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

3
4 Yann Hautier^{1*} [0000-0003-4347-7741](https://orcid.org/0000-0003-4347-7741), Forest Isbell², Elizabeth T. Borer², Eric W. Seabloom², W.
5 Stanley Harpole^{3,4,5}, Eric M. Lind², Andrew S. MacDougall⁶, Carly J. Stevens⁷, Peter B. Adler⁸,
6 Juan Alberti⁹, Jonathan D. Bakker¹⁰, Lars A. Brudvig¹¹, Yvonne M. Buckley¹², Marc Cadotte¹³,
7 Maria C. Caldeira¹⁴, Enrique J. Chaneton¹⁵, Chengjin Chu¹⁶, Pedro Daleo⁹, Christopher R.
8 Dickman¹⁷, John M. Dwyer¹⁸, Anu Eskelinen^{3,4,19}, Philip A. Fay²⁰, Jennifer Firn²¹, Nicole
9 Hagenah^{22,23}, Helmut Hillebrand²⁴, Oscar Iribarne²⁵, Kevin P. Kirkman²², Johannes M. H.
10 Knops²⁶, Kimberly J. La Pierre²⁷, Rebecca L. McCulley²⁸, John W. Morgan²⁹, Meelis Pärtel³⁰,
11 Jesus Pascual⁹, Jodi N. Price³¹, Suzanne M. Prober³², Anita C. Risch³³, Mahesh Sankaran^{34,35},
12 Martin Schuetz³⁶, Rachel J. Standish³⁷, Risto Virtanen^{3,4,19}, Glenda M. Wardle³⁸, Laura
13 Yahdjian¹⁵, Andy Hector³⁹

14
15 ¹ Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht,
16 Netherlands.

17 ² Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, USA.

18 ³ Department of Physiological Diversity, Helmholtz Center for Environmental Research – UFZ, Permoserstrasse 15,
19 Leipzig 04318, Germany.

20 ⁴ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, Leipzig
21 04103, Germany.

22 ⁵ Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, Halle (Saale) 06108, Germany.

23 ⁶ Department of Integrative Biology, University of Guelph, Guelph, Ontario Canada N1G 2W1.

24 ⁷ Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK.

- 25 ⁸ Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322, USA.
- 26 ⁹ Instituto de Investigaciones Marinas y Costeras, UNMDP, CONICET, 7600 Mar del Plata, Argentina.
- 27 ¹⁰ School of Environmental and Forest Sciences, University of Washington, Box 354115, Seattle, WA 98195-4115,
28 USA.
- 29 ¹¹ Department of Plant Biology and Program in Ecology, Evolutionary Biology and Behavior, Michigan State
30 University, East Lansing, MI 48824, USA.
- 31 ¹² School of Natural Sciences, Zoology, Trinity College Dublin, Dublin 2, Ireland.
- 32 ¹³ University of Toronto Scarborough, Toronto, Ontario, Canada M1C 1A4.
- 33 ¹⁴ Forest Research Center, ISA, University of Lisbon, 1349-017Lisbon, Portugal.
- 34 ¹⁵ IFEVA-CONICET, Facultad de Agronomia, Universidad de Buenos Aires, Av. San Martin 4453, 1417 Buenos
35 Aires, Argentina.
- 36 ¹⁶ State Key Laboratory of Grassland and Agro-Ecosystems, Research Station of Alpine Meadow and Wetland
37 Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000, China.
- 38 ¹⁷ Desert Ecology Research Group, School of Life and Environmental Sciences, The University of Sydney, NSW
39 2006, Australia.
- 40 ¹⁸ School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia & CSIRO Land &
41 Water, EcoSciences Precinct, Dutton Park, QLD 4102, Australia.
- 42 ¹⁹ Department of Ecology, University of Oulu, FI-90014 University of Oulu, Finland.
- 43 ²⁰ USDA-ARS, Grassland Soil and Water Lab, 808 E Blackland Road, Temple, TX, 76502, USA.
- 44 ²¹ School of Biological Sciences, Queensland University of Technology, Brisbane, Australia.
- 45 ²² School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
- 46 ²³ South African Environmental Network (SAEON), Grasslands, Forests and Wetlands Node, Queen Elizabeth Park,
47 1 Peter Brown Drive, Pietermaritzburg, South Africa
- 48 ²⁴ Institute for Chemistry and Biology of the marine Environment, University Oldenburg, Germany.

