

Relationships between plant community productivity and diversity vary with trampling disturbance in an Inner-Mongolian steppe

Yinzhan Liu

Henan University

Luna Zhang

Henan University

Yangyang Han

Henan University

Anqun Chen

Henan University

Renhui Miao

Henan University

Ji Chen

Aarhus University

Dong Wang (✉ wangdong19882005@163.com)

Henan University

Article

Keywords: functional group, grassland restoration, human disturbance, semi-arid grassland

Posted Date: August 18th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-775920/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

1 **Relationships between plant community productivity and diversity vary with**
2 **trampling disturbance in an Inner-Mongolian steppe**

3 Yinzhan Liu¹, Luna Zhang¹, Yangyang Han¹; Anqun Chen¹, Renhui Miao¹, Ji Chen²,
4 Dong Wang^{1*}

5 1 International Joint Research Laboratory for Global Change Ecology, Laboratory of
6 Biodiversity Conservation and Ecological Restoration, School of Life Sciences,
7 Henan University, Kaifeng 475004, Henan, China

8 2 Department of Agroecology, Aarhus University, 8830 Tjele, Denmark.

9 **Correspondence**

10 Dong Wang

11 wangdong19882005@163.com

12

13

14 **Abstract**

15 The relationship between diversity and productivity of plant communities is an
16 important issue in grassland restoration. However, the degree to which this
17 relationship varies during the restoration stage after trampling disturbance is not
18 clear. Here, we conducted a five-year study in a steppe after 4-year trampling to
19 detect restoration patterns of plant community and investigate variation in
20 diversity-productivity relationships. Our results showed that community cover,
21 abundance, height, and productivity recovered quickly after the trampling
22 disturbance ceased. However, the recovery of diversity was slower than biomass in
23 the steppe. In addition, grass, annual, and biennial recovery was more rapidly than
24 the recovery of forbs in the steppe. Moreover, following the restoration process, the
25 positive correlation between productivity and diversity was decoupled, and a
26 negative correlation between productivity and diversity developed. Our finding
27 provides the key evidence for the asynchronous relation between productivity and
28 diversity, and reveals that grass restored more rapidly than forbs in plant community
29 restoration after disturbance. This study indicates that the trade-off between plant
30 community structure and function can vary with the restoration process, and
31 implicates that future modeling and experimental studies should focus on the
32 different responses of productivity and diversity in plant community restoration.

33 **Key words:** functional group, grassland restoration, human disturbance, semi-arid
34 grassland.

35

36 Grasslands are among the most important terrestrial ecosystems in the world.
37 They cover 3.4 billion ha, occupy 40% of global terrestrial area and 69% of global
38 agricultural area ^[1-2], account for more than 30% of terrestrial net primary
39 productivity, and provide many services including food production, furs, tourism,
40 and climate change mitigation. However, grasslands are degrading rapidly^[2] due to
41 climate change (including warming and changing precipitation regimes) and human
42 disturbance (including the overgrazing, trampling by tourists, and vehicle
43 disturbance). Symptoms of grassland degradation include rodent outbreaks^[3-4],
44 decreases in the proportion of high-quality forage ^[5], and reductions in plant
45 diversity ^[5-6] and productivity ^[5]. In response to this degradation, several methods of
46 grassland restoration have been deployed, including grazing exclusion ^[7-8], replacing
47 grazing with mowing ^[4,9-10], grassland re-establishment ^[11-13], and some other
48 methods ^[14-15]. Trampling by domestic animals and humans is among the more
49 common disturbances in grassland ecosystems ^[16-18]. This disturbance often occurs in
50 conjunction with heavy grazing ^[19-20], tourism ^[21] and road construction ^[22].
51 Trampling can compact the soil, thus affecting water cycle ^[18, 23]. Additionally,
52 trampling can trigger injury of plant stalks and roots, suppressing plant growth,
53 limiting productivity ^[24-25] and decreasing diversity ^[19, 26-27], which can consequently
54 induce soil erosion ^[28]. Moreover, because plant functional groups differ in their
55 tolerance to trampling, trampling can alter community composition ^[29]. However, the
56 effects of trampling on community composition do not appear to be consistent. Some
57 studies have reported that trampling elevated the dominance of grass in grassland

58 communities ^[18, 30], but some others have reported that trampling supported forbs ^[31]
59 or did not affect community composition ^[20].

60 Reestablishing high biodiversity and productivity is an increasingly common
61 goal of restoration ecology ^[9, 32-34]. Thus, considering the relationships between plant
62 diversity and productivity is important for grassland ecology, and studies on the
63 relationships between plant diversity and productivity in the restoration stage after
64 disturbance have important theoretical implications for grassland conservation. A
65 meta-analysis has reported that in datasets of regional extent, most productivity–
66 richness relationships were positive, and only few studies have reported non-linear
67 relationships ^[35]. However, unimodal relationships were also reported in studies at
68 small and large scales ^[36-37]. In addition, it has also been reported that the
69 diversity-productivity relationship in a plant community can change over time ^[38].
70 However, variation in the diversity-productivity relationship during the restoration
71 stage has not been extensively studied. Furthermore, although most previous studies
72 have documented effects of trampling on ecosystem structure and function, only a
73 few studies have investigated changes in plant community composition during the
74 restoration stage after trampling. To our best knowledge, no study has reported the
75 variation in the relationship between plant diversity and productivity during the
76 restoration period after trampling. We conducted a five year investigation of the
77 plant community in a post-trampled natural grassland in an Inner-Mongolian steppe
78 to get a better understanding on the above questions. We assessed species richness,
79 plant community abundance, cover, height, and aboveground productivity, and

80 diversity was calculated in the experiment. The objectives of this study are 1) to
81 evaluate the pattern of restoration of the plant community after trampling in the
82 steppe, and 2) to test the variation in the relationship between plant community
83 diversity and productivity after trampling in the steppe.

