

1 **A cross-scale assessment of productivity-diversity** 2 **relationships**

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Running title: Cross-scale diversity-productivity

40 **Abstract**

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

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63 **Significance statement**

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

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84 **Introduction**

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

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

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

Running title: Cross-scale diversity-productivity

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

120 Here, we aim to address the dual nature by which productivity influences diversity (NPP→S) and
121 diversity influences on productivity (S→NPP) across spatial grains by combining structural equation
122 models (SEM) and Random Forest models (RFs) to explicitly account for the bidirectionality of NPP→S
123 and S→NPP. Using SEM, we propose and test hypothesis-based models (Fig. S2) that estimate the
124 direction and strength of NPP→S and S→NPP. Next, we use RFs, an assumption-free machine learning
125 approach (33), to quantify the relative importance of predictors of species richness and productivity. We
126 examine both hypothesized directions of the relationship, along with a number of important covariates
127 that influence both diversity and productivity, such as biomass, precipitation, temperature, and forest age,
128 using a comprehensive observational dataset of North American forests at fine (area = 672 m²; n =
129 46,211 plots), medium (median area = 1,386 km²; n = 1,956 spatial units), and coarse spatial grains
130 (median area = 35,677 km²; 98 spatial units). We specifically ask whether the influence of productivity
131 (and its environmental drivers) on diversity (NPP→S) played a predominant role, or whether the
132 influence of diversity on productivity (S→NPP) was predominant, and how these relationships manifest
133 across grains in real-world ecosystems.

Running title: Cross-scale diversity-productivity

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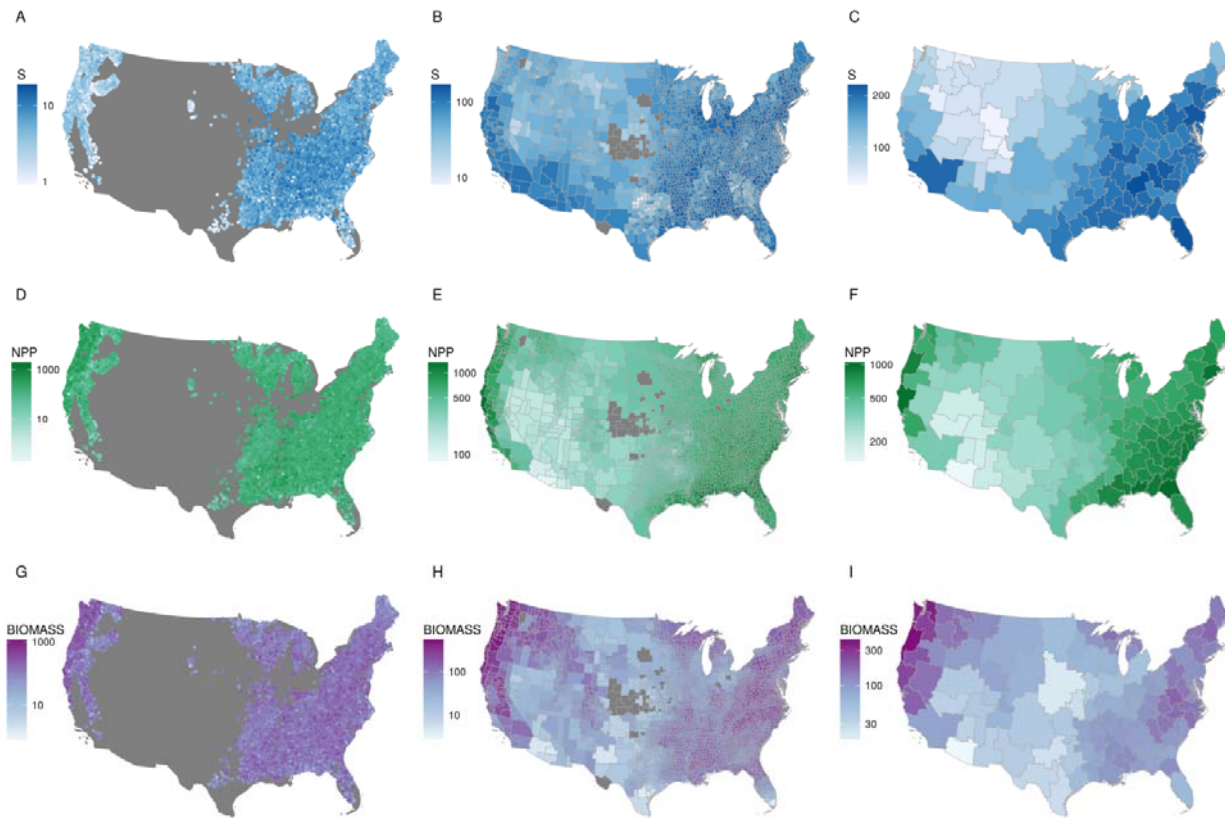
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138 **Table. 1** Overview of hypotheses predicting grain dependence of relationships between net primary
 139 productivity (NPP) and species richness (S).