- 49 ²⁵ Instituto de Investigaciones Marinas y Costeras, UNMdP, CONICET, 7600 Mar del Plata, Argentina.
- 50 ²⁶ School of Biological Sciences, University of Nebraska – Lincoln, USA.
- 51 ²⁷ Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgewater, Maryland, USA.
- 52 ²⁸ Department of Plant & Soil Sciences, University of Kentucky, Lexington KY 40546-0091, USA.
- 53 ²⁹ Department of Ecology, Environment and Evolution, La Trobe University, Bundoora 3083, Victoria, Australia.
- 54 ³⁰ Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu 51005, Estonia.
- 55 ³¹ Institute of Land, Water and Society, Charles Sturt University, Albury, NSW, 2640, Australia.
- 56 ³² CSIRO Land and Water, Private Bag 5, Wembley, WA 6913, Australia.
- 57 ³³ Swiss Federal Institute of Forest, Snow and Landscape Research, 8903 Birmensdorf, Switzerland.
- 58 ³⁴ School of Biology, University of Leeds, Leeds LS2 9JT, UK.
- 59 ³⁵ National Centre for Biological Sciences, GKVK Campus, Bangalore 560065, India.
- 60 ³⁶ Swiss Federal Institute of Forest, Snow and Landscape Research, 8903 Birmensdorf, Switzerland.
- 61 ³⁷ School of Veterinary and Life Sciences, Murdoch University, 90 South Street, Murdoch Western Australia 6150.
- 62 ³⁸ Desert Ecology Research Group, School of Life and Environmental Sciences, The University of Sydney, NSW
- 63 2006, Australia.
- 64 ³⁹ Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK.

65 ***corresponding author:** y.hautier@uu.nl

66

67 **Abstract:**

68 **Biodiversity is declining in many local communities while also becoming increasingly**

69 **homogenized across space. Experiments show that local plant species loss reduces**

70 **ecosystem functioning and services, but the role of spatial homogenization of community**

71 **composition and the potential interaction between diversity at different scales in**

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

87

88 **Introduction:**

89 There is consensus from experiments that higher numbers of plant species at small scales (α
90 diversity) contributes to higher levels of ecosystem functioning¹⁻⁶. However, it remains unclear
91 whether the variation in communities observed across landscapes (β diversity) and the interplay
92 between diversity at local and landscape scales also contributes to the functioning of real-world
93 ecosystems such as natural and semi-natural grasslands^{7,8}. This is of particular concern given that
94 large-scale variation in communities is being removed through local species loss^{9,10} and

95 immigration or widespread species replacements leading to homogenization¹¹⁻¹³. Furthermore,
96 given that ecosystems are managed for multiple functions simultaneously (multifunctionality),
97 and that conservation and management actions are usually implemented across different scales¹⁴,
98 understanding how plant diversity contributes to maintaining multiple functions is needed from
99 small to larger spatial scales¹⁵.

100

101 Spatial heterogeneity of community composition might contribute to ecosystem
102 multifunctionality through two main mechanisms. First, dissimilarity in functionally important
103 species can maintain functioning across landscapes if different species contribute to different
104 functions in different locations^{7,8,16,17}. Second, dissimilarity in species composition among local
105 communities can influence ecological interactions including the movement of organisms and
106 resources important for ecosystem functioning. For example, a local community providing
107 habitat for insect species might provide pollination and pest control to neighbouring
108 communities, thereby contributing to ecosystem functioning at both local and landscape scales¹⁸.

109 Although a couple of studies have shown that plant diversity contributes to ecosystem
110 multifunctionality at larger spatial scales, they were restricted to artificially constructed
111 landscapes based on simulations within a single experiment in a grassland⁸ or within a pan-
112 European study in forested ecosystems⁷. Thus, it remains unknown whether multifunctionality
113 relates to biodiversity at larger spatial scales in real-world ecosystems composed of
114 interconnected local communities.

115

116 Here, we assess the relationship between plant diversity and ecosystem multifunctionality at
117 local (1 m²) and larger (> 320 m², hereafter termed ‘landscape’) scales using small local plots

118 and larger spatial blocks (landscapes composed of interconnected local plots) within 65 grassland
119 sites on five continents, from the Nutrient Network collaborative experiment¹⁹ (Supplementary
120 Fig. 1, Supplementary Table 1). At each site, we sampled naturally occurring plant diversity and
121 measured ecosystem multifunctionality using eight ecosystem processes and properties^{3,17}
122 (hereafter functions): aboveground live biomass, resource capture aboveground (light
123 interception), resource pools belowground (% total soil nitrogen and extractable soil phosphorus
124 and potassium), soil carbon storage (% total soil carbon), litter decomposition and invasion
125 resistance (Methods, Supplementary Table 2). We use the term ‘functions’ in the broad sense to
126 refer to ecosystem processes and properties, including pools and fluxes of matter and
127 energy^{3,16,17,20}. Measurements were taken in 1 m² plots grouped into spatial blocks typically
128 spread over 1000 m² (most sites had three blocks (range: 1 to 6) with 10 plots (range: 8 to 12) per
129 study site; Supplementary Table 1).

130

131 **Results and discussion:**

132 We first assessed whether local plant species richness, community dissimilarity among local
133 communities, and their interaction were associated with ecosystem multifunctionality. We
134 measured species richness as the average number of plant species per 1m² plot within spatial
135 blocks ($\bar{\alpha}$, average α diversity), and community dissimilarity as the mean pairwise difference in
136 plant species composition among plots within spatial blocks (β diversity). The $\bar{\alpha}$ and β diversity
137 explanatory variables are both mathematically independent in principle and statistically
138 independent in practice ($R = 0.076$, $P = 0.28$, $N = 206$), allowing us to consider their independent
139 and interactive relationships with ecosystem multifunctionality. We quantified ecosystem
140 multifunctionality using two approaches²¹ (Methods). The *average multifunctionality*²² approach,

141 which provides a relatively interpretable metric and the *multiple-threshold multifunctionality*
142 approach²³ which assesses how many functions reach high levels. We calculated average
143 multifunctionality as the mean of all standardized functions within spatial blocks⁸ and multiple-
144 threshold multifunctionality as the mean number of functions per plot within spatial blocks that
145 exceeded threshold values between 5 and 95% of the observed maximum value for each
146 function.

