

1 **Title: Local loss and spatial homogenization of biodiversity reduce ecosystem**  
2 **multifunctionality**

3

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65

66 **Summary:**

67 **Biodiversity is declining in many local communities<sup>1</sup> while also becoming increasingly**  
68 **homogenized across space<sup>2-4</sup>. Experimental studies show that local plant species loss**  
69 **reduces ecosystem functioning and services<sup>5-10</sup>, but the role of spatial homogenization of**  
70 **community composition and the potential interaction between diversity at different scales**  
71 **in maintaining ecosystem functioning remains unclear, especially when many functions are**

72 **considered (ecosystem multifunctionality)<sup>11-14</sup>. We present a global analysis of eight**  
73 **ecosystem functions measured in 65 grasslands worldwide. We find that more diverse**  
74 **grasslands – those with both species-rich local communities (alpha diversity) and large**  
75 **compositional differences among localities (beta diversity) – had higher levels of**  
76 **multifunctionality. Moreover, alpha and beta diversity synergistically affected**  
77 **multifunctionality, with higher levels of diversity at one scale amplifying the contribution**  
78 **to ecological functions at the other scale. The identity of species influencing ecosystem**  
79 **functioning differed among functions and across local communities, explaining why more**  
80 **diverse grasslands maintained greater functionality when more functions and localities**  
81 **were considered. These results were general across continents and robust to variation in**  
82 **environmental drivers. Our findings reveal that plant diversity, at both local and landscape**  
83 **scales, contributes to the maintenance of multiple ecosystem services provided by**  
84 **grasslands. Preserving ecosystem functioning therefore requires conservation of**  
85 **biodiversity both within and among ecological communities.**

86

87 **Text:**

88 There is consensus from experiments that higher numbers of plant species at small scales ( $\alpha$   
89 diversity) contributes to higher levels of ecosystem functioning<sup>5-10</sup>. However, it remains unclear  
90 whether the variation in communities observed across landscapes ( $\beta$  diversity) and the interplay  
91 between diversity at local and landscape scales also contributes to the functioning of real-world  
92 ecosystems such as natural and semi-natural grasslands<sup>11,12</sup>. This is of particular concern given  
93 that large-scale variation in communities is being removed through local species loss<sup>1,15</sup> and  
94 immigration or widespread species replacements (homogenization)<sup>2-4</sup>. Furthermore, given that

95 ecosystems are managed for multiple functions simultaneously (multifunctionality), and that  
96 conservation and management actions are usually implemented at the local and landscape  
97 scales<sup>16</sup>, understanding how plant diversity contributes to maintain multiple functions is needed  
98 at both local and landscape scales<sup>14</sup>.

99

100 In addition to local diversity, spatial heterogeneity of community composition might contribute  
101 to ecosystem multifunctionality through two main mechanisms. First, dissimilarity in  
102 functionally important species can maintain functioning across landscapes if different species  
103 contribute to different functions in different locations<sup>11,12,17,18</sup>. Second, dissimilarity in species  
104 composition among local communities can influence ecological interactions including the  
105 movement of organisms and resources important for ecosystem functioning. For example, a local  
106 community providing habitat for insect species might provide pollination and pest control in  
107 neighbouring communities, thereby contributing to maintain ecosystem functioning at both local  
108 and landscape scales<sup>19</sup>. Although a couple of studies have shown that biodiversity contributes to  
109 ecosystem multifunctionality at larger spatial scales, they were restricted to artificially  
110 constructed landscapes based on simulations within a single experiment in grassland<sup>11</sup> or within  
111 a pan-European study in forest<sup>12</sup>. Thus, it remains unknown whether multifunctionality relates to  
112 biodiversity at larger spatial scales in real-world ecosystems composed of interconnected local  
113 communities.

114

115 Here, we assess the relationship between plant diversity and ecosystem multifunctionality at  
116 local (1 m<sup>2</sup>) and landscape (> 320 m<sup>2</sup>) scales using small local plots and larger spatial blocks  
117 (landscapes composed of interconnected local plots) within 65 grassland sites on five continents,

118 from the Nutrient Network collaborative experiment<sup>20</sup> (Extended Data Fig. 1, Supplementary  
119 Table 1). At each site, we sampled naturally occurring plant diversity and measured ecosystem  
120 multifunctionality using eight ecosystem processes and properties<sup>7,18</sup> (hereafter functions):  
121 aboveground live biomass, resource capture aboveground (light interception), resource pools  
122 belowground (% total soil nitrogen and extractable soil phosphorus and potassium), soil carbon  
123 storage (% total soil carbon), litter decomposition and invasion resistance (Methods, Extended  
124 Data Table 1). We use the term functions in the broad sense to refer to ecosystem processes and  
125 properties, including pools and fluxes of matter and energy<sup>7,13,17,18</sup>. Measurements were taken in  
126 1 m<sup>2</sup> plots grouped into spatial blocks typically spread over 1000 m<sup>2</sup> (most sites had three blocks  
127 (range: 1 to 6) of 10 plots (range: 8 to 12) per study site; Supplementary Table 1).

128

129 We first assessed whether local plant species richness, community dissimilarity among local  
130 communities and their interaction were associated with ecosystem multifunctionality. We  
131 measured species richness as the average number of plant species per 1 m<sup>2</sup> plot within spatial  
132 blocks ( $\bar{\alpha}$ , average  $\alpha$  diversity), and community dissimilarity as the mean pairwise difference in  
133 plant species composition among plots within spatial blocks ( $\beta$  diversity). The  $\bar{\alpha}$  and  $\beta$  diversity  
134 explanatory variables are both mathematically independent in principle and statistically  
135 independent in practice ( $R = 0.076$ ,  $P = 0.28$ ), allowing us to consider their independent and  
136 interactive relationships with ecosystem multifunctionality. We quantified ecosystem  
137 multifunctionality using the average multifunctionality<sup>21</sup> approach, as it is intuitive and easy to  
138 interpret. We calculated average multifunctionality as the mean of all standardized functions  
139 within spatial blocks<sup>11</sup>.

