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

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30 Acknowledgments

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39   **Biosketch**

40   The authors are a group of (mostly) early career researchers united by their interest in ecological

41   synthesis, in areas ranging from macroecology to experimental ecology, ecological theory, and ecological

42   modeling.

A cross-scale assessment of productivity-diversity relationships

Running title: Cross-scale diversity-productivity

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→NPP) at small spatial grains. In contrast, the influence of productivity on richness (NPP→S) has been explored at many grains in naturally assembled communities. Mismatches in spatial scale between approaches have fostered debate about the strength and direction of biodiversity-productivity relationships. Here we examine the direction and strength of productivity's influence on diversity (NPP→S) and of diversity's influence on productivity (S→NPP), and how this varies across spatial grains

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→NPP and NPP→S have similar magnitudes, meaning that processes underlying S→NPP and NPP→S either operate simultaneously, or that one of them is real and the other is an artifact. At all spatial grains, S was one of the weakest predictors of forest productivity, which was largely driven by biomass, temperature, and forest management and age.

67   **Main conclusions:** We conclude that spatial grain mediates relationships between biodiversity and

68   productivity in real-world ecosystems and that results supporting predictions from each approach

69   (NPP $\rightarrow$ S and S $\rightarrow$ NPP) serve as an impetus for future studies testing underlying mechanisms.

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

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

72   **Keywords:** spatial grain, biomass, carbon sequestration, climate, machine learning, more individuals
73   hypothesis, species-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 *et al.*, 2001; Cardinale *et al.*, 2009; Oberle *et al.*, 2009; Grace *et al.*, 2016).

100   The striking mismatch between the spatial grains of BEF experiments (cm^2 to m^2; Cardinale *et al.,* 2011),

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

102   macroecological diversity-productivity correlations (m^2 to thousands of km^2; Mittelbach *et al.,* 2001;

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

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

105   effects of productivity on diversity (NPP$\rightarrow$S) and of diversity on productivity (S$\rightarrow$NPP), which predict

106   effects to either strengthen or weaken as the spatial grain increases (Table 1). For example, spatial

107   turnover of species that are functionally equivalent within the regional grain can offset low species

108   richness at local grains, resulting in a strengthening of S$\rightarrow$NPP with increasing spatial grain. The effects

109   of NPP$\rightarrow$S are also hypothesized to increase with spatial grain, because higher NPP is associated with

110   greater heterogeneity at larger spatial grains, which enhances coexistence of more species at the regional

111   grain. Moreover, other components of a community, such as biomass, can mediate relationships between

112   productivity and diversity via their effects on competitive dominance (Grace *et al.,* 2016). These

113   theoretical expectations have been supported by observational data for the effects of productivity on

114   diversity (Mittelbach *et al.,* 2001; Chase & Leibold, 2002; Belmaker & Jetz, 2011). In the case of BEF

115   relationships (i.e. S$\rightarrow$NPP), there is also empirical and theoretical support for grain dependence, which

116   comes from a restricted range of small spatial grains (Luo *et al.*; Chalcraft, 2013; Hao *et al.,* 2018).

117 **Table. 1** Overview of hypotheses predicting grain dependence of relationships between net primary
118 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 the regional grain 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)

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

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

121 (SEM) and Random Forest models (RFs) to explicitly account for the bidirectionality of NPP→S and

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

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

124 (Hastie *et al.,* 2009), to quantify the relative importance of predictors of species richness and productivity.

125 We examine both hypothesized directions of the relationship, along with a number of important

126 covariates that influence both diversity and productivity, such as biomass, precipitation, temperature, and

127 forest age, using a comprehensive observational dataset of North American forests at fine (area = 672 m^2;

128 $n =$ 46,211 plots), medium (median area = 1,386 km^2; n = 1,956 spatial units), and coarse spatial grains

130   (median area = 35,677 km^2; 98 spatial units). We specifically ask whether the influence of productivity

131   (and its environmental drivers) on diversity (NPP$\rightarrow$S) played a predominant role, or whether the

132   influence of diversity on productivity (S$\rightarrow$NPP) was predominant, and how these relationships manifest

133   across grains in real-world ecosystems.

Methods

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Data

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

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137   (Fig. 1): (1) fine grain (46,211 plots, 672 m^2 or 0.000672 km^2 each), (2) intermediate grain (1956 units,

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

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

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

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

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

143   (Blackard *et al.,* 2008).

144   **Spatial aggregation algorithm.** To minimize variation in species diversity (defined below) due to

145   differences in area between spatial units within the intermediate and coarse spatial grains, we created an

146   algorithm that minimized variation of forested area at each spatial grain. The algorithm worked in an

147   iterative process as follows: (1) Calculate variance of area across all counties. (2) Randomly select a focal

148   county with a probability proportional to 1/sqrt(forest area+1), which will more likely select small rather

149   than large counties. This was because small counties can be merged to approach the grain of the large

150   counties, thus decreasing variation in area. (3) Select a random adjacent county and merge it with the

151   focal county. (4) Update the variance of area across all spatial units in the USA and compare it to the

152   original variance. If the new variance is lower than the original variance, the algorithm accepts the
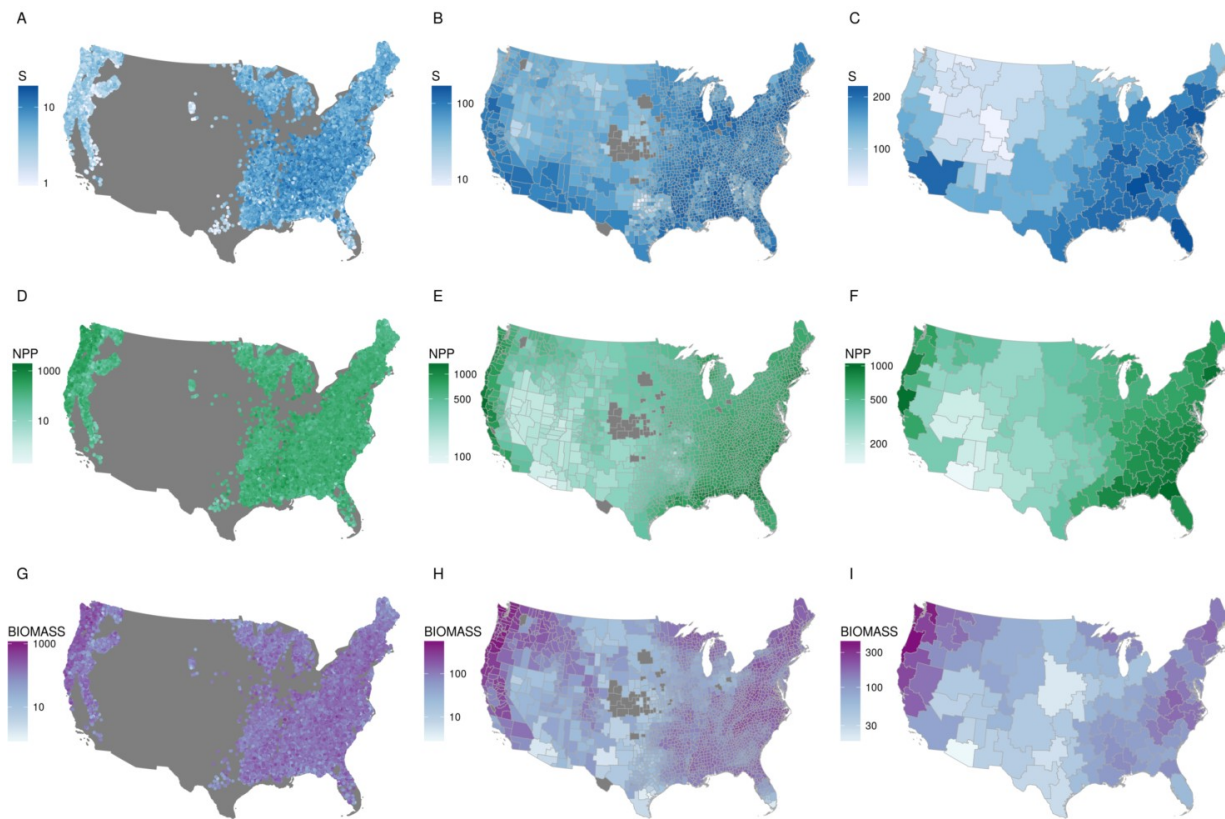
Fig.1. Maps of species richness (S), net primary productivity (NPP) [gC/m^2/year], and biomass [Mg/ha] of forests at three spatial grains across the contiguous USA. The values in all plots are on log$_{10}$ scale.

