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Environmental heterogeneity modulates the effect of biodiversity on the spatial

variability of grassland biomass

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70   **Abstract:**

71   Plant productivity varies due to environmental heterogeneity, and theory suggests that plant

72   diversity can reduce this variation. While there is strong evidence of diversity effects on temporal

73   variability of productivity, whether this mechanism extends to variability across space remains

74   elusive. Here we determine the relationship between plant diversity and spatial variability of

75   productivity in 83 grasslands, and quantify the effect of experimentally increased spatial

76   heterogeneity in environmental conditions on this relationship. We found that communities with

77   higher plant species richness (alpha and gamma diversity) have lower spatial variability of

78   productivity as reduced abundance of some species can be compensated for by increased abundance

79   of other species. In contrast, high species dissimilarity among local communities (beta diversity) is

80   positively associated with spatial variability of productivity, suggesting that changes in species

81   composition can scale up to affect productivity. Experimentally increased spatial environmental

82   heterogeneity weakens the effect of plant alpha and gamma diversity, and reveals that beta diversity

83   can simultaneously decrease and increase spatial variability of productivity. Our findings unveil the

84   generality of the diversity-stability theory across space, and suggest that reduced local diversity and

85   biotic homogenization can affect the spatial reliability of key ecosystem functions.

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88   **Introduction:**

89   Understanding the mechanisms linking biodiversity with ecosystem stability is essential to

90   anticipate the consequences of species loss for the sustainable delivery of critical ecosystem

91   services[1–5]. Theory and empirical tests have demonstrated that plant biodiversity can stabilize

92   primary productivity of communities through time[4], and a variety of mechanisms have been

93   proposed to explain this effect[6]. These mechanisms range from simple statistical relationships, such

94   as the portfolio effect (i.e., statistical averaging of the independent and random fluctuations in the

95   performance or abundance of different species[7]), to niche-based models like overyielding (i.e.,

96   increase of the mean productivity, relative to its variance, when a mixture exceeds the expected

97   productivity based on monocultures[8]). Previous studies, nevertheless, identified asynchronous

98   species responses to environmental fluctuations as the major underlying mechanism[9–12]. That is,

99   biodiversity buffers productivity against environmental fluctuations, because reduced abundance of

100 some species can be compensated for by increased abundance of other species[10,13]. Although this

101 "insurance effect" is usually considered over time[13], theory suggests that it should also apply across

102 space[13,14], because a larger species pool will be more likely to contain species that can grow well

103 under different environmental conditions in space, decreasing the variability of productivity (i.e.,

104 increasing stability) across space[13,15]. Although the potential effect of biodiversity on the spatial

105 variability of productivity has found some support in experimentally assembled communities[15–17]

106 and natural systems[14], whether these results can be generalized is unknown and, to our knowledge,

107 support for the different potentially involved mechanisms has not been evaluated empirically[13].

108   Similar to its temporal counterpart, the spatial version of the insurance hypothesis[15,18]

109 proposes stronger effects of plant biodiversity in heterogeneous environments compared to

110 homogeneous environments[18,19] (see Fig. 1). This is because the greater the number of species

111 present (i.e. either alpha or gamma diversity), the higher the probability of including the set of best-

112   performing species under different environmental conditions[18] (Fig. 1B). Despite these clear

113   predictions for alpha and gamma diversity, the potential relationship between the spatial turnover in

114   species composition (i.e. beta diversity) and the spatial variability of productivity is harder to

115   anticipate. Following the arguments above, as spatial turnover in species composition can emerge

116   from (compensatory) changes among species under heterogeneous environmental conditions,

117   increased beta diversity may reduce spatial variability of productivity (Fig. 1C). However, changes

118   in species composition can scale up to affect aggregate ecosystem properties, such as productivity[20]

119   (especially if different species imply different functional traits). Under the spatial insurance

120   theory[21], systems with high beta diversity are expected to have high spatial variability in

121   productivity across different patches at a given time, stabilizing productivity through time at larger

122   spatial scales (that integrate all patches)[21–24]. This positive effect of beta diversity on the spatial

123   variability of productivity may be especially important when patches are environmentally

124   similar[21,25,26] (see Fig. 1C). Thus, the opposite predictions for the potential effect of beta diversity on

125   spatial variability of productivity can be reconciled if the outcome is context dependent. Under low

126   environmental heterogeneity, beta diversity may mainly act as a destabilizing factor, because

127   communities with different species compositions can respond differently to the common

128   environment[21,27]. Under high environmental heterogeneity, in contrast, beta diversity may act as a

129   stabilizing factor, because different species may perform better under different environmental

130   conditions (Fig. 1C). Biodiversity loss at different scales[5] is an important consequence of

131   anthropogenic activities that also impacts the functioning of ecosystems. While biodiversity-

132   functioning research has predominantly focused on temporal stability of biomass, less is known

133   about spatial stability[13]. However, if biodiversity can buffer environmental change and stabilize

134   spatial ecosystem functions and services, then biodiversity restoration and conservation will

135   concurrently maximize functioning and spatial reliability[3] in changing conditions.

136   Here, we explore the relationship between different scales of plant species diversity and

137   spatial variability of productivity, measured as standing biomass, across 83 grasslands worldwide

138   (see Fig. 2; Supplementary Table 1) that are part of the Nutrient Network distributed experiment

139   (NutNet; http://www.nutnet.org[28]). Using sets of 10 unmanipulated plots (25 m^2) arranged in blocks

140   (250 m^2) from these grasslands, we first analyzed whether local plot diversity (alpha diversity),

141   larger site-scale diversity (gamma diversity), and among-plot variability in species composition

142   (beta diversity) are associated with the spatial variability of productivity, defined as the coefficient

143   of variation (i.e. standard deviation/mean)[13,14] of aboveground standing biomass among plots. We

144   also tested whether these associations are driven by two previously proposed niche-based

145   mechanisms: (1) overyielding, or enhancing productivity (see ref[29] for a temporal analog); and (2)

146   insurance provided by spatial compensation between species[13]. Second, we tested how the

147   association between different scales of diversity and spatial variability of productivity is affected by

148   imposed spatial environmental heterogeneity. For this second objective, we used a subset of 42

149   grasslands that implemented a factorial nutrient addition and herbivore exclusion experiment[28] (see

150   Fig. 2; Supplementary Table 1). This experimental approach (see Methods section) represents a set

151   of local plots (25 m^2), with different resource supply, collectively representing a larger scale (an

152   arrangement of 10 of those local plots resulting in 250 m^2) with spatial heterogeneity in

153   environmental conditions (sampling methods and spatial scales are the same than for the previously

154 described sampling; see Methods section). According to niche dimensionality theory[30,31], differences

155 in resource supply and associated nutrient ratios should create patches with different niches and

156 niche dimensions (i.e. different number of growth-limiting factors), increasing the spatial variability

157 of productivity. Sites with high species diversity may have a greater probability of including the set

158 of best-performing species in different patches (i.e. under different resource availability ratios),

159 decreasing spatial variability of productivity[32]. Thus, environmental heterogeneity may increase

160 variability of productivity across space and, in theory, alpha, beta and gamma diversity may

161 decrease this variability.