140

141 We found the interactive effect of local species richness ( $\bar{\alpha}$  diversity) and community  
142 dissimilarity ( $\beta$  diversity) to be the strongest contributor to average multifunctionality ( $F_{1,202} =$   
143 8.88,  $P = 0.003$ , Fig. 1, Extended Data Fig. 2 and 3). Specifically, average multifunctionality and  
144 local species richness were positively related at intermediate to high community dissimilarity but  
145 unrelated at low dissimilarity (Fig. 1A). Similarly, average multifunctionality and community  
146 dissimilarity were positively related at high species richness but unrelated at low to intermediate  
147 richness (Fig. 1B). These results indicate that diversity at the local (alpha) and landscape (beta)  
148 scale may synergistically affect multifunctionality, with higher levels of diversity at one scale  
149 amplifying the contribution to ecological functions at the other scale. This also suggests that  
150 losing diversity at one scale of diversity may have cascading effects on the other scale by  
151 weakening its potential to maintain high ecological functioning. In other words, the  
152 homogenization of biotic communities could also increase the effect of species loss on  
153 ecosystem functioning. Synergistic effects of  $\bar{\alpha}$  and  $\beta$  diversity were similar regardless of  
154 whether functions were considered separately or together (Extended Data Fig. 2). However, in  
155 terms of relative contribution to explained variation, some ecosystem functions depended mostly  
156 on  $\bar{\alpha}$  diversity, whereas others depended mostly on  $\beta$  diversity (Extended Data Fig. 3-4).  
157 Synergistic effects contributed the most to aboveground live biomass and litter decomposition,  $\bar{\alpha}$   
158 diversity to soil potassium and invasion resistance and  $\beta$  diversity to light interception, soil  
159 carbon, soil nitrogen, and soil phosphorus. These results suggest that high levels of diversity at  
160 any single scale may not maintain all functions at desirable levels, but instead that high levels of  
161 diversity at multiple scales may be required to maintain multiple functions simultaneously.

162

163 Addressing causation and biological mechanisms is challenging, especially with observational  
164 data. We used a multi-model inference approach to assess the relative importance of  $\bar{\alpha}$ ,  $\beta$   
165 diversity and their interaction and key environmental covariates including geographic, climatic  
166 and edaphic variables (Methods) on each individual function and on the average  
167 multifunctionality. We found that the interactive effect of  $\bar{\alpha}$  and  $\beta$  diversity was included in the  
168 four best and most parsimonious models which explained more than 32% of the variance in  
169 multifunctionality. Relative to other environmental predictors, the interactive effect of  $\bar{\alpha}$  and  $\beta$   
170 diversity was the third best predictor of multifunctionality after mean temperature during the  
171 wettest four months and mean annual precipitation (Extended Data Fig. 5). The importance of  
172 the interaction between local and landscape scale diversity further manifested through it being a  
173 better predictor of multifunctionality than many other environmental predictors including  
174 climatic variables such as mean annual temperature and edaphic variables such as soil pH.  
175 Effects of environmental variables included higher multifunctionality at sites with warmer  
176 temperatures during the wettest four months, larger variation in temperature and higher  
177 precipitation (Extended Data Table 2). Our results suggest that ongoing climate warming<sup>22</sup> may  
178 increase grassland multifunctionality during the wet season. However, large regional differences  
179 of projected changes in the seasonality of precipitation events and in the frequency of extreme  
180 climate events during this century<sup>22</sup> make this outcome uncertain. The relationship between plant  
181 diversity and average multifunctionality was generally robust across environmental gradients.  
182 The slope of the relationship between  $\bar{\alpha}$  diversity and multifunctionality did not vary with our  
183 environmental predictors while  $\beta$  diversity effects on multifunctionality increased with  
184 increasing soil silt and clay content (likely indicators of soil fertility) and decreased with  
185 increasing variation in both temperature and total soil nitrogen (Extended Data Table 3).



186

187 Similar to the multifunctionality analysis, the best and most parsimonious model describing  
188 individual functions included plant diversity ( $\bar{\alpha}$  and/or  $\beta$  and/or the interaction) (Extended Data  
189 Table 2), and a subset of environmental variables were the best predictors of individual functions  
190 relative to plant diversity (Extended Data Fig. 5). Plant diversity contributed much less to  
191 invasion resistance compared to other environmental factors. Effects of environmental variables  
192 on individual functions included among others lower plant biomass, percent total soil carbon,  
193 and invasion resistance and higher light interception, percent total soil nitrogen and extractable  
194 soil potassium at sites with warmer temperatures; higher plant biomass, light interception,  
195 percent total soil carbon and invasion resistance and lower percent total soil nitrogen, extractable  
196 soil phosphorus, extractable soil potassium and litter decomposition at sites with higher  
197 precipitation (Extended Data Table 2).