merged unit and returns to step one. If the variance does not decrease, the algorithm repeats step 3 until it decreases, with the maximum number of attempts of 1,000. If the variance still does not decrease even after 1,000 attempts, the algorithm rejects the merge, and returned to step one. The algorithm started with 3,107 US counties, and we first terminated it when 1,956 merged spatial units were created (intermediate grain dataset) and then after it reached 98 merged spatial units (coarse grain dataset) (Fig. 1). Although the algorithm substantially reduced variation in area within both spatial grains (Fig. S2), it did not eliminate the variation entirely, and thus we still used area as a covariate in the statistical analyses at the intermediate and coarse spatial grains.

Species richness (S). For all spatial grains, we estimated diversity as species richness (S) because it is the most commonly used and best understood metric of biodiversity, although other measures of diversity may be better predictors of net primary productivity (Paquette & Messier, 2011; Cadotte, 2015; Venail *et*

166 *al.*, 2015). We extracted S at the fine spatial grain from the Forest Inventory and Analysis National

167 Program (FIA) database v. 1.7.0 (USDA Forest Service, 2017). We restricted our analysis to plots on

168 forested land that were sampled using the national FIA design (plot design code 1)(Burrill *et al.*, 2018).

169 All plots were surveyed between 1998 and 2016 and contain four circular 168 m^2 sub-plots with a total

170 area of 0.067 ha in which all individuals larger than 12.7 cm diameter at 1.3 m were recorded and

171 identified to species level. In total, our final dataset included 344 woody species and 93,771 plots. To

172 estimate S at the intermediate and coarse spatial grains, we used data on the extant native species of trees

173 for the contiguous USA provided in The Biota of North America Program's (BONAP) North American

174 Plant Atlas (Kartesz, 2015).

175 **Taxonomic harmonization of species names.** We cleaned scientific names from the FIA data and the

176 BONAP data and harmonized them to accepted species based on The Plant List (The Plant List, 2013)

177 and the Taxonomic Name Resolution Service (TNRS)(The Taxonomic Name Resolution Service, 2018),

178 following the protocol described in Meyer et al. (2016). We included hybrid forms but excluded any

179 names that could not be resolved to the species level.

180 **Filtering of species occurrences.** We restricted our analyses to woody species occurring in forest. To this

181 end, we initially filtered the BONAP data to species classified as 'trees' in BONAP's taxonomic query

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

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

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

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

186 species. We also filtered out 8 FIA plot-level species occurrences and 1595 BONAP county-level species

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

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

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

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

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

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

193   BONAP dataset.

194   **Net primary productivity (NPP).** For a large subset of plots in the FIA database that have been

195   measured at least twice between 1999 and 2015 (n = 46,211, on average plots remeasured every 5.8

196   years), we calculated tree productivity. This was measured as the change in tree C over time due to

197   growth ($gC\ m^{-2}\ y^{-1}$), and is the sum of aboveground C increment of living trees between two

198   measurements and conservatively excludes recruits and dead trees (Paquette & Messier, 2011). Tree-level

199   carbon was estimated by multiplying tree-level biomass (see below) by 0.48, but recognize that

200   gymnosperms may have higher carbon content than that of angiosperms (Thomas & Martin, 2012). For

201   plots with more than two inventories, tree productivity was calculated for each period and then averaged.

202   At intermediate and coarse spatial grains, we calculated NPP using the MODIS-derived MOD17 A3

203   product (Zhao *et al.*, 2005; Zhao & Running, 2010), which gives annual values of NPP as $gC\ m^{-2}\ yr^{-1}$ in

204   30 arc-sec pixels (roughly 1 km^2 around the equator). Here, NPP is defined as the annual sum of daily net

205   photosynthesis minus the cost of growth and maintenance of living cells in permanent woody tissue. We

206   averaged the annual values from 2000 to 2015 for each pixel, and then averaged these across the

207   intermediate and coarse grains.

208   **Biomass.** At the fine scale, we estimated tree-level biomass using generalized biomass equations

209   developed for North American tree species (Chojnacky *et al.*, 2013). For each plot we calculated

210   aboveground biomass ($Mg\ ha^{-1}$) as the sum of individual biomass of living trees per hectare.

211   For the intermediate and coarse spatial grains we derived biomass values using a map of aboveground

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

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

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

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215 **Forest age and management.** For each plot in the fine-scale dataset, we extracted forest age and

216 management history from the FIA data set. Forest age is estimated using dendrochronological records

217 (Burrill *et al.*, 2018). Management regime was a binary variable that indicated whether any forest

218 management activity, e.g. harvest, thinning, tree planting, had been observed in any inventory or not.

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

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

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

222 unit.

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

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

225 variables in the analysis (Table 2, Fig. S3). Thus, only three variables that captured different aspects of

226 the climate were selected; mean annual temperature (BIO1), mean precipitation (BIO12), and temperature

227 seasonality (BIO4). At the fine scale, for each FIA plot we extracted the values of the 30 sec pixel in

228 which the plot was found. For the intermediate and coarse grains, we averaged the values across all pixels

229 within each spatial unit.

230 **Elevation range.** We used elevation range as a proxy for topographic and habitat heterogeneity, a

231 variable that has been shown to be a good predictor of species richness (Stein *et al.*, 2014). The USGS

232 SRTM1 dataset (USGS, 2009) with 1 sec (approx. 30 x 30 m^2) resolution was used for all spatial grains.

233 At the fine-scale, we calculated a 250 m diameter buffer around each FIA plot and calculated the

234 elevation range using all 1 sec SRTM pixels within the buffer. At the intermediate and coarse scale,

235 elevation range was calculated as the difference between the minimum and maximum elevation points

236 within each spatial unit.

