- Title Local nutrient addition drives plant diversity losses but not biotic homogenization in global 1
- 2 grasslands

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### 93 Abstract:

94 Nutrient enrichment typically causes local plant diversity declines. A common but untested 95 expectation is that nutrient enrichment also reduces variation in nutrient conditions among localities 96 and selects for a smaller pool of species, causing greater diversity declines at larger than local scales 97 and thus biotic homogenization. Here we apply a framework that links changes in species richness 98 across scales to changes in the numbers of spatially restricted and widespread species for a 99 standardized nutrient addition experiment across 72 grasslands on six continents. Overall, we find proportionally similar species loss at local and larger scales, suggesting similar declines of spatially 100 restricted and widespread species, and no biotic homogenization after 4 years and up to 14 years of 101 treatment. These patterns of diversity changes are generally consistent across species groups. Thus, 102 nutrient enrichment poses threats to plant diversity, including for widespread species that are often 103 critical for ecosystem functions. 104

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## 107 Introduction

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Agricultural fertilization practices and atmospheric nutrient deposition have led to increased 109 availability and redistribution of soil nutrients globally<sup>1-3</sup>. At local scales (i.e.,  $\alpha$  diversity), nutrient 110 enrichment tends to reduce plant diversity<sup>4,5</sup>. This diversity decline is typically ascribed to 111 disproportionate losses of rare species (i.e., species with relatively low cover) because small 112 populations are more susceptible to extinction<sup>6-8</sup>. In addition, nutrient enrichment often leads to the 113 removal of species with traits ill-suited for effectively competing in high nutrient conditions<sup>6</sup>. While 114 species can vary widely in their nutrient requirements and tolerances, groups of species with similar 115 (shared) characteristics can be lost from a flora. For example, native species are more likely to be 116 117 lost than non-native species when nutrients are enriched because non-natives are often betteradapted to nutrient-rich conditions<sup>6,9,10</sup>. Similarly, nitrogen-fixing legumes may be more vulnerable 118 than other species in high nutrient environments due to their decreased competitive advantage<sup>6,11</sup>. 119

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Despite clear evidence that nutrient enrichment causes losses of  $\alpha$  diversity in grasslands<sup>4,5</sup>, how 121 122 these losses are reflected at larger spatial scales (i.e.,  $\gamma$  diversity; calculated by aggregating local communities) is less straightforward<sup>12-14</sup>. Yet, it is diversity loss and change at larger spatial scales 123 that is most often relevant for biodiversity conservation and management as well as for the 124 provision of ecosystem functions and services<sup>15,16</sup>. It is often assumed that nutrient enrichment, like 125 126 many other global changes, results in biotic homogenization (i.e., increasing similarity in composition among local communities, quantified as a decrease in  $\beta$  diversity)<sup>17–21</sup>. This is because 127 local nutrient enrichment is expected to create homogeneous nutrient conditions among localities 128 129 and consistently select for a smaller pool of species that are nutrient-demanding, fast-growing, and highly competitive for light<sup>22,23</sup>. Previous investigations of scale-dependent diversity change under 130 nutrient enrichment have tended to be short term or limited in spatial extent<sup>24–28</sup>. These short-term or 131 132 spatially-restricted studies have found mixed results, indicating that nutrient enrichment leads to biotic homogenization<sup>29–31</sup>, no changes in  $\beta$  diversity<sup>24,26,27,32</sup> or even differentiation (i.e., increase in 133  $\beta$  diversity)<sup>25,28,33-37</sup>. 134

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A recent extension to Whittaker's multiplicative  $\beta$  diversity partition enables linking changes in 136 average  $\alpha$  diversity ( $\overline{\Delta \alpha}$ ),  $\gamma$ , and  $\beta$  diversity (in log scale) to changes in the numbers of spatially 137 restricted and widespread species (Fig. 1)<sup>12,38</sup>. This framework illustrates how nutrient enrichment 138 could cause biotic homogenization if local communities gain widespread species (Fig. 1: scenario 139 I), if spatially restricted species are replaced by widespread species (Fig. 1: scenario II), or if the 140 141 number of spatially restricted species decreases (Fig. 1: scenario III). Conversely, nutrient enrichment could cause biotic differentiation if local communities lose widespread species (Fig. 1: 142 scenario IV), if widespread species are replaced by spatially restricted species (Fig. 1: scenario V), 143 144 or if the number of spatially restricted species increases (Fig. 1: scenario VI). Finally, if gains or 145 losses of species at the  $\alpha$  and  $\gamma$  scale are similar (i.e., approximately equal or proportional), then we would observe no change in  $\beta$  diversity (1:1 diagonal line in Fig. 1). However, clear links between 146 changes in diversity across spatial scales and changes in the number of spatially restricted and 147 148 widespread species under nutrient enrichment are yet to be made.