147

148 We found the interactive effect of local species richness ($\bar{\alpha}$ diversity) and community
149 dissimilarity (β diversity) to be the strongest contributor to average multifunctionality ($F_{1,202} =$
150 8.88, $P = 0.003$, Fig. 1, Supplementary Fig. 2 and 3). Specifically, average multifunctionality and
151 local species richness were positively related at intermediate to high community dissimilarity but
152 unrelated at low dissimilarity (Fig. 1a, Fig. 2a). Similarly, average multifunctionality and
153 community dissimilarity were positively related at high species richness but unrelated at low to
154 intermediate richness (Fig. 1b, Fig. 2a). These interactions were generally consistent throughout
155 habitat types (Fig. 2b). These results indicate that diversity at the local ($\bar{\alpha}$) and landscape (β)
156 scale may synergistically affect multifunctionality, with higher levels of diversity at one scale
157 amplifying the contribution to ecological functions at the other scale. This also suggests that
158 losing diversity at one scale may have cascading effects on the other scale by weakening its
159 potential to maintain high ecological functioning. In other words, the homogenization of biotic
160 communities could increase the effect of local species loss on ecosystem functioning. Our results
161 were independent of the multifunctionality measure chosen; results of our analyses using
162 multiple-threshold multifunctionality did not differ qualitatively from the results using average
163 multifunctionality (Supplementary Fig. 4). Future studies could more completely consider

164 measuring all ecosystem functions related to realistic management objectives and address
165 scenarios representing different management objectives by calculating multifunctionality metrics
166 with different weighing for each ecosystem functions.

167

168 Synergistic effects of $\bar{\alpha}$ and β diversity were similar regardless of whether functions were
169 considered separately or together (Supplementary Fig. 2). However, in terms of relative
170 contribution to explained variation, some ecosystem functions depended mostly on $\bar{\alpha}$ diversity,
171 whereas others depended mostly on β diversity (Supplementary Fig. 3 and 5, Supplementary
172 Table 3). Synergistic effects contributed the most to aboveground live biomass and litter
173 decomposition, $\bar{\alpha}$ diversity to soil potassium and invasion resistance and β diversity to light
174 interception, soil carbon, soil nitrogen, and soil phosphorus. These results suggest that high
175 levels of diversity at any single scale may not maintain all functions at desirable levels, but
176 instead that high levels of diversity at multiple scales may be required to maintain multiple
177 functions simultaneously.

178

179 We used a multi-model inference approach to assess the relative importance of $\bar{\alpha}$, β diversity,
180 their interaction, and key environmental covariates including geographic, climatic and edaphic
181 variables (Methods) on each individual function and on the average multifunctionality. We found
182 that the interactive effect of $\bar{\alpha}$ and β diversity was included in the four best and most
183 parsimonious models which explained more than 32% of the variance in multifunctionality.
184 Relative to other environmental predictors, the interactive effect of $\bar{\alpha}$ and β diversity was the
185 third best predictor of multifunctionality after mean temperature during the wettest four months
186 and mean annual precipitation (Supplementary Fig. 6). The importance of the interaction

187 between local and landscape scale diversity further manifested through it being a better predictor
188 of multifunctionality than many other environmental predictors, including climatic variables
189 such as mean annual temperature and edaphic variables such as soil pH.

190

191 Higher multifunctionality was associated with warmer temperatures during the wettest four
192 months, larger variation in temperature and higher precipitation (Supplementary Table 4). The
193 relationship between plant diversity and average multifunctionality was generally robust across
194 environmental gradients. The slope of the relationship between $\bar{\alpha}$ diversity and multifunctionality
195 did not vary with our environmental predictors while β diversity effects on multifunctionality
196 increased with increasing soil silt and clay content (likely indicators of soil fertility) and
197 decreased with increasing variation in both temperature and total soil nitrogen (Supplementary
198 Table 5).

199

200 Similar to the multifunctionality analysis, the best and most parsimonious model describing
201 individual functions included plant diversity ($\bar{\alpha}$ and/or β and/or the interaction) (Supplementary
202 Table 4), and a subset of environmental variables were better predictors of individual functions
203 relative to plant diversity (Supplementary Fig. 6). Plant diversity contributed less to invasion
204 resistance compared to other environmental factors. Effects of environmental variables on
205 individual functions included an association of warmer temperatures with lower plant biomass,
206 percent total soil carbon, and invasion resistance and higher light interception, percent total soil
207 nitrogen and extractable soil potassium. Similarly, higher precipitation was associated with
208 higher plant biomass, light interception, percent total soil carbon and invasion resistance and

209 lower percent total soil nitrogen, extractable soil phosphorus, extractable soil potassium and litter
210 decomposition (Supplementary Table 4).