237 **Species pools.** We calculated regional species pools for each spatial grain as probabilistic dispersal pools

238 (Karger *et al.*, 2016). For each intermediate-grain spatial unit and each species in our data set, we first

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239   estimated the species' probability of being part of the unit's species pool as the joint probabilities that

240   dispersal might happen between that unit and any of the species' intermediate-grain occurrences within

241   the contiguous US. Due to insufficient data on species' dispersal abilities, we assumed that dispersal

242   probability between focal units and species' occurrences would decay with great-circle distance between

243   the respective regions' centroids. We explored five alternative exponential distance-decay functions, with

244   scaling coefficients that determined the probability of a species occurring in neighboring units would

245   disperse to the focal unit of 0.975, 0.95, 0.90, 0.80, and 0.60. We chose the function whose resulting

246   species pool estimate most strongly correlated with species richness. Finally, we calculated species pools

247   for each spatial unit as the sum of all species' individual probabilities of dispersal from any of their

248   respective occurrences. For each coarse-grain unit, we summed the species' joint probabilities of dispersal

249   between any of their intermediate-grain occurrences and any of the intermediate-grain units nested within

250   the coarse unit. For fine-grain units, we assumed that their species pools would equal those of the

251   intermediate-grain spatial units in which they were nested.

252   All of the variables used in our analyses are listed and summarized in Table 2 and visualized in Fig. S3.

253 **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 (80)	$1 km^2$
Biomass	BIOMASS	Mg/ha	fine	FIA	
			intermediate, coarse	(66)	$1 km^2$
Forest age	AGE	years	fine	FIA	
		years	intermediate, coarse	NACP (81)	$1 km^2$
Management regime	MGMT	managed or not	fine	FIA	
		proportion of managed FIA plots	intermediate, coarse	FIA	
Mean annual precipitation	MAP	average mm/y	all grains	WorldClim	$1 km^2$
Mean annual temperature	MAT	average ℃/y	all grains	WorldClim	$1 km^2$
Temperature seasonality	TEMP.SEAS	standard deviation of monthly ℃ * 100	all grains	WorldClim	$1 km^2$
Elevation range (altitudinal span)	ELEV.RANGE	m	all grains	SRTM v 2.1	30 arc-sec
Size of species pool	S.POOL	# of species	all grains	FIA, GBIF, BONAP	

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

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

256 1977) for the fine and intermediate spatial grains in order to (1) enhance environmental representativeness

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

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

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

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

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

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

263 sampling at the coarse spatial grain because the number of spatial units was small (N = 98) and spatial

264 autocorrelation was low. The spatial locations of the stratified samples are in Fig. S4. All of the analyses

265 presented here, as well as our main conclusions, are based on these stratified sub-samples of the data.

266 **Data transformation and standardization.** Prior to analysis, species richness, biomass, NPP, and area

267 were natural-log transformed.

Data Analyses

269 Two complementary statistical approaches were used. First, we fitted structural equation models (SEMs),

270 which allow the assessment of indirect effects including feedback loops, address causality, and take into

271 account potential collinearity among covariates (Grace *et al.,* 2010; Shipley, 2016). The paths in our

272 candidate SEMs were based on previous evidence of causal links between S, biomass, and NPP (Fig. S1;

273 18). Second, to better understand the relative importance of each variable in explaining variation in the

274 response variables within models, we fitted Random Forest models (RFs) (Hastie *et al.,* 2009). The results

275 from SEMs provide insight into differences among models (i.e. between the two causal pathways per

276 spatial grain, and among spatial grains), while results from RFs provide additional insights into the

277 relative importance of different predictors variables within models.

278 **Structural Equation Modelling (SEM).** To test the relative importance of S on NPP ('S→NPP') and

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

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

281 covariates on S, NPP, and biomass (except for area at the fine spatial grain) (Fig. S1). An effect of area on

282 NPP and biomass was included because in many models this proved necessary to obtain an accepted

283 model. The S→NPP model evaluated how S directly affects NPP and how NPP indirectly affects S via

284 biomass and, therefore, included a feedback loop. The NPP→S model tested the direct effect of NPP on

285 richness and, unlike the S→NPP model, did not include a feedback loop. This way, we tested the direct

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

287   NPP on S (included in both models).

288   To test the sensitivity of the relative importance of S on NPP to the direction of the relationships between

289   S and biomass ('S → Biomass') or biomass and NPP ('Biomass → NPP', we fitted two additional SEMs

290   per spatial grain as described above. The S → Biomass model evaluated how S directly affects NPP and

291   biomass and how S indirectly affects biomass via NPP. The Biomass → NPP model tested the direct

292   effect of S on NPP and the direct effect of biomass on S. Neither Biomass → NPP or S → Biomass

293   models includes an indirect effect of NPP on S, as was the case for the S → NPP or NPP → models.

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

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

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

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

298   remained qualitatively the same, and model fit to the data were still accepted (Chi-square test; P>0.05).

299   This indicates that the models are identifiable and their results are robust. Therefore, we did not further

300   reduce the model, and models maintained the same number of paths within each scale.

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

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

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

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

305   response variables within models, we used Random Forest models (RFs) (Breiman, 2001; Liaw &

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

307   'randomForest', with all RF models produced using the default settings: 500 trees, one third of predictors

308   sampled in each tree, sampling with replacement of the entire dataset, and terminal node size of 5.

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

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

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

312   decrease of squared error across all 500 trees using the function 'importance'. The importances were then

313   scaled between 0 and 1, with 1 being the most important predictor. Using the function 'partialPlot', we

314   extracted the partial responses of S and NPP to visualize the relationship between the two variables after

315   accounting for all other covariates.

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

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

318   license.