84 **Results**

85 **Abundance, cover, and height.** Community abundance, cover, and height were all
86 significantly different between R and C treatments (Table 1). In addition, the
87 differences in these three variables between the two treatments significantly varied
88 with year (Table 1). In the first two years, all three variables in the R plot were
89 significantly lower than in the C plot (Fig. 1). However, in 2016, although
90 abundance and cover in the R plot remained lower, height was significantly higher
91 than in the C plot (Fig. 1). In 2017, the difference in abundance and cover between R
92 and C plots disappeared (Fig. 1). In 2018, the abundance and height of the R plot
93 was higher, but cover was still lower than in the C plot (Fig. 1).

94 Moreover, abundance, cover and height of different functional groups also
95 differed with treatment and year (Fig. 1). Abundance, cover and height of AB in the
96 R plot were significantly lower than in the C plots in 2014 (Fig. 1). However, in
97 2015, none of the three variables were significantly different between the two
98 treatments (Fig. 1). In 2017 and 2018, all of the three variables of AB were
99 significantly higher in the R plot than in the C plot (Fig. 1). Abundance and cover of
100 PF were significantly lower in the R plot than in the C plot, though PF height was
101 significantly higher in the R plot than in the C plot (Fig. 1). The cover and height of

102 PG in the R plot was lower than in the C plot in 2014. The abundance and height of
103 PG was lower, but cover of PG was higher, in the R plot than in the C plot in 2015
104 (Fig. 1). In 2016, only the abundance of PG was lower, but the other two variables
105 were higher in the R plot than in the C plot (Fig. 1). In 2017 and 2018, all three
106 variables of PG were higher in the R plot than in the C plot (Fig. 1).

107 **Productivity and aboveground biomass.** Aboveground productivity varied
108 significantly with year (Table 1). The highest (212.9) and lowest (114.4) values
109 occurred in 2016 and 2014 (Fig. 2a), respectively. In addition, the treatment effect
110 varied significantly with year (Table 1). Community productivity in the R plot was
111 86.3% ($F = 53.29$, $P < 0.001$, Fig. 2a) and 87.0% ($F = 118.16$, $P < 0.001$, Fig. 2a)
112 lower than in C plots in 2014 and 2015, but 32.2% ($F = 64.46$, $P < 0.001$, Fig. 2a)
113 and 80.2% ($F = 21.48$, $P = 0.004$, Fig. 2a) higher than in C plots in 2016 and 2017,
114 respectively. In the last year, no difference was detected between the two treatments.

115 Biomass varied significantly among different functional groups and treatments
116 (Table 1). Biomass of AB and PF was lowest (2.6 g) and highest (131.9 g) in the C
117 plots (Fig. 2b, 2c, 2d). Biomass of PF and PG was lowest (7.5 g) and highest in the R
118 (138.5) plots (Fig. 2b, 2c, 2d), respectively. In addition, significant interactions were
119 detected between functional groups and year (Table 1). Biomass of AB in the R plots
120 was no different than in the C plots in 2014 ($F = 2.91$, $P = 0.139$, Fig. 2b), 2015 ($F =$
121 0.60 , $P = 0.468$, Fig. 2b), and 2016 ($F = 0.524$, $P = 0.496$, Fig. 2b), but became
122 significantly higher than in the C plots in 2017 ($F = 22.62$, $P = 0.003$, Fig. 2b), and
123 2018 ($F = 12.46$, $P = 0.012$, Fig. 2b). The biomass of PF in the R plot was 86.1 ($F =$

124 52.15, $P < 0.001$, Fig. 2c), 135.1 ($F = 150.07$, $P < 0.001$, Fig. 2c), 156.0 ($F = 404.48$,
125 $P < 0.001$, Fig. 2c), 124.9 ($F = 75.81$, $P < 0.001$, Fig. 2c), and 119.7 g ($F = 298.96$, P
126 < 0.001 , Fig. 2c); lower than in C plots in 2014, 2015, 2016, 2017, and 2018,
127 respectively. The biomass of PG in the R plot was 9.0 and 15.3 g lower than in the C
128 plot in 2014 ($F = 30.88$, $P < 0.001$, Fig. 2d) and 2015 ($F = 31.00$, $P < 0.001$, Fig. 2d),
129 but 223.2 ($F = 401.18$, $P < 0.001$, Fig. 2d), 241.3 ($F = 54.37$, $P < 0.001$, Fig. 2d), and
130 73.5 g ($F = 67.94$, $P < 0.001$, Fig. 2d) higher than in the C plot in 2016, 2017, and
131 2018, respectively.

