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A cross-scale assessment of productivity-diversity relationships

Running title: Cross-scale diversity-productivity

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Acknowledgments

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 modeling.

Data accessibility statement

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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Abstract

Aim: 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 ($S \rightarrow NPP$) 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 fostered debate about the strength and direction of biodiversity-productivity relationships. Here we examine the direction and strength of productivity's influence on diversity ($NPP \rightarrow S$) and of diversity's influence on productivity ($S \rightarrow NPP$), and how this varies 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 = $35,677$ 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 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.

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

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76   (NPP→S and S→NPP) serve as an impetus for future studies testing underlying mechanisms.

77   Productivity-diversity relationships emerge at multiple spatial grains, which should widen the focus of

78   national and global policy and research to larger spatial grains.

79   **Keywords:** spatial grain, biomass, biodiversity-ecosystem function, climate, machine learning, species-
80   energy

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Introduction

One of the most prominent questions in ecology is how to describe relationships between biodiversity and

ecosystem-level productivity (Currie, 1991; Rosenzweig, 1995; Mittelbach *et al.,* 2001; Balvanera *et al.,*

2006; Adler *et al.,* 2011; Cardinale *et al.,* 2011, 2012; Hooper *et al.,* 2012; Naeem *et al.,* 2012; Tilman *et*

al., 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 (Connell & Orias, 1964; Currie, 1991; Rosenzweig, 1995; Waide *et al.,* 1999; Mittelbach *et al.,*

2001; Adler *et al.,* 2011; Fraser *et al.,* 2015). The second aims to quantify changes in vital ecosystem

functions such as productivity following anthropogenically-induced changes in diversity (Schulze &

Mooney, 1993; Tilman, 1999; Cardinale *et al.,* 2012; Isbell *et al.,* 2017). 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 differing

spatial grains at which studies are conducted (Whittaker, 2010; Cardinale *et al.,* 2011).

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 (Liang *et al.,* 2016; Duffy

et al., 2017; van der Plas, 2019). 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 (Duffy *et al.,* 2017). 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 (Loreau

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121 *et al.,* 2001; Cardinale *et al.,* 2009; Oberle *et al.,* 2009; Grace *et al.,* 2016).

122 The striking mismatch between the spatial grains of BEF experiments (cm2 to m2; Cardinale *et al.,* 2011),

123 observational studies of BEF (0.04 to1.0 ha; Chisholm *et al.,* 2013; Liang *et al.,* 2016), and

124 macroecological diversity-productivity correlations (m2 to thousands of km2; Mittelbach *et al.,* 2001;

125 Hawkins *et al.,* 2003; Field *et al.,* 2009; Adler *et al.,* 2011) further obscures comparisons between

126 perspectives. However, there is a diverse array of theoretical expectations for grain dependency of the

127 effects of productivity on diversity (NPP→S) and of diversity on productivity (S→NPP), which predict

128 effects to either strengthen or weaken as the spatial grain increases (Table 1; Gonzalez *et al.,* 2020). For

129 example, spatial turnover of species that are functionally equivalent within the regional grain can offset

130 low species richness at local grains, resulting in a strengthening of S→NPP with increasing spatial grain.

131 The effects of NPP→S are also hypothesized to increase with spatial grain, because higher NPP is

132 associated with greater heterogeneity at larger spatial grains, which enhances coexistence of more species

133 at the regional grain. Moreover, other components of a community, such as biomass, can mediate

134 relationships between productivity and diversity via their effects on competitive dominance (Grace *et al.,*

135 2016). These theoretical expectations have been supported by observational data for the effects of

136 productivity on diversity (Mittelbach *et al.,* 2001; Chase & Leibold, 2002; Belmaker & Jetz, 2011). In the

137 case of BEF relationships (i.e. S→NPP), there is also empirical and theoretical support for grain

138 dependence, which comes from a restricted range of small spatial grains (Luo *et al.*; Chalcraft, 2013; Hao

139 *et al.,* 2018).

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145   **Table. 1** Overview of hypotheses predicting grain dependence of relationships between net primary
146   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	(Lande *et al.*, 2003)
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	(Abrams, 1988; Wright *et al.*, 1993; Chase & Leibold, 2002)
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	(Storch *et al.*, 2005)
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	(Jetz & Fine, 2012)
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	(Loreau *et al.*, 2003; Cardinale *et al.*, 2004)
VI	S→NPP	Functionally redundant species at intermediate or coarse grains can compensate for low richness at local grains.	S→NPP strengthens towards coarse grains	(Srivastava & Vellend, 2005)
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	(Thompson *et al.*, 2018)

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148   Here, we aim to address the dual nature by which productivity influences diversity (NPP→S) and

149   diversity influences productivity (S→NPP) across spatial grains by combining structural equation models

150   (SEM) and random forest models (RFs) to explicitly account for the bidirectionality of NPP→S and

151   S→NPP. Using SEM, we propose and test hypothesis-based models (Fig. S1) that estimate the direction

152   and strength of NPP→S and S→NPP. Next, we use RFs, an assumption-free machine learning approach

153   (Breiman, 2001; Hastie *et al.*, 2009), to quantify the relative importance of predictors of species richness

154   and productivity. We examine both hypothesized directions of the relationship, along with a number of

155   important covariates that influence both diversity and productivity, such as biomass, precipitation,

156   temperature, and forest age, using a comprehensive observational dataset of North American forests at

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157   fine (area = 672 m^2; n = 46,211 plots), medium (median area = 1,386 km^2; n = 1,956 spatial units), and

158   coarse spatial grains (median area = 35,677 km^2; 98 spatial units). We specifically ask whether the

159   influence of productivity on diversity (NPP→S) was stronger or weaker than the influence of diversity on

160   productivity (S→NPP), and how these relationships manifest across grains in real-world ecosystems.

161   **Methods**

162   **Data**

163   **Geographic extent and grain.** We conducted analyses across the contiguous USA at three spatial grains

164   (Fig. 1): (1) fine grain (46,211 plots, 672 m^2 or 0.000672 km^2 each), (2) intermediate grain (1,956 units,

165   median 1,386 km^2) created by aggregating US counties to larger units based on the forested area within

166   them (see 'spatial aggregation algorithm' below), and (3) coarse grain (95 units, median 35,677 km^2)

167   created by further aggregating the intermediate grain units. We restricted our analyses to forested areas to

168   make comparisons within and among spatial grains in similar ecosystems. For the intermediate and coarse

169   grains, we defined an area as forested if it fell into a 1 km^2 pixel with non-zero forest biomass following