Results

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

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

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

323   relationships among S and NPP exhibited scale dependence, with their slopes increasing with spatial grain
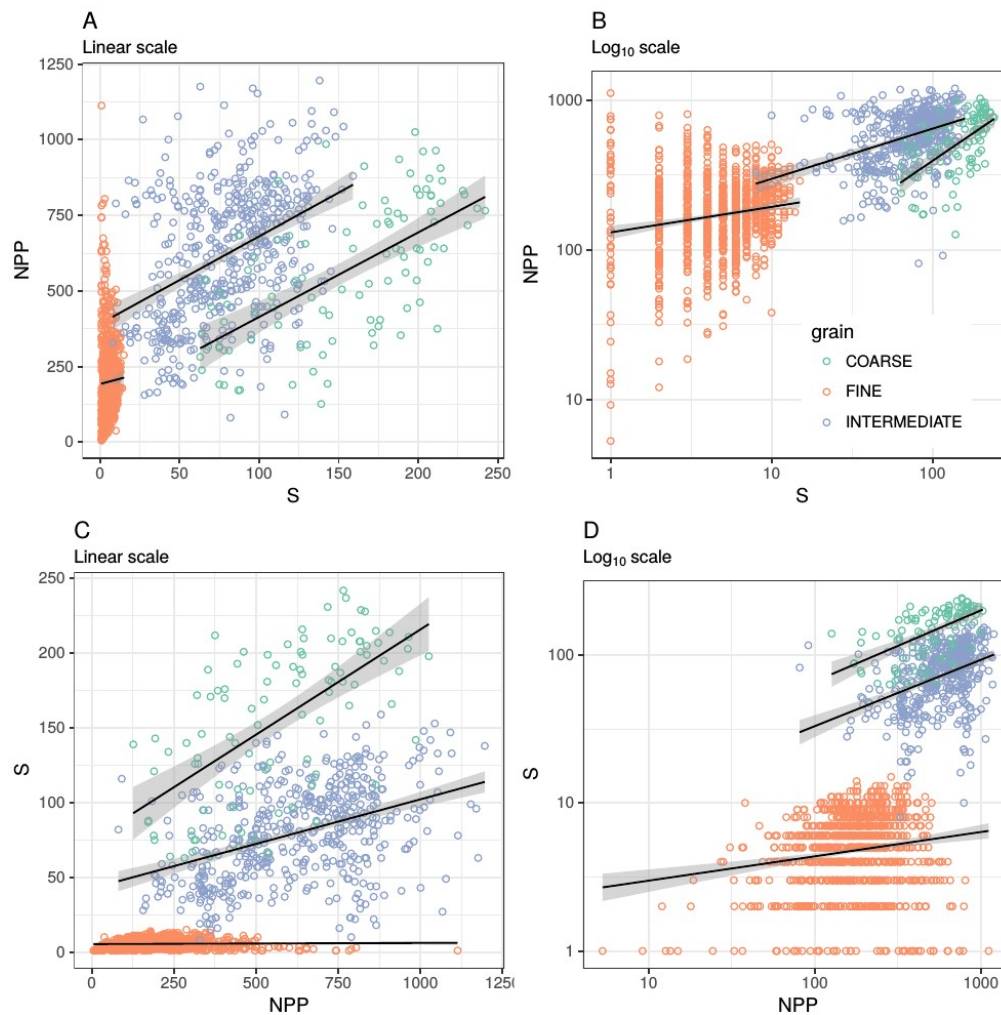
324   (Fig. 2).

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

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

18   18

337   used to explain variation in S, biomass, and NPP. At the intermediate and coarse grains, we also included

338   area (of each spatial unit) to account for variation in species richness due to the effects of area (see
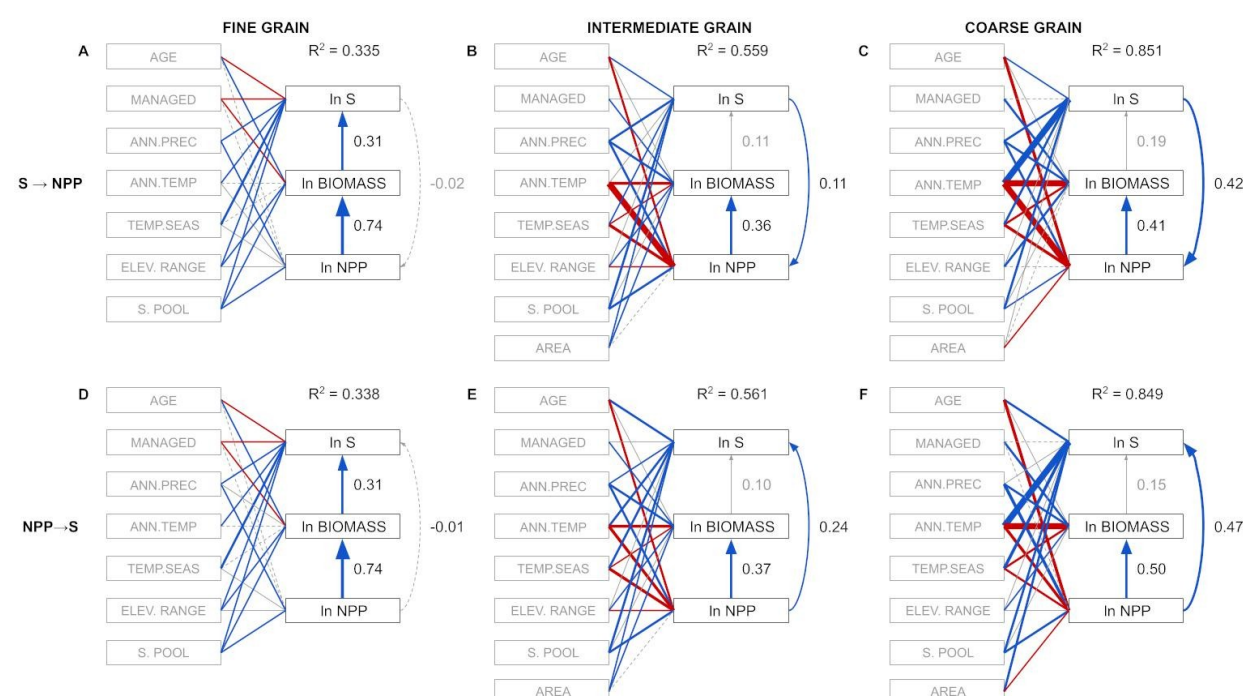
339   Methods).

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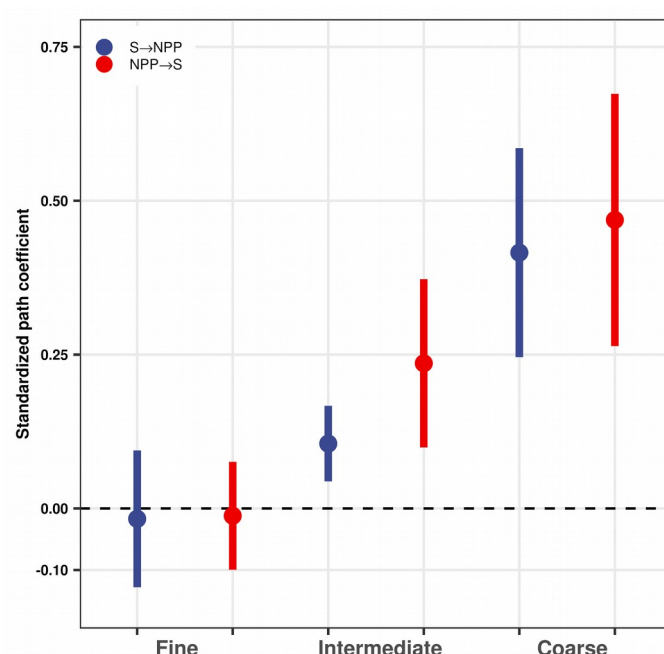352   AREA is area. S, BIOMASS, NPP, and AREA were natural log transformed prior to analysis.

19   19

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

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

20   20

368   3F and 4) and weak indirect effects of NPP on S (standardized path coefficient of indirect effect = 0.08;

369   Fig. 3F).

370   Overall, the SEMs show that the productivity-diversity relationship increases in strength with spatial

371   grain, and both relationships (S→NPP and NPP→S) explain similar amounts of variation, albeit with

372   some differences in the direct and indirect effects. At fine spatial grains, our SEMs show greater support

373   for a strong indirect effect of NPP on S via biomass, but do not support the inverse effect of S on NPP.

374   Towards coarser spatial grains, our SEMs do not conclusively show stronger support for one direction of

375   causality over the other. These patterns were robust to the direction of paths between S and biomass (Fig.