132 **Species richness, plant community diversity, and similarity.** Species richness in
133 the R plot was significantly lower than in the C plot across the five years (Table 1,
134 Fig. 3a). In addition, the difference in species richness between the two treatments
135 significantly varied with year (Table 1, Fig. 3a). Species richness in the R plots was
136 87.2% ($F = 230.46$, $P < 0.001$, Fig. 3a), 73.7% ($F = 273.80$, $P < 0.001$, Fig. 3a), 41.7%
137 ($F = 16.03$, $P = 0.007$, Fig. 3a), 25.8% ($F = 35.53$, $P < 0.001$, Fig. 3a), and 48.0% (F
138 $= 128.00$, $P < 0.001$, Fig. 3a) lower than in the C plot, respectively.

139 Species number was significantly different among the three groups, and the
140 difference varied with treatment (Table 1). In addition, significant interactions were
141 detected among functional group, year, and treatment (Table 1). Species number of
142 AB in the R plot was 2.7 lower in 2014 ($F = 21.43$, $P = 0.004$, Fig. 3b), but 2.4
143 higher in 2017 ($F = 10.57$, $P = 0.017$, Fig. 3b) than in the C plot. Species number did
144 not vary under the two treatments in 2015 ($F = 3.00$, $P = 0.134$, Fig. 3b), 2016 ($F =$
145 0.16 , $P = 0.705$, Fig. 3b), or 2018 ($F = 0.00$, $P = 1.000$, Fig. 3b). The species richness

146 of PF in the R plot was 6.3 ($F = 1323.00$, $P < 0.001$, Fig. 2c), 4.5 ($F = 170.46$, $P <$
147 0.001 , Fig. 2c), 5.4 ($F = 34.71$, $P < 0.001$, Fig. 2c), 6.2 ($F = 40.33$, $P < 0.001$, Fig.
148 2c), and 6.6 ($F = 54.00$, $P < 0.001$, Fig. 2c) lower than in the C plot in 2014, 2015,
149 2016, 2017, and 2018, respectively. The species richness of PF in the R plot was 3.3
150 ($F = 33.80$, $P < 0.001$, Fig. 3d), 2.3 ($F = 22.09$, $P = 0.003$, Fig. 3d), 1.2 ($F = 5.00$, $P =$
151 0.067 , Fig. 3d), and 6.6 ($F = 7.74$, $P = 0.032$, Fig. 3d) lower than in the C plot in
152 2014, 2015, 2016, and 2018, respectively. However, species richness of PF did not
153 differ between R and C plots in 2017 ($F = 1.42$, $P = 0.278$, Fig. 3d).

154 Shannon-Weiner diversity index significantly varied with year (Table 1), with
155 the highest (1.71) and lowest (1.31) values in the C plots in 2017 and 2015,
156 respectively (Fig. 3e). In addition, treatment effects on the Shannon-Weiner diversity
157 index differed across the five years (Table 1, Fig. 3e). The Shannon-Weiner diversity
158 index in the R plot was 0.9 ($F = 62.71$, $P < 0.001$, Fig. 3e), 0.7 ($F = 173.21$, $P <$
159 0.001 , Fig. 3e), 0.8 ($F = 40.62$, $P < 0.001$, Fig. 3e), and 0.5 ($F = 61.82$, $P < 0.001$, Fig.
160 3e) units lower than in the C plot in 2014, 2015, 2016, and 2017, respectively.
161 However, Shannon-Weiner diversity index did not differ between R and C plots in
162 2018 ($F = 0.11$, $P = 0.750$, Fig. 3e).

163 Similarity significantly varied with year (Table 1, Fig. 3f). Similarity in the last
164 3 years (2016, 2017, and 2018) was significantly higher than in the first two years
165 (2014 and 2015, Fig. 3f). No other significant difference in similarity was observed
166 in the experiment (Fig. 3f)

167 **Restoration trends of AGB and diversity, and relationships between AGB and**

168 **diversity.** The relationship between R:C diversity and year was a quadratic curve
169 with a get down to openings ($R^2 = 0.978$, $P < 0.001$, Fig. 4). However, the
170 relationship between R:C productivity and year was a quadratic curve going upwards
171 to openings ($R^2 = 0.715$, $P = 0.034$, Fig. 4). Productivity in the R plot linearly
172 increased with diversity in 2014 ($R^2 = 0.437$, $P = 0.027$, Fig. 4b) and 2015 ($R^2 =$
173 0.491 , $P = 0.011$, Fig. 5), did not correlate with diversity in 2016 ($R^2 = 0.196$, $P =$
174 0.149 , Fig. 4b) and 2017 ($R^2 = 0.089$, $P = 0.346$, Fig. 5), and linearly decreased with
175 diversity in 2018 ($R^2 = 0.274$, $P = 0.080$, Fig. 5).

176 **Discussion**

177 We found that the plant community was drastically degraded after four years of
178 severe trampling. The reductions in abundance, cover, ANPP, as well as species
179 richness and diversity after trampling were consistent with many previous studies
180 which have demonstrated that trampling inhibited plant growth ^[17, 26, 38], but
181 inconsistent with studies that have recorded minimal effects of trampling on plant
182 communities ^[29, 39-41]. This latter discrepancy can be attributed to the much higher
183 trampling intensity (more than 3500 passes per year) in our study than in some other
184 study systems. Severe trampling can compact soil, and triggered serious damage on
185 stalks, foliage, and roots ^[24-25, 38], decreasing recruitment and survival of plants ^[42],
186 and consequently inducing decreases in plant community variables.