170   Blackard *et al.* (2008).

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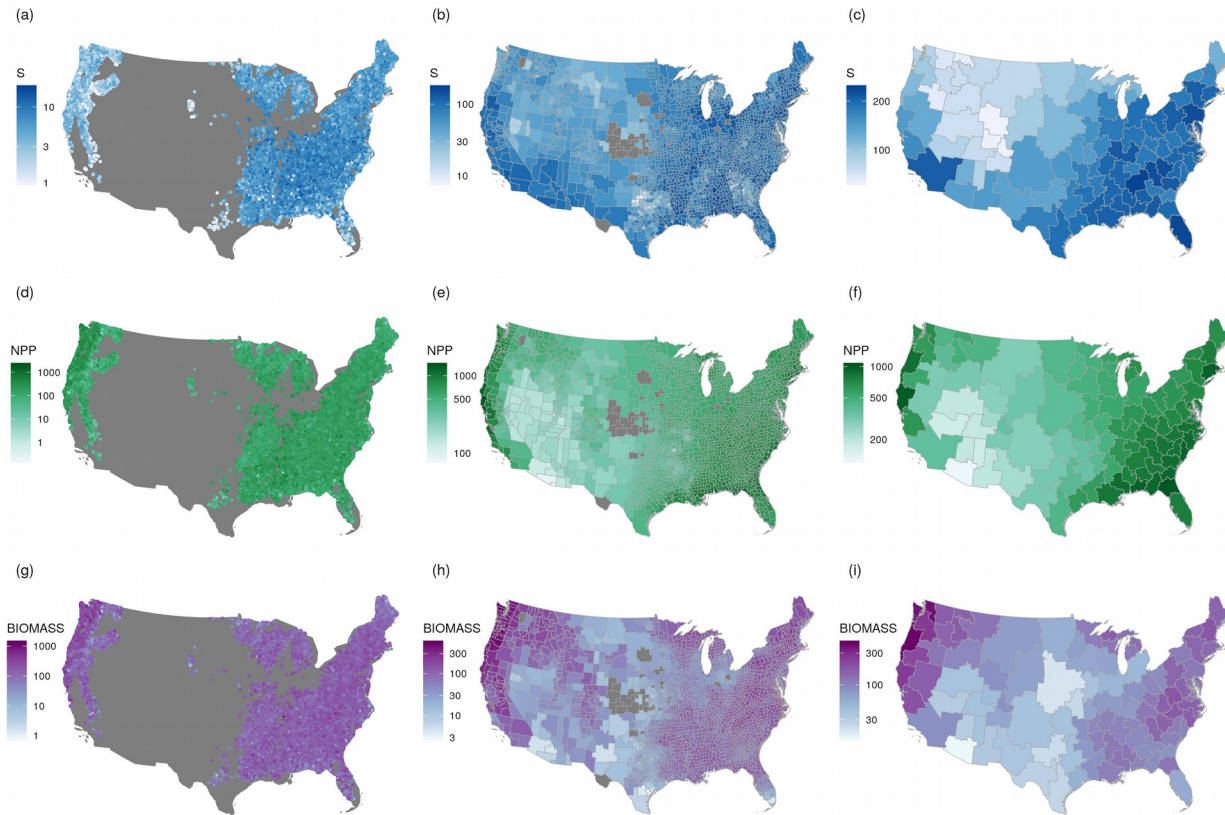
Fig.1. Maps of species richness (S), MODIS-derived net primary productivity (NPP) [gC/m^2/year], and biomass [Mg/ha] of forests at three spatial grains across the contiguous USA. The values in all plots are on log$_{10}$ scale.

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 (Paquette & Messier, 2011; Cadotte, 2015; 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 m^2 sub-plots with a total area of 672 m^2 ha 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

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186 contiguous USA provided in The Biota of North America Program's (BONAP) North American Plant

187 Atlas (Kartesz, 2015).

188 **Taxonomic harmonization of species names.** We cleaned scientific names from the FIA and BONAP

189 datasets and harmonized them to accepted species based on The Plant List (2013) and the Taxonomic

190 Name Resolution Service (2018), following the protocol described in Meyer et al. (2016). We included

191 hybrid forms, but excluded any names that could not be resolved to the species level.

192 **Filtering of species occurrences.** We restricted our analyses to tree species that likely occur in forests.

193 At the fine spatial grain, we included native and alien species. At the intermediate and coarse spatial

194 grains, however, we excluded alien species because we could not be certain if they occurred in forests as

195 many are cultivated, particularly in urban ecosystems (Kowarik, 2008; Pearse *et al.,* 2018). We therefore

196 filtered the BONAP data to native species classified as 'trees' in BONAP's taxonomic query database

197 (Kartesz, 2015). We further filtered out 70 county-level occurrences of 5 non-woody species from the

198 BONAP dataset. Species woodiness was inferred from woodiness data (Zanne *et al.,* 2013) and species

199 lists of trees, shrubs and subshrubs (USDA NRCS, 2018), except for 37 species without such data for

200 which we instead inferred woodiness from online searches or assumed resemblance among congeneric

201 species. We also filtered out 8 FIA plot-level species occurrences and 1,595 BONAP county-level species

202 occurrences that we deemed unlikely to be forest occurrences, as inferred from independent species

203 occurrences within forested pixels recorded in FIA plots and Global Biodiversity Information Facility

204 (GBIF) point-occurrence records (Downloaded via https://www.gbif.org/ on 26th September 2016;

205 doi:10.15468/dl.mka2y5; Supplementary Note 1). To make species richness data internally consistent

206 across the different spatial grains, we added a further 6,593 quality-vetted county-level forest occurrences

207 of woody species from FIA plot records to the 282,991 occurrences in the taxonomically harmonized

208 BONAP dataset.

209 **Net primary productivity (NPP).** At all spatial grains, we calculated NPP using MODIS-derived

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210   estimates, which we further supplemented with plot-derived estimates at the fine spatial grain. Briefly, we

211   calculated NPP using the MODIS-derived MOD17 A3 product (Zhao *et al.*, 2005; Zhao & Running,

212   2010), which gives annual values of NPP as gC m^{-2} yr^{-1} in 30 arc-sec pixels (roughly 1 km^2 around the

213   equator). Here, NPP is defined as the annual sum of daily net photosynthesis minus the cost of growth

214   and maintenance of living cells in permanent woody tissue. We averaged the annual values from 2000 to

215   2015 for each pixel, and then averaged these across the intermediate and coarse grains. We use MODIS-

216   derived NPP in the analyses presented in the main text to ensure comparability across spatial grains.

217   At the fine spatial grain, we also estimated NPP using plot-derived data. For a large subset of plots in the

218   FIA database that have been measured at least twice between 1999 and 2015 (n = 46,211, on average

219   plots re-measured every 5.8 years), we calculated net annual net aboveground C change (gC m^{-2} y^{-1}). This

220   was measured as the net change in aboveground tree C between two measurements as the sum of

221   aboveground C growth of living trees, ingrowth by recruitment, and loss from tree mortality (NPPmort;

222   Chen & Luo, 2015). Tree-level carbon was estimated by multiplying tree-level biomass (see below) by

223   0.48, but we recognize that gymnosperms may have higher carbon content than that of angiosperms

224   (Thomas & Martin, 2012). For plots with more than two inventories, tree productivity was calculated for

225   each period and then averaged. NPPmort was weakly correlated with MODIS-derived NPP at the fine

226   spatial grain ($r = 0.19$), suggesting that it may capture different processes. Therefore, we provide the

227   analyses using the plot-derived NPP at the fine spatial grain in the Supplementary Information.