211

212 Next, we assessed whether ecological interactions between interconnected communities
213 contribute to the positive relationship between plant diversity and ecosystem multifunctionality.
214 To do so, we compared the results from our observed landscapes composed of interconnected
215 local plots within blocks with results of artificially constructed landscapes simulating reduced
216 interconnection between local communities. Each simulated landscape was composed of ten
217 plots randomly drawn from local plots belonging either to different blocks within sites (average
218 interconnection) or to different sites within habitat type (low interconnection); and from which $\bar{\alpha}$
219 and β diversity and average multifunctionality were calculated. In our simulated landscapes,
220 local species richness ($\bar{\alpha}$ diversity) and community dissimilarity (β diversity) interacted to affect
221 the average multifunctionality (simulated landscapes within sites $F_{1,6496} = 225.26$, $P < 0.001$,
222 $N=6500$, simulated landscapes within habitats $F_{1,4996} = 30.43$, $P < 0.001$, $N=5000$). When
223 compared to our observed landscapes (Fig. 2a and b), artificially reducing interconnection
224 between communities either within sites (Fig. 2c) or within habitats (Fig. 2d) did not influence
225 the relationships of $\bar{\alpha}$ and β diversity with average multifunctionality. Similar to our observed
226 landscapes, simulated landscapes generally showed stronger association between species
227 richness and average multifunctionality at high community dissimilarity and between community
228 dissimilarity and average multifunctionality at high species richness.

229

230 Finally, we assessed whether dissimilarity in functionally important species contribute to
231 ecosystem multifunctionality. We identified the sets of species most important for maintaining

232 ecosystem functioning for each function in each locality (spatial block) at each site using three
233 analytical approaches that range in how conservative they are in identifying species effects
234 (Methods): stepwise backward-deletion multiple regression^{16,17}, randomization²⁴, and
235 multimodel inference²⁵. For each approach, we quantified the degree of functional and spatial
236 overlap between species sets^{16,17}. For example, we quantified functional overlap between all
237 pairs of functions within spatial blocks. Functional overlap values of one or zero would indicate
238 respectively that completely identical or completely unique sets of species were important for
239 maintaining different functions in any particular spatial block. Finally, for each site, we
240 quantified the proportion of unique species that maintained ecosystem functioning at least once
241 across all combinations of functions for each spatial block and across all combinations of spatial
242 blocks for each function considered.

243

244 We found low functional and spatial overlap in the sets of species influencing ecosystem
245 functions (Supplementary Fig. 7). Thus, the identity of the species most important for
246 maintaining ecosystem functioning differed between ecosystem functions and among local
247 communities, resulting in a higher proportion of species required for maintaining ecosystem
248 functioning when more functions (Fig. 3a) or localities (spatial blocks, Fig. 3b) were
249 independently considered¹⁶; and explaining why greater overall ecosystem functioning was
250 found to be associated with greater local plant species and greater spatial heterogeneity in
251 community composition (Fig. 1). These positive associations between the proportion of species
252 maintaining functioning and the range of functions or localities considered were observed for
253 each of the three approaches investigated (Fig. 3). For example, predictions from the most to the
254 least conservative method show that between 10 and 28% of the species pool maintained one

255 function in one block, while between 19 and 37% maintained the same function in three blocks,
256 and between 39 and 54% maintained the same function in six blocks simultaneously (Fig. 3b).
257 This suggests that while estimates of the number of species important for maintaining
258 functioning may vary with analytical approach, the qualitative results are robust to methodology.
259 Analyses using presence-absence instead of percent species cover, or using only sites with three
260 or fewer spatial blocks, yielded qualitatively similar results (Supplementary Fig. 7). Our results
261 indicate that no single plant species maintains all ecosystem functions in all locations, but rather
262 that more species and greater heterogeneity in species composition across the landscape both
263 contribute to and enhance ecosystem multifunctionality (Supplementary Fig. 8). Together, these
264 analyses suggest that the effects of diversity on multifunctionality are mainly due to species traits
265 and how these traits interact with local environmental conditions and do not point to any
266 additional effects of ecological interactions between interconnected communities.

267

268 Our results, based on standardized data collected from grasslands around the world, provide
269 robust, general evidence that plant diversity at the local and landscape scale is associated with
270 more reliable functioning of grassland ecosystems and contribute to the increasing body of
271 knowledge cautioning about the functional consequences of local species loss and biotic
272 homogenization^{7,8,11,16,17,20,22,26-28}. Consequently, human activities that simplify ecosystems
273 through the loss of plant diversity^{9,11-13} are likely to diminish the capacity of natural systems to
274 supply essential ecosystem functions, while the maintenance and restoration of plant diversity at
275 local and landscape scales should help ensure the reliable provision of ecosystem services.