162 **Results**

163 **Global patterns of biodiversity-spatial variability of productivity relationships**

164   Using unmanipulated (i.e., pre-treatment) data from the 83 grasslands, we found that alpha

165 (linear mixed-effects models, $\chi^2 = 17.41$; P < 0.001) and gamma ($\chi^2 = 5.59$, P < 0.05) diversity were

166 both negatively associated with spatial variability of productivity (Fig. 3A, B), whereas beta

167 diversity was positively associated with spatial variability of productivity ($\chi^2 = 9.77$, P < 0.005, Fig.

168 3C). We found no significant relationship between the different scales of biodiversity and the two

169 separate components of spatial variability (i.e., μ, the mean plot biomass; alpha: $\chi^2 = 0.52$; beta: $\chi^2 =$

170 0.74; gamma: $\chi^2 = 0.04$; all P> 0.05; Supplementary Fig. 1; and σ, the standard deviation of plot

171 biomass; alpha: $\chi^2 = 0.03$; beta: $\chi^2 = 0.81$; gamma: $\chi^2 = 1.29$; all P> 0.05; Supplementary Fig. 1). The

172 patterns were consistent when modeled with type II regression (Supplementary Fig. 2) and for

173 different diversity indices (Supplementary Table 2; Supplementary Fig. 3). The patterns also

174 persisted after accounting for differences in site environmental conditions, such as precipitation,

175 temperature and seasonality (Supplementary Table 3; Supplementary Table 4). Both alpha and

176 gamma diversity were negatively associated with species covariation, a spatial analog of species

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176   synchrony that (inversely) measures the degree of spatial biomass compensation between species

177   (alpha: χ^2= 33.43, P< 0.001; gamma: χ^2= 28.56, P< 0.001; Fig. 3D, E). Species covariation was, in

178   turn, strongly associated with spatial variability (χ^2= 247.83, P< 0.0001; Fig. 3G). However, we

179   found no significant relationship between beta diversity and species covariation (χ^2= 2.31, P= 0.13;

180   Fig. 3F).

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182   Direct and indirect effects of biodiversity on the spatial variability of productivity

183   To explicitly evaluate overyielding and compensatory changes between species[13] as

184   mechanisms by which increased biodiversity could decrease spatial variability of biomass, we

185   constructed a Structural Equation Model (SEM). The final model showed a good fit (Fisher's C=

186   8.82, df= 6, P= 0.2) and explained a high proportion of the total variance of spatial variability of

187   productivity (marginal R^2= 0.66; conditional R^2= 0.90). Spatial variability of productivity was

188   influenced primarily (and negatively) by species covariation (Fig. 3H). Higher alpha diversity

189   contributed to lower spatial variability through lower species covariation (Fig. 3H). Higher gamma

190   diversity also contributed to lower spatial variability, but this effect was mainly because of a strong

191   correlation with alpha diversity (Fig. 3H). The indirect negative effect of gamma diversity on spatial

192   variability (through alpha diversity) was partially offset by a direct positive effect (Fig. 3H). Higher

193   beta diversity, in contrast, contributed to spatial variability via two processes. First, beta diversity

194   positively contributed to spatial variability (Fig. 3H). Second, this positive effect was partially

195   offset by a negative contribution of beta diversity to spatial variability through lower species

196   covariation (Fig. 3H). The model did not include pathways from any level of diversity to spatial

197   variability mediated by biomass production (Fig. 3H), confirming the absence of overyielding in

198   contributing to spatial variability seen in bivariate relationships. After refitting the SEM using a

199   smaller set of sites (54 sites in which soil samples were collected to include an estimation of spatial

200   environmental heterogeneity), we found a positive direct effect of edaphic spatial heterogeneity on

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beta diversity but global model remained qualitatively unchanged (Supplementary Fig. 4).

The effect of increased environmental heterogeneity

Next, we evaluated the effect of increased environmental heterogeneity on the relationship between spatial variability of productivity and species diversity using data from a subset of 42 grasslands (Fig. 2A) that experimentally enhanced environmental heterogeneity via nutrient and fencing treatments. Enhanced environmental heterogeneity increased the spatial standard deviation and the spatial variability of productivity, as well as beta diversity (Supplementary Fig. 5). As experimental manipulation implied nutrient additions in most plots, it also increased μ, the mean plot biomass and decreased alpha diversity (Supplementary Fig. 5). However, enhanced environmental heterogeneity did not affect species covariation or gamma diversity (Supplementary Fig. 5). In addition, experimentally enhanced environmental heterogeneity flattened the relationships between the three scales of diversity and spatial variability (diversity*heterogeneity interaction, alpha: $\chi^2= 23.41$; beta: $\chi^2= 3.89$; gamma: $\chi^2= 14.92$; all P< 0.01; Fig. 4A-C; see also Supplementary Fig. 6 for an analysis including an intermediate level of heterogeneity).

Finally, using the data from the subset of grasslands that experimentally enhanced environmental heterogeneity, we refitted the SEM analysis, including experimentally increased spatial heterogeneity as a factor. Results identified two major changes in the pathways, compared to the model using data from unmanipulated (i.e. pre-treatment) plots, in which increased spatial environmental heterogeneity weakened the diversity-variability relationship for the three scales of diversity (i.e., there were two paths that varied between pre- and post-treatment; Fig. 4D,E). First, the negative relationship between alpha diversity and species covariation under ambient conditions became non-significant under increased heterogeneity (Fig. 4D,E). Second, the neutral relationship between beta diversity and species covariation under ambient conditions became negative under increased heterogeneity.

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Discussion

Greater plant diversity is known to contribute to decreased temporal variability of
community productivity through higher asynchronous temporal dynamics among species in
response to environmental fluctuations (species asynchrony[13]). Adding to this theory, we
demonstrate that these same processes also occur through space. Across a wide range of global
grasslands, spatial variability of site productivity declines with increasing plant diversity because of
compensatory species responses to spatial heterogeneity (i.e., reduced species covariation across
space). An obvious alternative explanation is that spatial environmental heterogeneity drives both
spatial variability of productivity and biodiversity, but basic community theory predicts that more
spatially variable environments should have higher biodiversity at both site (gamma) and local
(alpha) scales due to niche partitioning (increasing heterogeneity in environmental conditions
promote species diversity by adding different niches)[33] and spatial mass effects (sink-source
dynamics in which local species diversity can be enriched by species from the heterogeneous
surrounding areas)[34]. Thus, this explanation would predict a positive association between
biodiversity and spatial variability of productivity, contrary to the negative association we observed.
In contrast to the observed decline in spatial variability of productivity with increasing alpha and
gamma diversity, greater beta diversity was positively associated with spatial variability of
productivity. These contrasting associations have been suggested by theoretical metacommunity
studies (i.e. the spatial insurance theory)[21] that postulate that beta diversity plays a key role in the
temporal stability of productivity at regional scales, as it involves higher variation in temporal
dynamics among local communities (spatial asynchrony), implying high spatial variability of
productivity at a given time[13,21]. To our knowledge, nevertheless, this is the first study to provide
empirical evidence. Finally, we demonstrate that spatial environmental heterogeneity,
experimentally created by the addition of multiple types and combinations of nutrients and

251 herbivore exclusions, increases (as expected) the spatial variability of productivity but weakens the

252 relationships between different scales of plant diversity and this spatial variability.