228   Importantly, results concerning the strength of the S-NPP relationship were qualitatively similar for both

229   NPP measures.

230   **Biomass (BIOMASS).** At all spatial grains, we derived biomass values using a map of aboveground

231   forest biomass of the USA, which is derived by modeling FIA plot biomass as a function of geospatial

232   predictor variables (Blackard *et al.*, 2008). This data layer had a grain of 250 x 250 m^2, therefore, the

233   average within each of the intermediate- and coarse-grain spatial units was taken.

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234   For analyses using plot-derived NPP, we estimated tree-level biomass at the fine spatial grain using

235   generalized biomass equations developed for North American tree species (Chojnacky *et al.*, 2013). For

236   each FIA plot we calculated aboveground biomass (Mg ha^{-1}) as the sum of individual biomass of living

237   trees per hectare.

238   **Number of trees (N).** At the fine scale, we estimated the number of trees directly from each FIA plot. For

239   the intermediate and coarse spatial grains, we estimated the number of trees using a global map of tree

240   density (Crowther *et al.*, 2015). As the grain of the data layer was 1 x 1 km^2, average tree density was

241   calculated within each spatial unit at the intermediate and coarse spatial grains.

242   **Forest age (AGE) and management (MANAGED).** For each plot in the fine-scale dataset, we

243   extracted forest age and management history from the FIA data set. Forest age is estimated using

244   dendrochronological records (Burrill *et al.*, 2018). Management regime was a binary variable that

245   indicated whether any forest management activity, e.g. harvest, thinning, tree planting, had been observed

246   in any inventory or not.

247   At the intermediate and coarse grain, forest age was calculated as the average forest age from NASA

248   NACP 1 km^2 resolution layer (Pan *et al.*, 2012). Management regime at the intermediate and coarse grains

249   was calculated as the proportion of managed FIA plots within all FIA plots that were within each spatial

250   unit.

251   **Climatic variables.** For all grains, we used WorldClim (Hijmans *et al.*, 2005) bioclimatic variables at 30

252   sec resolution. Many of the WorldClim variables are strongly collinear with one another, or with other

253   variables in the analysis (Table S1, Fig. S1). Thus, only three variables that captured different aspects of

254   the climate were selected; mean annual temperature (BIO1; ANN.TEMP), mean precipitation (BIO12;

255   ANN.PREC), and temperature seasonality (BIO4; TEMP.SEAS). At the fine scale, for each FIA plot we

256   extracted the values of the 30 sec pixel in which the plot was found. For the intermediate and coarse

257   grains, we averaged the values across all pixels within each spatial unit.

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258   **Elevation range (ELEV.RANGE).** We used elevation range as a proxy for topographic and habitat

259   heterogeneity, a variable that has been shown to be a good predictor of species richness (Stein *et al.*,

260   2014). The USGS SRTM1 dataset (USGS, 2009) with 1 sec (approx. 30 x 30 m^2) resolution was used for

261   all spatial grains. At the fine-scale, we calculated a 250 m diameter buffer around each FIA plot and

262   calculated the elevation range using all 1 sec SRTM pixels within the buffer. At the intermediate and

263   coarse scale, elevation range was calculated as the difference between the minimum and maximum

264   elevation points within each spatial unit.

265   **Species pools (S.POOL).** We calculated regional species pools for each spatial grain as probabilistic

266   dispersal pools (Karger *et al.*, 2016). For each intermediate-grain spatial unit and each species in our data

267   set, we first estimated the species' probability of being part of the unit's species pool as the joint

268   probabilities that dispersal might happen between that unit and any of the species' intermediate-grain

269   occurrences within the contiguous US. Due to insufficient data on species' dispersal abilities, we assumed

270   that dispersal probability between focal units and species' occurrences would decay with great-circle

271   distance between the respective regions' centroids. We explored five alternative exponential distance-

272   decay functions, with scaling coefficients P that determined the probability of a species occurring in

273   neighboring units would disperse to the focal unit of 0.975, 0.95, 0.90, 0.80, and 0.60. We chose the

274   function with $P = 0.8$, which exhibited the strongest correlation between species pool and species richness

275   at all spatial grains (Fig. S2). Finally, we calculated species pools for each spatial unit as the sum of all

276   species' individual probabilities of dispersal from any of their respective occurrences. For each coarse-

277   grain unit, we summed the species' joint probabilities of dispersal between any of their intermediate-grain

278   occurrences and any of the intermediate-grain units nested within the coarse unit. For fine-grain units, we

279   assumed that their species pools would equal those of the intermediate-grain spatial units in which they

280   were nested.

281   All of the variables used in our analyses are listed and summarized in Table S1 and visualized in Fig. S1.

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282 **Spatial aggregation algorithm.** Because US counties vary dramatically in their area (Fig. S3), from Falls

283 Church (VA) being as small as 5.1 km^2, to San Bernardino (CA) with 52,109 km^2, it is difficult to assign

284 one categorical grain size to county-level data. Thus, we aggregated county data for species richness to

285 create new spatial units, with the goal to minimize variation in forested area (A) between spatial units. We

286 achieved this using a greedy algorithm which worked as follows: (1) Calculate variance (V_1) of forested

287 area (A) across all counties. (2) Randomly select a focal county with a probability proportional to $1/\sqrt{\square}$,

288 which will most likely select counties with small A. (3) Randomly choose a county adjacent to the focal

289 county and merge it with the focal county. (4) Update the variance (V_2) of forested area across all spatial

290 units in the USA and compare it to the original variance V_1. If the $V_2 < V_1$, the algorithm accepts the

291 merged unit and returns to step one. If the variance does not decrease, the algorithm repeats step 3 until

292 $V_2 < V_1$, with the maximum number of attempts of 1,000. If the variance still does not decrease even after

293 1,000 attempts, the algorithm rejects the merge, and returns to step one. The algorithm started with 3,107

294 counties, and we first terminated it when 1,956 merged spatial units were created. We classified these

295 spatial units as the intermediate spatial grain (Fig. 1). We then allowed the algorithm to continue until it

296 reached 98 merged spatial units, which we classified as the coarse spatial grain (Fig. 1). Although the

297 algorithm substantially reduced variation in area within both spatial grains (Fig. S3), it did not eliminate

298 the variation entirely. For this reason, we used area as a covariate in the statistical analyses at the

299 intermediate and coarse spatial grains.