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

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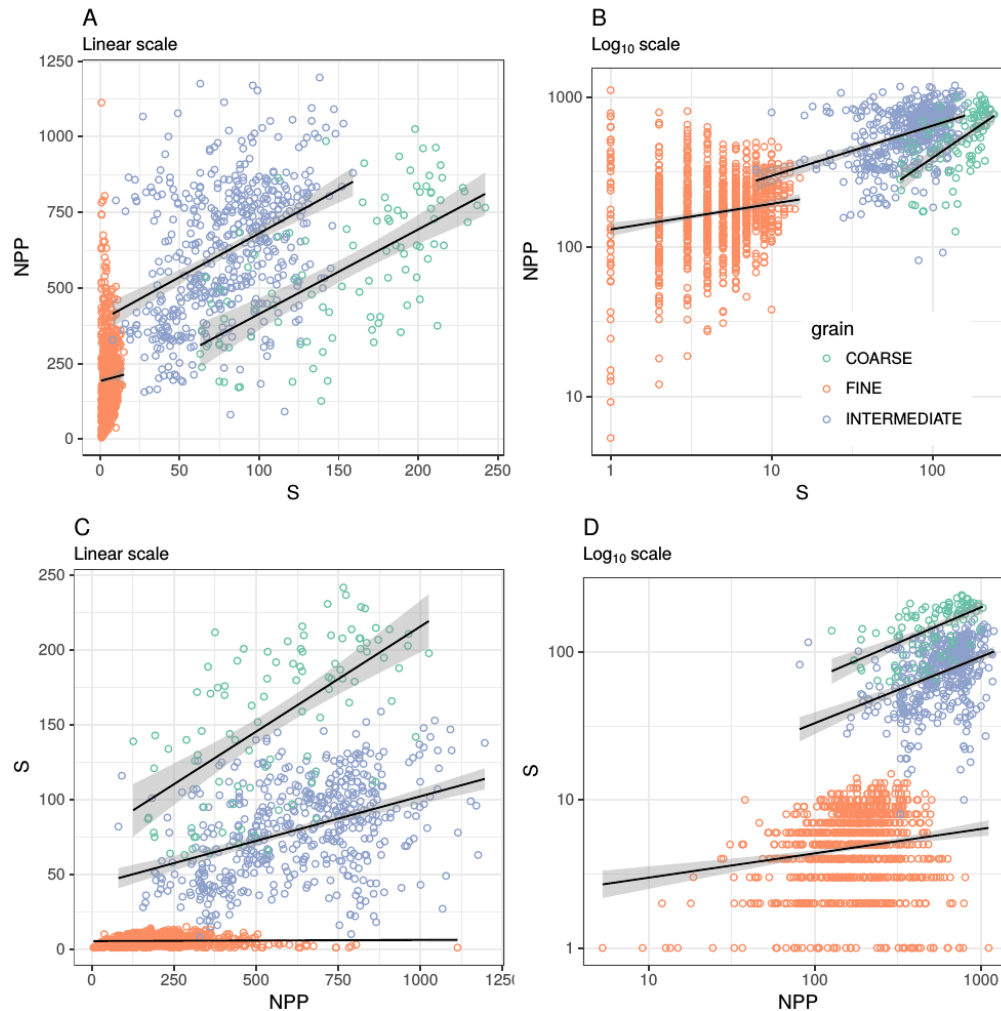
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142 **Fig.1.** Maps of species richness (S), net primary productivity (NPP) [$\text{gC}/\text{m}^2/\text{year}$], and biomass [Mg/ha]
143 of forests at three spatial grains across the contiguous USA. The values in all plots are on \log_{10} scale.

