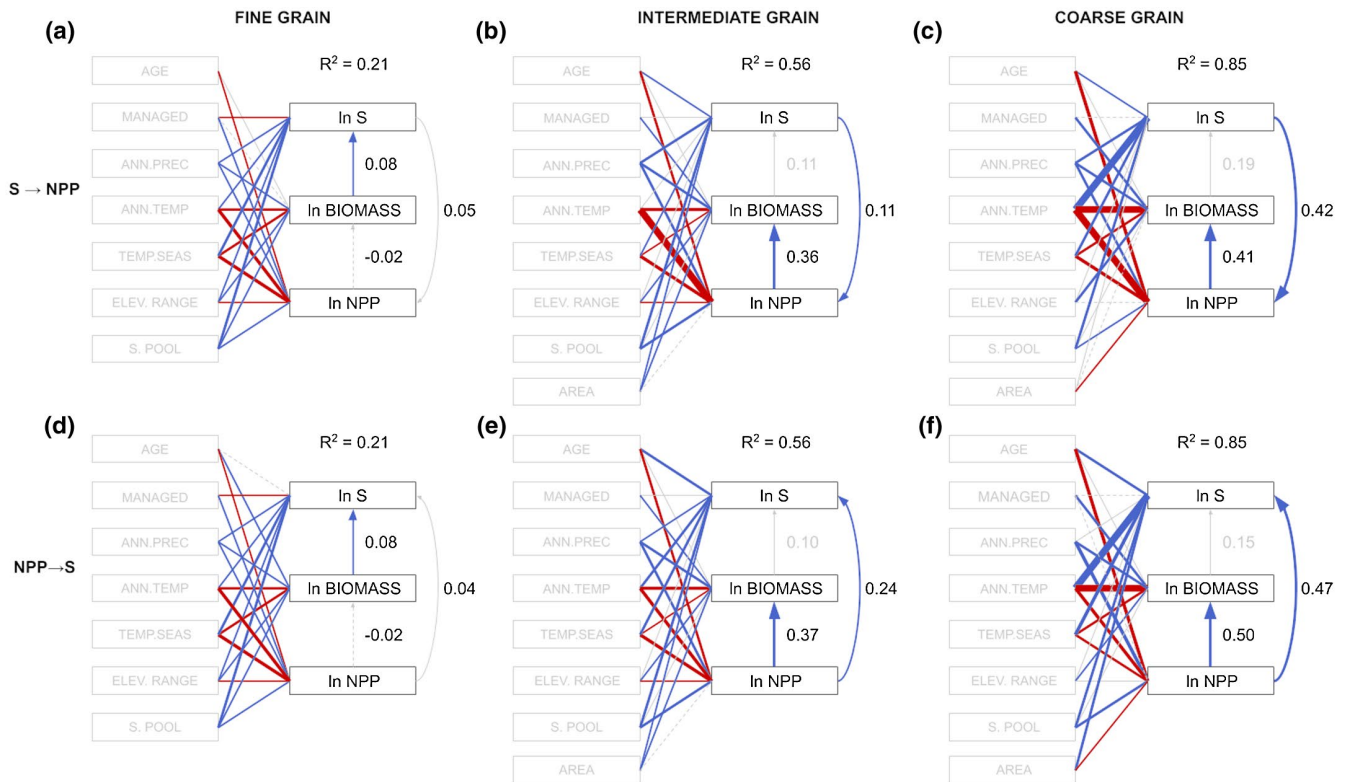


FIGURE 4 Structural equation models (SEMs) testing the influence of diversity (S) on net primary productivity (NPP; $S \rightarrow$ NPP; a–c) and that of NPP on S (NPP \rightarrow S; d–f), after controlling for environmental variables (e.g., mean annual precipitation, mean annual temperature, temperature seasonality and elevation range), size of the species pool, forest age and management, in forests across the contiguous USA at three spatial grains. All models fitted the data well at all spatial grains (p -value of the chi-square test $>.1$; Supporting Information Table S1). Boxes represent measured variables and arrows represent relationships among variables. Continuous blue and red arrows represent significant ($p < .05$) positive and negative standardized path coefficients, respectively, and their width is scaled by the corresponding standardized path coefficient. Continuous and dashed grey arrows represent non-significant ($p > .05$) positive and negative standardized path coefficients, respectively. R^2 is the average of R^2 values for S , BIOMASS and NPP. NPP is MODIS derived at all spatial grains. AGE is forest age, ANN.PREC is mean annual precipitation, ANN.TEMP is mean annual temperature, AREA is area, ELEV.RANGE is elevation range, MANAGED is forest management, S.POOL is the regional species pool, and TEMP.SEAS is temperature seasonality. S , BIOMASS, NPP and AREA were natural logarithmically transformed before analysis [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Random forest models