187 In addition, we found that trampling completely eliminated the forbs, but left
188 few grasses, annuals, and biennials in the steppe, which supported the results of
189 many previous studies which have reported that trampling can alter community

190 composition ^[29, 31, 43]. These trampling-induced changes in community composition
191 can be explained by many factors. First, perennial grasses are often more tolerant of
192 trampling than perennial forbs ^[18, 30, 44] because of their greater root strength ^[25, 30].
193 Second, trampling often decreases soil water infiltration, reducing the soil water
194 content in deep soil ^[18]. Most grass roots are concentrated in the shallow soil layers,
195 but forbs allocate a certain part of their root mass in the deeper layers of the soil.
196 Compacted soil may inhibit root growth in the deep layer, and thus suppress the
197 growth of forbs. Trampling-induced changes in soil water may stimulate grass
198 growth, but inhibit growth of forbs, consequently altering the community structure.
199 Third, differences in morphological traits, life forms, and reproductive strategies
200 among different functional groups can also explain the trampling-induced variation
201 in plant community composition ^[45-46]. Previous studies have reported that
202 stoloniferous, matted or rosette plants are more resistant to trampling than erect forbs
203 ^[45-46]. Annuals and biennials often have great ability to survive under adverse
204 situation due to their high seed production and high seed germination rates ^[47]. Most
205 of the forb species in our study site are chamaephytes or hemicryptophytes, which
206 have buds that are easily hurt by trampling. All in all, our results suggest that
207 perennial grasses, annuals, and biennials have higher tolerance to trampling than
208 perennial forbs, which has important implications for restoration management in
209 grassland ecosystems.

210 Our results show that plant abundance, cover and height gradually returned to
211 and even exceeded pre-disturbance conditions after restoration, which is consistent

212 with studies that reported fast recovery of community parameters after ceasing
213 disturbance in grasslands ^[11,48]. However, the recovery of these traits varied across
214 different functional groups in our study. Annual and biennial herbs and perennial
215 grasses recovered more quickly than perennial forbs, which are consistent with one
216 study that reported fast recovery of graminoid biomass after ceasing disturbance in a
217 grassland meadow on the Tibetan Plateau ^[49]. The differences in rates of restoration
218 among different functional groups can be attributed to the initial status of the plant
219 community after trampling. Almost all forb individuals disappeared after trampling
220 in our study, but some grasses survived after trampling. In turn, grasses that survived
221 could recover quickly because trampling reduced resource competition among the
222 different functional groups. Annual and biennial plants are usually pioneer species in
223 the steppe ^[50-51], have much higher seed germination rate than forbs, and can quickly
224 occupy a niche after trampling because of the large amount of open spaces created
225 by trampling. However, forbs must reenter the community through seed germination
226 and seedling recruitment, and thus their competitive capacity and recovery is lower
227 than grasses, annuals, and biennials at the early stage of restoration. In addition, our
228 result showed that community biomass recovered from a very low value to a peak
229 that exceed biomass in the undisturbed grassland, and then decreased to a value
230 similar to the undisturbed grassland. This pattern is inconsistent with some studies.
231 For example, it has been reported sustained increases in cover and biomass over 8
232 years of restoration of a Tibetan alpine meadow ^[19]. Several factors are responsible
233 for the restoration pattern we observed in the steppe. After trampling ceases, the gaps

234 formed by trampling are beneficial for the recovery of remaining plants and the
235 establishment of pioneer species. Residual grasses can quickly grow due to minimal
236 competitive pressure and compensatory effects after disturbance. Annuals and
237 biennials can also easily grow due to the lack of competitors^[41]. Thus biomass can
238 quickly recover in the steppe. After initial recovery, inter- and intraspecific
239 competition may prohibit further increases in biomass, and biomass may eventually
240 decrease because plants may allocate resources to traits that maintain their
241 competitive advantages.

242 The continuously increasing species richness in the restored grassland indicates
243 that recovery of species richness is more difficult than other simple community
244 parameters, which supports conclusions found in previous studies^[11, 52], which
245 documented that diversity is difficult to recover in severely disturbed area. However,
246 the restoration rate we observed was slower than that observed in a study in the
247 Tibetan meadow^[19]. This slower restoration rate may be because the species
248 richness of the semi-arid steppe is much lower than in the meadow, so the
249 opportunity for a new plant species to enter the disturbed area is lower than it is in
250 the meadow. In addition, the slower restoration rate is correlated with arid soil
251 conditions, which only allow species with strong arid resistance to germinate and
252 recruit in the trampled area. Furthermore, many previous studies have reported that
253 trampling can lead to soil erosion^[24, 53]. The loss of soil nutrients in the erosion
254 process may exacerbate the difficulty of plant establishment in the restored grassland.
255 Another interesting pattern in our study is that at the 4th year of restoration, the

256 diversity index recovered to the level of control plots, but the species richness
257 remained much lower than in the control treatment. This result indicates that the
258 plant communities in the trampled plots are more homogeneous than those in the
259 control plots, and also suggests that the evaluation of many more parameters is
260 necessary, rather than relying solely on diversity indices as metrics of restoration
261 success.