253   The negative association of alpha and gamma diversity with spatial variability of

254 productivity can result from a combination of processes[6]. For instance, higher plant diversity often

255 increases productivity (overyielding[35]). If this increase in the mean is not compensated by a

256 proportional increase in its standard deviation, high diversity sites should have lower spatial

257 variability of productivity[8]. In contrast, as the effect of diversity on productivity may change along

258 productivity gradients (shifting from positive in low-productivity communities to neutral or

259 negative in high-productivity communities), diversity may decrease spatial variability by

260 maintaining community productivity at intermediate levels (thus decreasing its standard

261 deviation)[14]. In the present study, both the bivariate relationships and the SEM analysis showed no

262 significant direct relationship between diversity and the mean or the standard deviation of

263 productivity when individually analyzed. But, when analyzing the spatial variability of productivity

264 as a composite variable (i.e. coefficient of variation), our results suggest a combined effect on the

265 two components (i.e., the ratio between standard deviation and mean productivity is a relative

266 measure of variability that removes the impact of mean productivity). Results further suggest that

267 the main underlying mechanism by which alpha and gamma diversity decrease spatial variability of

268 productivity is by decreasing species covariation (see also Fig. S4). Different species can present

269 non-correlated or negatively correlated changes in biomass production in different patches; thus,

270 highly diverse systems have lower spatial variability in aggregate productivity. Our results thus

271 highlight the importance of compensatory species responses to environmental variation, as a general

272 stabilizing mechanism for ecosystem function, not only in the temporal[4,23,36], but also in the spatial

273 dimension as recently suggested[13].

274   The stabilizing mechanism of compensatory changes between species, contributing to more

275 consistent biomass[6,13] may involve shifts in relative species abundances rather than abrupt

276 compositional changes (i.e. species turnover), as our results show that large changes in species

277 composition (i.e. high beta diversity) are related to increases in the spatial variability of

278 productivity. This pattern can arise because changes in species composition and spatial variability

279 of productivity (or other aggregate functions) are both related to spatial heterogeneity in

280 environmental conditions. The SEM analysis, nevertheless, only detected an indirect path between

281 spatial environmental heterogeneity and spatial variability, a path that was mediated by beta

282 diversity. This suggests that at least part of the observed relationship between beta diversity and

283 spatial variability cannot be explained by its simultaneous correlation with environmental

284 heterogeneity.

285   Experimentally imposed environmental heterogeneity weakened the bivariate negative

286 relationship between spatial variability and both alpha and gamma diversity on the one hand, and

287 the bivariate positive relationship with beta diversity on the other hand. Our SEM model suggests

288 that this effect is due to a weaker relationship between alpha diversity and species covariation.

289 Thus, under experimentally increased environmental heterogeneity, biomass production of different

290 species was no longer negatively correlated, i.e., they may have more coupled responses to spatial

291 environmental variation, disabling the potential compensation between them. Our experimental

292 design, in addition to the intended increased environmental heterogeneity (through varying

293 combinations of nutrient additions), also led to higher mean plot biomass, and lower alpha diversity

294 as a consequence of increased mean nutrient inputs[37]. However, these effects should mostly affect

295 variability rather than the relationships between diversity and variability as observed. Our SEM

296 analysis also suggests that, under increased environmental heterogeneity, the weaker relationship

297 between beta diversity and spatial variability resulted from an enhanced negative contribution of

298 beta diversity to species covariation. Although of lower magnitude, this path was also detected

299 using the full set of observational sites, but it was overcome by the stronger and positive direct path

300 between beta diversity and spatial variability. If different species are able to respond differently to

13

301 environmental heterogeneity, higher dissimilarity in species composition among communities may

302 decrease species covariation[13]. As this indirect path had a similar magnitude but opposite sign

303 compared to the direct positive path, the two paths canceled each other out. Our results support

304 theoretical work suggesting that beta diversity acts as a destabilizing factor, as changes in species

305 composition can involve shifts in functional traits that scale up to affect community

306 production[20,21,26]. At the same time, beta diversity can also act as a stabilizing factor, because

307 different species may perform better under different environmental conditions[32]. When

308 environmental variability is large enough, high contrast in environmental conditions drives coupled

309 biomass covariation of shared species, but species divergence may partially offset this effect

310 decreasing the spatial variability of productivity (Fig. 1C).

311   The most likely driver of spatial heterogeneity at the spatial scale of our study design (i.e.

312 hundreds of meters) is plot-scale variability of biotic or abiotic conditions. Spatial heterogeneity in

313 environmental conditions is usually the result of concurrent, superimposed gradients occurring at

314 multiple spatial scales, or multiple disturbances interacting with each other[38]. Biomass production

315 often varies in response to this combination of coarse and fine-scale heterogeneity. Results of

316 studies evaluating the effect of biodiversity on ecosystem function are often scale-dependent. For

317 example, small-scale studies are more likely to be at the spatial scales at which niche-partitioning

318 and competitive exclusion operate. Large-scale studies, on the other hand, are likely to detect the

319 effects of site-scale factors (e.g., climate, herbivory) that may covary with diversity, thereby

320 reducing the ability to detect niche partitioning and competition[39]. At larger spatial scales, the

321 importance of alpha diversity may decrease (niche partitioning becomes less important relative to

322 extrinsic factors). Concurrently, the importance of beta diversity may increase (as different species

323 are filtered into environmental conditions where their traits most efficiently convert resources into

324 biomass)[40]. Thus, even among the largest patches, diversity may continue to have an additional

325 buffering effect on spatial variability in biomass production[41]. This natural spatial heterogeneity

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326 (even at small-scale) also contrasts with our experimentally increased heterogeneity, because our

327 experimental landscape was characterized by high-contrast patches with sharp boundaries (i.e.

328 clearly delimited experimental plots presenting within-plot homogeneous nutrient conditions and

329 contrasting nutrient conditions among-plots). Perhaps the most clear natural analogy takes place in

330 some grazed systems, where a combination of abiotic (salinity, fire frequency, nutrients, water

331 content) and biotic variables (grazer density, bioturbation, nutrient cycling) creates distinct patches

332 of contrasting plant height, biomass and composition[42–44]. Those characteristics are also common

333 features of some anthropogenic biomes (heterogeneous landscape mosaics, combining a variety of

334 different land uses or land use histories[45,46]) and similar to the management-driven landscape

335 heterogeneity implemented to restore ecosystem complexity and diversity[47–50]. Thus, although the

336 application of spatially variable management tools (such as patch-burning, patch-grazing, and land-

337 use diversification) can increase spatial heterogeneity and restore diversity, they can potentially

338 disrupt biodiversity-spatial variability relations.