300
301 **Stratified random sampling.** Large areas of the contiguous US are environmentally homogeneous, while

302 other parts are environmentally unique and small. We employed stratified random sampling (Cochran,

303 1977) for the fine and intermediate spatial grains in order to (1) enhance environmental representativeness

304 of the data, (2) prevent excessive statistical leverage of the large number of data points from

305 homogeneous areas and (3) reduce spatial pseudoreplication (autocorrelation) by increasing the

306 geographic distance between data points. We first identified 11 strata at the fine and intermediate grains

307 respectively, using multivariate regression trees with S, NPP and biomass as response variables and all

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308   covariates as predictors (Fig. 1). We then took a random and proportionally sized sample of spatial units

309   from each strata (fine grain, N = 1,000; intermediate grain, N = 500). We did not use stratified random

310   sampling at the coarse spatial grain because of the small number of spatial units (N = 98). The spatial

311   locations of the stratified samples are in Fig. S4. All of the analyses presented here, as well as our main

312   conclusions, are based on these stratified sub-samples of the data.

313   **Data transformation and standardization.** Prior to analysis, species richness, biomass, N, NPP, and

314   area were natural-log transformed to meet normality assumptions of the standardised major-axis

315   regressions and SEMs.

316   # Data Analyses

317   We quantified simple bivariate relationships between diversity and productivity for each spatial grain

318   using standardised major-axis regression with the 'sma' function in the R package 'smatr' (Warton *et al.*,

319   2012). We then used two complementary statistical approaches to assess the impacts of diversity and

320   productivity and vice versa while simultaneously accounting for covariates that influence both.

321   First, we fitted structural equation models (SEMs), which allow the assessment of indirect effects

322   including feedback loops, address causality, and take into account potential collinearity among covariates

323   (Grace *et al.*, 2010; Shipley, 2016). The paths in our candidate SEMs were based on previous evidence of

324   causal links between S, biomass, and NPP (Fig. 2; Grace *et al.*, 2016). Second, to better understand the

325   relative importance of each variable in explaining variation in the response variables within models, we

326   fitted random forest models (RFs) (Hastie *et al.*, 2009). The results from SEMs provide insight into

327   differences among models (i.e. between the two causal pathways per spatial grain, and among spatial

328   grains), while results from RFs provide additional insights into the relative importance of different

329   predictors variables within models.

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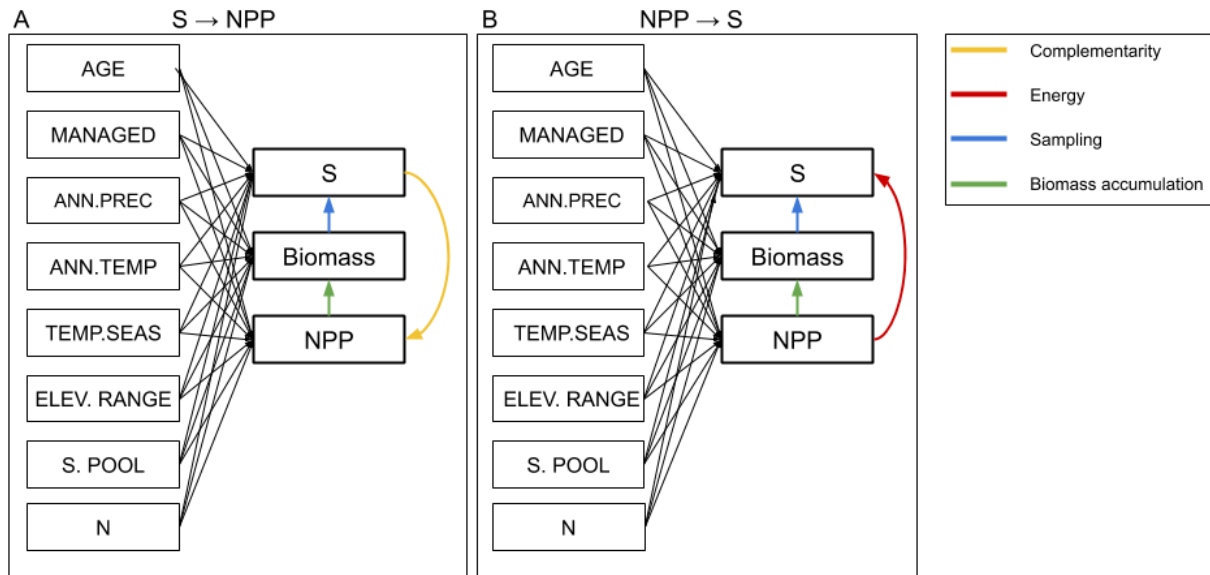
330
331 **Fig. 2.** Hypothetical causal models for structural equation models (SEM) testing the relative importance
332 of species richness (S) on net primary productivity (NPP) ('S→NPP'; A) and NPP on S ('NPP→S'; B) in
333 forests across the contiguous USA at three spatial grains. Paths in color represent possible ecological
334 mechanisms influencing the direction of the relationship; yellow paths represent complementarity effects,
335 red paths represent 'species-energy' relationships, blue paths represent sampling (or niche) effects and
336 green paths represent biomass accumulation. Black paths are relationships of additional covariates with S,
337 NPP, and BIOMASS and are not hypothesized to occur in a particular direction. AGE is forest age,
338 MANAGED is forest management, ANN.PREC is mean annual precipitation, ANN.TEMP is mean
339 annual temperature, TEMP.SEAS is temperature seasonality, ELEV.RANGE is elevation range, S.POOL
340 is the regional species pool, and N is the number of individuals. At the intermediate and coarse spatial
341 grains, we added AREA to the SEMs to account for differences in the area of spatial units. S, BIOMASS,
342 NPP, and AREA were natural log transformed prior to analysis.
343
344 **Structural Equation Modelling (SEM).** To test the relative importance of S on NPP ('S→NPP') and

345 NPP on S ('NPP→S') we fitted two SEMs per spatial grain. For each SEM, we started with a 'saturated'

346 model, which included the relationships between S, NPP, and biomass, and relationships of all additional

347 covariates on S, NPP, and biomass (except for area at the fine spatial grain) (Fig. 2). The S→NPP model

348 evaluated how S directly affects NPP and how NPP indirectly affects S via biomass and, therefore,

349 included a feedback loop. The NPP→S model tested the direct effect of NPP on richness and, unlike the

350 S→NPP model, did not include a feedback loop. This way, we tested the direct effect of S on NPP

351 (S→NPP model), the direct effect of NPP on S (NPP→S), and the indirect effect of NPP on S (included

352 in both models).

353 Model fit can only be tested on unsaturated models, i.e. those that have at least one missing path.

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354   Therefore, we removed the path with the lowest standardized path coefficient from the model. As SEMs

355   had an equal number of paths, we could compare model fit across all models within each spatial grain

356   using their unadjusted R^2 values. After excluding the additional paths, path coefficients of S, NPP, and

357   biomass remained qualitatively the same, and model fit to the data were still accepted (Chi-square test;

358   P>0.05). This indicates that the models are identifiable and their results are robust. Therefore, we did not

359   further reduce the model, and models maintained the same number of paths within each scale. Because

360   models at the fine spatial grain including the number of individuals (N) did not fit the data well (P <

361   0.05), we excluded this variable. Models at the intermediate and coarse spatial grains including N fit the

362   data well (P >0.05), but we present models without N for consistency with the fine spatial grain and

363   because the sampling effects captured by N are also captured by area.