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Here, we use this framework to synthesize scale-dependent plant diversity change (for the entire 150 community and groups of species) under nutrient enrichment using a long-term standardized 151 experiment in 72 grasslands distributed across six continents (i.e., NutNet<sup>39</sup>; Fig. S1; Table S1). We 152 use two treatments: Ambient (Control) and fertilization by nitrogen, phosphorus, and potassium 153 154 together (i.e., NPK). Nutrients were added at a rate of 10 g m<sup>-2</sup> annually. Treatments were randomly assigned to 5 m  $\times$  5 m plots and were replicated in three or more blocks. Species cover was 155 recorded in one 1 m  $\times$  1 m permanent subplot using a standardized protocol. At each site,  $\alpha$ 156 157 diversity is determined as the number of species in each permanent subplot (i.e., species richness),

and  $\gamma$  diversity as the total number of species occurring in three permanent subplots (for each 158 159 treatment separately). We exclude additional blocks from sites that have more than three because  $\gamma$ 160 and  $\beta$  diversity depend on the number of local communities used. We calculate  $\Delta \alpha$  as the richness difference in local communities (subplots) and  $\Delta \gamma$  as the difference in the sum of the subplots under 161 162 nutrient addition relative to that of control on the log scale. That is,  $\Delta \alpha = \log(\alpha_{\text{NPK}}/\alpha_{\text{Control}})$  and  $\Delta \gamma =$ 163  $\log(\gamma_{\text{NPK}}/\gamma_{\text{Control}})$ . We then calculate  $\Delta\beta$  as  $\Delta\gamma$  minus  $\overline{\Delta\alpha}$ , where  $\overline{\Delta\alpha}$  is the average of  $\Delta\alpha$  over three blocks. Overall, we find proportionally similar species loss at local and larger scales, suggesting 164 similar magnitudes of declines of spatially restricted and widespread species. Thus, we find no clear 165 166 biotic homogenization or differentiation four years, and even up to 14 years, after nutrient additions began. Moreover, these overall patterns of little change in  $\beta$  diversity hold consistent across species 167 groups. 168

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#### 170 Results and discussion

- 171
- 172 Changes in  $\alpha$ -,  $\gamma$ -, and  $\beta$  diversity for the entire communities

Overall, adding nutrients decreased  $\alpha$  and  $\gamma$  diversity, but it had no significant effects on  $\beta$  diversity 173  $(\Delta\beta = 0.03; 95\%$  credible interval: -0.02 to 0.08) (Fig. 2; Table S3), see also<sup>27</sup>. While we observed 174 175 substantial variation in  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and to a lesser extent,  $\Delta \beta$  among sites (Table S4), we found no strong relationships between site-level  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  and distance among blocks, drought 176 intensity, grazing intensity, productivity, and/or the size of the species pool<sup>24,25,34,40</sup> (Fig. S3). On a 177 site level, we found biotic homogenization at 24 sites, differentiation at 47 sites, and no change in  $\beta$ 178 diversity at one site. However, the site-level 95% credible intervals (see Methods) overlapped 0 for 179 all sites, suggesting no significant change in  $\beta$  diversity under nutrient addition (Table S4). 180 Importantly, the overall effects of nutrient addition on  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity were similar when we 181 used effective numbers of species based on either Shannon diversity or Simpson diversity that 182 account for species relative abundances<sup>40</sup> (Fig. S4; Table S3). Because species richness is more 183 strongly influenced by rare species, while Shannon and Simpson diversity increasingly weigh 184 abundant species, this result suggests that relatively rare and abundant species responded similarly 185 186 to nutrient addition.