198

199 Next, we assessed whether ecological interactions between interconnected communities  
200 contribute to the positive relationship between plant diversity and ecosystem multifunctionality.  
201 To do so, we compared the results from our observed landscapes composed of interconnected  
202 local plots within blocks with results of artificially constructed landscapes simulating reduced  
203 interconnection between local communities. Each simulated landscape was composed of ten  
204 plots randomly drawn from local plots belonging either to different blocks within sites (average  
205 interconnection) or to different sites within habitats (low interconnection); and from which  $\bar{\alpha}$  and  
206  $\beta$  diversity and average multifunctionality were calculated. In our simulated landscapes, local  
207 species richness ( $\bar{\alpha}$  diversity) and community dissimilarity ( $\beta$  diversity) interacted to affect the  
208 average multifunctionality (simulated landscapes within sites  $F_{1,6496} = 225.26$ ,  $P < 0.001$ ,

209 simulated landscapes within habitats  $F_{1,4996} = 30.43$ ,  $P < 0.001$ ). When compared to our observed  
210 landscapes (Fig. 2A), artificially reducing interconnection between communities either within  
211 sites (Fig. 2B) or within habitat (Fig. 2C) did not influence the relationships of  $\bar{\alpha}$  and  $\beta$  diversity  
212 with average multifunctionality. Similar to our observed landscapes, simulated landscapes  
213 generally showed stronger association between species richness and average multifunctionality at  
214 high community dissimilarity and between community dissimilarity and average  
215 multifunctionality at high species richness (Fig. 2B-C).

216

217 Finally, we assessed whether dissimilarity in functionally important species contribute to  
218 ecosystem multifunctionality. We identified the sets of species most important for maintaining  
219 ecosystem functioning for each function in each locality (spatial block) at each site using three  
220 analytical approaches that range in how conservative they are in identifying species effects  
221 (Methods): stepwise backward-deletion multiple regression<sup>17,18</sup>, randomization<sup>23</sup>, and  
222 multimodel inference<sup>24</sup>. For each approach, we quantified the degree of functional and spatial  
223 overlap between species sets<sup>17,18</sup>. For example, we quantified functional overlap between all  
224 pairs of functions within spatial blocks. Functional overlap values of one or zero would indicate  
225 respectively that completely identical or completely unique sets of species were important for  
226 maintaining different functions in any particular spatial block. Finally, for each site, we  
227 quantified the proportion of unique species that maintained ecosystem functioning at least once  
228 across all combinations of functions for each spatial block and across all combinations of spatial  
229 blocks for each function considered.

230

231 We found low functional and spatial overlap in the sets of species influencing ecosystem  
232 functions (Extended Data Fig. 6). Thus, the identity of the species most important for  
233 maintaining ecosystem functioning differed between ecosystem functions and among local  
234 communities, resulting in a higher proportion of species required for maintaining ecosystem  
235 functioning when more functions (Fig. 3A) or localities (spatial blocks, Fig. 3B) were  
236 independently considered<sup>17</sup>; and explaining why greater overall ecosystem functioning was  
237 found to be associated with greater local plant species and greater spatial heterogeneity in  
238 community composition (Fig. 1). These positive associations between the proportion of species  
239 maintaining functioning and the range of functions or localities considered were observed for  
240 each of the three approaches investigated (Fig. 3). For example, predictions from the most to the  
241 least conservative method show that between 10 and 28% of the species pool maintained one  
242 function in one block, while between 19 and 37% maintained the same function in three blocks,  
243 and between 39 and 54% maintained the same function in six blocks simultaneously (Fig. 3B).  
244 This suggests that while estimates of the number of species important for maintaining  
245 functioning may vary with analytical approach, the qualitative results are robust to methodology.  
246 Analyses using presence-absence instead of percent species cover, or using only sites with three  
247 or fewer spatial blocks, yielded qualitatively similar results (Extended Data Fig. 6). Our results  
248 indicate that no single plant species maintains all ecosystem functions in all locations, but rather  
249 that more species and greater heterogeneity in species composition across the landscape both  
250 contribute to and strengthen each other's impact on maintaining multifunctional ecosystems  
251 (Extended Data Fig. 7). Together, these analyses suggest the effects of diversity on  
252 multifunctionality are mainly due to species traits and do not detect any additional effects of  
253 species interactions.

254

255 Our results, based on standardized data collected from grasslands around the world, provide  
256 robust, general evidence that plant diversity at the local and landscape scale is associated with  
257 more reliable functioning of grassland ecosystems and contribute to the increasing body of  
258 knowledge cautioning about the functional consequences of local species loss and biotic  
259 homogenization<sup>3,11-13,17,18,21,25-27</sup>. Consequently, human activities that simplify ecosystems  
260 through the loss of plant diversity<sup>1-4</sup> are likely to diminish the capacity of natural systems to  
261 supply essential ecosystem functions, while the maintenance and restoration of plant diversity at  
262 local and landscape scales should help ensure the reliable provision of ecosystem services.

263

#### 264 **Methods:**

265

266 **The Nutrient Network experiment.** The 65 study sites are part of the Nutrient Network Global  
267 Research Cooperative (NutNet, Extended Data Fig. 1, Supplementary Table 1,  
268 <http://nutnet.org/>)<sup>20</sup>. Detailed description of site selection, methods and measurements are  
269 available in Borer et al.<sup>20</sup>. Plots at all sites were 5 x 5 m (separated by at least 1 m walkways)  
270 spread over an area of at least 1000 m<sup>2</sup>. Sampling was done in 1m<sup>2</sup> plots grouped into spatial  
271 blocks spread over > 320 m<sup>2</sup> (typically three blocks (range: 1 to 6) of 10 plots (range: 8 to 12)  
272 per study site; Supplementary Table 1) and followed a standardized protocol at all sites<sup>20</sup>. The  
273 analyses presented here include all NutNet sites that contributed to pre-treatment data on  
274 community-level functions in all plots and therefore do not include either of the nutrient addition  
275 or consumer enclosure treatments. Two sites that contributed data were excluded from these  
276 analyses because they did not lay out plots in separate spatial blocks (sevi.us and jorn.us).