364   To assess the differences among scales in the relationships between S, NPP and biomass for each model,

365   we compared the standardized regression coefficients using their 95% confidence intervals. All SEMs

366   were fitted using the 'sem' function of the 'lavaan' package in R (Rosseel, 2012).

367   **Random forest models (RFs).** To assess the relative importance of each variable in predicting the

368   response variables within models, we used random forest models (RFs) (Breiman, 2001; Liaw & Wiener,

369   2002; Hastie *et al.*, 2009). We used the 'randomForest' function in the R package 'randomForest', with

370   all RF models produced using the default settings: 500 trees, one third of predictors sampled in each tree,

371   sampling with replacement of the entire dataset, and terminal node size of 5.

372   At each of the three spatial grains we fitted two RFs, one with S as a response variable and the other with

373   NPP as a response variable. All predictors that were used in the SEMs were used in the RF models

374   (including biomass). To quantify the relative importance of each predictor, we calculated the mean

375   decrease of squared error across all 500 trees using the 'importance' function. The importance values

376   were then scaled between 0 and 1, with 1 being the most important predictor. Using the function

377   'partialPlot', we extracted the partial responses of S and NPP to visualize the relationship between the

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35

378   two variables after accounting for all other covariates.

379   **Non-linear responses and spatial autocorrelation**. SEMs offer the advantage of modelling complex,

380   causal relationships (Grace *et al.*, 2010; Shipley, 2016), but they can be difficult to fit to data with non-

381   linear responses or spatial pseudoreplication. While it is possible to model non-linearity in SEMs, e.g.

382   using polynomials (Grace *et al.,* 2010; Shipley, 2016), this often comes at the cost of interpretability. A

383   similar problem applies when it comes to another prevalent problem of observational geographic data:

384   spatial autocorrelation, which statistical models have so far addressed by modelling it either in residuals,

385   or in the response (Dormann *et al.,* 2007). However, because of the causal loop in the SEMs (Fig. 2), the

386   key response variables are also predictors, which prevented us from estimating spatial autocorrelation. In

387   our analyses, we account for these issues in the following manner: (1) In the SEM analyses, we keep the

388   relationships linear, given the approximately linear pairwise relationships between the raw NPP, S and

389   biomass data (Figs. S5-7). (2) In the SEM analyses we do not directly model spatial autocorrelation. (3)

390   We address spatial autocorrelation in the random forest analysis by allowing the algorithm to model

391   smooth geographic trends in the response (by including the X and Y spatial coordinates as predictors),

392   and we measure spatial autocorrelation in the response and in residuals. (4) We allow the random forest

393   analysis to detect non-linear responses.

394   **Reproducibility.** All data on species richness, biomass, NPP, covariates, and R code used for the data

395   processing and analyses are available on Figshare (DOI: 10.6084/m9.figshare.5948155) under a CC-BY

396   license.

Results

398   Spatial patterns in productivity (NPP) and richness (S) emerged at coarser spatial grains, with higher S

399   and NPP usually observed in the eastern USA than in the western USA (Fig. 1). Biomass, a time-

400   integrated measure of NPP that also influences diversity, also exhibited similar patterns (Fig. 1). Bivariate

401   relationships between S and NPP exhibited scale dependence (Fig. 3). While not significantly correlated

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402   at the fine spatial grain (standardised major axis regression: $R^2 = 0.00$, $P = 0.73$), S and NPP were

403   significantly correlated at the intermediate (standardised major axis regression: $R^2 = 0.15$, $P < 0.001$) and

404   coarse spatial grains (standardised major axis regression: $R^2 = 0.35$, $P < 0.001$). The slope of S-NPP

405   increased from 0.86 (95% confidence intervals: 0.80, 0.94) at the intermediate spatial grain to 1.23 (95%

406   confidence intervals: 1.05, 1.45) at the coarse spatial grain. Similar patterns were observed when using

407   plot-derived estimates of NPP at the fine spatial grain (Fig. S8).
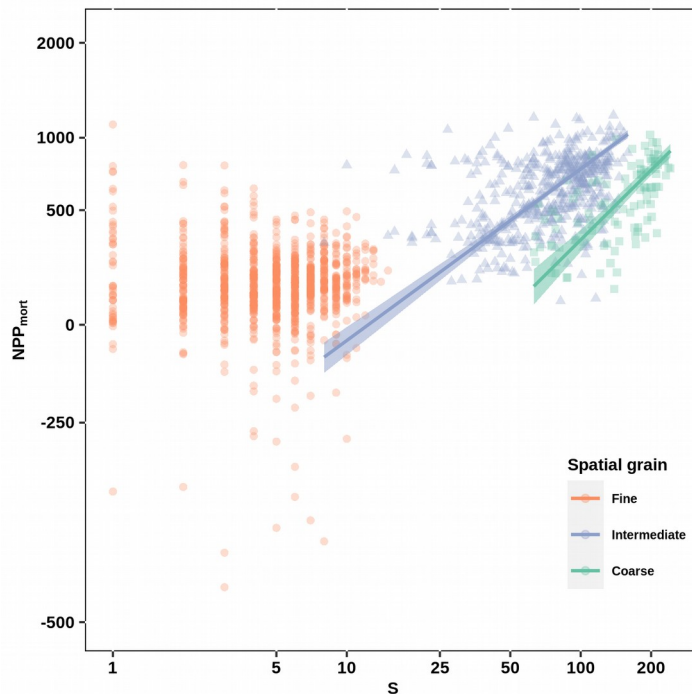
408

409   **Fig. 3.** Bivariate relationships between observed species richness (S) and productivity (NPP) of forests at
410   three spatial grains across the contiguous USA. Solid lines are standardised major-axis regressions fitted
411   at each spatial grain and shaded areas are 95% confidence intervals; only regressions with statistically
412   significant slopes (P<0.05) were visualised. NPP is MODIS-derived at all spatial grains. Note that axes
413   are on the natural log scale. Analyses were performed using stratified random samples of 1000, 500 and
414   98 spatial units at the fine, intermediate and coarse spatial grains, respectively.

415

416   **Structural Equation Models (SEM).** We examined relationships between species richness and net

417   primary productivity (NPP) across spatial grains using two SEMs for each spatial grain: the first

418   (S→NPP) testing the direct effect of S on NPP and the indirect effect of NPP on S (via biomass), and the

419   second (NPP → S) testing both the direct and indirect effects of NPP on S (Fig. 4). In both SEMs,

420   environmental variables (e.g., mean annual precipitation, mean annual temperature , temperature

421   seasonality, and elevation range), size of the species pool, forest age, and management were used to

422   explain variation in S, biomass, and NPP. At the intermediate and coarse grains, we also included area (of

423   each spatial unit) to account for variation in species richness due to sampling effects.