262 The results of our experiment indicate that following the restoration process, the
263 positive correlation between biomass and diversity is decoupled, and a negative
264 correlation between biomass and diversity is formed. This pattern is inconsistent
265 with the common pattern that high diversity often represents high productivity in
266 undisturbed area. However, this relationship has also been reported in many studies
267 conducted in ecosystems that have suffered human disturbance. For example, in
268 some nitrogen addition experiments, nitrogen elevated biomass but often decreased
269 diversity^[49]. One mechanism can explain the variation in relationships between
270 biomass and diversity. At the early stages of restoration, trampling has formed many
271 gaps in the community, and competition is very low. Under this situation, the more
272 species, the higher the resource use efficiency in the community. However, as
273 restoration progresses, plant density and species number increase quickly. Thus
274 competitive pressures become much higher. Plants may allocate more energy to
275 competition rather than growth, so although diversity increases after a period of
276 restoration, biomass stops increasing and may even decrease. This result suggests
277 that we must consider variation in the relationship between diversity and biomass

278 when we predict plant community productivity in restoration ecology.
279 In conclusion, our results show that community abundance, cover, height, and
280 biomass recovered more quickly than did diversity. Furthermore, annuals, biennials,
281 and grasses were more responsive than forbs. Moreover, the diversity-biomass
282 relationship changed from a negative correlation to a positive correlation following
283 the restoration process. Our study documented an important implication of the
284 trade-off between community structure and function for typical grassland restoration,
285 suggesting that we must simultaneously focus on the productivity and diversity in
286 the evaluation of grassland restoration process.

287 **Materials and Methods**

288 **Site Description.** The study area was conducted at the Duolun Restoration Ecology
289 Station of the Institute of Botany, Chinese Academy of Sciences (42°20'N, 116°17'E),
290 a semi-arid temperate steppe in Inner-Mongolia. The altitude is 1324m a.s.l. Mean
291 annual temperature is 2.4 °C, and temperatures range from the annual low (-17.5 °C)
292 in January to the annual high (18.9 °C) in July. The long-term (1953-2017) mean
293 annual precipitation at this site is about 380 mm, but it ranged from 286 to 422mm in
294 the growing season (from May to August) from 2014 to 2018. The soil is classified
295 as chestnut (Chinese classification). The study site is dominated by a perennial grass
296 *Stipa krylovii* and a semi-shrub *Artemisia frigida*. Other species such as *Agropyron*
297 *crisatum*, *Melissilus ruthenicus*, *Potentilla acaulis*, *Cleistogenes squarrosa*, and
298 *Allium bidentatum* are also abundant in the natural grassland.

299 **Experimental design.** The experiment was conducted in an abandoned trackway

300 and adjacent natural grassland. The natural grassland was fenced to exclude
301 disturbance, kept enclosed since 2000, and referred to as control grassland (C). The
302 trackway, next to the C plots, was trampled by humans (with an intensity of 30
303 passes each day in the growing season (from early May to late October) and 4 passes
304 each day in the non-growing season) from 2011 to 2014, but has been restored since
305 2015, and is referred to as restoration grassland (R). Four blocks of 30 m x 6 m were
306 selected along the trackway in late July 2014. Three pairs of 1 m x 1 m plots were
307 selected in each block from 2014 to 2018 along the direction of the trackway. The
308 distance between two adjacent pairs of plots was 7-9 m. Each set of paired plots
309 contained a C plot and an R plot. The distance between the C and R plot in each
310 paired-plot was <5 m to minimize spatial heterogeneity.

311 **Plant community parameters.** Plant community parameters were assessed in
312 mid-August in each year. Plant species were divided into three functional groups
313 including annuals and biennials (AB), perennial grasses (PG), and perennial forbs
314 (PF). The number of species, and number of individuals per species, was counted in
315 each plot. The cover of each plant species, functional group, and community was
316 estimated visually following methods used in previous grassland studies (Liu et al.,
317 2018). Three individuals of each plant species in the plot were selected, and their
318 heights were measured and then averaged to estimate the mean height of the species.
319 The aboveground live part of each measured plant was harvested and separated by
320 species, oven dried for 48 hours at 65 °C to a constant weight, and then weighed to
321 determine the biomass of each species. Biomass of all species in a plot was summed

322 to estimate productivity. The functional group and community level species richness,
323 abundance, cover, aboveground biomass, height, Shannon-Weiner diversity index,
324 and Similarity coefficients were calculated with the following functions:

325 Species richness: $R = S$

326 Abundance: $A = \sum_1^S N_i$

327 Aboveground biomass: $AGB = \sum_1^S b_i$

328 Height: $H = \sum_1^S (H_i \times \frac{C_i}{\sum_1^S C_i})$

329 Shannon-Weiner diversity index: $H = - \sum_1^S \left(\frac{B_i}{\sum_1^S B_i} \times \ln \left(\frac{B_i}{\sum_1^S B_i} \right) \right)$

330 Similarity coefficients: $J = \frac{j}{a+b-j}$

331 Where: S is the number of the plant species. N_i , c_i , B_i , and H_i is the individual
332 number, cover, biomass, and height of i species, respectively. Letter j is the number
333 of species common to both plots and “a” and “b” are the number of species only in
334 the first (a) or second (b) plot in each of the paired plots⁵⁴.