277

278 **Diversity and abundance.** A 1 x 1 m area within each plot was permanently marked and  
279 sampled for species richness during the season of peak biomass. Alpha diversity was the number  
280 of plant species per 1 m<sup>2</sup> plot and average alpha diversity ( $\bar{\alpha}$ ) the average number of plant species  
281 per plot within spatial blocks. Beta diversity ( $\beta$ ) was the dissimilarity in plant species  
282 composition among plots within spatial blocks (differences in 1 m<sup>2</sup> plots among blocks within  
283 each site), which is the complement to Sørensen's similarity index ( $\alpha$ ) ( $\beta = 1 - \alpha$ ) ranging from 0  
284 (completely similar, homogeneous) to 1 (completely dissimilar, heterogeneous). Percent cover  
285 was estimated independently for each species, so that total summed cover can exceed 100% for  
286 multilayer canopies.

287

288 **Ecosystem functions and properties.** Aboveground live biomass (g m<sup>-2</sup>) was estimated  
289 destructively at growing season peak by clipping at ground level all aboveground biomass of  
290 individual plants rooted within two 0.1 m<sup>2</sup> (10 x 100 cm) strips immediately adjacent to the  
291 permanent 1 x 1 m subplot. Biomass was sorted into current (live and recently senescent  
292 material) and previous year's growth (litter). For shrubs and subshrubs, leaves and current year's  
293 woody growth were collected. Biomass was dried at 60°C to a constant mass and weighed to the  
294 nearest 0.01 g. Resource capture aboveground was measured as photosynthetically active  
295 radiation (PAR) at the same time and in the same 1 x 1 m plot sample for species richness. Light  
296 readings were taken using a 1 m PAR sensor (e.g., Decagon, Apogee) on a cloudless day as close  
297 to solar noon as possible (i.e. 11 am to 2 pm). For each plot, we took two light measurements at  
298 ground level (at opposite corners of the 1 x 1 m plot, diagonal to each other) and one above the  
299 canopy. The complement to the ratio represents the percentage of light intercepted at the ground

300 (percentage of intercepted PAR). Adjacent to each plot, resource pools belowground were  
301 estimated using 250 grams of air-dried soil. Total soil %C and %N were measured using dry  
302 combustion GC analysis (COSTECH ESC 4010 Element Analyzer) at the University of  
303 Nebraska. Extractable soil P and K (p.p.m.) were quantified using the Mehlich-3 extraction  
304 method and p.p.m. concentration was estimated using ICP (A&L Analytical Laboratory,  
305 Memphis, TN, USA). Litter turnover ( $y^{-1}$ ) ( $k$ ) as a proxy for litter decomposition was estimated  
306 using an equation derived from Olson<sup>28,29</sup> for deciduous forest decay rates:

$$307 \quad k = -\log\left(1 - \left(\frac{\text{live biomass}}{\text{total biomass}}\right)\right),$$

308 where live biomass is the standing stock during peak season and total biomass is live biomass  
309 plus litter collected at the same time<sup>29</sup>. Although our experimental system is not a forested  
310 system as modeled in Olson's paper, both are deciduous with annual biomass contributions to the  
311 litter pool. Native dominance as a proxy for invasion resistance was estimated as the ratio of  
312 native to invasive species cover. Note that some sites measured only a subset of these eight  
313 functions (Table S1). In the calculation of multifunctionality, we used the inverse of soil N, P  
314 and K as lower levels of unconsumed resources are consistent with higher uptake and lower  
315 potential for leaching.

316

317 **Trade-offs between functions.** To investigate potential trade-offs between individual functions,  
318 we calculated Pearson's correlation coefficients between each pair of individual standardized  
319 functions. Of the possible 28 combinations of pairs of functions, we found significant positive  
320 correlations between eleven pairs and significant negative correlations between five pairs  
321 (Extended Data Table 1). We found a strong negative correlation between our inverse measure of  
322 percent total N and percent total C (-0.96). We kept both variables in our analyses because a

323 negative correlation meant that choosing one function or the other would favour either a positive  
324 or negative impact of diversity on average multifunctionality. In contrast, retaining both  
325 variables demonstrates a trade-off between them. Moreover, our results were qualitatively  
326 similar when we used either percent total N or the soil C:N ratio. All the other correlations were  
327 lower than 0.30.

328

### 329 **Community-level analyses.**

330 *Ecosystem multifunctionality.* We quantified ecosystem multifunctionality in whole communities  
331 of interacting species using two methods<sup>30</sup>: the average and multiple threshold approaches.

332 The average approach<sup>11,29,31</sup> tests whether the average level of multiple functions is related to  
333 diversity. We standardized each function by the maximum observed value across all sites to  
334 remove the effects of differences in measurement scale between functions<sup>30</sup>. We then calculated  
335 block *average multifunctionality* as the mean of all standardized functions within spatial  
336 blocks<sup>11</sup>. The average multifunctionality metric is intuitive and easy to interpret, but it does not  
337 incorporate potential tradeoffs between functions that perform at high levels when others  
338 perform at low levels.

339 The multiple threshold approach<sup>11,31-33</sup> overcomes this limitation and tests whether diversity is  
340 associated with higher numbers of functions exceeding discrete threshold values considered to be  
341 minimal for desirable ecosystem functioning. We calculated the number of functions per plot that  
342 exceeded a given threshold value, expressed as a percentage of each maximum function value.

343 Here, we defined maximum level of functioning for each function as the average of the top four  
344 values for each function across all sites. We then calculated *multiple-threshold*  
345 *multifunctionality*<sup>31</sup> as the mean number of functions that exceeded a given threshold within

346 spatial blocks. In practice, a range of thresholds is usually explored. We calculated the average  
347 number of functions exceeding functional thresholds between 5 and 95% of this maximum per  
348 plot. Thus, for each block, 91 values (counts of functions) were generated, one for each discrete  
349 threshold value between 5 and 95%.