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#### 188 Changes in $\alpha$ -, $\gamma$ -, and $\beta$ diversity for species groups

The overall proportional species loss within the community at local and larger scales on average 189 190 may result if different species groups have contrasting patterns of response to nutrient addition. For 191 instance, this result could be the case if native species loss is greater at the larger spatial scale than 192 at the local scale, while non-native species loss is lower at the larger than the local scale. To test this possibility, we investigate changes in  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity for native and non-native species 193 194 separately. Extending previous studies<sup>6,41</sup>, we found that nutrient addition decreased native species more than non-native species. Compared to non-native species, nutrient addition resulted in a 10% 195 196 greater reduction in  $\alpha$  diversity and a 16% greater reduction in  $\gamma$  diversity of native plant species, respectively (Table S5). The overall pattern of diversity change across spatial scales for native 197 species largely followed that of the entire communities with similar magnitudes of decline in  $\alpha$  and 198 199  $\gamma$  diversity and little change in  $\beta$  diversity ( $\Delta\beta = 0$ ; 95% credible interval: -0.05 to 0.06; Fig. 3A). 200 For non-native species, overall, nutrient addition decreased  $\alpha$  diversity 6% more than  $\gamma$  diversity 201 (Table S5). But nutrient addition had no significant effects on  $\beta$  diversity of non-native species ( $\Delta\beta$ 202 = 0.04; 95% credible interval: -0.05 to 0.14; Fig. 3B).

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We also separated species into graminoid, forb, legume, and woody species to investigate scaledependent diversity change within species groups. Nutrient addition led to the greatest reduction of  $\alpha$  diversity in forb species and of  $\gamma$  diversity in woody species (Table S6). Similar to that of entire communities, nutrient addition decreased  $\alpha$  and  $\gamma$  diversity by similar magnitudes and it had no effects on  $\beta$  diversity for graminoid species ( $\Delta\beta = 0.01$ ; 95% credible interval: -0.04 to 0.05; Fig. 4B; Table S6) and legume species ( $\Delta\beta = 0.00$ ; 95% credible interval: -0.17 to 0.18; Fig. 4C; Table 210 S6). Overall, nutrient addition decreased  $\alpha$  diversity 8% more than  $\gamma$  diversity for forb species, 211 while it decreased  $\gamma$  diversity 11% more than  $\alpha$  diversity for woody species (Table S6). However, 212 nutrient addition also did not have significant effects on  $\beta$  diversity for forb species ( $\Delta\beta = 0.09$ ; 213 95% credible interval: -0.02 to 0.19; Fig. 4C; Table S6). Nutrient addition caused a weak biotic 214 homogenization for woody species ( $\Delta\beta = -0.14$ ; 95% credible interval: -0.30 to 0.003; Table S6), 215 this was primarily linked to loss of spatially restricted species (Fig. 4D).

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## 217 Robustness and limitations

218 We tested the robustness of our results by performing multiple sensitivity tests. We redid the analyses for the effects of nutrient addition on  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity for the entire communities as 219 well as for species groups using a subset of 16 sites that had data 14 years after nutrient additions 220 221 began (Fig. S5 ~ Fig. S7). In all, we found that the overall effects were largely similar in these 222 longer-term sites to that of 72 sites that had data four years after nutrient additions began. Because 223 three spatial blocks may be somewhat limited in spatial extent for estimating effects on  $\beta$  diversity, 224 we tested whether including more blocks to create the  $\gamma$  scale altered our results. We redid the analyses for the effects of nutrient addition on  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity for the entire communities as 225 226 well as for species groups using using 11 sites that had five spatial blocks (Fig. S8~Fig. S10). 227 Again, the overall effects were largely similar to that we found for the full analysis of the 72 sites 228 with three blocks.