335 **Statistical analysis.** The differences in species richness, abundance, cover,
336 aboveground biomass, productivity, and height among time, functional group, and
337 grassland types were tested with three way ANOVAs. Two-way ANOVAs and LSD
338 Post-Hoc tests were used to determine the differences in species richness, abundance,
339 cover, aboveground biomass, productivity, height, and Simpson's diversity index
340 among the five years and two grassland types. Paired t-test was used to analyze the
341 differences in the above plant community parameters between the natural and
342 restored grassland. One way ANOVA and LSD Post-Hoc tests were used to test the
343 differences in similarity coefficients among different years. The variation trend for

344 the ratio of AGB between R and C plots (R: C productivity) and ratio of diversity
345 between R and C plots (R:C diversity) during the experiment was estimated with
346 curve-estimated regression. The relationships between productivity and diversity in
347 each year under restoration were determined with linear regression. All statistics
348 were performed with SPSS 21.0 software package (SPSS Inc., CHI, IL, USA).

349 Reference

- 350 1. Blair, J., Nippert J. & Briggs J. *Grassland Ecology. In: Monson R. (eds) Ecology and the*
351 *Environment*. Springer, New York, NY. (2014).
- 352 2. Stevens, C. J. Recent advances in understanding grasslands. *F1000 Res.* **7**, 1363 (2018).
- 353 3. Li, G., Liu, Y., Frelich, L. E. & Sun, S. Experimental warming induces degradation of a
354 Tibetan alpine meadow through trophic interactions. *J. Appl. Ecol.* **48**, 659-667 (2011).
- 355 4. Liu, Y., Ma, G., Zan, Z., Chen, A., Miao, Y., Wang, D. & Miao, R. Effects of nitrogen addition
356 and mowing on rodent damage in an Inner Mongolian steppe. *Ecol. Evol.* **8**, 3919-3926
357 (2018).
- 358 5. Klein, J. A., Harte, J. & Zhao, X. Experimental warming causes large and rapid species loss,
359 dampened by simulated grazing, on the Tibetan Plateau. *Ecol. Lett.* **7**, 1170-1179 (2004).
- 360 6. Yang, H., Wu, M., Liu, W., Zhang, Z., Zhang, N. & Wan, S. Community structure and
361 composition in response to climate change in a temperate steppe. *Global Change Biol.* **17**,
362 452-465 (2011).
- 363 7. Wu, G., Du, G., Liu, Z. & Thirgood, S. Effect of fencing and grazing on a kobresia-dominated
364 meadow in the Qinghai-Tibetan plateau. *Plant Soil* **319**, 115-126 (2009).
- 365 8. Deng, L., Zhang, Z. & Shanguan, Z. Long-term fencing effects on plant diversity and soil
366 properties in China. *Soil Till. Res.* **137**, 7-15 (2014).
- 367 9. Liu, Y., Wu, G., Ding, L., Tian, F. & Shi, Z. Diversity-Productivity Trade - off During
368 Converting Cropland to Perennial Grassland in the Semi - arid Areas of China. *Land*
369 *Degrad. Dev.* **28**, 699-707 (2017).
- 370 10. Wang, D., Chi, Z., Yue, B., Huang, X., Zhao, J., Song, H., Yang, Z., Miao, R., Liu, Y., Zhang,
371 Y., Miao, Y., Han, S. & Liu, Y. Effects of mowing and nitrogen addition on the ecosystem C
372 and N pools in a temperate steppe: A case study from northern China. *Catena* **185**, 104332
373 (2020).
- 374 11. Miao, R., Song, Y., Sun, Z., Guo, M., Zhou, Z. & Liu, Y. Soil seed bank and plant community
375 development in passive restoration of degraded sandy grasslands. *Sustainability* **8**, 581-581
376 (2016).
- 377 12. Bischoff, A., Hoboy, S., Winter, N. & Warthemann, G. Hay and seed transfer to re-establish
378 rare grassland species and communities: How important are date and soil preparation? *Biol.*
379 *Conserv.* **221**, 182-189 (2018).
- 380 13. Vidaller, C., Dutoit, T., Ramone, H. & Bischoff, A. Factors limiting early establishment of the
381 Mediterranean grassland species *Brachypodium retusum* at disturbed sites. *Basic Appl. Ecol.*