376   S5A, B, and C; Table S1) and between biomass and NPP (Fig. S5D, E, and F; Table S1).

377   **Random Forest models (RFs).** To assess the relative importance of each predictor of species richness

378   and NPP, and to provide an assumption-free alternative to the SEMs, we fitted two random forest models

379   for each of the three spatial grains: one with NPP and the other with S as response variables. We found

380   that NPP was an important predictor of S at the fine and intermediate spatial grains (Fig. 5A), with

381   unimodal and linear effects respectively (Fig. 5), but was less important relative to other predictors at the

382   coarse spatial grain. For S, we found that species pool, MAT, MAP, and forest age were the best

383   predictors at all spatial grains (Fig. 5). In line with the SEM analyses, the overall explained variation of S

384   increased towards coarse spatial grains, from 0.38 at the fine grain to 0.51 at the intermediate and 0.85 at

385   coarse grains (see Fig. S6 for predicted vs. observed values). For NPP, we found that species richness was

386   one of the weakest predictors relative to other predictors at all spatial grains (Fig. 5B), with management,

387   forest age, MAP, and especially biomass being the most important predictors (Fig. 5B). The overall

388   explained variation of NPP also increased towards coarse spatial grains, from 0.62 at the fine spatial, to

389   0.82 at the intermediate spatial grain and 0.83 at the coarse spatial grain (Fig. S6).
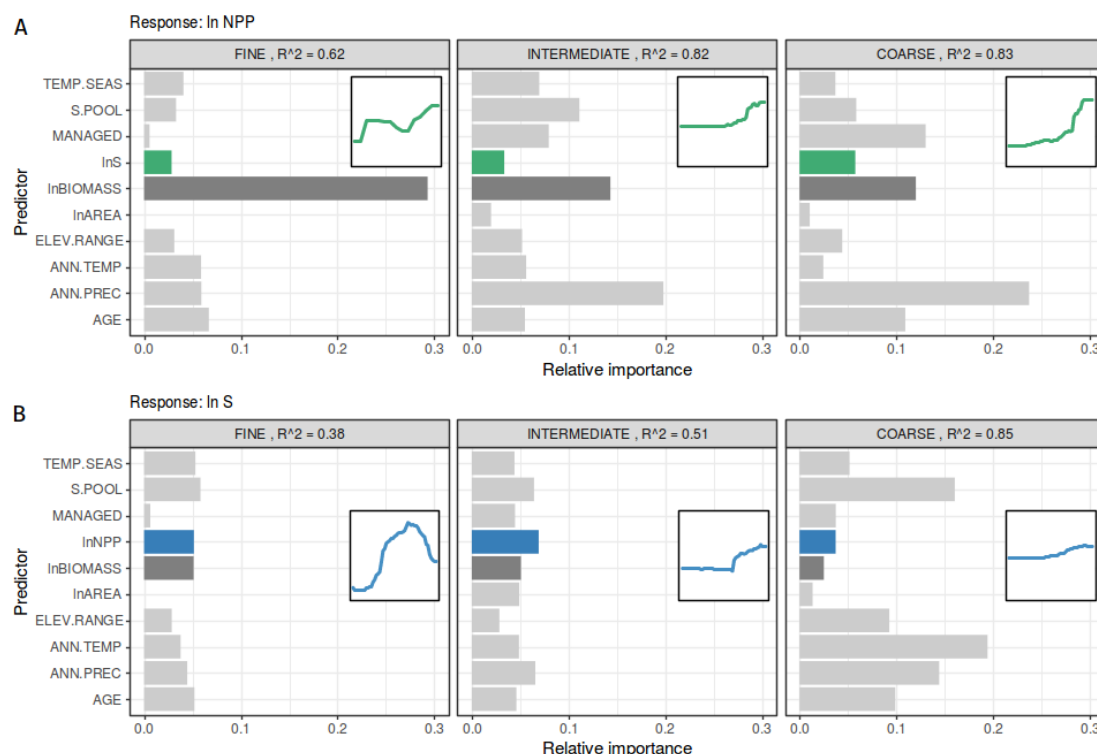
Fig. 5. Relative variable importance from random forest models explaining NPP and species richness (S) and NPP at three spatial grains, which is the mean decrease in squared error caused by each of the variables, rescaled such that it sums up to the total pseudo R^2. The curves in the insets show shapes of the partial response of ln NPP or ln S (after accounting for all of the covariates); all of the insets have the same span of the y-axis. For complete responses with axis scales and tick-marks see Fig. S7.

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

408   2016; Hillebrand *et al.,* 2018; Manning *et al.,* 2019), we see little hope for resolving this with

409   contemporary data and approaches.

410   Our second important result is that both $S \rightarrow NPP$ and $NPP \rightarrow S$ strengthen from the fine to the intermediate

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

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

413   empirical data for $S \rightarrow NPP$ using spatial grains coarser than several hectares (Luo *et al.*; Chisholm *et al.,*

414   2013; Hao *et al.,* 2018). If the $S \rightarrow NPP$ direction is the real causal one, then our results from SEM and RF

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

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

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

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

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

420   results. Intriguingly, a third possibility is that both $NPP \rightarrow S$ and $S \rightarrow NPP$ are real and that they operate

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

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

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

424   demographic stochasticity (mechanism I in Table1), which may weaken both $NPP \rightarrow S$ and $S \rightarrow NPP$, or

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

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

427   (12.24 ± 0.02 trees per plot; range = 1- 157 trees per plot) therein. This would suggest that temporal

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

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

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

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

432   a clear increase in the effect of annual temperature (but not precipitation) on both S and NPP towards

433   coarse grains, which supports the notion that either temperature-dependent diversification (Rohde, 1992;

434   Allen *et al.*, 2002) or ecological limits (Šímová *et al.*, 2011) shape diversity at these spatial grains. The

435   consistently weak effect of precipitation is expected since we focus on forests, which only grow above

436   certain precipitation thresholds (Whittaker, 1975). Second, we found a positive, indirect effect of NPP on

437   species richness via forest biomass at the fine spatial grain, which supports multiple hypotheses (Table 1)

438   such as the view that higher ecosystem productivity enhances species diversity by enabling larger

439   numbers of individuals per species to persist due to lower extinction rates (Wright *et al.*, 1993; Evans *et*

440   *al.*, 2005; Storch *et al.*, 2005), particularly at fine grains where stochastic extinctions occur (34). The clear

441   importance of temperature, biomass, and other predictors such as forest age, seasonality, or species pool

442   (Figs. 3 & 5) highlights that even when the NPP→S relationship holds across grains, other drivers are

443   considerably more important in predicting both (e.g., Ratcliffe *et al.*, 2017). Hence, integrating the

444   environmental context surrounding ecological communities into modeling diversity-productivity

445   relationships is a necessary step towards making robust predictions of either biodiversity or ecosystem

446   functioning at any spatial grain.