424

425
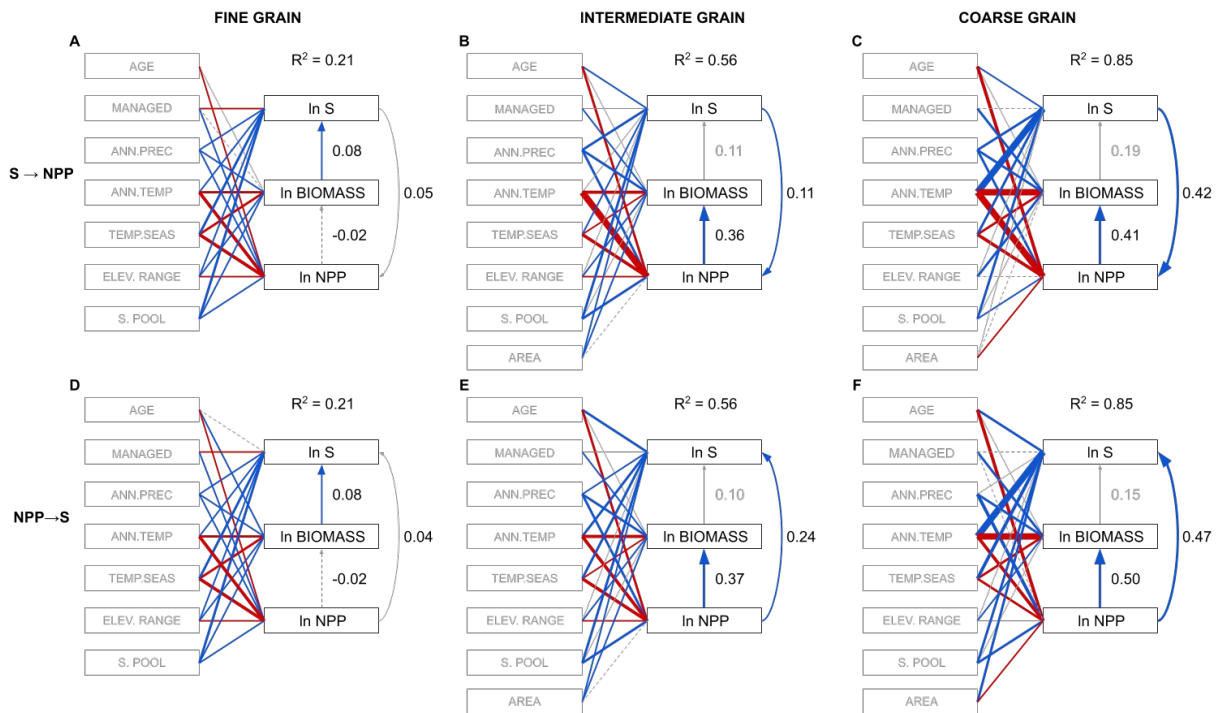
Fig. 4. Structural equation models (SEM) testing the influence of diversity (S) on productivity (NPP)('S → NPP'; A, B, C) and that of NPP on S ('NPP → S'; D, E, F), once controlling for environmental variables (e.g., mean annual precipitation, mean annual temperature, temperature seasonality, and elevation range), size of the species pool, forest age, and management, in forests across the contiguous USA at three spatial grains. All 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. 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, 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,

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439   BIOMASS, NPP, and AREA were natural log transformed prior to analysis.

440

441
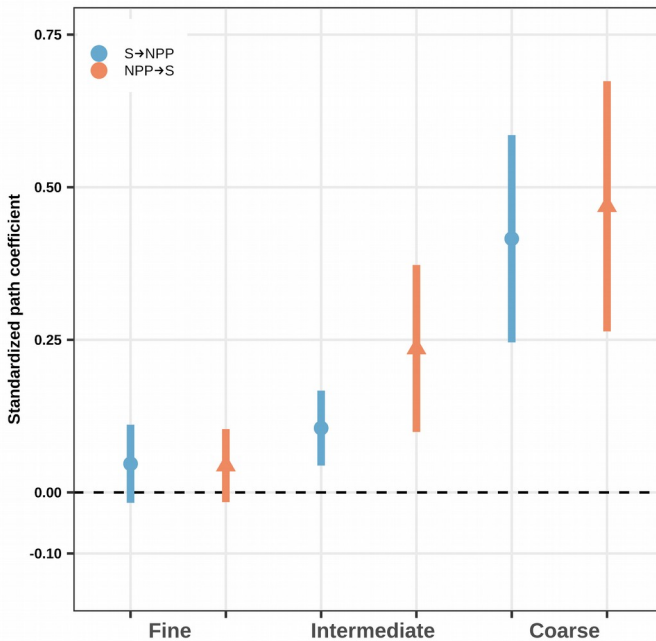
Fig. 5. Direct effects of diversity on productivity (S → NPP) and productivity on diversity (NPP → S) estimated with structural equation models (SEM) in forests across the contiguous USA at three spatial grains. Points are standardized path coefficients and solid lines are 95% confidence intervals.

445

446   Both models fit the data well for all spatial grains (P-value of the Chi-square test > 0.1; Table S2). At

447   each spatial grain, both SEMs had similar R^2 values averaged over S, biomass and NPP, indicating a

448   similar fit of the model to the data. R^2 values for both SEMs increased with spatial grain, from 0.21 at the

449   fine grain, to 0.56 at the intermediate grain and 0.85 at the coarse grain. Generally, the strength of effects

450   of S → NPP and NPP → S were similar within each spatial grain, but both increased in strength with

451   increasing spatial grain (Figs. 4 & 5). At the fine spatial grain, we found a weak direct effect of S → NPP

452   (Fig. 4A) and NPP → S (Fig. 4D), and effectively a null indirect effect of NPP on S via biomass

453   (standardized path coefficient of indirect effect = -0.002; Fig. 4A). At the intermediate spatial grain, we

454   found a similarly strong direct effect of S on NPP (standardized path coefficient of direct effect = 0.11,

455   Figs. 4B and 5) as NPP on S (standardized path coefficient of direct effect = 0.24; Figs. 4E and 5) and

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456 weak indirect effects of NPP on S via biomass (standardized path coefficient of indirect effect = 0.04; Fig.

457 4B). Similarly at the coarse spatial grain, we found strong direct effects of S on NPP (0.42, Fig. 4C and 5)

458 and of NPP on S (0.47, Fig. 4F and 5) and weak indirect effects of NPP on S via biomass (standardized

459 path coefficient of indirect effect = 0.08; Fig. 4C).

460 Overall, the SEMs suggest that the productivity-diversity relationship increases in strength with spatial

461 grain, and both relationships (S→NPP and NPP→S) explain similar amounts of variation. At all spatial

462 grains, our SEMs do not conclusively show stronger support for one direction of causality over the other.