350

351 *Association between plant diversity and ecosystem functioning (average multifunctionality).* We  
352 explored the direct relationships of plant diversity, measured as the average species richness ( $\bar{\alpha}$ ),  
353 community dissimilarity ( $\beta$ ) and their interaction ( $\bar{\alpha}:\beta$ ), with each individual function and the  
354 average multifunctionality across the 65 sites using ordinary least squares (OLS) regression. In  
355 order to visualize the interactive effect of  $\bar{\alpha}$  and  $\beta$  diversity on average multifunctionality, we  
356 divided the data set into three equal groups corresponding to low (Low), intermediate (Int) and  
357 high (High) levels of  $\bar{\alpha}$  or  $\beta$  diversity and fitted separate models for each group. This means that  
358 we fitted relationships between  $\bar{\alpha}$  diversity and average multifunctionality at low, intermediate  
359 and high levels of  $\beta$  diversity. Similarly, we fitted relationships between  $\beta$  diversity and average  
360 multifunctionality at low, intermediate and high levels of  $\bar{\alpha}$  diversity. Due to similar fit we  
361 subsequently grouped the intermediate and high levels (Int-High) of  $\bar{\alpha}$  diversity and the low and  
362 intermediate levels (Low-Int) of  $\beta$  diversity (Fig. 1, Extended Data Fig. 4). We also assessed the  
363 relative contribution of  $\bar{\alpha}$ ,  $\beta$  diversity and  $\bar{\alpha}:\beta$  to average multifunctionality by using multivariate  
364 models to calculate standardized regression coefficients (Extended Data Fig. 2) and the  
365 percentage of variance explained (percent of  $R^2$ , Extended Data Fig. 3) for each diversity metric.

366

367 *Association between plant diversity and ecosystem functioning (multiple-threshold*  
368 *multifunctionality).* To assess the relationship between plant diversity and multiple-threshold



369 multifunctionality, we fitted separate models for each of the 91 discrete threshold values between  
370 5 and 95%, and recorded the slope and associated 95% confidence intervals. Because some  
371 functions were not measured for all sites, we ran two separate analyses. For the first analysis, we  
372 measured the mean number of functions that exceeded a given threshold values of the observed  
373 maximum value for each function, for 44 sites that measured more than six ecosystem functions  
374 (Extended Data Fig. 8). Because the responses in each of the 91 models were integers (counts of  
375 functions exceeding the particular threshold) we used generalized linear models (GLMs) with a  
376 quasipoisson error distribution (to account for observed over-dispersion) and identity link  
377 function<sup>30</sup>. For the second analysis, we used data from all 65 sites, adjusting for the fact that  
378 some functions were not measured for all sites, and measured the percentage of measured  
379 functions exceeding a given threshold. Results did not qualitatively differ between the two  
380 analyses. Because the responses in each of the 91 models were percentages we fitted generalized  
381 linear models (GLMs) with a quasibinomial error distribution and logit link function<sup>30</sup>. For both  
382 analyses, we included environmental variables because the relationship between plant diversity  
383 and multifunctionality may covary with environmental factors correlated to both plant diversity  
384 and ecosystem multifunctionality. Our results were independent of the multifunctionality  
385 measure chosen; results of our analyses using multiple-threshold multifunctionality data did not  
386 differ qualitatively from the results presented in the text using average multifunctionality.

387

388 *Relative importance of plant diversity and environmental predictors.* We used a multi-model  
389 inference approach based on Akaike information criterion (AIC) and OLS regression to assess  
390 the relative importance of  $\bar{\alpha}$ ,  $\beta$  diversity and  $\bar{\alpha}:\beta$  and key environmental predictors on each  
391 individual function and on the average multifunctionality (Extended Data Fig. 5, Extended Data

392 Table 2). We fitted separate models for each function and the average multifunctionality as  
393 response variables and fifteen potential environmental predictors including geographic, climatic  
394 and edaphic variables. Geographic variables included latitude and longitude. Climatic variables  
395 were derived from the WorldClim Global Climate database (version 1.4;  
396 <http://www.worldclim.org/>)<sup>34</sup>. Due to multicollinearity between many of the climatic variables,  
397 we first fitted a principal component analysis (PCA) to reduce their number, resulting in a subset  
398 of bioclimatic variables representing annual trends (mean annual temperature (°C) and  
399 precipitation (mm)), seasonality (mean annual range in temperature, standard deviation in  
400 temperature, coefficient of variation of precipitation) and extreme or limiting environmental  
401 factors (mean temperature during the wettest four months)<sup>35</sup>. Edaphic variables included pH,  
402 bulk density, soil nutrient heterogeneity (coefficient of variation in total soil nitrogen, extractable  
403 soil phosphorus and extractable soil potassium) and soil texture (percent silt, percent clay and  
404 percent sand). Again due to multicollinearity between soil texture variables, we used percent silt  
405 and percent clay in our analyses.

406

407 *Relationship between plant diversity and average multifunctionality across environmental*  
408 *gradients.* To assess whether the relationship between plant diversity and average  
409 multifunctionality varied across environmental gradients, we first determined the slopes of the  
410 relationships of  $\bar{\alpha}$  and  $\beta$  diversity with average multifunctionality within each site using linear  
411 mixed-effects models and site as random effect allowing both the intercepts and slopes of the  
412 regression to vary among sites. We then assessed the relationships between the slopes of  
413 relationships of  $\bar{\alpha}$  and  $\beta$  diversity with average multifunctionality as response variable and each  
414 environmental variable as explanatory variables (Extended Data Table 3).

415

416 **Assessing whether ecological interactions between interconnected communities contribute**  
417 **to ecosystem multifunctionality.**

418 To assess the contribution of ecological interactions to multifunctionality, we constructed  
419 artificial landscapes from our grassland plots belonging either to different blocks within sites  
420 (average interconnection) or to different sites within habitats (low interconnection); and from  
421 which  $\bar{\alpha}$  and  $\beta$  diversity and average multifunctionality were calculated as described above.