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

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

449   different spatial grain. For example, the positive, indirect effect of NPP on species richness via forest

450   biomass at the fine spatial grain provides support for the more individuals hypothesis (Storch *et al.*,

451   2005), although it is typically tested at regional to continental spatial scales. Increasingly,

452   macroecological mechanisms such as speciation gradients (Schluter & Pennell, 2017) and water-energy

453   variables are being examined in small-grain experimental grasslands to explore their role in mediating

454   niche-based processes (Zuppinger-Dingley *et al.*, 2014) and biodiversity effects (Wagg *et al.*, 2017),

455   respectively. Similarly, efforts to upscale biodiversity effects on productivity - developed initially to

456   identify local scale mechanisms (Loreau & Hector, 2001; Turnbull *et al.,* 2016) - may identify new

457   mechanisms that determine spatial variation in ecosystem functioning at large spatial scales. Rather than

458   uniquely focusing on the direction and strength of S-NPP once accounting for other factors, our results

459   show that mechanisms associated with $S \rightarrow NPP$ and $NPP \rightarrow S$ likely underpin the context dependency of

460   diversity-productivity relationships across spatial grains (Table 1). These recent developments in BEF

461   research and macroecology suggest that conceptual integration between these two disciplines is just

462   beginning (Craven *et al.,* 2019), yet further efforts to bridge disciplinary gaps are essential to deepen

463   current understanding of mechanisms that underpin the shifts in diversity-productivity relationships

464   across spatial scales.

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

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

467   from macroecological studies on $NPP \rightarrow S$, and highlights the potential of demographic stochasticity to

468   distort diversity-productivity relationships at fine grains. Moreover, we find similar support for both

469   directions of diversity-productivity relationships across spatial grains, revealing that biodiversity and

470   productivity can be both cause and effect. Future research on this relationship needs to move from fine-

471   grain experiments and observational studies to coarse grains in order to fully understand and predict the

472   impacts of anthropogenic biodiversity change on ecosystem function.

References

474   Abrams, P.A. (1988) Resource Productivity-Consumer Species Diversity: Simple Models of Competition
475   in Spatially Heterogeneous Environments. *Ecology,* **69**, 1418–1433.
476   Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S.,
477   O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S.,
478   Buckley, Y.M., Calabrese, L.B., Chu, C.-J., Cleland, E.E., Collins, S.L., Cottingham, K.L.,
479   Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P.,
480   Gasarch, E.I., Gruner, D.S., Hagenah, N., Hille Ris Lambers, J., Humphries, H., Jin, V.L., Kay,
481   A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W.,
482   MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W.,
483   Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D.,
484   Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P. & Yang, L.H. (2011)
485   Productivity Is a Poor Predictor of Plant Species Richness. *Science*, **333**, 1750–1753.
486   Allen, A.P., Brown, J.H. & Gilloolly, J.F. (2002) Global Biodiversity, Biochemical Kinetics, and the

487   Energetic-Equivalence Rule. *Science*, **297**, 1545–1548.

488   Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. & Schmid, B.
489   (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services.
490   *Ecology Letters*, **9**, 1146–1156.

491   Bannar Martin, K.H., Kremer, C.T., Ernest, S.K.M., Leibold, M.A., Auge, H., Chase, J., Declerck,
492   S.A.J., Eisenhauer, N., Harpole, S., Hillebrand, H., Isbell, F., Koffel, T., Larsen, S., Narwani, A.,
493   Petermann, J.S., Roscher, C., Cabral, J.S. & Supp, S.R. (2018) Integrating community assembly
494   and biodiversity to better understand ecosystem function: the Community Assembly and the
495   Functioning of Ecosystems (CAFE) approach. *Ecology Letters*, **21**, 167–180.

496   Belmaker, J. & Jetz, W. (2011) Cross-scale variation in species richness–environment associations.
497   *Global Ecology and Biogeography*, **20**, 464–474.

498   Blackard, J.A., Finco, M.V., Helmer, E.H., Holden, G.R., Hoppus, M.L., Jacobs, D.M., Lister, A.J.,
499   Moisen, G.G., Nelson, M.D., Riemann, R., Ruefenacht, B., Salajanu, D., Weyermann, D.L.,
500   Winterberger, K.C., Brandeis, T.J., Czaplewski, R.L., McRoberts, R.E., Patterson, P.L. &
501   Tymcio, R.P. (2008) Mapping U.S. forest biomass using nationwide forest inventory data and
502   moderate resolution information. *Remote Sensing of Environment*, **112**, 1658–1677.

503   Breiman, L. (2001) Random forests. *Machine learning*, **45**, 5–32.

504   Burrill, E.A., Wilson, A.M., Turner, J.A., Pugh, S.A., Menlove, J., Christiansen, G., Conkling, B.L. &
505   David, W. (2018) *The Forest Inventory and Analysis Database: database description and user
506   guide version 8.0 for Phase 2*, U.S. Department of Agriculture, Forest Service.

507   Cadotte, M.W. (2015) Phylogenetic diversity and productivity: gauging interpretations from experiments
508   that do not manipulate phylogenetic diversity. *Functional Ecology*, **29**, 1603–1606.

509   Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace,
510   G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie,
511   A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*,
512   **486**, 59–67.

513   Cardinale, B.J., Hillebrand, H., Harpole, W., Gross, K. & Ptacnik, R. (2009) Separating the influence of
514   resource 'availability'from resource 'imbalance'on productivity–diversity relationships. *Ecology
515   Letters*, **12**, 475–487.

516   Cardinale, B.J., Ives, A.R. & Inchausti, P. (2004) Effects of species diversity on the primary productivity
517   of ecosystems: extending our spatial and temporal scales of inference. *Oikos*, **104**, 437–450.

518   Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P.,
519   Connor, M.I.O.' & Gonzalez, A. (2011) The functional role of producer diversity in ecosystems.
520   *American Journal of Botany*, **98**, 1–21.

521   Chalcraft, D.R. (2013) Changes in ecological stability across realistic biodiversity gradients depend on
522   spatial scale. *Global Ecology and Biogeography*, **22**, 19–28.

523   Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship.
524   *Nature*, **416**, 427–430.

525   Chisholm, R.A., Muller Landau, H.C., Rahman, K.A., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg,
526   N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.-W.,
527   Chiang, J.-M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C.,
528   Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.-F., Hubbell, S.P.,
529   Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma,
530   K., Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Razman, S.M., Morecroft, M.D.,
531   Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi Manage, R., Romero Saltos, H., Sang,
532   W., Schurman, J., Su, S.-H., Sukumar, R., Sun, I.-F., Suresh, H.S., Tan, S., Thomas, D., Thomas,
533   S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. & Zimmerman, J.K. (2013)
534   Scale-dependent relationships between tree species richness and ecosystem function in forests.
535   *Journal of Ecology*, **101**, 1214–1224.

536   Chojnacky, D.C., Heath, L.S. & Jenkins, J.C. (2013) Updated generalized biomass equations for North
537   American tree species. *Forestry*, **87**, 129–151.

538 Cochran, W.G. (1977) *Sampling techniques*, 3rd edn. John Wiley and Sons, New York, USA.

539 Connell, J.H. & Orias, E. (1964) The Ecological Regulation of Species Diversity. *The American*
540   *Naturalist*, **98**, 399–414.

541 Craven, D., Winter, M., Hotzel, K., Gaikwad, J., Eisenhauer, N., Hohmuth, M., König Ries, B. & Wirth,
542   C. (2019) Evolution of interdisciplinarity in biodiversity science. *Ecology and Evolution*, **9**,
543   6744–6755.