To assess the relative importance of each predictor of species richness and NPP and to provide an assumption-free alternative to the SEMs that also accounts for spatial autocorrelation, we fitted two RFs for each of the three spatial grains: one with NPP and the other with S as the response variable. We found that species richness was one of the weakest predictors of NPP relative to other predictors at all spatial grains (Figure 6a), with management, forest age, MAP and biomass being the most important predictors (Figure 6a). The overall explained variation of NPP also increased from the fine to the two coarser spatial grains, from .64 at the fine spatial grain to .89 at the intermediate spatial grain and .88 at the coarse spatial grain.

We found that NPP was an important predictor of S (with a positive effect) only at the intermediate spatial grain (Figure 6b) but was less important relative to other predictors at fine and coarse spatial grains. For S , we found that species pool, mean

annual temperature and precipitation, and forest age were the best predictors, and their importance increased towards coarse spatial grains (Figure 6). In line with the SEM analyses, the overall explained variation of S increased towards coarse spatial grains, from .39 at the fine grain to .55 at the intermediate grain and .87 at the coarse grain (for predicted versus observed values, see Supporting Information Figure S10).

In all RF analyses, there is a clear east–west spatial component in both S and NPP (represented by the X coordinate in Figure 6), which was not explained by any of the other predictors. This spatial component was stronger for NPP than for S . Residual autocorrelation in all of the RFs was negligible (Supporting Information Figure S11). Finally, we also fitted all the RFs with local plot-derived measures of productivity (as an alternative to the MODIS-derived productivity used in the main analyses), showing that the strengths of the S –NPP relationships were similar across all NPP measures (Supporting Information Figure S12).