422 *Simulated landscapes within sites.* Within each site, we constructed 100 artificial landscapes  
423 each composed of ten plots randomly selected, without replacement, across the different blocks.  
424 With 65 sites, this resulted in 6500 landscapes.

425 *Simulated landscapes within habitats.* Within each habitat, we constructed 1000 artificial  
426 landscapes each composed of ten plots randomly selected, without replacement, across the  
427 different sites. The number of sites within each habitat was relatively low (ranging between one  
428 and eight) and many habitats were represented by only a few sites. In order to ensure that our  
429 landscape were composed of unique plot combinations, we selected the habitats represented by  
430 more than four sites. Due to their similarity, alpine and montane grasslands were subsequently  
431 grouped together. This resulted in five habitats with a total of 5000 landscapes.

432 For each of the observed and simulated landscapes within sites and within habitats, we quantified  
433 the standardized regression coefficients of the relationships of plant diversity, measured as the  
434 average species richness ( $\bar{\alpha}$ ), community dissimilarity ( $\beta$ ) and their interaction ( $\bar{\alpha}:\beta$ ), with  
435 average multifunctionality using ordinary least squares (OLS) regression. Again, in order to  
436 visualize the interactive effect of  $\bar{\alpha}$  and  $\beta$  diversity on average multifunctionality, we divided the

437 data set into three equal groups corresponding to low (Low), intermediate (Int) and high (High)  
438 levels of  $\bar{\alpha}$  or  $\beta$  diversity and fitted separate models for each group (Fig. 2).

439

440 **Species-level analyses: assessing whether dissimilarity in functionally important species**  
441 **contribute to ecosystem multifunctionality.**

442 *Identifying sets of species most important for maintaining ecosystem functioning.* We started by  
443 identifying the sets of species most important for maintaining ecosystem functioning for each  
444 function in each spatial block at each site, based on three approaches proposed in the ecological  
445 literature that range in how conservative they are in identifying species effects: stepwise-deletion  
446 multiple regression<sup>17,18,36</sup>, randomization<sup>23</sup> and multimodel inference<sup>24</sup>. For each approach, we  
447 modeled ecosystem functioning in response to the abundance (percent cover, Fig. 3) or the  
448 presence-absence of each species in each plot (Extended Data Fig. 6). For the presence-absence  
449 analysis, some species were present in every plot within spatial blocks and could not be included  
450 in the analyses as their contributions could not be statistically estimated. However, all species  
451 could be included in analyses using abundance data, as abundance values varied among plots for  
452 each species. Where the results overlapped with the presence/absence data they were  
453 qualitatively similar (Fig. 3, Extended Data Fig. 6).

454 Stepwise-deletion multiple regression identified the most parsimonious set of species influencing  
455 each ecosystem function based on information criteria<sup>37</sup>. We implemented this procedure using  
456 the stepAIC function in the MASS library<sup>38</sup> of R<sup>17,18,36</sup>. In stepwise-deletion analyses, multiple  
457 models can have nearly equivalent support, making it misleading to choose a single best model  
458 in that case. Multimodel inference addresses this problem by accounting for model selection  
459 uncertainty and reducing model selection bias<sup>39</sup>. In this sense multimodel inference is more

460 robust and conservative than stepwise-deletion. We implemented multimodel inference using the  
461 `glmulti` function in the `glmulti` R package<sup>24</sup>. While stepwise-deletion and multimodel inference  
462 require designs that include each species in a variety of compositional treatments (typical of most  
463 but not all biodiversity experiments)<sup>30</sup>, randomization is advocated for observational studies  
464 lacking imposed compositional treatments<sup>23</sup>. The effect of each species on each function is  
465 measured in multiple plots as the difference between the average of a function in the presence  
466 and absence of a particular species. The sets of species that show strong influences on each  
467 function are then identified by randomly reassigning the values of the ecosystem function to the  
468 different plots for a large number of iterations<sup>23</sup>.

469

470 *Comparing sets of species most important for maintaining ecosystem functioning.* After  
471 identifying the sets of species most important for maintaining ecosystem functioning in each  
472 plot, we quantified overlap  $o$  between species sets for each of the stepwise-deletion multiple  
473 regression, randomization and multimodel inference approaches. To test whether different sets of  
474 species maintained ecosystem functioning for different functions in different spatial blocks, we  
475 quantified functional and spatial overlap between species sets. All comparisons were made  
476 within spatial blocks so that differences between pairs of functions or pairs of spatial blocks were  
477 not due to sampling from multiple species pools. We quantified functional overlap between  
478 functions  $a$  and  $b$  in a particular spatial block and spatial overlap between spatial blocks  $a$  and  $b$   
479 for a particular function using Sørensen's similarity index<sup>17,18</sup>:

$$o = \frac{|E_a \cap E_b|}{0.5(|E_a| + |E_b|)}$$

480 Where  $|E_a|$  is the number of species that promoted ecosystem functioning for function or spatial  
481 block  $a$ ,  $|E_b|$  is the number of species that promoted ecosystem functioning for function or

482 spatial block  $b$  and  $|E_a \cap E_b|$  is the number of species that promoted ecosystem functioning for  
483 both functions or spatial blocks. This allowed us to test whether identical (overlap = 1), unique  
484 (overlap = 0) or somewhat different ( $0 < \text{overlap} < 1$ ) sets of species promoted ecosystem  
485 functioning for different functions at different spatial blocks.