463 Similar patterns were observed when using plot-derived estimates of NPP (Fig. S9; Table S2), except for

464 the direction of direct effects of S on NPP and NPP on S, which was negative.

465 **Random forest models (RFs).** To assess the relative importance of each predictor of species richness and

466 NPP, and to provide an assumption-free alternative to the SEMs that also accounts for spatial

467 autocorrelation, we fitted two random forest models for each of the three spatial grains: one with NPP and

468 the other with S as response variables. We found that species richness was one of the weakest predictors

469 of NPP relative to other predictors at all spatial grains (Fig. 6A), with management, forest age, MAP, and

470 biomass being the most important predictors (Fig. 6A). The overall explained variation of NPP also

471 increased from the fine to the two coarser spatial grains, from 0.64 at the fine spatial, to 0.89 at the

472 intermediate spatial grain and 0.88 at the coarse spatial grain.

473 We found that NPP was an important predictor of S (with a positive effect) only at the intermediate

474 spatial grain (Fig. 6B), but was less important relative to other predictors at fine and coarse spatial grains.

475 For S, we found that species pool, mean annual temperature and precipitation, and forest age were the

476 best predictors, and their importance increased towards coarse spatial grains (Fig. 6). In line with the

477 SEM analyses, the overall explained variation of S increased towards coarse spatial grains, from 0.39 at

478 the fine grain to 0.55 at the intermediate and 0.87 at coarse grains (see Fig. S10 for predicted vs. observed

479 values).

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480   In all RF analyses, there is a clear East-West spatial component in both S and NPP (represented by the X

481   coordinate in Fig. 6), which was not explained by any of the other predictors. This spatial component was

482   stronger for NPP than for S. Residual autocorrelation in all of the RF models was negligible (Fig S11).

483   Finally, we also fitted all of the RFs with local plot-derived measures of productivity (as an alternative to

484   the MODIS-derived productivity used in the main analyses), showing that the strength of the S-NPP

485   relationships were similar across all NPP measures (Fig. S12).

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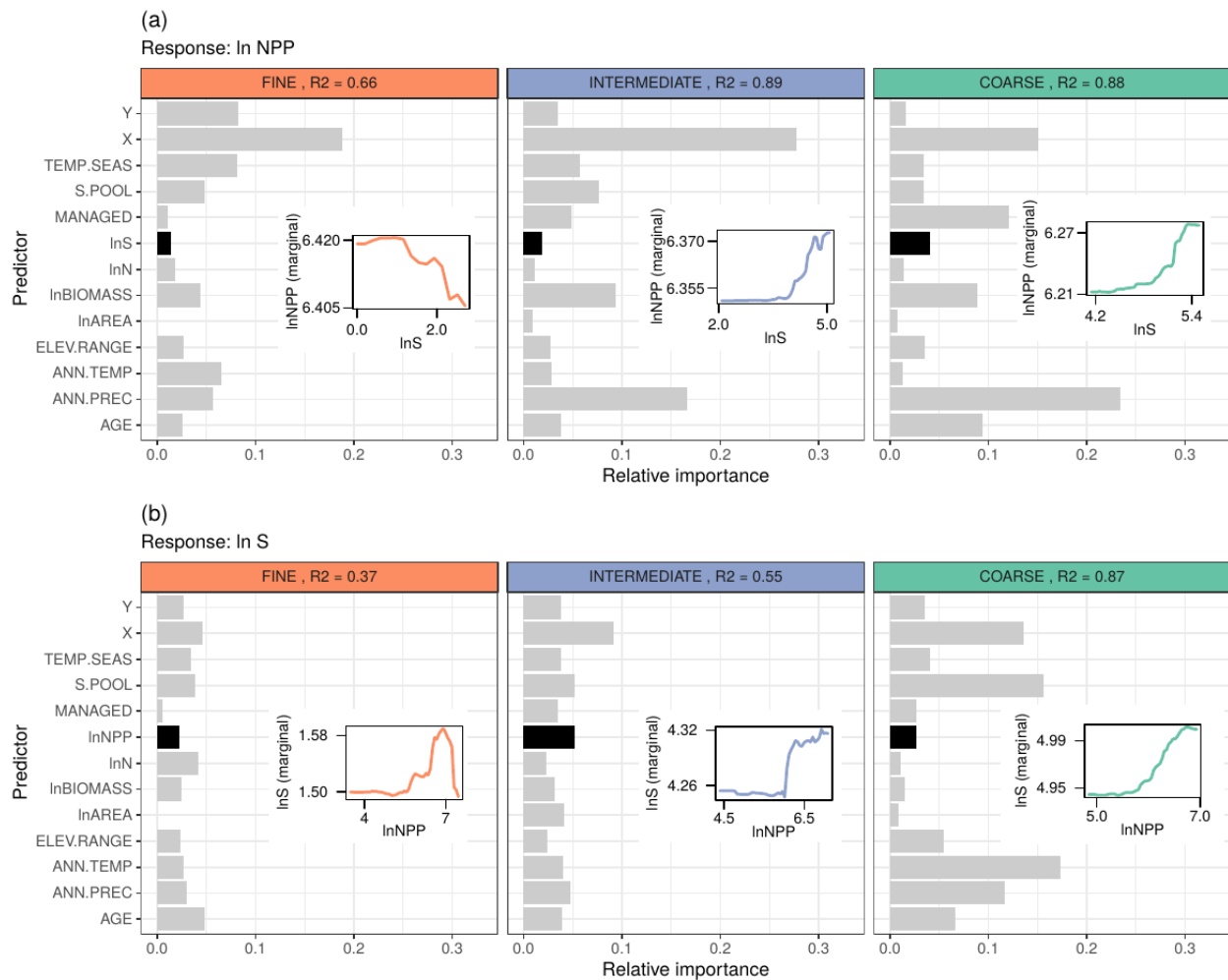
487
488   **Fig. 6.** Relative variable importance from random forest models explaining (a) MODIS-derived NPP and
489   (b) species richness (S) at three spatial grains. Relative variable importance is the mean decrease in
490   squared error caused by each of the variables, rescaled such that it sums up to the total pseudo R^2 of the
491   whole random forest model. The curves in the insets show shapes of the marginal responses of ln NPP or
492   ln S after accounting for all of the covariates. Y and X are latitudinal and longitudinal coordinates of the
493   US National Atlas projection, TEMP.SEAS is temperature seasonality, S.POOL is the regional species
494   pool, MANAGED is forest management, lnNPP is MODIS-derived NPP, lnN is the number of

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495 individuals, lnBIOMASS is biomass, lnAREA is area of the spatial unit, ELEV.RANGE is elevation

496 range, ANN.TEMP is mean annual temperature, ANN.PREC is mean annual precipitation, and AGE is

497 forest age. For explanation of variables see Table S1.