339 Large-scale human impacts on ecosystems, such as land use intensification, N deposition or

340 species invasions, have been driving biotic homogenization, including losses in beta diversity[51–54].

341 Our results suggest that those losses may lead to lower spatial variability in ecosystem-scale

342 processes. The spatial homogenization in species composition may also imply higher spatial

343 correlations in ecosystem temporal dynamics[21,23,25,55], increasing temporal variability of ecosystem

344 functions at the landscape scale[21,23,56]. In addition, most of the drivers of biotic homogenization (e.g.

345 eutrophication and trophic simplification[37]) also lead to reductions in alpha diversity (but see ref[57]).

346 Thus, the potential loss of species at a local scale may still cause increased spatial (our results) and

347 temporal[23,58] variability of ecosystem function, even in this biologically homogenized scenario.

348 Biodiversity is thus a necessary prerequisite to ensure greater stability of key ecosystem functions in

349 the face of an ever expanding human footprint on environmental heterogeneity.

350

Methods:

To explore the relationship between different scales of plant biodiversity and spatial variability of productivity, we used observational (i.e. pre-treatment) data from 83 natural and semi-natural grassland ecosystems in 18 countries across 6 continents (see Fig. 2; Supplementary Table 1) that are part of the Nutrient Network collaborative experiment (NutNet)[28]. All sites are dominated by herbaceous species, and together cover a wide range of grassland habitats that range from alpine grassland, to prairie, pasture, shrub steppe, savanna and old field. These grasslands also cover a wide range in elevation (0 to 4400 masl), mean annual precipitation (192 to 2566 mm yr^{-1}), mean annual temperature (-7 to 27° C), latitude (52 degrees S to 69 degrees N), and aboveground productivity (0.5 to 1445 g m^{-2} yr^{-1}; Fig. 2B). Study sites contained three replicate blocks each composed of ten 5 m × 5 m plots (see Supplementary Table 1 for exceptions). Here, we consider each plot as a "patch", and the block of 10 plots as the "larger scale"[23]. Thus, each "larger scale" is composed of 10 "patches" (but see Supplementary Table 1 for exceptions) and there are at least 3 "larger scales" per site, for a total of 83 sites, 271 "larger scales", and 2700 "patches". We defined alpha diversity as species richness at the "patch" level, gamma diversity as species richness at the "larger scale" level, and beta diversity as the dissimilarity in species composition across the 10 "patches" within each "larger scale" (see details below).

To evaluate the effect of increased environmental heterogeneity on the relationship between spatial variability of productivity and species diversity, we used data from 42 of those sites (Fig. 2A) that implemented, for at least 4 years, an experiment with three nutrient addition treatments (Nitrogen (N), Phosphorus (P), Potassium plus micronutrients (Kµ)) and vertebrate herbivore exclusion. At most sites plots were arranged in 3 blocks, each block containing the 10 focal treatments: control (unfenced and unfertilized), +N, +P, +Kµ, +NP, +NKµ, +PKµ, +NPKµ, fenced (unfertilized), and fenced +NPKµ. Thus, each "larger scale" was composed of 10 "patches" with different environmental conditions, that include variations in the availability of the most important

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376 limiting nutrients and variations in herbivory pressure. Here we used data from the 4th year of

377 treatments. Nitrogen, P and K were applied annually to experimental plots while micronutrients

378 were applied just once, at the start of the experiment, to avoid toxic levels from over-application.

379 Nutrient addition rates and sources were: 10 g N m^{-2} yr^{-1} as timed-release urea ($(NH_2)_2CO$), 10 g P

380 m^{-2} yr^{-1} as triple-super phosphate ($Ca(H_2PO_4)_2$), 10 g K m^{-2} yr^{-1} as potassium sulphate (K_2SO_4) and

381 100 g m^{-2} yr^{-1} of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn

382 (1%), B (0.2%) and Mo (0.05%). Fences were 2.1 m tall and excluded aboveground, non-climbing,

383 vertebrate herbivores. The lower 0.9 m was composed of 10 mm woven wire mesh with a 0.3 m

384 outward-facing flange stapled to the ground to exclude digging animals. The top 1.2 m was

385 composed of five rows of wire. Minor variations in fence design are described by [28]. Each plot was

386 separated by at least 1.5 m from neighboring plots (1 m walkway and 0.5 m within-plot buffer),

387 which served to minimize indirect effects of treatments in one plot on adjacent plots (for example,

388 nutrient leaching, shading or mycelial networks). Although different sites started the experiment in

389 different years, we used data from the 4th year of treatment implementation. Thus, sites have the

390 same length of treatment years.

391

392 *Data acquisition and calculations*

393 The variables described in this section were calculated separately for the pre-treatment and

394 post-treatment (4th year of treatment implementation) sampling. Thus, we created two datasets, one

395 based on pre-treatment (natural) conditions from 83 grasslands, and one with increased

396 environmental heterogeneity from a subset of 42 grasslands.

397 We used aboveground live biomass as a surrogate measure of primary productivity.

398 Aboveground live biomass was estimated destructively each year, at peak standing biomass, by

399 clipping all aboveground biomass of individual plants rooted within two 0.1 m^2 (10 cm x 100 cm)

400 quadrats at ground level. Biomass was sorted into current (live and recently senescent material) and

17

401 previous year's growth. For shrubs and subshrubs, all leaves and the current year's stems were

402 collected. All biomass was dried to a constant mass at 60°C prior to weighing to the nearest 0.01 g.

403 Cover of each species was estimated non-destructively at a permanent 1 m x 1 m subplot within

404 each plot. Plant species cover was recorded to the nearest 1% for each species in the plot. Cover

405 was estimated independently for each species so that total summed cover can exceed 100% for

406 multilayer canopies. During pre-treatment sampling, soil samples were collected from each plot

407 (three 25 mm diameter cores to 100 mm depth); because of missing samples, this dataset includes a

408 subset of 54 of the 83 sites. Soils were air dried to constant mass, weighed, and analyzed for pH,

409 total carbon (C in %), total N (in %), P (ppm), and K (ppm) concentrations. C and N analyses were

410 done at the University of Minnesota and the University of Nebraska via dry combustion GC

411 analysis (COSTECH ESC 4010 Element Analyzer) using cross-calibrated machines. Data also were

412 generated on soil phosphorus, potassium, and micronutrients, soil pH, organic matter, and texture

413 from each sample (A&L Analytical Laboratory, Memphis, TN, USA). Full details of Nutrient

414 Network methods can be found in Borer *et al*. (2014)[28].

415   We estimated alpha, beta and gamma diversity separately for each block, using the approach

416 described in[56]. Alpha diversity was estimated as the mean plant species richness per plot across all

417 plots within a block, whereas gamma diversity was estimated as the total plant species richness

418 within each block (i.e., block richness [56]). Beta diversity was estimated as the Jaccard Dissimilarity

419 Index across the 10 plots within each block[56]; we calculated this index using the function 'vegdist'

420 from the 'vegan' package[59] in R and then calculated the mean multivariate distance between the 10

421 plots and their centroid using the function 'betadisper' (also from the 'vegan' package). We used

422 these diversity indexes because they are all based on presence/absence. However, we evaluated if

423 our results still hold using other common biodiversity indexes, such as the Shannon Entropy index,

424 Inverse Simpson index and the Effective Number of Species (ENS) needed to reach the observed

425 Probability of Interspecific Encounter (S_{PIE})[60] for alpha and gamma diversity as well as Whittaker´s

426   multiplicative (i.e. alpha/gamma), additive (i.e. gamma-alpha) beta diversity[61] and abundance-based

427   multivariate beta diversity (Supplementary Table 2; Supplementary Fig. 3).