276

277 **Methods:**

278

279 **The Nutrient Network experiment.** The 65 study sites are part of the Nutrient Network Global
280 Research Cooperative (NutNet, Supplementary Fig. 1, Supplementary Table 1,
281 <http://nutnet.org/>)¹⁹. Detailed description of site selection, methods and measurements are
282 available in Borer et al.¹⁹. Plots at all sites were 5 x 5 m (separated by at least 1 m walkways)
283 spread over an area of at least 1000 m². Sampling was done in 1m² plots grouped into spatial
284 blocks spread over > 320 m² (typically three blocks (range: 1 to 6) of 10 plots (range: 8 to 12)
285 per study site; Supplementary Table 1) and followed a standardized protocol at all sites¹⁹. The
286 analyses presented here include all NutNet sites that contributed to pre-treatment data on
287 community-level functions in all plots and therefore do not include either of the nutrient addition
288 or consumer exclosure treatments. Two sites that contributed data were excluded from these
289 analyses because they did not lay out plots in separate spatial blocks (sevi.us and jorn.us).

290

291 **Diversity and abundance.** A 1 x 1 m area within each plot was permanently marked and
292 sampled for species richness during the season of peak biomass. Alpha diversity was the number
293 of plant species per 1 m² plot and average alpha diversity ($\bar{\alpha}$) the average number of plant species
294 per plot within spatial blocks. Beta diversity (β) was the dissimilarity in plant species
295 composition among plots within spatial blocks (differences in 1 m² plots among blocks within
296 each site), which is the complement to Sørensen's similarity index (o) ($\beta = 1 - o$) ranging from 0
297 (completely similar, homogeneous) to 1 (completely dissimilar, heterogeneous). Percent cover
298 was estimated independently for each species, so that total summed cover can exceed 100% for
299 multilayer canopies.

300

301 **Ecosystem functions and properties.** Aboveground live biomass (g m^{-2}) was estimated
302 destructively at growing season peak by clipping at ground level all aboveground biomass of
303 individual plants rooted within two 0.1 m^2 ($10 \times 100 \text{ cm}$) strips immediately adjacent to the
304 permanent $1 \times 1 \text{ m}$ subplot. Biomass was sorted into current (live and recently senescent
305 material) and previous year's growth (litter). For shrubs and subshrubs, leaves and current year's
306 woody growth were collected. Biomass was dried at 60°C to a constant mass and weighed to the
307 nearest 0.01 g . Resource capture aboveground was measured as photosynthetically active
308 radiation (PAR) at the same time and in the same $1 \times 1 \text{ m}$ plot sample for species richness. Light
309 readings were taken using a 1 m PAR sensor (e.g., Decagon, Apogee) on a cloudless day as close
310 to solar noon as possible (i.e. 11 am to 2 pm). For each plot, we took two light measurements at
311 ground level (at opposite corners of the $1 \times 1 \text{ m}$ plot, diagonal to each other) and one above the
312 canopy. The complement to the ratio represents the percentage of light intercepted at the ground
313 (percentage of intercepted PAR). Adjacent to each plot, resource pools belowground were
314 estimated using 250 grams of air-dried soil. Total soil %C and %N were measured using dry
315 combustion GC analysis (COSTECH ESC 4010 Element Analyzer) at the University of
316 Nebraska. Extractable soil P and K (p.p.m.) were quantified using the Mehlich-3 extraction
317 method and p.p.m. concentration was estimated using ICP (A&L Analytical Laboratory,
318 Memphis, TN, USA). Litter turnover (y^{-1}) (k) as a proxy for litter decomposition was estimated
319 using an equation derived from Olson^{29,30} for deciduous forest decay rates:

$$320 \quad k = -\log\left(1 - \left(\frac{\text{live biomass}}{\text{total biomass}}\right)\right),$$

321 where live biomass is the standing stock during peak season and total biomass is live biomass
322 plus litter collected at the same time³⁰. Although our experimental system is not a forested
323 system as modeled in Olson's paper, both are deciduous with annual biomass contributions to the

324 litter pool. Native dominance as a proxy for invasion resistance was estimated as the ratio of
325 native to invasive species cover. Note that some sites measured only a subset of these eight
326 functions (Supplementary Table 1). In the calculation of multifunctionality, we used the inverse
327 of soil N, P and K as lower levels of unconsumed resources are consistent with higher uptake and
328 lower potential for leaching.

329

330 **Trade-offs between functions.** To investigate potential trade-offs between individual functions,
331 we calculated Pearson's correlation coefficients between each pair of individual standardized
332 functions. Of the possible 28 combinations of pairs of functions, we found significant positive
333 correlations between eleven pairs and significant negative correlations between five pairs
334 (Supplementary Table 2). We found a strong negative correlation between our inverse measure
335 of percent total N and percent total C (-0.96). We kept both variables in our analyses because a
336 negative correlation meant that choosing one function or the other would favour either a positive
337 or negative impact of diversity on average multifunctionality. In contrast, retaining both
338 variables demonstrates a trade-off between them. Moreover, our results were qualitatively
339 similar when we used either percent total N or the soil C:N ratio. All the other correlations were
340 lower than 0.30.

341

342 **Community-level analyses.**

343 *Ecosystem multifunctionality.* We quantified ecosystem multifunctionality in whole communities
344 of interacting species using two methods²¹: the average and multiple threshold approaches.