486

487 *Accumulation of species across functions and spatial blocks.* For each approach, we then  
488 assessed how the proportion of species maintaining functioning changed as more functions or  
489 spatial blocks were considered. We quantified the accumulation of species that maintained  
490 ecosystem functioning across all combinations of functions for each spatial block and across all  
491 combinations of spatial blocks for each function considered. For example, to estimate how the  
492 proportion of species maintaining functioning changed as more functions were considered, we  
493 sampled all combinations of the eight functions (that is, all pairs, groups of three, etc.), and  
494 recorded the number of unique species that maintained functioning, the total number of species,  
495 for each combination. The proportion of species was then calculated by dividing the number of  
496 species that maintained functioning by the total number of species per spatial block. This was  
497 repeated for each spatial block, at each site. We modelled the relationships between the  
498 proportion of species that maintained ecosystem functioning and the number of functions or  
499 spatial blocks, for each of the stepwise-deletion multiple regression, randomization tests and  
500 multimodel inference approaches, using quasibinomial GLMs including “approaches” as a factor  
501 with three levels. The number of spatial blocks per site range between one and six, meaning that  
502 the relationship between the proportion of species that maintained ecosystem functioning and the  
503 number of spatial blocks could be driven by the few sites with more than three blocks (Fig. 3).

504 We therefore re-run the analyses using a subset of the data including only sites with three or  
505 fewer spatial blocks (Extended Data Fig. 6). All analyses were conducted in R 2.15.1<sup>40</sup>.

506

507

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597

598 **Supplementary Information** is linked to the online version of the paper at

599 [www.nature.com/nature](http://www.nature.com/nature).

600

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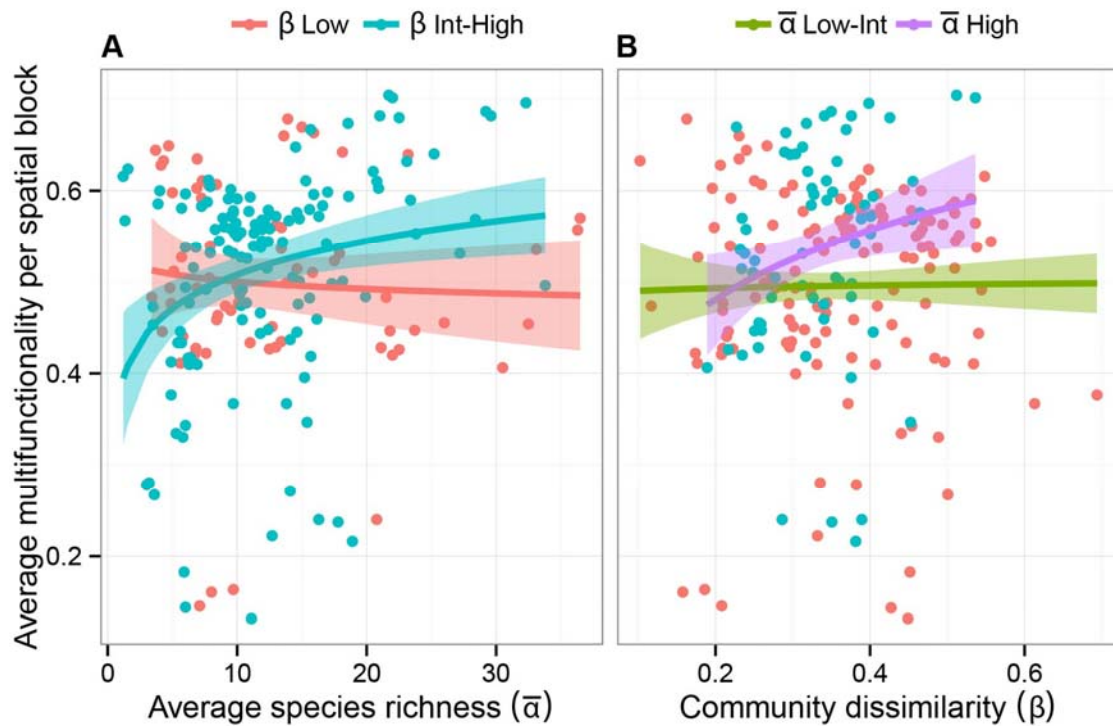
614 Y.H., F.I. and A.H. developed and framed research questions. Y.H., F.I. and A.H. analysed the  
615 data and wrote the paper with contributions and input from all authors. E.T.B., E.W.S., K.L.P.,  
616 and J.D.B. contributed to data analysis. E.W.S., E.T.B., W.S.H. and E.M.L. are Nutrient  
617 Network coordinators. All authors collected data used in this analysis. Author contribution  
618 matrix provided as Supplementary Table 2.

619

620 **Author Information:**

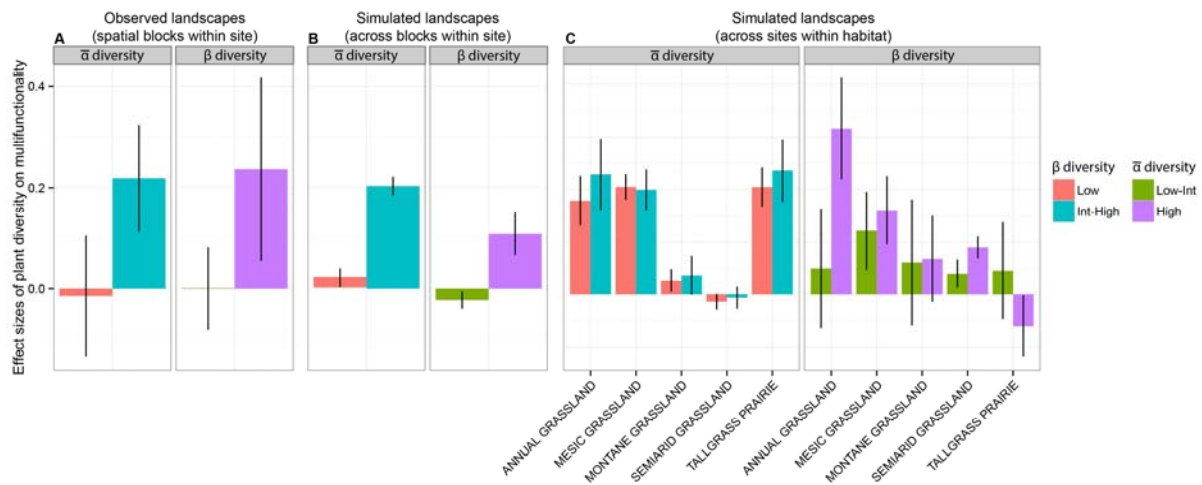
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624 **Figures:**