498

Discussion

500 The first important result is the similar magnitude of the S→NPP (Grace *et al.*, 2016) and NPP→S

501 (Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003; Šímová *et al.*, 2011) relationships at all grains. This

502 reflects, in part, that both productivity and species richness have many environmental and geographical

503 drivers in common (Lavers & Field, 2006), which complicates distinguishing correlation from causation,

504 even when using SEMs (Grace *et al.*, 2010; Shipley, 2016). There are two possible interpretations of this

505 result: (i) it may indicate that diversity's causal effects on productivity and productivity's causal effects

506 on diversity operate simultaneously, which was suggested by (Grace *et al.*, 2016), but never demonstrated

507 on observational data from large spatial grains. Alternatively (ii), if only one direction of the diversity-

508 productivity relationship is real and causal, it may be possible to fit another model assuming the opposite

509 direction because of multicollinearity in the data or non-identifiability of the causal direction (Petersen &

510 van der Laan, 2014). Without large-grain experiments that manipulate diversity in ways that mimic

511 biodiversity change (i.e. species gains and losses) in real-world ecosystems (Loreau *et al.*, 2001; Wardle,

512 2016; Hillebrand *et al.*, 2018; Manning *et al.*, 2019; Gonzalez *et al.*, 2020), we see little hope for

513 resolving this with contemporary data and approaches.

514 Our second important result is that both S→NPP and NPP→S strengthen from the fine to the intermediate

515 grain, and in the case of the SEM both relationships continue strengthening towards the coarsest grain.

516 While grain-dependent shifts are often expected (Table 1), this had not been shown previously with

517 empirical data for S→NPP using spatial grains coarser than several hectares (Luo *et al.*; Chisholm *et al.*,

518 2013; Hao *et al.*, 2018). If the S→NPP direction is the real causal one, then our results from SEM and RF

519 analyses support several theoretical expectations (Table 1) and give further impetus to efforts quantifying

520 biodiversity effects in naturally assembled ecosystems at broad spatial scales (Isbell *et al.*, 2018). If the

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521   NPP→S direction is the real causal one, then our results are in line with (Lavers & Field, 2006; Field *et*

522   *al.*, 2009), but are in contrast with (Storch *et al.*, 2005; Belmaker & Jetz, 2011), particularly when

523   upscaling from the fine grain to intermediate grain, where both the SEM and RF analyses give congruent

524   results. Intriguingly, a third possibility is that both NPP→S and S→NPP are real and that they operate

525   simultaneously, as suggested by our SEM results. In this case, we are unaware of any theory that

526   considers how this reciprocal relationship would be expected to change with increasing spatial grain. The

527   one caveat applicable to interpreting any direction of diversity-productivity relationships is that of

528   demographic stochasticity (mechanism I in Table1), which may weaken both NPP→S and S→NPP, or

529   their synergistic interplay, at fine spatial grains. In our study, the strong local effect of demographic

530   stochasticity appears plausible given the small area of the forest plots (672 m^2) and small population sizes

531   (12.24 ± 0.02 trees per plot; range = 1- 157 trees per plot) therein. This would suggest that temporal

532   changes in local scale biodiversity (Dornelas *et al.*, 2014; Magurran *et al.*, 2018) may have under-

533   appreciated effects on ecosystem function (Bannar-Martin *et al.*, 2018).

534   The third key result is that other predictors, such as temperature and biomass, were particularly influential

535   in all our analyses. That is, the grain dependence of the relationship between S and NPP was coupled with

536   a clear increase in the combined effect of annual temperature and precipitation on both S and NPP

537   towards coarse grains, which supports the notion that either temperature-dependent diversification

538   (Rohde, 1992; Allen *et al.*, 2002), niche conservatism (Qian & Ricklefs, 2016), or ecological limits

539   (Šímová *et al.*, 2011) shape diversity at these spatial grains. The weaker (relatively to temperature) effect

540   of precipitation is expected since we focus on forests, which only grow above certain precipitation

541   thresholds (Whittaker, 1975). The clear importance of temperature, biomass, longitude, and other

542   predictors such as forest age, temperature seasonality, or species pool (Figs. 4 & 6) highlights that even

543   when the NPP→S relationship holds across grains, other drivers are considerably more important in

544   predicting both (e.g., Ratcliffe *et al.*, 2017). Hence, integrating the environmental context surrounding

545   ecological communities into modeling diversity-productivity relationships is a necessary step towards

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546   making robust predictions of either biodiversity or ecosystem functioning at any spatial grain.

547   Our results reveal that mechanisms associated with one direction of diversity-productivity relationships

548   may provide insight to observed patterns of either direction, despite being initially formulated at a

549   different spatial grain. For example, the strong effect of the East-West spatial coordinate on both S and

550   NPP at the fine spatial grain (Fig. 6) suggests that biogeographical history may play a role in shaping the

551   diversity and ecosystem functioning of plant communities, which was initially tested at larger spatial

552   grains (e.g., Hawkins *et al.*, 2011; Conradi *et al.*, 2020). Increasingly, macroecological mechanisms such

553   as speciation gradients (Schluter & Pennell, 2017) and water-energy variables are being examined in

554   small-grain experimental grasslands to explore their role in mediating niche-based processes (Zuppinger-

555   Dingley *et al.*, 2014) and biodiversity effects (Wagg *et al.*, 2017), respectively. Similarly, efforts to

556   upscale biodiversity effects on productivity - developed initially to identify local scale mechanisms

557   (Loreau & Hector, 2001; Turnbull *et al.*, 2016) - may identify new mechanisms that underpin spatial

558   variation in ecosystem functioning at large spatial scales (Gonzalez *et al.*, 2020). An emerging challenge

559   to these efforts is the creation of data products that capture similar processes across spatial scales and are

560   independent (Supplemental Note 2 and Table S3); many of the variables used in this study share similar

561   data sources (e.g. MODIS and LANDSAT sensors), but are ultimately derived from different types of

562   intermediate products. Rather than uniquely focusing on the direction and strength of S-NPP once

563   accounting for other factors, our results show that mechanisms associated with $S \rightarrow NPP$ and $NPP \rightarrow S$

564   likely underpin the context dependency of diversity-productivity relationships across spatial grains (Table

565   1). These recent developments in BEF research and macroecology suggest that conceptual integration

566   between these two disciplines is just beginning (Craven *et al.*, 2019), yet further efforts to bridge

567   disciplinary gaps are essential to deepen current understanding of mechanisms that underpin the shifts in

568   diversity-productivity relationships across spatial scales.

569   To conclude, we show that the relationship between diversity and productivity strengthens toward coarse

570   grains. This result is in line with expectations from both BEF theory, and some (but not all) expectations

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571   from macroecological studies on NPP→S, and highlights the potential of demographic stochasticity and

572   sampling effects to distort or mask diversity-productivity relationships at fine grains. Moreover, we find

573   similar support for both directions of diversity-productivity relationships across spatial grains, revealing

574   that biodiversity and productivity can be both cause and effect. Future research on this relationship needs

575   to move from fine-grain experiments and observational studies to coarse grains in order to fully

576   understand and predict the impacts of anthropogenic biodiversity change on ecosystem function.

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