144 Results

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

Running title: Cross-scale diversity-productivity



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

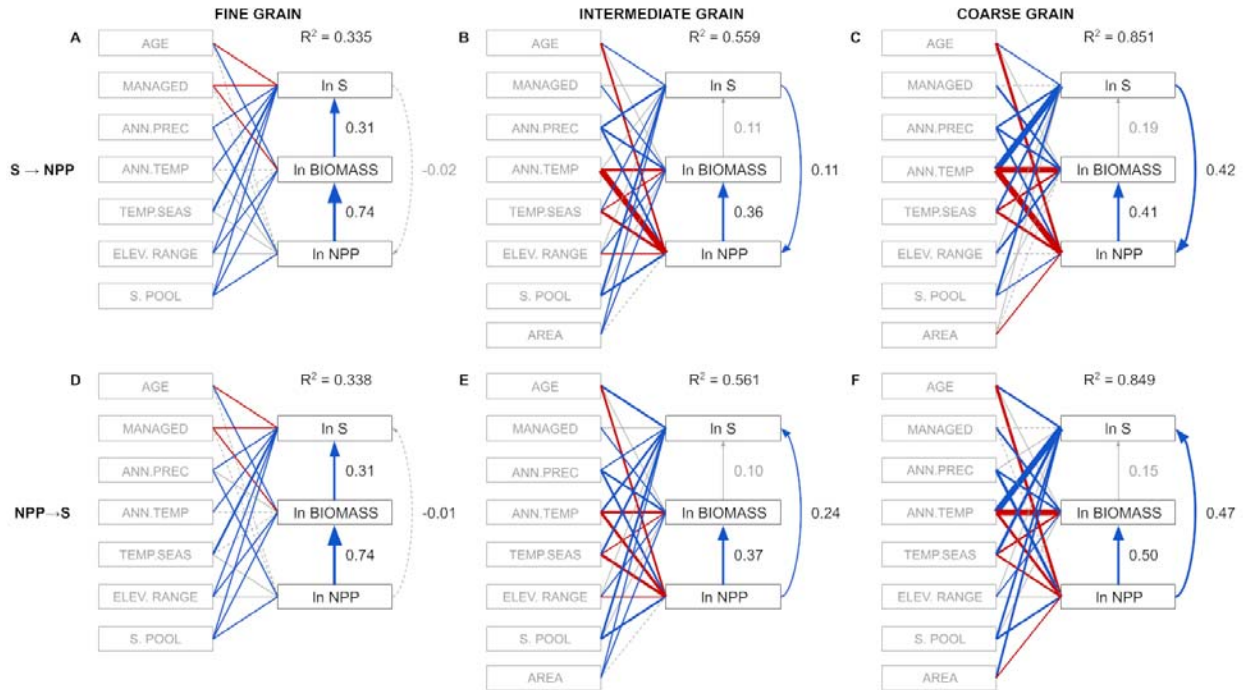
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158 **Structural Equation Models (SEM).** We examined relationships between species richness and net
159 primary productivity (NPP) across spatial grains using two SEMs for each spatial grain: the first
160 ($S \rightarrow NPP$) testing the direct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

Running title: Cross-scale diversity-productivity

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

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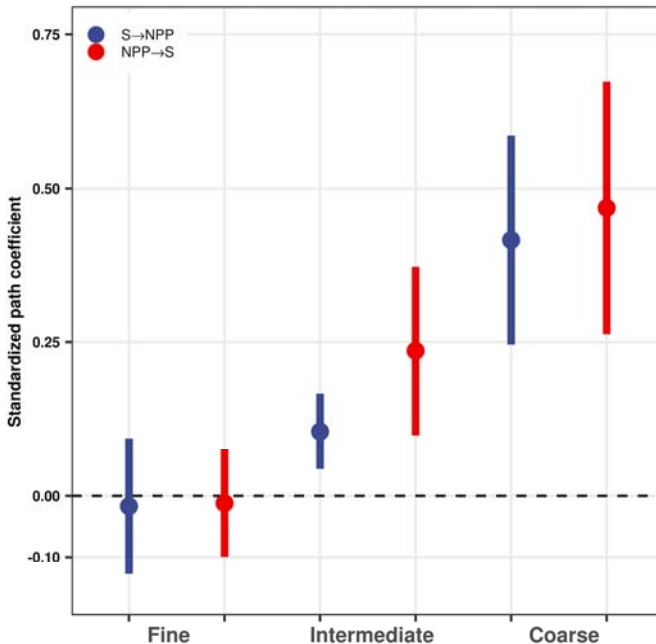


