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Local Loss and Spatial Homogenization of Plant Diversity Reduce Ecosystem Multifunctionality

Yann Hautier
Utrecht University, The Netherlands

Forest Isbell
University of Minnesota - Twin Cities

Elizabeth T. Borer
University of Minnesota - Twin Cities

Eric W. Seabloom
University of Minnesota - Twin Cities

W. Stanley Harpole
Helmholtz Center for Environmental Research, Germany

See next page for additional authors

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Authors

Yann Hautier, Forest Isbell, Elizabeth T. Borer, Eric W. Seabloom, W. Stanley Harpole, Eric M. Lind, Andrew S. MacDougall, Carly J. Stevens, Peter B. Adler, Juan Alberti, Jonathan D. Bakker, Lars A. Brudvig, Yvonne M. Buckley, Marc Cadotte, Maria C. Caldeira, Enrique J. Chaneton, Chengjin Chu, Pedro Daleo, Christopher R. Dickman, John M. Dwyer, Anu Eskelinen, Philip A Fay, Jennifer Firn, Nicole Hagenah, Helmut Hillebrand, Oscar Iribarne, Kevin P. Kirkman, Johannes M. H. Knops, Kimberly J. La Pierre, and Rebecca L. McCulley

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Due to the large number of authors, only the first 30 and the authors affiliated with the University of Kentucky are listed in the author section above. For the complete list of authors, please download this article or visit: https://doi.org/10.1038/s41559-017-0395-0

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

Yann Hautier[1]*0000-0003-4347-7741, Forest Isbell[2], Elizabeth T. Borer[2], Eric W. Seabloom[2], W. Stanley Harpole[3,4,5], Eric M. Lind[2], Andrew S. MacDougall[6], Carly J. Stevens[7], Peter B. Adler[8], Juan Alberti[9], Jonathan D. Bakker[10], Lars A. Brudvig[11], Yvonne M. Buckley[12], Marc Cadotte[13], Maria C. Caldeira[14], Enrique J. Chaneton[15], Chengjin Chu[16], Pedro Daleo[9], Christopher R. Dickman[17], John M. Dwyer[18], Anu Eskelinen[3,4,19], Philip A. Fay[20], Jennifer Firn[21], Nicole Hagenah[22,23], Helmut Hillebrand[24], Oscar Iribarne[25], Kevin P. Kirkman[22], Johannes M. H. Knops[26], Kimberly J. La Pierre[27], Rebecca L. McCulley[28], John W. Morgan[29], Meelis Pärtel[30], Jesus Pascual[9], Jodi N. Price[31], Suzanne M. Prober[32], Anita C. Risch[33], Mahesh Sankaran[34,35], Martin Schuetz[36], Rachel J. Standish[37], Risto Virtanen[3,4,19], Glenda M. Wardle[38], Laura Yahdjian[15], Andy Hector[39]

[1] Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, Netherlands.

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

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

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

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

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

[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**

3

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 functioning[1-6]. 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 homogenization[11-13]. Furthermore,

96   given that ecosystems are managed for multiple functions simultaneously (multifunctionality),

97   and that conservation and management actions are usually implemented across different scales[14],

98   understanding how plant diversity contributes to maintaining multiple functions is needed from

99   small to larger spatial scales[15].

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 scales[18].

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 grassland[8] or within a pan-

112   European study in forested ecosystems[7]. 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 m^2) and larger (> 320 m^2, 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 experiment[19] (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 $1 \ m^2$ plots grouped into spatial blocks typically

128 spread over $1000 \ m^2$ (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 $1m^2$ plot within spatial

135 blocks ($\overline{\alpha}$, average α diversity), and community dissimilarity as the mean pairwise difference in

136 plant species composition among plots within spatial blocks (β diversity). The $\overline{\alpha}$ 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 approaches[21] (Methods). The *average multifunctionality*[22] approach,

6

141   which provides a relatively interpretable metric and the *multiple-threshold multifunctionality*

142   approach[23] which assesses how many functions reach high levels. We calculated average

143   multifunctionality as the mean of all standardized functions within spatial blocks[8] 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 ($\overline{\alpha}$ 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 ($\overline{\alpha}$) 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 $\overline{\alpha}$ 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 $\overline{\alpha}$ 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, $\overline{\alpha}$ 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 $\overline{\alpha}$, 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 $\overline{\alpha}$ 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 $\overline{\alpha}$ 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 $\overline{\alpha}$ 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 ($\overline{\alpha}$ 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

9

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 $\overline{\alpha}$

219   and β diversity and average multifunctionality were calculated. In our simulated landscapes,

220   local species richness ($\overline{\alpha}$ 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 $\overline{\alpha}$ 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], randomization[24], and

235 multimodel inference[25]. 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 considered[16]; 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

The Nutrient Network experiment. The 65 study sites are part of the Nutrient Network Global

Research Cooperative (NutNet, Supplementary Fig. 1, Supplementary Table 1,

http://nutnet.org/)[19]. Detailed description of site selection, methods and measurements are

available in Borer et al.[19]. Plots at all sites were 5 x 5 m (separated by at least 1 m walkways)

spread over an area of at least 1000 m^2. Sampling was done in 1m^2 plots grouped into spatial

blocks spread over > 320 m^2 (typically three blocks (range: 1 to 6) of 10 plots (range: 8 to 12)

per study site; Supplementary Table 1) and followed a standardized protocol at all sites[19]. The

analyses presented here include all NutNet sites that contributed to pre-treatment data on

community-level functions in all plots and therefore do not include either of the nutrient addition

or consumer exclosure treatments. Two sites that contributed data were excluded from these

analyses because they did not lay out plots in separate spatial blocks (sevi.us and jorn.us).