428   Stability is a multifaceted concept[62] that is commonly empirically measured as the inverse of

429   variability (i.e. invariability)[63]; the mean of an ecosystem property or function divided by its

430   standard deviation. However, the term "stability" has a temporal connotation so, to avoid confusion,

431   we defined spatial variability as the coefficient of variation (i.e., standard deviation divided by

432   mean)[13,14]. Spatial variability of productivity was defined for each larger scale (i.e. block) as σ/μ,

433   where σ is the spatial standard deviation of total live biomass, and μ is the spatial mean among the

434   10 plots of each larger scale. We estimated species covariation across space as a spatial analog of

435   species synchrony (insurance effects may emerge from asynchronous species fluctuations[10,13,22]). It

436   was measured for each block as:

437

438    $$\sigma^2 / \left(\sum_{i=1}^{S} \sigma_i \right)^2$$

439

440   where σ^2 is the variance in total plot live biomass, and σ_i is the standard deviation of species i

441   live biomass in a block with S species. Thus, if all species respond equally to spatial environmental

442   variability, species covariation approaches 1, but if different species are capable of differently

443   responding to this variability, species complement each other and species covariation approaches 0.

444   As we do not have per-species biomass data, we used species' relative cover as a proxy. Cover of

445   each species across the whole plot was multiplied by the total living biomass for the plot[36].

446

447   *Data analysis*

448   We first explored the relationship between different scales of biodiversity (i.e. alpha, beta and

449   gamma diversity) and the spatial variability of productivity using pre-treatment data from the 83

450   grasslands. We modeled these relationships with linear mixed-effects models using the 'lmer'

451   function in the 'lme4' package[64] in R version 4.0.5 (R Core Team 2021). To improve normality,

452   spatial variability was log-transformed before analysis. We used sites as random effects, allowing

453   the intercepts and slopes of the regression to vary between sites if supported by model selection. We

454   used a model-selection approach based on minimization of BIC following ref [65], in which we

455   compared models with and without a given random structure to determine which level of variation

456   was required in the model. In all cases, model selection retained only variation among sites in the

457   intercept. We also modeled these relationships using type II regression (ranged major axis method)

458   using the 'lmodel2' package[66] in R to take into account the existence of sampling error of both

459   predictor and response variables. As this model does not allow the inclusion of random structures

460   (i.e. to reflect or multi-level design), we averaged values at the site level (i.e. instead of using 3

461   replicates per site, and to avoid pseudoreplication, we used the average value per site). To evaluate

462   the two previously proposed niche-based mechanisms (i.e overyielding, which implies increases in

463   the spatial mean of productivity as diversity increases *versus* insurance, which implies decreases in

464   species covariation as diversity increases), we also separately explored the relationship between

465   biodiversity and each component of variability (i.e., σ and μ) and species covariation, using mixed-

466   effects models as described above.

467   To remove the possible influence of key abiotic factors on the relationship between different

468   scales of biodiversity and the spatial variability of productivity, we used a subset of bioclimatic

469   variables representing (i) annual trends (mean annual temperature (°C) and precipitation (mm);

470   seasonality (mean annual range in temperature (°C), standard deviation in temperature, coefficient

471   of variation of precipitation) and (ii) extreme or limiting environmental factors (mean temperature

472   during the wettest 4 months (°C)). We performed a multiple regression of spatial variability against

473   these climatic variables, kept the residuals, and then modeled the relationship between different

474   scales of diversity and the obtained residuals, using type II regression. We also performed a multi-

20

475 model inference (using the 'MuMIn' package)[67] to select the simplest models that explained the

476 most variation (of spatial variability) based on Akaike's information criterion (AIC). Candidate

477 models represented every possible combination of explanatory variables (i.e. the subset of

478 bioclimatic variables along with the different scales of diversity) and the interactions between

479 bioclimatic variables and the different scales of diversity.

480   We then fit a Piecewise Structural Equation Model (Piecewise SEM)[68] to infer the direct and

481 indirect effects of biodiversity on the spatial variability of productivity. Our model also aimed to

482 explicitly evaluate whether increased biodiversity can decrease spatial variability of biomass

483 production by the two previously proposed mechanisms (i.e. overyielding and decreased species

484 covariation; see Supplementary Table 5). We began with a full conceptual model (see

485 Supplementary Fig. 7) and followed a model simplification process in which non-significant paths

486 were iteratively removed until only significant paths remained[69] and/or model fit was higher (i.e.

487 minimization of BIC) than with further path removals. We incorporated site as a random effect in

488 individual models[68] and model fit was assessed using Shipley's test of d-separation, which yields a

489 Fisher's C statistic that is χ^2 distributed[68]. In order to include an estimation of spatial environmental

490 heterogeneity, we repeated the SEM analysis using the subset of 54 sites in which soil chemistry

491 was measured. Environmental heterogeneity was estimated as the average Euclidean distance using

492 the 'vegan' package[59] in R for standardized soil parameters (soil C, N, P and K contents, and pH)

493 and ambient light[56] among the 10 plots within each block.

494   Lastly, we explored the effect of increased environmental heterogeneity using data from the

495 42 sites with experimental nutrient addition (see Supplementary table 1). We first evaluated whether

496 increased environmental heterogeneity affects the observed bivariate relationships between different

497 scales of biodiversity and spatial variability of productivity, and then fitted the same SEM described

498 above. For comparisons we re-fit pre-treatment models for the subset of 42 experimental sites, and

499 then performed a multigroup analysis to evaluate differences in path coefficients between pre- and

500 post-treatment models using the 'multigroup' function from the 'piecewiseSEM' package[68] in R. In

501 short, this analysis implements a model-wide interaction in which every term in the model interacts

502 with the grouping variable (i.e. pre- *versus* post-treatment). If the interaction is significant, then the

503 path is free to vary by group; if not, then the path is constrained and takes on the estimate from the

504 global dataset.