- 382 **37**, 10-19 (2019).
- 383 14. Dong, S., Shang, Z., Gao, J. & Boone, R. B. Enhancing sustainability of grassland
384 ecosystems through ecological restoration and grazing management in an era of climate
385 change on Qinghai-Tibetan Plateau. *Agr. Ecosyst. Environ.* **287**, 106684 (2020).
- 386 15. Scasta, J. D., Duchardt, C., Engle, D. M., Miller, J. R., Debinski, D. M. & Harr, R. N.
387 Constraints to restoring fire and grazing ecological processes to optimize grassland
388 vegetation structural diversity. *Ecol. Eng.* **95**, 865-875 (2016).
- 389 16. Liu, S. & Wang, T. Aeolian processes and landscape change under human disturbances on the
390 Sonid grassland of Inner Mongolian Plateau, northern China. *Environ. Earth Sci.* **71**,
391 2399-2407 (2014).
- 392 17. Pickering, C. M. & Growcock, A. J. Impacts of experimental trampling on tall alpine
393 herbfields and subalpine grasslands in the Australian Alps. *J. Environ. Manage.* **91**, 532-540
394 (2010).
- 395 18. Su, L., Yang, Y., Li, X., Wang, D., Liu, Y. & Liu, Y. Increasing plant diversity and forb ratio
396 during the revegetation processes of trampled areas and trails enhances soil infiltration.
397 *Land Degrad. Dev.* **29**, 4025-4034 (2018).
- 398 19. Du C., Jing, J., Shen, Y., Liu, H. & Gao, Y. Short-term grazing exclusion improved topsoil
399 conditions and plant characteristics in degraded alpine grasslands. *Ecol. Indic.* **108**, 105680
400 (2020).
- 401 20. Yang, X., Shen, Y., Liu, N., Wilson, G. W. T., Cobb, A. B. & Zhang, Y. Defoliation and
402 arbuscular mycorrhizal fungi shape plant communities in overgrazed semi-arid grasslands.
403 *Ecology* **99**, 1847-1856 (2018).
- 404 21. Zhang, J., Xiang, C. & Li, M. Effects of tourism and topography on vegetation diversity in
405 the subalpine meadows of the Dongling Mountains of Beijing, China. *Environ. Manage.* **49**,
406 403-411 (2012).
- 407 22. Komonen, A. & Elo, M. Ecological response hides behind the species abundance distribution:
408 community response to low-intensity disturbance in managed grasslands. *Ecol. Evol.* **7**,
409 8558-8566 (2017).
- 410 23. Wu, X., Wang, Y. & Sun, S. Long-term fencing decreases plant diversity and soil organic
411 carbon concentration of the Zoige alpine meadows on the eastern Tibetan plateau. *Plant*
412 *Soil*, **458**, 191-200 (2021).
- 413 24. Dunne, T., Western, D. & Dietrich, W. E. Effects of cattle trampling on vegetation,
414 infiltration, and erosion in a tropical rangeland. *J. Arid Environ.* **75**, 58-69 (2011).
- 415 25. Striker, G. G., Insausti, P., Grimold A. A. & León, R. J. C. Root strength and trampling
416 tolerance in the grass *Paspalum dilatatum* and the dicot *Lotus glaber* in flooded soil. *Funct.*
417 *Ecol.* **20**, 4-10 (2006).
- 418 26. Farrell, H. L. & Fehmi, J. S. Seeding alters plant community trajectory: impacts of seeding,
419 grazing and trampling on semi-arid re-vegetation. *Appl. Veg. Sci.* **21**, 240-249 (2018).
- 420 27. Lezama, F. & Paruelo, J. M. Disentangling grazing effects: trampling, defoliation and urine
421 deposition. *Appl. Veg. Sci.* **19**, 557-566 (2016).
- 422 28. Munkhtsetseg, E., Shinoda, M., Ishizuka, M., Mikami, M., Kimura, R. & Nikolich, G.
423 Anthropogenic dust emissions due to livestock trampling in a Mongolian temperate
424 grassland. *Atmos. Chem. Phys.* **17**, 1-27 (2017).
- 425 29. Brunbjerg, A. K., Svenning, J. C. & Ejrnaes, R. Experimental evidence for disturbance as key

- 426 to the conservation of dune grassland. *Biol. Conserv.* **174**, 101-110 (2014).
- 427 30. Striker, G.G., Mollard, F. P. O., Grimoldi, A. A., León, R. J. C. & Insausti, P. Trampling
428 enhances the dominance of graminoids over forbs in flooded grassland mesocosms. *Appl.*
429 *Veg. Sci.* **14**, 95-106 (2011).
- 430 31. Ludvíková, V, Pavlu, V. V., Gaisler, J., Hejcman, M. & Pavlu, L. Long term defoliation by
431 cattle grazing with and without trampling differently affects soil penetration resistance and
432 plant species composition in *agrostis capillaris* grassland. *Agr. Ecosyst. Environ.* **197**,
433 204-211 (2014).
- 434 32. Frouz, J. et al. Soil biota in post-mining sites along a climatic gradient in the USA: simple
435 communities in shortgrass prairie recover faster than complex communities in tallgrass
436 prairie and forest. *Soil Biol. Biochem.* **67**, 212-225 (2013).
- 437 33. Frouz, J., Dvorščík, P., Vávrová, A., Doušová, O., Kadochová, Š. & Matějčík, L.
438 Development of canopy cover and woody vegetation biomass on reclaimed and
439 unreclaimed post-mining sites. *Ecol. Eng.* **84**, 233-239 (2015).
- 440 34. Martin, L. M., Moloney, K. A. & Wilsey, B. J. An assessment of grassland restoration success
441 using species diversity components. *J. Appl. Ecol.* **42**, 327-336 (2005).
- 442 35. Gillman, L. N. & Wright, S. D. The influence of productivity on the species richness of plants:
443 a critical assessment. *Ecology* **87**,1234-1243 (2006).
- 444 36. Kelemen, A., Török, P., Valkó, O., Miglécz, T., & Tóthmérész, B. Mechanisms shaping
445 plant biomass and species richness: plant strategies and litter effect in alkali and loess
446 grasslands. *J. Veg. Sci.* **24**, 1195-1203 (2013).
- 447 37. Fraser, L. H. et al. Worldwide evidence of a unimodal relationship between productivity and
448 plant species richness. *Science* **349**, 302-305 (2015).
- 449 38. van Klink, R., Schrama, M., Nolte S., Bakker, J. P., WallisDeVries M. F. & Berg, M. P.
450 Defoliation and soil compaction jointly drive large-herbivore grazing effects on plants and
451 soil arthropods on clay soil. *Ecosystems* **18**, 671-685 (2015).
- 452 39. Conradi, T., Strobl, K., Wurfer, A. L., Kollmann, J. & Paruelo, J. Impacts of visitor trampling
453 on the taxonomic and functional community structure of calcareous grassland. *Appl. Veg.*
454 *Sci.* **18**, 359-367 (2015).
- 455 40. Liu, N., Kan H. M., Yang, G. W. & Zhang Y. J. Changes in plant, soil, and microbes in a
456 typical steppe from simulated grazing: explaining potential change in soil C. *Ecol. Monog.*
457 **85**, 269-286 (2015).
- 458 41. Wang, D., Zhang, B., Zhu, L., Yang, Y. & Li, M. Soil and vegetation development along a
459 10-year restoration chronosequence in tailing dams in the Xiaoqinling gold region of
460 Central China. *Catena* **167**, 250-256 (2018).
- 461 42. Cumming, D. & Cumming, G. S. Ungulate community structure and ecological processes:
462 body size, hoof area and trampling in African savannas. *Oecologia* **134**, 560-568 (2003).
- 463 43. Plassmann, K., Jones, M. L. M., & Edwards-Jones, G. Effects of long-term grazing
464 management on sand dune vegetation of high conservation interest. *Appl. Veg. Sci.* **13**,
465 100-112 (2010).
- 466 44. Cole, D. N. Experimental trampling of vegetation. ii. predictors of resistance and resilience. *J.*
467 *of Appl. Ecol.* **32**, 215-224 (1995).
- 468 45. Cole, D. N. & Monz, C. A. Trampling disturbance of high-elevation vegetation, wind river
469 mountains, Wyoming, U.S.A. *Arct. Antarct. Alp. Res.* **34**, 365-376 (2002).