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169 **Fig. 3.** Structural equation models (SEM) testing the influence of diversity (S) on productivity (NPP) ('S
 170 → NPP'; A, B, C) and that of NPP on S ('NPP → S'; D, E, F), once controlling for environmental
 171 variables (e.g., mean annual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

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

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

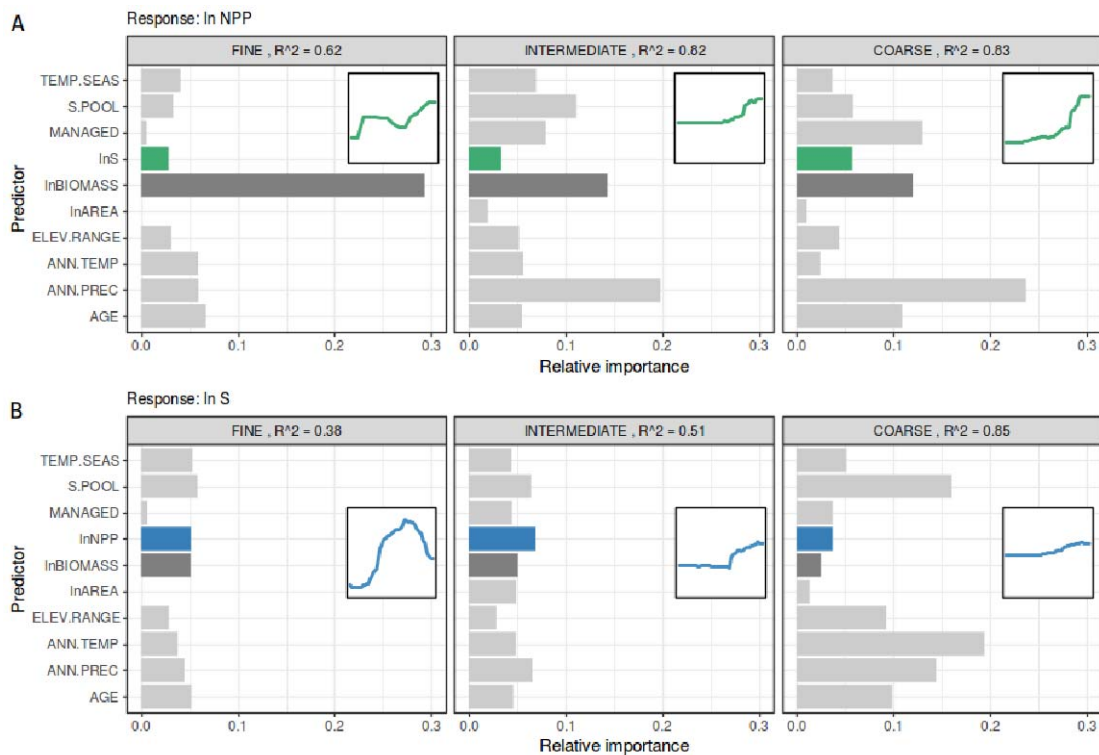
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200 3F and 4) and weak indirect effects of NPP on S (standardized path coefficient of indirect effect = 0.08;
201 Fig. 3F).

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

209 **Random Forest models (RFs).** To assess the relative importance of each predictor of species richness
210 and NPP, and to provide an assumption-free alternative to the SEMs, we fitted two random forest models
211 for each of the three spatial grains: one with NPP and the other with S as response variables. We found
212 that NPP was an important predictor of S at the fine and intermediate spatial grains (Fig. 5A), with
213 unimodal and linear effects respectively (Fig. 5), but was less important relative to other predictors at the
214 coarse spatial grain. For S, we found that species pool, MAT, MAP, and forest age were the best
215 predictors at all spatial grains (Fig. 5). In line with the SEM analyses, the overall explained variation of S
216 increased towards coarse spatial grains, from 0.38 at the fine grain to 0.51 at the intermediate and 0.85 at
217 coarse grains. For NPP, we found that species richness was one of the weakest predictors relative to other
218 predictors at all spatial grains (Fig. 5B), with management, forest age, MAP, and especially biomass
219 being the most important predictors (Fig. 5B). The overall explained variation of NPP also increased
220 towards coarse spatial grains, from 0.62 at the fine spatial, to 0.82 at the intermediate spatial grain and
221 0.83 at the coarse spatial grain.