505

506 **Data availability:** All data and code for these analyses will be published and publicly available via

507 EDI after this paper is accepted. Currently, the raw data that support these findings are available via

508 GitHub (https://github.com/juanalberti/spatial_variability).

509

510 **Code availability:** The complete R code supporting the findings of this study has been

511 archived online (https://github.com/juanalberti/spatial_variability).

512

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652

665   **Author Contributions:** P.D., J.A. E.J.C., O.I. and Y.H. developed and framed research questions.

666   P.D. and J.A. analyzed the data with contributions and inputs from E.J.C., O.I., Y.H., E.T.B, J.T.B.,

667   E.W.S., A.S.M., S.W., P.M.T. and S.B. P.D. and J.A.wrote the paper with contributions and input

668   from all authors. E.W.S., E.T.B. and P.A.W. are Nutrient Network coordinators.

669

670   **Competing interests:** The authors declare no competing interests.

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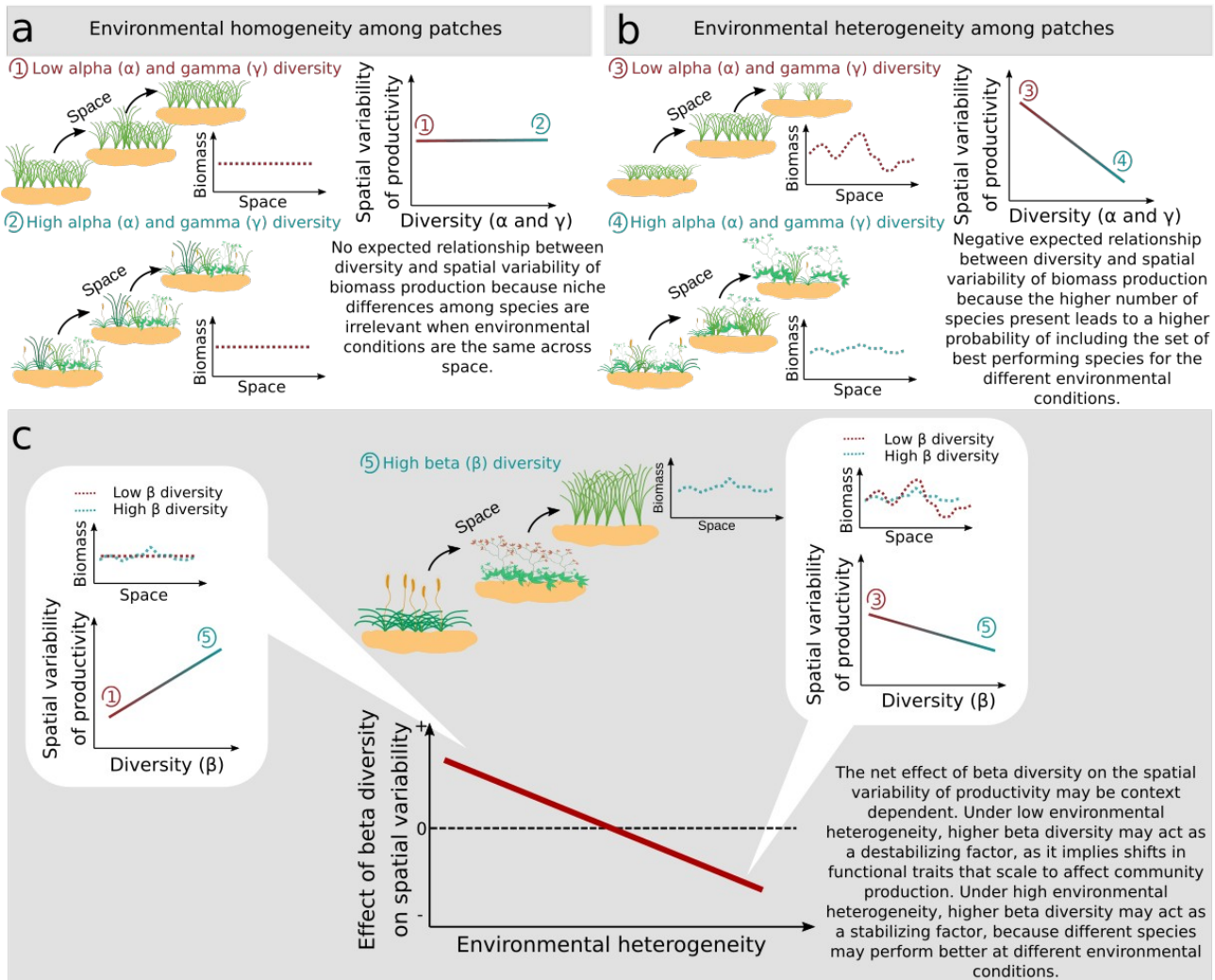
Figure 1. Conceptual figure illustrating the effect of different scales of biodiversity on the spatial variability of aggregate ecosystem functions. The insurance hypothesis postulates that biodiversity buffers aggregate ecosystem functions (e.g., biomass production) against environmental fluctuations, resulting in less variation within more diverse systems. This hypothesis was originally postulated for environmental fluctuations over time, but may also apply to spatial heterogeneity. **a** When environmental conditions are homogeneous, niche differences among species are non-important, and the variability of an aggregate ecosystem function is unaffected by alpha or gamma diversity. **b** In contrast, in heterogeneous environments, different environmental conditions provide an array of niches. In this scenario, a species may be functionally insignificant under some environmental conditions, but more abundant or functionally important under other

686 conditions. Thus, a highly diverse system may exhibit decreased variability of an aggregated

687 ecosystem function compared to low diversity systems. In this scenario, a negative relationship is

688 expected between alpha or gamma diversity and the spatial variability of the function. **c** The net

689 effect of beta diversity on spatial variability of an aggregated ecosystem function may be context

690 dependent. When environmental heterogeneity is low, beta diversity (that can be the result of

691 priority effect or other stochastic processes) may act as a destabilizing factor as it can imply shifts

692 in functional traits that scale up to affect community production. In contrast, when environmental

693 heterogeneity is high, beta diversity may act as a stabilizing factor because of niche

694 complementarity.