625

626 **Figure 1. Local species richness ( $\bar{\alpha}$  diversity) and community dissimilarity ( $\beta$  diversity)**  
 627 **interact to affect average multifunctionality. A**, average number of species per plot within  
 628 spatial blocks ( $\bar{\alpha}$  diversity); **B**, dissimilarity in species composition among plots within spatial  
 629 blocks ( $\beta$  diversity). The average level of multiple functions increased with  $\bar{\alpha}$  diversity at  
 630 intermediate to high (Int-High)  $\beta$  diversity (slope and 95% CI on the log  $\bar{\alpha}$  scale = 0.05 (0.021 –  
 631 0.086)), and with  $\beta$  diversity at high (High)  $\bar{\alpha}$  diversity (0.10 (0.015 – 0.23)), but was unrelated  
 632 to  $\bar{\alpha}$  diversity at low (Low)  $\beta$  diversity (-0.011 (-0.057 – 0.034) and to  $\beta$  diversity at low to  
 633 intermediate (Low-Int)  $\bar{\alpha}$  diversity (-0.0044 (-0.051 – 0.059)).



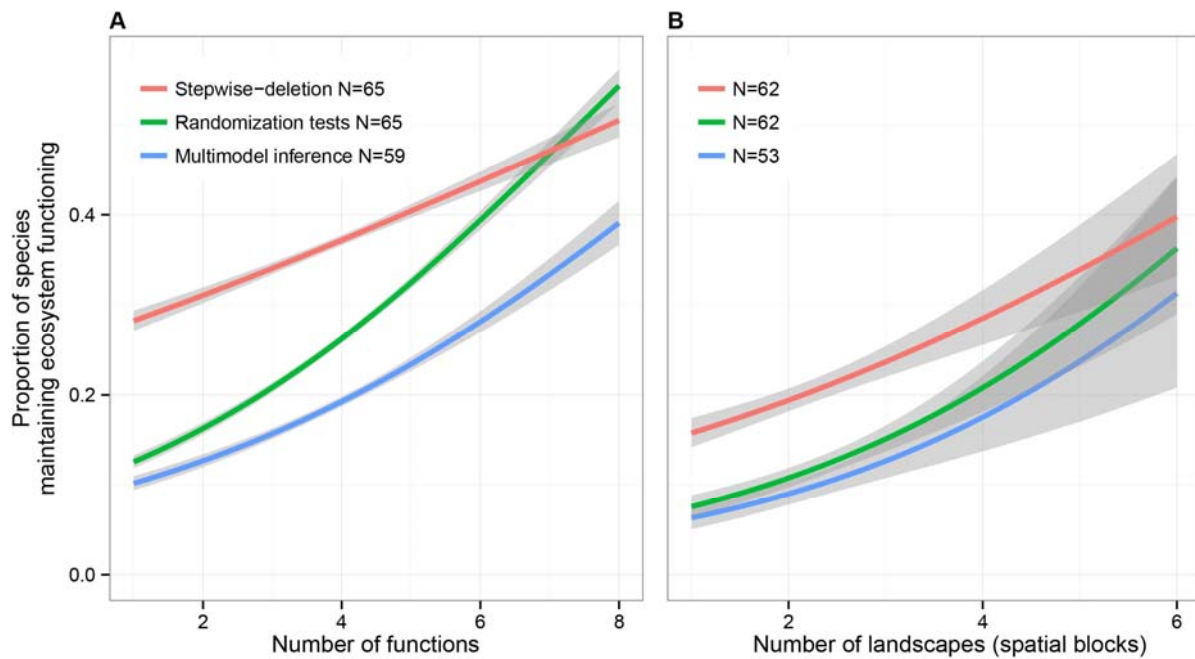
634

635 **Figure 2. Simulating reduced ecological interactions between local communities did not**636 **influence the relationships of plant diversity with average multifunctionality.** Standardized637 regression coefficients of local species richness ( $\bar{\alpha}$ ) and community dissimilarity ( $\beta$ ) with638 average multifunctionality for **A**, observed landscapes (spatial blocks) composed of639 interconnected local plots within site, **B and C**, artificially constructed landscapes simulating640 reduced interconnection between local communities within sites (**B**) or within habitat (**C**).

641 Standardized regression coefficients are shown with their 95% confidence intervals such that

642 diversity effect on multifunctionality is significant when the intervals do not overlap zero.





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**Figure 3. Relationships between the proportion of species maintaining ecosystem functioning and the number of ecosystem functions (A) or the number of spatial blocks (B) considered for each of three analytical approaches: stepwise-deletion multiple regression, randomization tests and multimodel inference.** A higher proportion of species maintained ecosystem functioning with the independent consideration of **A**, more functions (slopes and 95% CI: stepwise-deletion 0.136 (0.130 – 0.142), randomization tests 0.302 (0.295 – 0.308), multimodel inference 0.247 (0.239 – 0.256)) or **B**, more spatial blocks (slopes and 95% CI: stepwise-deletion 0.252 (0.233 – 0.271), randomization tests 0.387 (0.364 – 0.410), multimodel inference 0.381 (0.345 – 0.418)). Regression lines indicate generalized linear model fits for each method with 95% confidence intervals. N denotes the number of sites included in each approach.