345 We standardized each function by the maximum observed value across all sites to remove the
346 effects of differences in measurement scale between functions²¹. We then calculated block

347 *average multifunctionality* as the mean of all standardized functions within spatial blocks⁸. The
348 average multifunctionality metric is intuitive and easy to interpret, but it does not incorporate
349 potential tradeoffs between functions that perform at high levels when others perform at low
350 levels.

351 The multiple threshold approach^{8,23,31,32} overcomes this limitation and tests whether diversity is
352 associated with higher numbers of functions exceeding discrete threshold values considered to be
353 minimal for desirable ecosystem functioning. We calculated the number of functions per plot that
354 exceeded a given threshold value, expressed as a percentage of each maximum function value.
355 Here, we defined maximum level of functioning for each function as the average of the top four
356 values for each function across all sites. We then calculated *multiple-threshold*
357 *multifunctionality*²³ as the mean number of functions that exceeded a given threshold within
358 spatial blocks. In practice, a range of thresholds is usually explored. We calculated the average
359 number of functions exceeding functional thresholds between 5 and 95% of this maximum per
360 plot. Thus, for each block, 91 values (counts of functions) were generated, one for each discrete
361 threshold value between 5 and 95%.

362

363 *Association between plant diversity and ecosystem functioning (average multifunctionality)*. We
364 explored the direct relationships of plant diversity, measured as the average species richness ($\bar{\alpha}$),
365 community dissimilarity (β) and their interaction ($\bar{\alpha}:\beta$), with each individual standardized
366 function and the average multifunctionality across the 65 sites (Fig. 1, Fig. 2a) and within habitat
367 types (Fig. 2b) using generalized linear models (GLMs) with a quasibinomial error distribution
368 and logit link function. See the section hereafter ‘Assessing whether ecological interactions
369 between interconnected communities contribute to ecosystem multifunctionality’ for a

370 description of how the habitat types were selected. In order to visualize the interactive effect of $\bar{\alpha}$
371 and β diversity on average multifunctionality, we divided the data set into three equal groups
372 corresponding to low (Low), intermediate (Int) and high (High) levels of $\bar{\alpha}$ or β diversity and
373 fitted separate models for each group. This means that we fitted relationships between $\bar{\alpha}$ diversity
374 and average multifunctionality at low, intermediate and high levels of β diversity. Similarly, we
375 fitted relationships between β diversity and average multifunctionality at low, intermediate and
376 high levels of $\bar{\alpha}$ diversity. Due to similar fit we subsequently grouped the intermediate and high
377 levels (Int-High) of $\bar{\alpha}$ diversity and the low and intermediate levels (Low-Int) of β diversity (Fig.
378 1, Supplementary Fig. 5). We also assessed the relative contribution of $\bar{\alpha}$, β diversity and $\bar{\alpha}:\beta$ to
379 average multifunctionality by using multivariate models to calculate standardized regression
380 coefficients (Supplementary Fig. 2) and the percentage of variance explained (percent of R^2 ,
381 Supplementary Fig. 3) for each diversity metric.

382

383 *Association between plant diversity and ecosystem functioning (multiple-threshold*
384 *multifunctionality)*. To assess the relationship between plant diversity and multiple-threshold
385 multifunctionality, we fitted separate models for each of the 91 discrete threshold values between
386 5 and 95%, and recorded the slope and associated 95% confidence intervals (Supplementary Fig.
387 4). Because the responses in each of the 91 models were integers (counts of functions exceeding
388 the particular threshold) we used GLMs with a quasipoisson error distribution (to account for
389 observed over-dispersion) and identity link function²¹. We rerun the analysis adjusting for the
390 fact that some functions were not measured for all sites by measuring the percentage of measured
391 functions exceeding a given threshold. Because the responses in each of the 91 models were
392 percentages we fitted GLMs with a quasibinomial error distribution and logit link function²¹.

393 Results did not qualitatively differ between the two analyses. For both analyses, we included
394 environmental variables because the relationship between plant diversity and multifunctionality
395 may covary with environmental factors correlated to both plant diversity and ecosystem
396 multifunctionality.

397

398 *Relative importance of plant diversity and environmental predictors.* We used a multi-model
399 inference approach based on Akaike information criterion (AIC) and ordinary least square (OLS)
400 regression to assess the relative importance of $\bar{\alpha}$, β diversity and $\bar{\alpha}:\beta$ and key environmental
401 predictors on each individual function and on the average multifunctionality (Supplementary Fig.
402 6, Supplementary Table 4). We fitted separate models for each function and the average
403 multifunctionality as response variables and fifteen potential environmental predictors including
404 geographic, climatic and edaphic variables. Geographic variables included latitude and
405 longitude. Climatic variables were derived from the WorldClim Global Climate database
406 (version 1.4; <http://www.worldclim.org/>)³³. Due to multicollinearity between many of the
407 climatic variables, we first fitted a principal component analysis (PCA) to reduce their number,
408 resulting in a subset of bioclimatic variables representing annual trends (mean annual
409 temperature (°C) and precipitation (mm)), seasonality (mean annual range in temperature,
410 standard deviation in temperature, coefficient of variation of precipitation) and extreme or
411 limiting environmental factors (mean temperature during the wettest four months)³⁴. Edaphic
412 variables included pH, bulk density, soil nutrient heterogeneity (coefficient of variation in total
413 soil nitrogen, extractable soil phosphorus and extractable soil potassium) and soil texture
414 (percent silt, percent clay and percent sand). Again due to multicollinearity between soil texture
415 variables, we used percent silt and percent clay in our analyses.