544 Currie, D.J. (1991) Energy and large-scale patterns of animal-and plant-species richness. *The American*
545   *Naturalist*, **137**, 27–49.

546 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014)
547   Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*, **344**,
548   296–299.

549 Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017) Biodiversity effects in the wild are common and as
550   strong as key drivers of productivity. *Nature*, **549**, 261–264.

551 Evans, K.L., Greenwood, J.J.D. & Gaston, K.J. (2005) Dissecting the species–energy relationship.
552   *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2155–2163.

553 Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz Filho, J.A.F., Guégan, J.-F., Kaufman, D.M.,
554   Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial
555   species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

556 Fraser, L.H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., Bartha, S., Beierkuhnlein,
557   C., Bennett, J.A., Bittel, A., Boldgiv, B., Boldrini, I.I., Bork, E., Brown, L., Cabido, M., Cahill,
558   J., Carlyle, C.N., Campetella, G., Chelli, S., Cohen, O., Csergo, A.-M., Díaz, S., Enrico, L.,
559   Ensing, D., Fidelis, A., Fridley, J.D., Foster, B., Garris, H., Goheen, J.R., Henry, H.A.L., Hohn,
560   M., Jouri, M.H., Klironomos, J., Koorem, K., Lawrence-Lodge, R., Long, R., Manning, P.,
561   Mitchell, R., Moora, M., Müller, S.C., Nabinger, C., Naseri, K., Overbeck, G.E., Palmer, T.M.,
562   Parsons, S., Pesek, M., Pillar, V.D., Pringle, R.M., Roccaforte, K., Schmidt, A., Shang, Z.,
563   Stahlmann, R., Stotz, G.C., Sugiyama, S., Szentes, S., Thompson, D., Tungalag, R.,
564   Undrakhbold, S., van Rooyen, M., Wellstein, C., Wilson, J.B. & Zupo, T. (2015) Worldwide
565   evidence of a unimodal relationship between productivity and plant species richness. *Science*,
566   **349**, 302–305.

567 Grace, J.B., Anderson, T.M., Olff, H. & Scheiner, S.M. (2010) On the specification of structural equation
568   models for ecological systems. *Ecological Monographs*, **80**, 67–87.

569 Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., Hautier, Y.,
570   Hillebrand, H., Lind, E.M., Pärtel, M., Bakker, J.D., Buckley, Y.M., Crawley, M.J., Damschen,
571   E.I., Davies, K.F., Fay, P.A., Firn, J., Gruner, D.S., Hector, A., Knops, J.M.H., MacDougall,
572   A.S., Melbourne, B.A., Morgan, J.W., Orrock, J.L., Prober, S.M. & Smith, M.D. (2016)
573   Integrative modelling reveals mechanisms linking productivity and plant species richness.
574   *Nature*, **529**, 390–393.

575 Hao, M., Zhang, C., Zhao, X. & Gadow, K. von (2018) Functional and phylogenetic diversity determine
576   woody productivity in a temperate forest. *Ecology and Evolution*, **8**, 2395–2406.

577 Hastie, T., Tibshirani, R. & Friedman, J.H. (2009) *The elements of statistical learning: data mining,*
578   *inference, and prediction*, 2nd edn. New York, NY: Springer.

579 Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T.,
580   Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy,
581   water, and broad scale geographic patterns of species richness. *Ecology*, **v. 84**, 3105–3117.

582 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution
583   interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**,
584   1965–1978.

585 Hillebrand, H., Blasius, B., Borer, E.T., Chase, J.M., Downing, J.A., Eriksson, B.K., Filstrup, C.T.,
586   Harpole, W.S., Hodapp, D., Larsen, S., Lewandowska, A.M., Seabloom, E.W., Van de Waal,
587   D.B. & Ryabov, A.B. (2018) Biodiversity change is uncoupled from species richness trends:
588   Consequences for conservation and monitoring. *Journal of Applied Ecology*, **55**, 169–184.

589 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A.,
590   Duffy, J.E., Gamfeldt, L. & O/'Connor, M.I. (2012) A global synthesis reveals biodiversity loss
591   as a major driver of ecosystem change. *Nature*, **486**, 105–108.
592 Isbell, F., Cowles, J., Dee, L.E., Loreau, M., Reich, P.B., Gonzalez, A., Hector, A. & Schmid, B. (2018)
593   Quantifying effects of biodiversity on ecosystem functioning across times and places. *Ecology*
594   *Letters*, **21**, 763–778.
595 Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Diaz, S., Hector, A., Mace, G.M., Wardle, D.A.,
596   O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L. & Larigauderie, A. (2017) Linking
597   the influence and dependence of people on biodiversity across scales. *Nature*, **546**, 65–72.
598 Jetz, W. & Fine, P.V.A. (2012) Global Gradients in Vertebrate Diversity Predicted by Historical Area-
599   Productivity Dynamics and Contemporary Environment. *PLOS Biology*, **10**, e1001292.
600 Karger, D.N., Cord, A.F., Kessler, M., Kreft, H., Kühn, I., Pompe, S., Sandel, B., Sarmento Cabral, J.,
601   Smith, A.B., Svenning, J.-C., Tuomisto, H., Weigelt, P. & Wesche, K. (2016) Delineating
602   probabilistic species pools in ecology and biogeography. *Global Ecology and Biogeography*, **25**,
603   489–501.
604 Kartesz, J.T. (2015) The Biota of North America Program (BONAP). *Taxonomic Data Center*.
605 Lande, R., Engen, S. & Saether, B.-E. (2003) *Stochastic population dynamics in ecology and*
606   *conservation*, Oxford University Press.
607 Lavers, C. & Field, R. (2006) A resource-based conceptual model of plant diversity that reassesses
608   causality in the productivity–diversity relationship. *Global Ecology and Biogeography*, **15**, 213–
609   224.
610 Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A.D.,
611   Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett,
612   C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C.,
613   Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H.,
614   Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim,
615   H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S.,
616   Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J.,
617   Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T.,
618   Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski,
619   A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero,
620   F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F.,
621   Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L. &
622   Reich, P.B. (2016) Positive biodiversity-productivity relationship predominant in global forests.
623   *Science*, **354**, aaf8957.
624 Liaw, A. & Wiener, M. (2002) Classification and regression by randomForest. *R news*, **2**, 18–22.
625 Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments.
626   *Nature*, **412**, 72–76.
627 Loreau, M., Mouquet, N. & Gonzalez, A. (2003) Biodiversity as spatial insurance in heterogeneous
628   landscapes. *Proceedings of the National Academy of Sciences*, **100**, 12765–12770.
629 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A.,
630   Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and Ecosystem
631   Functioning: Current Knowledge and Future Challenges. *Science*, **294**, 804–808.
632 Luo, W., Liang, J., Gatti, R.C., Zhao, X. & Zhang, C. Parameterization of biodiversity–productivity
633   relationship and its scale dependency using georeferenced tree-level data. *Journal of Ecology*, **0**.
634 Magurran, A.E., Deacon, A.E., Moyes, F., Shimadzu, H., Dornelas, M., Phillip, D.A.T. & Ramnarine,
635   I.W. (2018) Divergent biodiversity change within ecosystems. *Proceedings of the National*
636   *Academy of Sciences*, 201712594.
637 Manning, P., Loos, J., Barnes, A.D., Batáry, P., Bianchi, F.J.J.A., Buchmann, N., De Deyn, G.B.,
638   Ebeling, A., Eisenhauer, N., Fischer, M., Fründ, J., Grass, I., Isselstein, J., Jochum, M., Klein,
639   A.M., Klingenberg, E.O.F., Landis, D.A., Lepš, J., Lindborg, R., Meyer, S.T., Temperton, V.M.,

640   Westphal, C. & Tscharntke, T. (2019) *Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems*. *Advances in Ecological Research*, Academic Press.