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230 Despite our evidence for little change in  $\beta$  diversity under nutrient addition across the entire experiment, we recognize limitations of extrapolating these results to the landscape scale (e.g., >1 231  $km \times 1 km$ ). This is because many ecological processes that directly and indirectly influence plant 232 diversity can be very different at the landscape scales<sup>14,42</sup>. The scale at which we inferred changes in 233 the number of spatially restricted and widespread species, by examining how many local 234 235 communities they were lost from, is a relatively small spatial scale. Linking estimates of species' geographic range size and other key traits with changes in plant diversity across larger spatial 236 scales<sup>19,42</sup> will deepen our understanding of the mechanisms of diversity change. 237

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239 To summarize, we apply a framework to a globally distributed long-term experiment to provide a 240 comprehensive synthesis of the impact of nutrient addition on scale-dependent plant diversity 241 change in grasslands. The framework links changes in species richness across scales to that changes 242 in the numbers of spatially restricted and widespread species. Overall, we found similar 243 proportional plant diversity declines at local and larger spatial scales under nutrient addition, and 244 little evidence for either biotic homogenization or differentiation within sites. These overall patterns were largely consistent for diversity metrics that incorporate relative species covers, across species 245 246 groups, and over long time periods. This demonstrates that nutrient enrichment poses a potential 247 threat to all plant species groups, including widespread and native species that often drive 248 ecosystem functions and services.

249

# 250 Methods

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# 252 Experimental setup

The experimental sites used in this study are part of the Nutrient Network (NutNet, Fig. S1 and 253 Table S1). The experimental design includes a factorial manipulation of nutrients (N, P, and K) plus 254 two fences to exclude herbivores, see ref<sup>39</sup> for more details. For the analyses here, we used plots 255 256 under two treatments: Ambient (Control) and fertilization by nitrogen, phosphate, and potassium 257 together (i.e., NPK). Treatments were randomly assigned to 5 m  $\times$  5 m plots and were replicated in three or more blocks. A micronutrient mix consists of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), 258 Cu (1%), Zn (1%), B (0.2%), and Mo (0.05%) was added once only at the start of the experiment 259 260 (i.e., year 1) for the nutrient addition plots, but not in subsequent years to avoid toxicity. Nitrogen, 261 phosphate, potassium were added annually before the growing season of each treatment year at 262 most sites. Nitrogen was added as  $10 \text{ g m}^{-2} \text{ yr}^{-1}$  time-release urea [(NH<sub>2</sub>)<sub>2</sub>CO], phosphate was added 263 as  $10 \text{ g m}^{-2} \text{ yr}^{-1}$  triple-super phosphate [Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>], while potassium was added as  $10 \text{ g m}^{-2} \text{ yr}^{-1}$ 264 sulfate [K<sub>2</sub>SO<sub>4</sub>].

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Data were retrieved from the NutNet database in November 2023. We analyzed data from 72 sites
where 1) nutrients were applied for at least four years; and 2) each site had at least three blocks.
These sites are distributed across six continents and include a wide range of grassland types. See
Fig. S1 and Table S1 for details of geolocation, grassland types, and experimental years used.

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# 271 Sampling protocol

Scientists at NutNet sites followed standard sampling protocols<sup>39</sup>. Specifically, a 1 m  $\times$  1 m subplot 272 273 within each plot was permanently marked for annual recording of plant species composition. 274 Species cover (%) was estimated visually for individual species in the subplots; thus the total cover 275 of living plants may sometimes exceed 100% for multilayer canopies. At most sites, cover was 276 recorded once per year at peak biomass. At some sites with strong seasonality, cover was recorded 277 twice per year to include a complete list of species. For those sites, the maximum cover for each 278 species and total biomass were used in the analyses. When taxa could not be identified to the species level, they were aggregated at the genus level but referred to as "species" for simplicity. 279

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## 281 Quantifying changes in $\alpha$ , $\gamma$ , and $\beta$ diversity