Running title: Cross-scale diversity-productivity



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224 **Fig. 5.** Relative variable importance from random forest models explaining NPP and species richness (S)
225 and NPP at three spatial grains, which is the mean decrease in squared error caused by each of the
226 variables, rescaled such that it sums up to the total pseudo R². The curves in the insets show shapes of the
227 partial response of ln NPP or ln S (after accounting for all of the covariates); all of the insets have the
228 same span of the y-axis. For complete responses with axis scales and tick-marks see Fig. S5.

229 **Discussion**

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

Running title: Cross-scale diversity-productivity

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

242 Our second important result is that both $S \rightarrow NPP$ and $NPP \rightarrow S$ strengthen from the fine to the intermediate
243 grain, and in the case of the SEM both relationships continue strengthening towards the coarsest grain.

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

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

Running title: Cross-scale diversity-productivity

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

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

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

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

301 **Methods**

302 **Data**

303 **Geographic extent and grain.** We conducted analyses across the contiguous USA at three spatial grains
304 (Fig. 1): (1) fine grain (46,211 plots, 672 m² or 0.000672 km² each), (2) intermediate grain (1956 units,
305 median 1,386 km²) created by aggregating US counties to larger units based on the forested area within
306 them (see ‘spatial aggregation algorithm’ below), and (3) coarse grain (95 units, median 35,677 km²)
307 created by further aggregating the intermediate grain units. We restricted our analyses to forested areas to
308 make comparisons within and among spatial grains in similar ecosystems. For the intermediate and coarse
309 grains, we defined an area as forested if it fell into a 1 km² pixel with non-zero forest biomass following
310 (66).

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

Running title: Cross-scale diversity-productivity

313 algorithm that minimized variation of forested area at each spatial grain. The algorithm worked in an
314 iterative process as follows: (1) Calculate variance of area across all counties. (2) Randomly select a focal
315 county with a probability proportional to $1/\sqrt{\text{forest area}+1}$, which will more likely select small rather
316 than large counties. This was because small counties can be merged to approach the grain of the large
317 counties, thus decreasing variation in area. (3) Select a random adjacent county and merge it with the
318 focal county. (4) Updated the variance of area across all spatial units in the USA and compare it to the
319 original variance. If the new variance is lower than the original variance, the algorithm accepts the
320 merged unit and returns to step one. If the variance does not decrease, the algorithm repeats step 3 until it
321 decreases, with the maximum number of attempts of 1,000. If the variance still does not decrease even
322 after 1,000 attempts, the algorithm rejects the merge, and returned to step one. The algorithm started with
323 3,107 US counties, and we first terminated it when 1,956 merged spatial units were created (intermediate
324 grain dataset) and then after it reached 98 merged spatial units (coarse grain dataset) (Fig. 1). Although
325 the algorithm substantially reduced variation in area within both spatial grains (Fig. S9), it did not
326 eliminate the variation entirely, and thus we still used area as a covariate in the statistical analyses at the
327 intermediate and coarse spatial grains.

328 **Species richness (S).** For all spatial grains, we estimated diversity as species richness (S) because it is the
329 most commonly used and best understood metric of biodiversity, although other measures of diversity
330 may be better predictors of net primary productivity (67–69). We extracted S at the fine spatial grain from
331 the Forest Inventory and Analysis National Program (FIA) database v. 1.7.0 (70). We restricted our
332 analysis to plots on forested land that were sampled using the national FIA design (plot design code 1)
333 (71). All plots were surveyed between 1998 and 2016 and contain four circular 168 m² sub-plots with a
334 total area of 0.067 ha in which all individuals larger than 12.7 cm diameter at 1.3 m were recorded and
335 identified to species level. In total, our final dataset included 344 woody species and 93,771 plots. To
336 estimate S at the intermediate and coarse spatial grains, we used data on the extant native species of trees
337 for the contiguous USA provided in The Biota of North America Program's (BONAP) North American