642 Meyer, C., Weigelt, P. & Kreft, H. (2016) Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters*, **19**, 992–1006.

644 Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What Is the Observed Relationship Between Species Richness and Productivity? *Ecology*, **82**, 2381–2396.

647 Naeem, S., Duffy, J.E. & Zavaleta, E. (2012) The Functions of Biological Diversity in an Age of Extinction. *Science*, **336**, 1401–1406.

649 Oberle, B., Grace, J.B. & Chase, J.M. (2009) Beneath the veil: plant growth form influences the strength of species richness–productivity relationships in forests. *Global Ecology and Biogeography*, **18**, 416–425.

652 Pan, Y., Chen, J.M., Birdsey, R., McCullough, K., He, L. & Deng, F. (2012) *NACP Forest Age Maps at 1-km Resolution for Canada (2004) and the U.S.A. (2006). Data set.*, ORNL DAAC, Oak Ridge, Tennessee, USA.

655 Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

657 Petersen, M.L. & van der Laan, M.J. (2014) Causal models and learning from data: integrating causal modeling and statistical estimation. *Epidemiology (Cambridge, Mass.)*, **25**, 418–426.

659 van der Plas, F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, **94**, 1220-1245.

661 Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C.C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Chećko, E., Dawud, S.M., Wandeler, H.D., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L. & Baeten, L. (2017) Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, **20**, 1414–1426.

671 Rohde, K. (1992) Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos*, **65**, 514–527.

673 Rosenzweig, M.L. (1995) *Species diversity in space and time*, Cambridge University Press.

674 Rosseel, Y. (2012) lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software*, **48**, 1–36.

676 Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, **546**, 48–55.

678 Schulze, E. & Mooney, H. (1993) *Biodiversity and Ecosystem Function*, Springer, Berlin.

679 Shipley, B. (2016) *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference with R*, 2nd edn. Cambridge University Press.

681 Šímová, I., Storch, D., Keil, P., Boyle, B., Phillips, O.L. & Enquist, B.J. (2011) Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Global Ecology and Biogeography*, **20**, 842–856.

684 Srivastava, D.S. & Vellend, M. (2005) Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation? *Annual Review of Ecology, Evolution, and Systematics*, **36**, 267–294.

686 Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, **17**, 866–880.

688 Storch, D., Evans, K.L. & Gaston, K.J. (2005) The species–area–energy relationship. *Ecology Letters*, **8**, 487–492.

690 The Plant List (2013) Version 1.1 URL: http://www.theplantlist.org/ [accessed 1 December 2017].

691   The Taxonomic Name Resolution Service iPlant Collaborative. (2018) Version 4.0. [Accessed September
692   2018]. Available from http://tnrs.iplantcollaborative.org.
693   Thomas, S.C. & Martin, A.R. (2012) Carbon Content of Tree Tissues: A Synthesis. *Forests*, **3**, 332–352.
694   Thompson, P.L., Isbell, F., Loreau, M., O'Connor, M.I. & Gonzalez, A. (2018) The strength of the
695   biodiversity–ecosystem function relationship depends on spatial scale. *Proceedings of the Royal*
696   *Society B: Biological Sciences*, **285**.
697   Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general
698   principles. *Ecology*, **80**, 1455–1474.
699   Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and Ecosystem Functioning. *Annual Review of*
700   *Ecology, Evolution, and Systematics*, **45**, 471–493.
701   Turnbull, L.A., Isbell, F., Purves, D.W., Loreau, M. & Hector, A. (2016) Understanding the value of plant
702   diversity for ecosystem functioning through niche theory. *Proceedings of the Royal Society of*
703   *London B: Biological Sciences*, **283**.
704   USDA Forest Service (2017) *Forest Inventory and Analysis National Program (FIA) database v. 1.7.0*.
705   USDA NRCS (2018) The PLANTS Database (http://plants.usda.gov).
706   USGS (2009) SRTM v2.1 Topography.
707   Venail, P., Gross, K., Oakley, T.H., Narwani, A., Allan, E., Flombaum, P., Isbell, F., Joshi, J., Reich,
708   P.B., Tilman, D., van Ruijven, J. & Cardinale, B.J. (2015) Species richness, but not phylogenetic
709   diversity, influences community biomass production and temporal stability in a re-examination of
710   16 grassland biodiversity studies. *Functional Ecology*, **29**, 615–626.
711   Wagg, C., O'Brien, M.J., Vogel, A., Scherer   Lorenzen, M., Eisenhauer, N., Schmid, B. & Weigelt, A.
712   (2017) Plant diversity maintains long-term ecosystem productivity under frequent drought by
713   increasing short-term variation. *Ecology*, **98**, 2952–2961.
714   Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. &
715   Parmenter, R. (1999) The Relationship Between Productivity and Species Richness. *Annual*
716   *Review of Ecology and Systematics*, **30**, 257–300.
717   Wardle, D.A. (2016) Do experiments exploring plant diversity–ecosystem functioning relationships
718   inform how biodiversity loss impacts natural ecosystems? *Journal of Vegetation Science*, **27**,
719   646-653.
720   Whittaker, R. (1975) *Communities and Ecosystems*, 2nd edn. MacMillan, New York, USA.
721   Whittaker, R.J. (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species
722   richness–productivity relationship. *Ecology*, **91**, 2522–2533.
723   Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local
724   and regional scales. *Species diversity in ecological communities: historical and geographical*
725   *perspectives*, 66–74.
726   Zanne, A., Tank, D., Cornwell, W., Eastman, J., Smith, S., FitzJohn, R., McGlinn, D., O'Meara, B.,
727   Moles, A., Reich, P., Royer, D., Soltis, D., Stevens, P., Westoby, M., Wright, I., Aarssen, L.,
728   Bertin, R., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M., Oleksyn, J., Soltis, P.,
729   Swenson, N., Warman, L., Beaulieu, J. & Ordonez, A. (2013) *Data from: Three keys to the*
730   *radiation of angiosperms into freezing environments*, Dryad Digital Repository.
731   Zhao, M., Heinsch, F.A., Nemani, R.R. & Running, S.W. (2005) Improvements of the MODIS terrestrial
732   gross and net primary production global data set. *Remote Sensing of Environment*, **95**, 164–176.
733   Zhao, M. & Running, S.W. (2010) Drought-induced reduction in global terrestrial net primary production
734   from 2000 through 2009. *Science*, **329**, 940–943.
735   Zuppinger-Dingley, D., Schmid, B., Petermann, J.S., Yadav, V., De Deyn, G.B. & Flynn, D.F.B. (2014)
736   Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*,
737   **515**, 108–111.