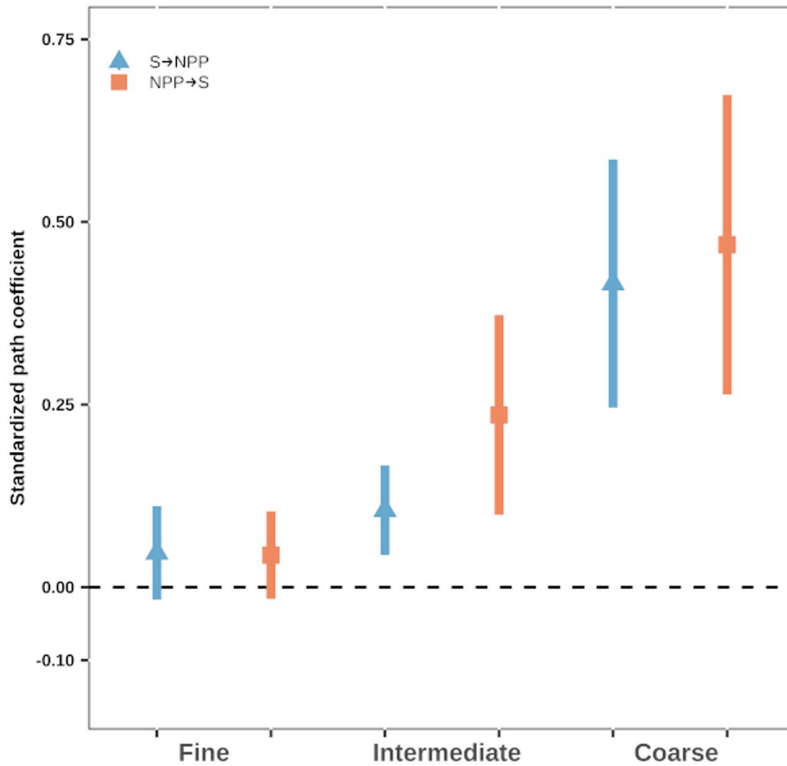


FIGURE 5 Direct effects of diversity on net primary productivity ($S \rightarrow \text{NPP}$) and productivity on diversity ($\text{NPP} \rightarrow S$) estimated with structural equation models (SEMs) in forests across the contiguous USA at three spatial grains. Points are standardized path coefficients and continuous lines are 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

The first important result is the similar magnitude of the $S \rightarrow \text{NPP}$ (Grace et al., 2016) and $\text{NPP} \rightarrow S$ (Hawkins et al., 2003; Mittelbach et al., 2001; Šimová et al., 2011) relationships at all grains. This reflects, in part, that both productivity and species richness have many environmental and geographical drivers in common (Lavers & Field, 2006), which complicates distinguishing correlation from causation, even when using SEMs (Grace et al., 2010; Shipley, 2016). There are two possible interpretations of this result. It might indicate that the causal effects of diversity on productivity and the causal effects of productivity on diversity operate simultaneously, which was suggested by Grace et al. (2016) but never demonstrated on observational data from large spatial grains. Alternatively, if only one direction of the diversity–productivity relationship is real and causal, it might be possible to fit another model assuming the opposite direction because of multicollinearity in the data or non-identifiability of the causal direction (Petersen & van der Laan, 2014). Without large-grain experiments that manipulate diversity in ways that mimic biodiversity change (i.e., species gains and losses) in real-world ecosystems (Gonzalez et al., 2020; Hillebrand et al., 2018; Loreau et al., 2001; Manning et al., 2019; Wardle, 2016), we see little hope for resolving this with contemporary data and approaches.

Our second important result is that both $S \rightarrow \text{NPP}$ and $\text{NPP} \rightarrow S$ strengthen from the fine to the intermediate grain, and in the case of the SEM both relationships continue strengthening towards the coarsest grain. Although grain-dependent shifts are often expected (Table 1), this had not been shown previously with empirical data for $S \rightarrow \text{NPP}$ using spatial grains coarser than several

hectares (Chisholm et al., 2013; Hao et al., 2018; Luo et al., 2019). If the $S \rightarrow \text{NPP}$ direction is the causal direction, 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 (Isbell et al., 2018). If the $\text{NPP} \rightarrow S$ direction is the causal direction, then our results are in line with Lavers and Field (2006) and Field et al. (2009) but contrast with Storch, Evans, and Gaston (2005) and Belmaker and Jetz (2011), particularly when scaling up from the fine grain to intermediate grain, where both the SEM and RF analyses give congruent results. Intriguingly, a third possibility is that both $\text{NPP} \rightarrow S$ and $S \rightarrow \text{NPP}$ are real and that they operate simultaneously. 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 Table 1), which might weaken both $\text{NPP} \rightarrow S$ and $S \rightarrow \text{NPP}$, 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 (672 m^2) 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 (Dornelas et al., 2014; Magurran et al., 2018) might have under-appreciated effects on ecosystem function (Bannar-Martin et al., 2018).