416

417 *Relationship between plant diversity and average multifunctionality across environmental*
418 *gradients.* To assess whether the relationship between plant diversity and average
419 multifunctionality varied across environmental gradients, we first determined the slopes of the
420 relationships of $\bar{\alpha}$ and β diversity with average multifunctionality within each site using linear
421 mixed-effects models and site as random effect allowing both the intercepts and slopes of the
422 regression to vary among sites. We then assessed the relationships between the slopes of
423 relationships of $\bar{\alpha}$ and β diversity with average multifunctionality as response variable and each
424 environmental variable as explanatory variables (Supplementary Table 5).

425

426 **Assessing whether ecological interactions between interconnected communities contribute**
427 **to ecosystem multifunctionality.**

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

432 *Simulated landscapes within sites.* Within each site, we constructed 100 artificial landscapes
433 each composed of ten plots randomly selected, without replacement, across the different blocks.

434 With 65 sites, this resulted in 6500 landscapes.

435 *Simulated landscapes within habitats.* Within each habitat (Supplementary Table 1), we
436 constructed 1000 artificial landscapes each composed of ten plots randomly selected, without
437 replacement, across the different sites. The number of sites within each habitat was relatively low
438 (ranging between one and eight) and many habitats were represented by only a few sites. In order
439 to ensure that our landscape were composed of unique plot combinations, we selected the

440 habitats represented by more than four sites. Due to their similarity, alpine and montane
441 grasslands were subsequently grouped together. This resulted in five habitats with a total of 5000
442 landscapes.

443 For each of the observed and simulated landscapes within sites and within habitats, we quantified
444 the standardized regression coefficients of the relationships of plant diversity, measured as the
445 average species richness ($\bar{\alpha}$), community dissimilarity (β) and their interaction ($\bar{\alpha}:\beta$), with
446 average multifunctionality using OLS regression. Again, in order to visualize the interactive
447 effect of $\bar{\alpha}$ and β diversity on average multifunctionality, we divided the data set into three equal
448 groups corresponding to low (Low), intermediate (Int) and high (High) levels of $\bar{\alpha}$ or β diversity
449 and fitted separate models for each group (Fig. 2).

450

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

453 *Identifying sets of species most important for maintaining ecosystem functioning.* We started by
454 identifying the sets of species most important for maintaining ecosystem functioning for each
455 function in each spatial block at each site, based on three approaches proposed in the ecological
456 literature that range in how conservative they are in identifying species effects: stepwise-deletion
457 multiple regression^{16,17,35}, randomization²⁴ and multimodel inference²⁵. For each approach, we
458 modeled ecosystem functioning in response to the abundance (percent cover, Fig. 3) or the
459 presence-absence of each species in each plot (Supplementary Fig. 7). For the presence-absence
460 analysis, some species were present in every plot within spatial blocks and could not be included
461 in the analyses as their contributions could not be statistically estimated. However, all species
462 could be included in analyses using abundance data, as abundance values varied among plots for

463 each species. Where the results overlapped with the presence/absence data they were
464 qualitatively similar (Fig. 3, Supplementary Fig. 7).
465 Stepwise-deletion multiple regression identified the most parsimonious set of species influencing
466 each ecosystem function based on information criteria³⁶. We implemented this procedure using
467 the stepAIC function in the MASS library³⁷ of R^{16,17,35}. In stepwise-deletion analyses, multiple
468 models can have nearly equivalent support, making it misleading to choose a single best model
469 in that case. Multimodel inference addresses this problem by accounting for model selection
470 uncertainty and reducing model selection bias³⁸. In this sense multimodel inference is more
471 robust and conservative than stepwise-deletion. We implemented multimodel inference using the
472 glmulti function in the glmulti R package²⁵. While stepwise-deletion and multimodel inference
473 require designs that include each species in a variety of compositional treatments (typical of most
474 but not all biodiversity experiments)²¹, randomization is advocated for observational studies
475 lacking imposed compositional treatments²⁴. The effect of each species on each function is
476 measured in multiple plots as the difference between the average of a function in the presence
477 and absence of a particular species. The sets of species that show strong influences on each
478 function are then identified by randomly reassigning the values of the ecosystem function to the
479 different plots for 1000 iterations²⁴.