Fig. 2

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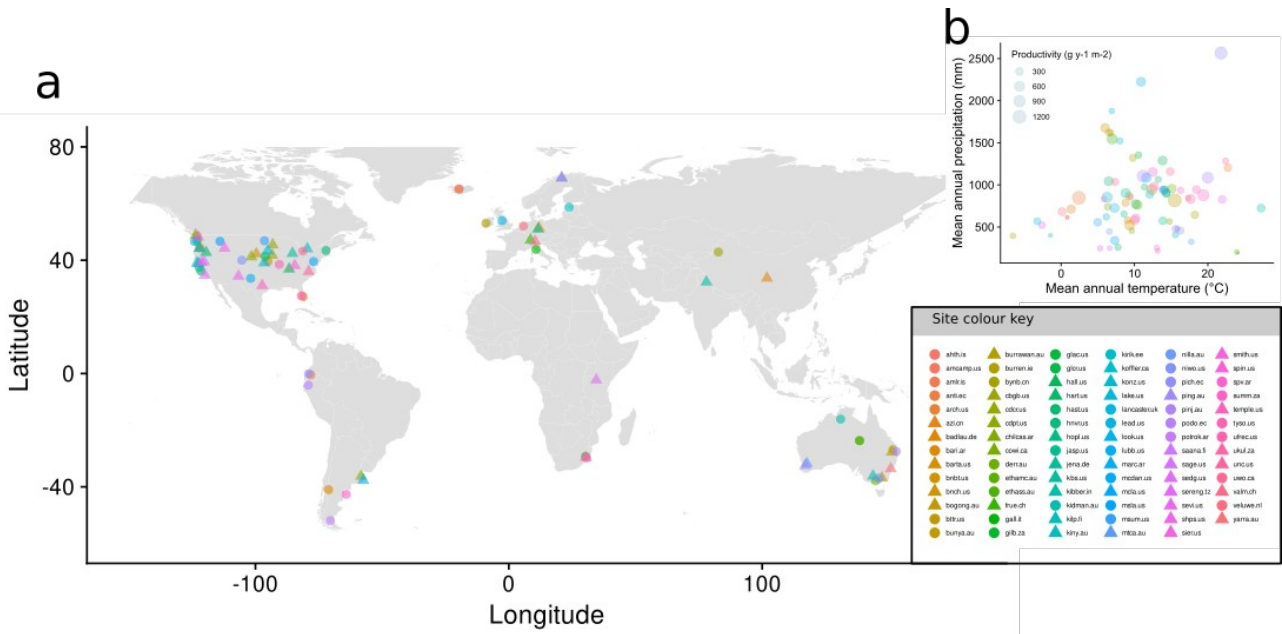
Fig. 2. Geographic and climatic distribution of grassland sites. a Global map showing the

locations of the 83 grassland sites included in this study. All sites were used to analyze diversity-

variability relationships under ambient spatial environmental heterogeneity (pre-treatment

conditions). Triangles denote the 42 sites that implemented the experimental protocol used to

evaluate the effect of increased environmental heterogeneity on diversity-variability relationships. **b**

The grassland sites span a wide range of mean annual productivity, mean annual temperature

(MAT), and mean annual precipitation (MAP). Site color key shows the color assignment to each

site, which is consistent in all figures.

708

Fig. 3
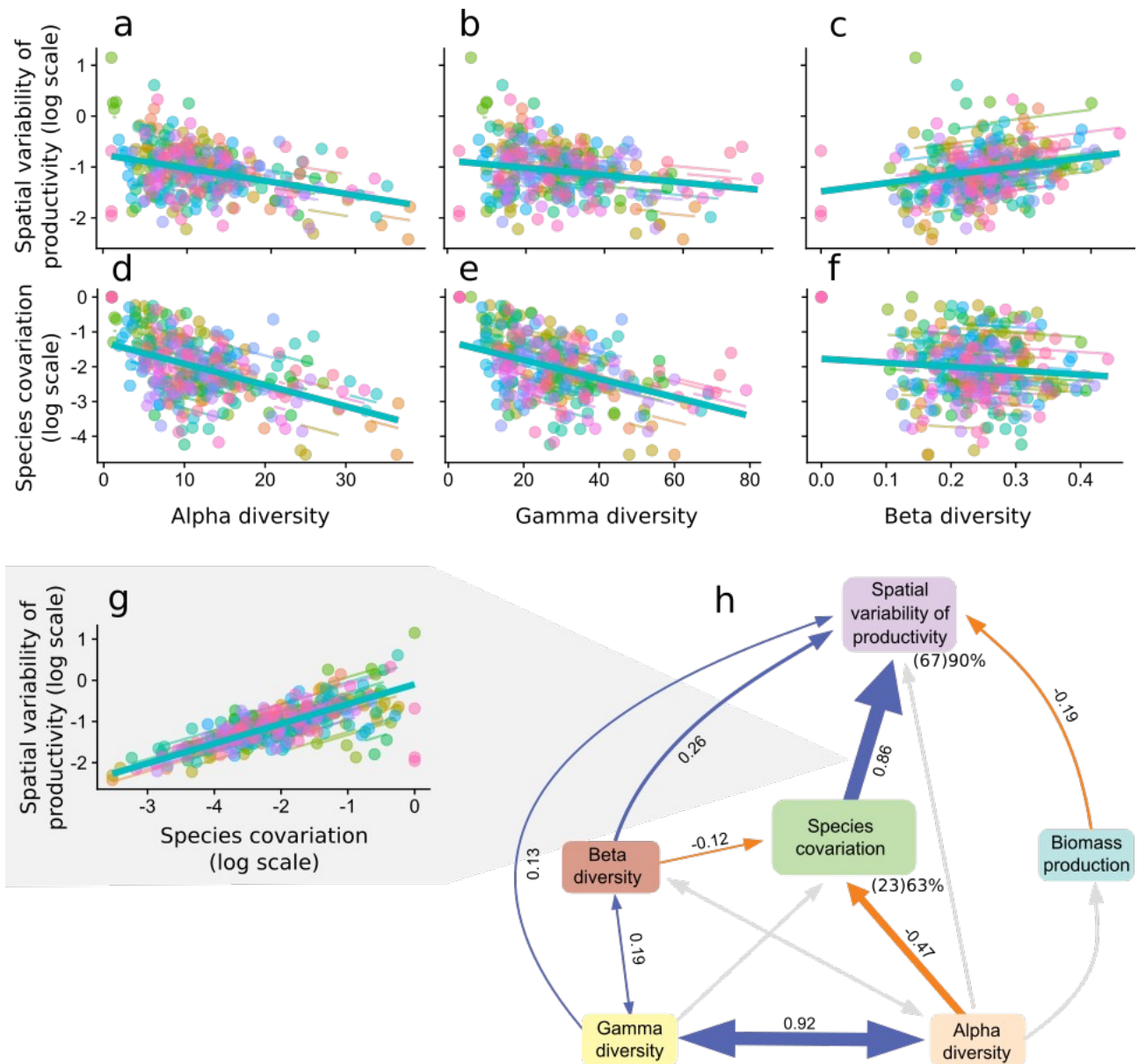
Figure 3. The relationships between plant species diversity and spatial variability of productivity across 83 globally distributed grasslands sites of the Nutrient Network. Both **a** alpha **(**slope and 95% CIs= -0.026 (-0.038 to -0.015)) and **b** gamma (-0.007 (-0.013 to -0.001)) diversity were negatively associated with the spatial variability. **c** Beta diversity, in contrast, was positively associated with spatial variability (1.57 (0.59 to 2.54)); **d** Alpha (-0.06 (-0.08 to -0.04)) and **e** gamma (-0.03 (-0.04 to -0.02)) diversity were negatively associated with species covariation. **f** Beta diversity, in contrast, was not associated with species covariation (-1.27 (-2.92 to 0.38)). **g** Species covariation, in turn, was positively associated with spatial variability of productivity (0.48 (0.44 to 0.53)). For panels **a-g,** different colors represent different sites (See Fig 2 for site color key

720　assignment), major lines (in turquoise) represent the fixed-effect linear regression slopes among

721　sites and small colored lines show patterns within sites. **h** Structural equation model (SEM) analysis

722　showing the direct and indirect pathways through which different scales of diversity determine

723　spatial variability of biomass. Solid blue arrows and solid orange arrows represent significant ($P \leq$

724　0.05) positive and negative paths, respectively, and light gray arrows represent non-significant paths

725　that were included in the initial model. Bidirectional arrows represent paths that were modeled as

726　correlated errors (i.e., bidirectional relationships instead of causal and unidirectional relationships).