282 We measured  $\alpha$  and  $\gamma$  diversity using species richness (i.e., number of species) because it is the most commonly examined diversity metric<sup>43</sup>. At each site,  $\alpha$  diversity was estimated as the number 283 of species in each permanent subplot  $(1 \text{ m} \times 1 \text{ m})$ , and  $\gamma$  diversity as the total number of species 284 285 occurring in three permanent subplots (for each treatment separately). To standardize sampling 286 effort, for sites with more than three blocks, we selected the first three blocks according to the block number recorded by site PIs. The framework relies on Whittaker's multiplicative  $\beta$  diversity 287 partition, and it quantifies  $\beta$  diversity using the effective number of communities<sup>12</sup>. As such, if all 288 289 subplots share the same species, then  $\beta$  diversity would equal to one. In contrast, if each subplot has 290 unique species, then  $\beta$  diversity would equal to three. We calculated  $\Delta \alpha$  as the richness difference in local communities (subplots) and  $\Delta \gamma$  as the difference in the sum of the subplots under nutrient 291 addition relative to that of control treatment on the log scale. That is,  $\Delta \alpha = \log(\alpha_{\text{NPK}}/\alpha_{\text{Control}})$  and  $\Delta \gamma =$ 292  $\log(\gamma_{\text{NPK}}/\gamma_{\text{Control}})$ . We calculated  $\Delta\beta$  as  $\Delta\gamma$  minus  $\overline{\Delta\alpha}$ , where  $\overline{\Delta\alpha}$  is the average of  $\Delta\alpha$  over three 293 blocks. A decrease in  $\Delta\beta$  indicates nutrient addition causes species composition to be more similar 294 295 among three subplots than that among control subplots. Because sites are not evenly distributed 296 around the world, many sites are aggregated in North America, we checked spatial autocorrelation 297 of diversity change under nutrient addition using Moran's I<sup>44</sup>. We found that  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  did not appear to be more similar for sites that are closer to each other (Table S2). 298

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300 We fitted multilevel (also referred as mixed effects or hierarchical) models for  $\Delta \alpha$ ,  $\Delta \gamma$ , and  $\Delta \beta$  (as the response variable; all on the log scale) separately. We included random intercept for each site, 301 302 model was coded as: richness change  $\sim 1 + (1 | \text{sites})$  to estimate site-level variation. We used Bayesian analysis because it yields full posterior distributions of parameters rather than point 303 304 estimates and p-values, which provides a deeper understanding of the uncertainty and variability in the results<sup>45</sup>. Models described above were fitted using the Hamiltonian Monte Carlo (HMC) 305 sampler in Stan and coded using the package 'brms' (version 2.21.0) in R (version 4.4.1)<sup>46,47</sup>. 306 Models were fitted without explicitly specifying priors, allowing brms to assign its default priors. 307 Models were fitted with 6 chains and 3000 iterations (1000 iterations for warm up). Visual 308 309 inspection of the HMC chains and Rhat summaries showed model convergence (all Rhats < 1.03; 310 Table S3; Table S5; Table S6). We visually checked posterior predictive plots to determine how 311 well models can reproduce the data (Fig. S2).

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313 To examine whether diversity changes were sensitive to species relative covers, we redid the above 314 analyses (i.e., based on species richness) using Shannon diversity and Simpson diversity (both 315 converted to effective numbers)<sup>48</sup>(Fig. S4). Species richness is most sensitive to rare species, 316 followed by Shannon diversity, and Simpson diversity is more sensitive to the numbers of 317 relatively abundant species. We calculated the exponential of Shannon diversity and the inverse 318 form of Simpson diversity using the R package vegan (version 2.6-6.1)<sup>49</sup>. These three diversity 319 metrics equal to diversity with order  $q = \{0, 1, 2\}$ , where increasing q decreases the influence of

320 rare species, and  $D_q = \left(\sum_{i=1}^{s} p_i^q\right)^{1/(1-q)}$ , where p is the relative cover of species i, s is the total number

321 of species. These diversity metrics are also referred to as Hill numbers<sup>48,50</sup>.