480

481 *Comparing sets of species most important for maintaining ecosystem functioning.* After
482 identifying the sets of species most important for maintaining ecosystem functioning in each
483 plot, we quantified overlap o between species sets for each of the stepwise-deletion multiple
484 regression, randomization and multimodel inference approaches. To test whether different sets of
485 species maintained ecosystem functioning for different functions in different spatial blocks, we

486 quantified functional and spatial overlap between species sets. All comparisons were made
487 within spatial blocks so that differences between pairs of functions or pairs of spatial blocks were
488 not due to sampling from multiple species pools. We quantified functional overlap between
489 functions a and b in a particular spatial block and spatial overlap between spatial blocks a and b
490 for a particular function using Sørensen's similarity index^{16,17}:

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

491 Where $|E_a|$ is the number of species that promoted ecosystem functioning for function or spatial
492 block a , $|E_b|$ is the number of species that promoted ecosystem functioning for function or
493 spatial block b and $|E_a \cap E_b|$ is the number of species that promoted ecosystem functioning for
494 both functions or spatial blocks. This allowed us to test whether identical (overlap = 1), unique
495 (overlap = 0) or somewhat different ($0 < \text{overlap} < 1$) sets of species promoted ecosystem
496 functioning for different functions at different spatial blocks.

497

498 *Accumulation of species across functions and spatial blocks.* For each approach, we then
499 assessed how the proportion of species maintaining functioning changed as more functions or
500 spatial blocks were considered. We quantified the accumulation of species that maintained
501 ecosystem functioning across all combinations of functions for each spatial block and across all
502 combinations of spatial blocks for each function considered. For example, to estimate how the
503 proportion of species maintaining functioning changed as more functions were considered, we
504 sampled all combinations of the eight functions (that is, all pairs, groups of three, etc.), and
505 recorded the number of unique species that maintained functioning, the total number of species,
506 for each combination. The proportion of species was then calculated by dividing the number of
507 species that maintained functioning by the total number of species per spatial block. This was

508 repeated for each spatial block, at each site. We modelled the relationships between the
509 proportion of species that maintained ecosystem functioning and the number of functions or
510 spatial blocks, for each of the stepwise-deletion multiple regression, randomization tests and
511 multimodel inference approaches, using quasibinomial GLMs including “approaches” as a factor
512 with three levels. The number of spatial blocks per site range between one and six, meaning that
513 the relationship between the proportion of species that maintained ecosystem functioning and the
514 number of spatial blocks could be driven by the few sites with more than three blocks (Fig. 3).
515 We therefore re-run the analyses using a subset of the data including only sites with three or
516 fewer spatial blocks (Supplementary Fig. 7). All analyses were conducted in R 2.15.1³⁹.

517

518 **Data availability.** The datasets generated during and/or analysed during the current study are
519 available from the corresponding author on reasonable request.

520

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533

534 **Author Contributions:**

535 Y.H., F.I. and A.H. developed and framed research questions. Y.H., F.I. and A.H. analysed the
536 data and wrote the paper with contributions and input from all authors. E.T.B., E.W.S., K.L.P.,
537 and J.D.B. contributed to data analysis. E.W.S., E.T.B., W.S.H. and E.M.L. are Nutrient
538 Network coordinators. All authors collected data used in this analysis. Author contribution
539 matrix provided as Supplementary Table 6.

540

541 **Declaration of Financial Competing Interests**

542 The authors declare no competing financial competing interests.

543

544 **Additional information**

545 Supplementary information is available for this paper.

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547 Correspondence and requests for materials should be addressed to Y.H.

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636

637

638

639 **Figure legends:**

640

641 **Figure 1. Local species richness ($\bar{\alpha}$ diversity) and community dissimilarity (β diversity)**

642 **interact to affect average multifunctionality. a**, average number of species per plot within

643 spatial blocks ($\bar{\alpha}$ diversity); **b**, dissimilarity in species composition among plots within spatial

644 blocks (β diversity). The average level of multiple functions increased with $\bar{\alpha}$ diversity at

645 intermediate to high (Int-High) β diversity (slope and 95% CI on the log $\bar{\alpha}$ scale = 0.05 (0.021 –

646 0.086)), and with β diversity at high (High) $\bar{\alpha}$ diversity (0.10 (0.015 – 0.23)), but was unrelated

647 to $\bar{\alpha}$ diversity at low (Low) β diversity (-0.011 (-0.057 – 0.034) and to β diversity at low to

648 intermediate (Low-Int) $\bar{\alpha}$ diversity (-0.0044 (-0.051 – 0.059).

649

650 **Figure 2. Simulating reduced ecological interactions between local communities did not**

651 **influence the relationships of plant diversity with average multifunctionality.** Standardized

652 regression coefficients of local species richness ($\bar{\alpha}$) and community dissimilarity (β) with

653 average multifunctionality for **a and b**, observed landscapes (spatial blocks) composed of

654 interconnected local plots within site (**a**) or within habitat (**b**), **c and d**, artificially constructed

655 landscapes simulating reduced interconnection between local communities within sites (**c**) or

656 within habitat (**d**). Standardized regression coefficients are shown with their 95% confidence

657 intervals such that diversity effect on multifunctionality is significant when the intervals do not

658 overlap zero.

659

660 **Figure 3. Relationships between the proportion of species maintaining ecosystem**

661 **functioning and the number of ecosystem functions (a) or the number of spatial blocks (b)**

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