727　Numbers next to the arrows are averaged effect sizes as standardized path coefficients; arrow

728　widths reflect these standardized effect sizes. For spatial variability of biomass and species

729　covariation, the marginal (i.e., explained by the fixed factors alone) and conditional (i.e., explained

730　by both the fixed and the random factors; in parentheses) percent of variance explained is shown

731　below and to the right of the variable name.

Fig. 4
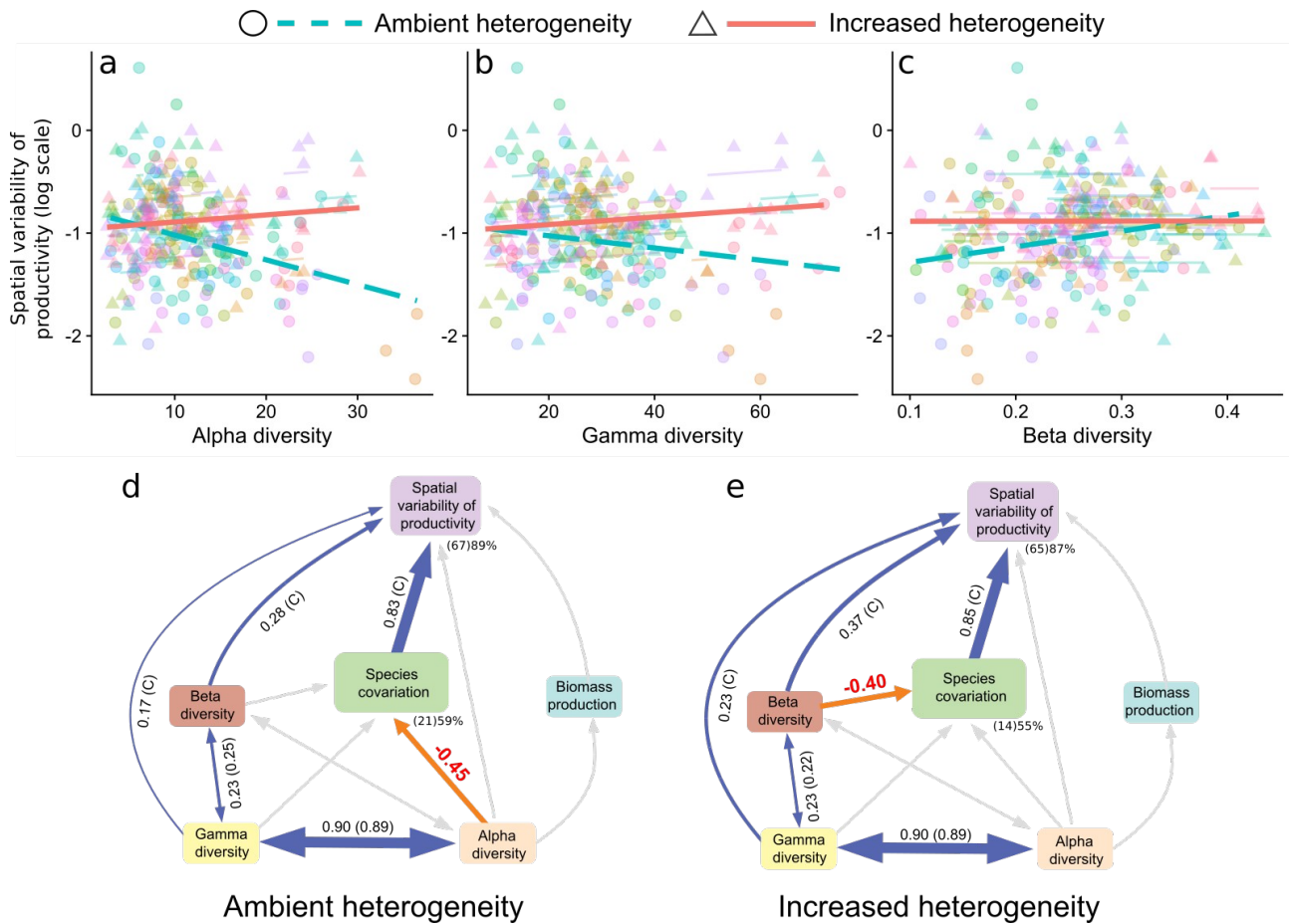
Figure 4. Experimentally increased heterogeneity weakened the diversity-spatial variability relationships. a Alpha diversity (diversity*heterogeneity interaction slopes and 95% confidence intervals: 0.0046 (0.0077 to 0.0108)). **b** Gamma diversity (0.0029 (0.0015 to 0.0043)). **c** Beta diversity (-0.309 (-0.617 to -0.002)). Different colors represent different sites (see Fig 2 for site color key assignment), major lines represent the fixed-effect linear regression slopes among sites and small colored lines show patterns within sites. Comparison of SEM models with **c** ambient and **d** experimentally increased spatial heterogeneity, using the subset of 42 sites that implemented the experimental protocol, identified two major changes (red numbers; P ≤ 0.05 in multigroup analysis) in the pathways whereby increased heterogeneity weakened the three diversity-variability relationships: (1) the negative relationship between alpha diversity and species covariation under ambient conditions was neutral under increased spatial heterogeneity; (2) the neutral relationship

6

746   between beta diversity and species covariation under ambient conditions became negative under

747   increased heterogeneity. Solid blue arrows and solid orange arrows represent significant ($P \leq 0.05$)

748   positive and negative paths, respectively, and light gray arrows represent non-significant paths that

749   were included in the initial model, bidirectional arrows represent paths that were modeled as

750   correlated errors (i.e. bidirectional relations instead of causal and unidirectional relations). Numbers

751   next to the arrows are averaged effect sizes as standardized path coefficients. Path coefficients that

752   have been constrained (multigroup analysis; $P > 0.05$) are the same between the two models and are

753   followed by a (C) (path coefficients are globally estimated, but standardized coefficients differ

754   because the variance differs between groups, and thus the standardization). Numbers within

755   brackets show bidirectional path coefficients estimated for the global model (i.e., as if they were

756   conditional). Width of arrows reflects standardized effect sizes. The marginal (i.e. explained by the

757   fixed factors alone) and conditional (i.e. explained by both the fixed and the random factors)

758   percent variance of endogenous variables (R^2) are shown next to them (marginal between brackets).

7