322

Site covariates. We investigated whether the effects of nutrient addition on  $\overline{\Delta \alpha}$ ,  $\gamma$ , and  $\beta$  diversity 323 324 based on species richness were mediated by site characteristics. We included site characteristics that have been shown in previous literature to influence  $\Delta \alpha$ ,  $\Delta \gamma$ , and  $\Delta \beta$  in grasslands: site species pool, 325 site productivity, drought intensity, and grazing intensity<sup>24,25,34,40</sup>. We quantified drought intensity as 326 the sum of annual evapotranspiration/precipitation, and averaged it from year 0 to 4 at each site. 327 328 Precipitation and potential evapotranspiration used to calculate SPEI were downloaded from 329 https://crudata.uea.ac.uk/cru/data/hrg/cru ts 4.07/. We quantified the site species pool as the total 330 number of species and site productivity as the average aboveground biomass from year 0 to 4 under 331 the control treatment in the three blocks at each site. Aboveground biomass was harvested within two  $1 \times 0.1$  m strips (in total 0.2 m<sup>2</sup>), strips were moved from year to year to avoid resampling the 332 333 same location. For subshrubs and shrubs occurring within strips, we collected all leaves and current 334 year's woody growth. All biomass was dried at 60 °C (to constant mass) before weighing to the 335 nearest 0.01 g. We used published methods to quantify an integrated grazing intensity metric from vertebrate herbivores at each site. Specifically, herbivore species (> 2 kg) that consume grassland 336 337 biomass were documented at each site by site PIs, and each species was assigned an importance 338 value from 1 (present, but low impact and frequency) to 5 (high impact and frequency). An index 339 value was calculated for each site as the sum of herbivore importance values for all herbivores following ref<sup>51,52</sup>. We also investigated relationships between change in diversity and distance 340 among blocks, because species composition may become less similar as the distance between 341 342 sampled communities increases. The average pairwise distance among the three blocks within sites 343 ranged from 23.04 to 12538.09 m, with a mean of 513.01 m and a median of 118.7 m across 54 sites that have geolocation data for each block. We first calculated three Euclidean distances 344 between pairs of blocks, we then used the mean of these pairwise distances as the average distance 345 346 among blocks. We used the average distance among blocks instead of area, because blocks are arranged in parallel at some sites. We fitted linear regression models with  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  as the 347 response variable separately, and each of the site characteristics was used as a predictor variable. 348 349

350 **Species groups.** We then investigated the effects of nutrient addition on  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity within groups of species with similar characteristics following the method for changes in  $\alpha$ ,  $\gamma$ , and  $\beta$ 351 352 diversity in the entire communities. We eliminated sites where no species occurred in control, 353 nutrient addition, or both plots for a particular group because the value of the log (0) is undefined. 354 We ran the analyses separately for native and non-native species. Native and non-native species were classified by site PIs. Then, we investigated effects of nutrient addition on species richness for 355 different life forms including forb, graminoid, legume, and woody species because previous studies 356 have shown that different life forms may show distinct responses to nutrient addition<sup>6,11,53</sup>. 357

358

**Sensitivity test.** We tested whether effects of nutrient addition on species richness across spatial scales depend on experimental duration because a few single-site experiments have shown that the effects of nutrient additions on changes in diversity, especially  $\beta$  diversity, may take several years to emerge<sup>29,31</sup>. To that end, we used a subset of 16 sites that had data 14 years after nutrient

363 additions began. Also, because three blocks may be limited in spatial extent, we tested whether 364 combining more blocks to create the  $\gamma$  scale would alter our results. We redid the analyses using 365 data from 11 sites that had five spatial blocks.

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367 Data availability: The species cover and species richness data, site abiotic and biotic 368 environmental data used and generated in this study have been deposited in the Figshare database and are publicly available (https://doi.org/10.6084/m9.figshare.26412295.v3). The NutNet data are 369 the 370 publicly available on Environmental Data Initiative (EDI) 371 (https://portal.edirepository.org/nis/advancedSearch.jsp). Source data are provided with this paper. 372

# 373 Code Availability

**374** The R codes used to produce results in this study have been deposited in the GitHub **375** (https://github.com/chqq365/plant-diversity-and-biotic-homogenization.git) and archived through **376** Zenodo (https://doi.org/10.5281/zenodo.14902812).

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#### **398 Author Contributions Statement**

Q.C., J.M.C., S.A.B., E.L., W.S.H. conceived the study; Q.C., J.M.C., S.A.B. developed the
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#### 410 Competing Interests Statement