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

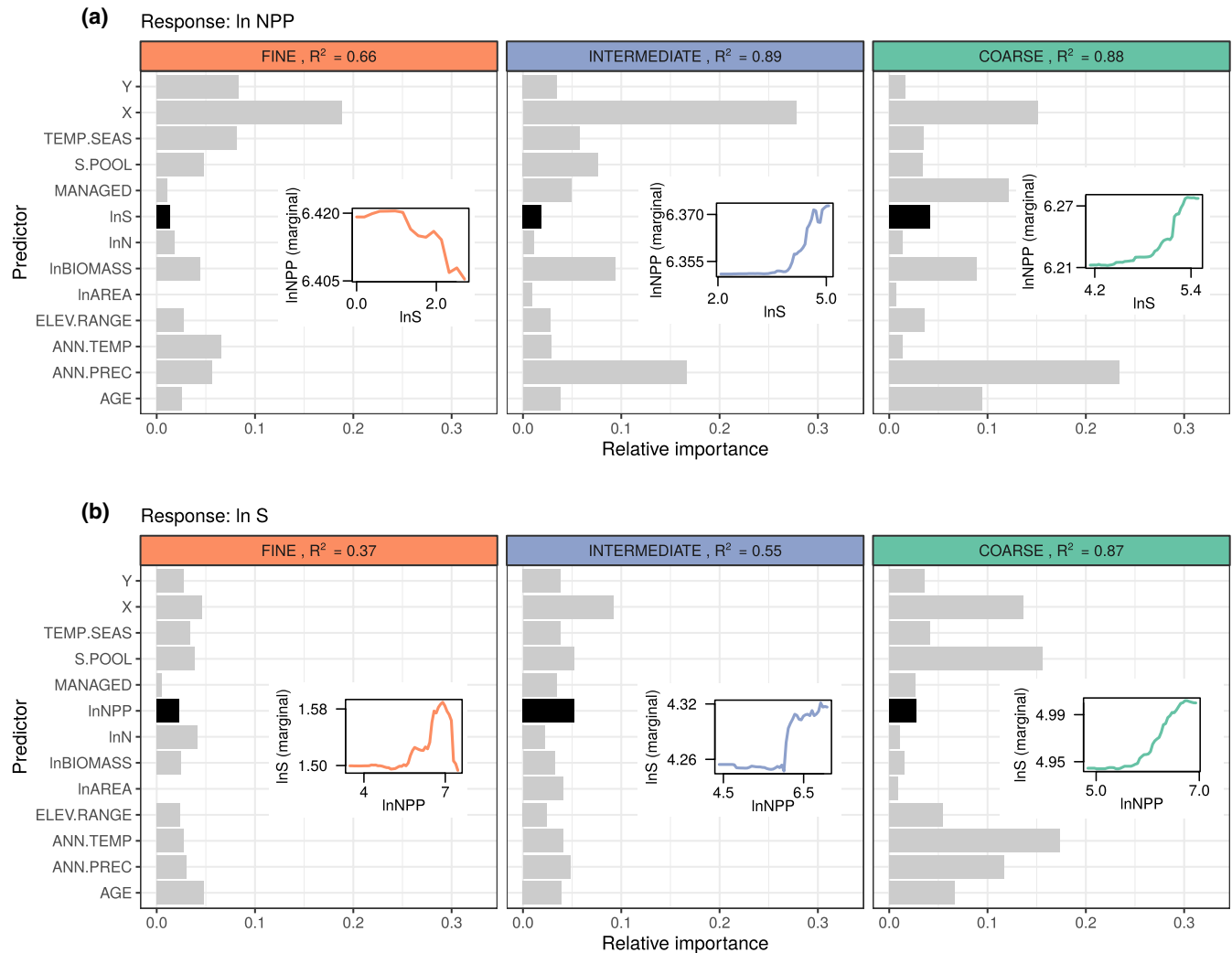


FIGURE 6 Relative variable importance from random forest models explaining (a) MODIS-derived net primary productivity (NPP) and (b) species richness (S) at three spatial grains. Relative variable importance is the mean decrease in squared error caused by each of the variables, rescaled such that it sums up to the total pseudo- R^2 of the whole random forest model. The curves in the insets show shapes of the marginal responses of In NPP or In S after accounting for all the covariates. AGE is forest age, ANN.PREC is mean annual precipitation, ANN.TEMP is mean annual temperature, ELEV.RANGE is elevation range, InAREA is area of the spatial unit, InBIOMASS is biomass, InN is the number of individuals, InNPP is MODIS-derived NPP, MANAGED is forest management, S.POOL is the regional species pool, TEMP.SEAS is temperature seasonality, and Y and X are latitudinal and longitudinal coordinates of the U.S. National Atlas projection. For explanation of variables, see the Supporting Information (Table S1) [Colour figure can be viewed at wileyonlinelibrary.com]

coupled with a clear increase in the combined effect of annual temperature and precipitation on both S and NPP towards coarse grains, which supports the notion that temperature-dependent diversification (Allen, Brown, & Gillooly, 2002; Rohde, 1992), niche conservatism (Qian & Ricklefs, 2016) or ecological limits (Šímová et al., 2011) shape diversity at these spatial grains. The weaker (relatively to temperature) effect of precipitation is expected because we focus on forests, which only grow above certain precipitation thresholds (Whittaker, 1975). The clear importance of temperature, biomass, longitude and other predictors, such as forest age, temperature seasonality or species pool (Figures 4 and 6), highlights that even when the $NPP \rightarrow S$ relationship holds across grains, other drivers are considerably more important in predicting both (e.g., Ratcliffe et al., 2017). Hence, integration of the environmental context

surrounding ecological communities into modelling 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 might provide insight into observed patterns of either direction, despite initially being formulated at a different spatial grain. For example, the strong effect of the east–west spatial coordinate on both S and NPP at the fine spatial grain (Figure 6) suggests that biogeographical history might play a role in shaping the diversity and ecosystem functioning of plant communities, which was initially tested at larger spatial grains (e.g., Conradi, Meerbeek, Ordonez, & Svenning, 2020; Hawkins, Rodríguez, & Weller, 2011). Increasingly, macroecological