Running title: Cross-scale diversity-productivity

338 Plant Atlas (72).

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

343 **Filtering of species occurrences.** We restricted our analyses to woody species occurring in forest. To this
344 end, we initially filtered the BONAP data to species classified as ‘trees’ in BONAP's taxonomic query
345 database (72). We further filtered out 70 county-level occurrences of 5 non-woody species from the
346 BONAP dataset. Species woodiness was inferred from woodiness data (76) and species lists of trees,
347 shrubs and subshrubs (77), except for 37 species without such data for which we instead inferred
348 woodiness from online searches or assumed resemblance among congeneric species. We also filtered out
349 8 FIA plot-level species occurrences and 1595 BONAP county-level species occurrences that we deemed
350 unlikely to be forest occurrences, as inferred from independent species occurrences within forested pixels
351 recorded in FIA plots and Global Biodiversity Information Facility (GBIF) point-occurrence records
352 (Downloaded via <https://www.gbif.org/> on 26th September 2016; doi:10.15468/dl.mka2y5;
353 Supplementary Note). To make species richness data internally consistent across the different spatial
354 grains, we added a further 6,593 quality-vetted county-level forest occurrences of woody species from
355 FIA plot records to the 282,991 occurrences in the taxonomically harmonized BONAP dataset.

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

Running title: Cross-scale diversity-productivity

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

364 At intermediate and coarse spatial grains, we calculated NPP using the MODIS-derived MOD17 A3
365 product (79, 80), which gives annual values of NPP as $\text{gC m}^{-2} \text{yr}^{-1}$ in 30 arc-sec pixels (roughly 1 km^2
366 around the equator). Here, NPP is defined as the annual sum of daily net photosynthesis minus the cost of
367 growth and maintenance of living cells in permanent woody tissue. We averaged the annual values from
368 2000 to 2015 for each pixel, and then averaged these across the intermediate and coarse grains.

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

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

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

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

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

Running title: Cross-scale diversity-productivity

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

389 **Elevation range.** We used elevation range as a proxy for topographic and habitat heterogeneity, a
390 variable that has been shown to be a good predictor of species richness (84). The USGS SRTM1 dataset
391 (85) with 1 sec (approx. 30 x 30 m²) resolution was used for all spatial grains. At the fine-scale, we
392 calculated a 250 m diameter buffer around each FIA plot and calculated the elevation range using all 1 sec
393 SRTM pixels within the buffer. At the intermediate and coarse scale, elevation range was calculated as
394 the difference between the minimum and maximum elevation points within each spatial unit.

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

Running title: Cross-scale diversity-productivity

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

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

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

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

Running title: Cross-scale diversity-productivity

423 (3) reduce spatial pseudoreplication (autocorrelation) by increasing the geographic distance between data
424 points. We first identified 11 strata at the fine and intermediate grains respectively, using multivariate
425 regression trees with S, NPP and biomass as response variables and all covariates as predictors (Fig. 1).
426 We then took a random and proportionally sized sample of spatial units from each strata (fine grain, N =
427 1,000; intermediate grain, N = 500). We did not use stratified random sampling at the coarse spatial grain
428 because the number of spatial units was small (N = 98) and spatial autocorrelation was low. The spatial
429 locations of the stratified samples are in Fig. S1. All of the analyses presented here, as well as our main
430 conclusions, are based on these stratified sub-samples of the data.

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

433 **Data Analyses**

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

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

Running title: Cross-scale diversity-productivity

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

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

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

460 Therefore, we removed the path with the lowest standardized path coefficient from the model. As SEMs
461 had equal number of paths, we could compare model fit across all models within each spatial grain using
462 their unadjusted R^2 values. After excluding the additional paths, path coefficients of S, NPP, and biomass
463 remained qualitatively the same, and model fit to the data were still accepted (Chi-square test; $P > 0.05$).

464 This indicates that the models are identifiable and their results are robust. Therefore, we did not further
465 reduce the model, and models maintained the same number of paths within each scale.

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

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

Running title: Cross-scale diversity-productivity

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

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

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

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Running title: Cross-scale diversity-productivity

493 **Author contributions**

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

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

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