411 Authors declare that they have no competing interests.

- 413 Figure Legends/Captions
- 414

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415 Fig 1. A framework linking diversity changes at the  $\alpha$ -,  $\gamma$ -, and  $\beta$ -scales to changes in the number of spatially restricted and widespread species.  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  are log response ratios 416 417 (LRR) of average  $\alpha$ -,  $\gamma$ - and  $\beta$ - diversity under nutrient enrichment relative to that under ambient 418 conditions (control).  $\Delta\beta$  is equal to zero along the 1:1 diagonal line. Below the diagonal line,  $\Delta\gamma < \infty$ 419  $\overline{\Delta \alpha}$ ,  $\Delta \beta < 0$ , nutrient enrichment causes biotic homogenization. Above the diagonal line,  $\Delta \gamma > 0$ 420  $\overline{\Delta \alpha}$ ,  $\Delta \beta > 0$ , nutrient enrichment causes biotic differentiation. Moreover, homogenization can be attributed to three scenarios including I: gain of widespread species ( $\Delta\gamma < \overline{\Delta\alpha}$ , and  $\Delta\gamma > 0$ ,  $\overline{\Delta\alpha} > 0$ 421 0); II: spatially restricted species replaced by widespread species ( $\Delta \gamma < \overline{\Delta \alpha}$ ,  $\Delta \gamma < 0$  and  $\overline{\Delta \alpha} >$ 422 0); III: Loss of spatially restricted species ( $\Delta \gamma < \overline{\Delta \alpha}$ , and  $\Delta \gamma < 0$ , 423  $\overline{\Delta \alpha} < 0$ ). Conversely, 424 differentiation can be attributed to three scenarios that include IV: Loss of widespread species ( $\Delta \gamma >$ 425  $\overline{\Delta \alpha}$ , and  $\Delta \gamma < 0$ ,  $\overline{\Delta \alpha}$ < 0); V: Widespread species replaced by spatially restricted species ( $\Delta \gamma >$  $\overline{\Delta \alpha}$ ,  $\Delta \gamma > 0$  and  $\overline{\Delta \alpha} < 0$ ; VI: gain of spatially restricted species ( $\Delta \gamma > \overline{\Delta \alpha}$ , and  $\Delta \gamma > 0$ ,  $\overline{\Delta \alpha}$ 426 427 > 0). Adapted from<sup>12</sup>.

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Fig. 2. Changes in average  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity ( $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ ) with nutrient addition. 429 430 LRR: log response ratio. The white 1:1 diagonal line indicates no effects of nutrient addition on  $\beta$ 431 diversity. Numbers in the parentheses are the number of sites. When a site has  $\overline{\Delta \alpha} = 0$ ,  $\Delta \gamma = 0$ , or  $\Delta\beta = 0$ , it was not counted into any of the six scenarios as shown in the framework. The small 432 points represent site-level  $\overline{\Delta \alpha}$  and  $\Delta \gamma$  at 72 sites. The large open point and error bars are the 433 434 estimated mean and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  across all sites. See Table S3 for 435 model fit and estimated overall means and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ . See Table S4 for site-level estimates and 95% credible intervals. Source data are provided as a Source Data 436 437 file.

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Fig. 3. Changes in average  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity ( $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ ) with nutrient addition for 439 440 native and non-native species groups. (A) native and (B) non-native species. LRR: log response 441 ratio. The white 1:1 diagonal line indicates no effects of nutrient addition on  $\beta$  diversity. Numbers in the parentheses are the number of sites. When a site has  $\overline{\Delta \alpha} = 0$ ,  $\Delta \gamma = 0$ , or  $\Delta \beta = 0$ , it was not 442 counted into any of the six scenarios as shown in the framework. The small points represent site-443 444 level  $\overline{\Delta \alpha}$  and  $\Delta \gamma$ . The large open point and error bars are the estimated mean and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  across all sites. See Table S5 for model fit and estimated overall 445 446 means and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ . Source data are provided as a Source Data 447 file.

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Fig. 4. Changes in average  $\alpha$ ,  $\gamma$ , and  $\beta$  diversity ( $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ ) with nutrient addition for 449 450 different functional species groups. (A) forb, (B) graminoid, (C) legume, and (D) woody 451 species. LRR: log response ratio. The white 1:1 diagonal line indicates no effects of nutrient addition on  $\beta$  diversity. Numbers in the parentheses are the number of sites. When a site has  $\overline{\Delta \alpha}$  = 452 453  $0, \Delta \gamma = 0$ , or  $\Delta \beta = 0$ , it was not counted into any of the six scenarios as shown in the framework. The small points represent site-level  $\overline{\Delta \alpha}$  and  $\Delta \gamma$ . The large open point and error bars are the 454 estimated mean and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$  across all sites. See Table S6 for 455 model fit and estimated overall means and 95% credible intervals for  $\overline{\Delta \alpha}$ ,  $\Delta \gamma$ , and  $\Delta \beta$ . Source data 456

457 are provided as a Source Data file.