290

Diversity and abundance. A 1 x 1 m area within each plot was permanently marked and

sampled for species richness during the season of peak biomass. Alpha diversity was the number

of plant species per 1 m^2 plot and average alpha diversity ($\overline{\alpha}$) the average number of plant species

per plot within spatial blocks. Beta diversity (β) was the dissimilarity in plant species

composition among plots within spatial blocks (differences in 1 m^2 plots among blocks within

each site), which is the complement to Sørensen's similarity index (o) ($\beta = 1 - o$) ranging from 0

(completely similar, homogeneous) to 1 (completely dissimilar, heterogeneous). Percent cover

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

multilayer canopies.

300

13

Ecosystem functions and properties. Aboveground live biomass (g m^{-2}) was estimated

destructively at growing season peak by clipping at ground level all aboveground biomass of

individual plants rooted within two 0.1 m^2 (10 x 100 cm) strips immediately adjacent to the

permanent 1 x 1 m subplot. Biomass was sorted into current (live and recently senescent

material) and previous year's growth (litter). For shrubs and subshrubs, leaves and current year's

woody growth were collected. Biomass was dried at 60°C to a constant mass and weighed to the

nearest 0.01 g. Resource capture aboveground was measured as photosynthetically active

radiation (PAR) at the same time and in the same 1 x 1 m plot sample for species richness. Light

readings were taken using a 1 m PAR sensor (e.g., Decagon, Apogee) on a cloudless day as close

to solar noon as possible (i.e. 11 am to 2 pm). For each plot, we took two light measurements at

ground level (at opposite corners of the 1 x 1 m plot, diagonal to each other) and one above the

canopy. The complement to the ratio represents the percentage of light intercepted at the ground

(percentage of intercepted PAR). Adjacent to each plot, resource pools belowground were

estimated using 250 grams of air-dried soil. Total soil %C and %N were measured using dry

combustion GC analysis (COSTECH ESC 4010 Element Analyzer) at the University of

Nebraska. Extractable soil P and K (p.p.m.) were quantified using the Mehlich-3 extraction

method and p.p.m. concentration was estimated using ICP (A&L Analytical Laboratory,

Memphis, TN, USA). Litter turnover (y^{-1}) (k) as a proxy for litter decomposition was estimated

using an equation derived from Olson[29,30] for deciduous forest decay rates:

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

where live biomass is the standing stock during peak season and total biomass is live biomass

plus litter collected at the same time[30]. Although our experimental system is not a forested

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 methods[21]: 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 functions[21]. We then calculated block

15

347   *average multifunctionality* as the mean of all standardized functions within spatial blocks[8]. 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 ($\overline{\alpha}$),

365   community dissimilarity (β) and their interaction ($\overline{\alpha}$:β), 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

16

370   description of how the habitat types were selected. In order to visualize the interactive effect of $\overline{\alpha}$

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 $\overline{\alpha}$ or β diversity and

373   fitted separate models for each group. This means that we fitted relationships between $\overline{\alpha}$ 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 $\overline{\alpha}$ diversity. Due to similar fit we subsequently grouped the intermediate and high

377   levels (Int-High) of $\overline{\alpha}$ 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 $\overline{\alpha}$, β diversity and $\overline{\alpha}$:β 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 function[21]. 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 function[21].

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 $\bar{\alpha}$:β 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

19

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 ($\bar{\alpha}$:β), 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], randomization [24] and multimodel inference[25]. 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 criteria[36]. We implemented this procedure using

467   the stepAIC function in the MASS library[37] 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 bias[38]. 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 package[25]. 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 treatments[24]. 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 iterations[24].

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 ($0 <$ 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 2.15.1[39].

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

23

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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

543

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637

638

Figure legends:

640

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

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

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

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

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

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

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

648 intermediate (Low-Int) $\overline{\alpha}$ 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 ($\overline{\alpha}$) 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.

a Observed landscapes (spatial blocks within site)

b Observed landscapes (spatial blocks within habitat)

c Simulated landscapes (across blocks within site)

d Simulated landscapes (across sites within habitat)

β diversity: Low, Int-High
ᾱ diversity: Low-Int, High

a

- Stepwise−deletion N=65
- Randomization tests N=65
- Multimodel inference N=59

Proportion of species maintaining ecosystem functioning

Number of functions

b

- N=62
- N=62
- N=53

Number of landscapes (spatial blocks)