mechanisms, such as speciation gradients (Schluter & Pennell, 2017) and water–energy variables, are being examined in small-grain experimental grasslands to explore their role in mediating niche-based processes (Zupping-Dingley et al., 2014) and biodiversity effects (Wagg et al., 2017), respectively. Likewise, efforts to scale up the effects of biodiversity on productivity, developed initially to identify local-scale mechanisms (Loreau & Hector, 2001; Turnbull, Isbell, Purves, Loreau, & Hector, 2016), might identify new mechanisms that underpin spatial variation in ecosystem functioning at large spatial scales (Gonzalez et al., 2020). An emerging challenge to these efforts is the creation of data products that capture similar processes across spatial scales and are independent (Supporting Information Supplemental Note 2; Table S3); many of the variables used in the present study share similar data sources (e.g. MODIS and LANDSAT sensors) but are ultimately derived from different types of intermediate products. Rather than focusing uniquely on the direction and strength of S –NPP after accounting for other factors, our results show that mechanisms associated with $S \rightarrow$ NPP and NPP \rightarrow S are likely to underpin the context dependence 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 only beginning (Craven et al., 2019). Nevertheless, 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 BEF theory and some (but not all) expectations from macroecological studies on NPP \rightarrow S and highlights the potential of demographic stochasticity and sampling effects to distort or mask diversity–productivity relationships at fine grains. Moreover, we found similar support for both directions of diversity–productivity relationships across spatial grains, but could not distinguish between causation and correlation because productivity and species richness share many environmental and geographical drivers. Future research on this relationship needs to move from fine-grain experiments and observational studies to coarse grains in order to understand fully and predict the impacts of anthropogenic biodiversity change on ecosystem function.

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DATA AVAILABILITY STATEMENT

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

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BIOSKETCH

The authors are a group of (mostly) early career researchers united by their interest in ecological synthesis, in areas ranging from macroecology to experimental ecology, ecological theory and ecological modelling.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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