- 470 46. Xiao, H., Peng, Z., Xu, C., Zhang, D., Chai, J. & Pan, T. Yak and Tibetan sheep trampling
471 inhibit reproductive and photosynthetic traits of *Medicago ruthenica* var. *inschanica*.
472 *Environ. Monit. Assess.* **190**, 507 (2018).
- 473 47. Liu, Y. et al. Understanding the wide geographic range of a clonal perennial grass: plasticity
474 versus local adaptation. *AoB Plants* **8**, plv141 (2015).
- 475 48. Monz, C. A. The response of two arctic tundra plant communities to human trampling
476 disturbance. *J. Environ. Manage.* **64**, 207-217 (2002).
- 477 49. Wang, D., Chen, J., Felton, A. J., Xia, L., Zhang, Y., Luo, Y., Cheng, X. & Cao, J. Post-fire
478 co-stimulation of gross primary production and ecosystem respiration in a meadow
479 grassland on the Tibetan Plateau. *Agr. Forest Meteorol.* **303**, 108388 (2021).
- 480 50. Qian, J., Liu, Z., Hatier, J. & Liu, B. The vertical distribution of soil seed bank and its
481 restoration implication in an active sand dune of northeastern Inner Mongolia, china. *Land*
482 *Degrad. Dev.* **27**, 305-315. (2016).
- 483 51. Yan, S. & Liu, Z. Effects of dune stabilization on the plant diversity of inter dune wetlands in
484 northeastern Inner Mongolia, China. *Land Degrad. Dev.* 2010, **21**, 40-47 (2010).
- 485 52. Whinam, J. & Chilcott, N. M. Impacts after four years of experimental trampling on
486 alpine/sub-alpine environments in western Tasmania. *J. Environ. Manage.* **67**, 339-351
487 (2003).
- 488 53. Stavi, I., Barkai, D., Knoll, Y. M. & Zaddy, E. Livestock grazing impact on soil wettability
489 and erosion risk in post-fire agricultural lands. *Sci. Total Environ.* **573**, 1203-1208 (2016).
- 490 54. Kerr, J. T., Southwood, T. & Cihlar, J. Remotely sensed habitat diversity predicts butterfly
491 species richness and community similarity in Canada. *P. Natl. Acad. Sci. USA* **98**,
492 11365-11365 (2001).

493

494 **Acknowledgements**

495 Authors thank Yuan Miao, Zhiman Zan, and Juanxuan for the field measurement.
496 This study was supported by the National Natural Science Foundation of China
497 (31670477, 31600380). We would like to thank Dr. Julia Monk at Yale University for
498 his assistance with English language and grammatical editing. We would like to
499 thank the editor and anonymous reviewers for their helpful comments on the draft of
500 this paper.

501 **Author contributions**

502 Y.L. and D.W. designed the experiment. Y.L., L.Z., Y.H. and A.C. collected the data.
503 Y.L. and D.W. wrote the first draft of the MS, R.M. and J. C. revised the draft of the
504 MS. All authors contributed to the final version of the manuscript.

505 **Competing interests**

506 The authors declare no competing interests.

507 **Data availability statement**

508 Data available from <https://doi.org/10.5061/dryad.dv41ns1xs>

Figures

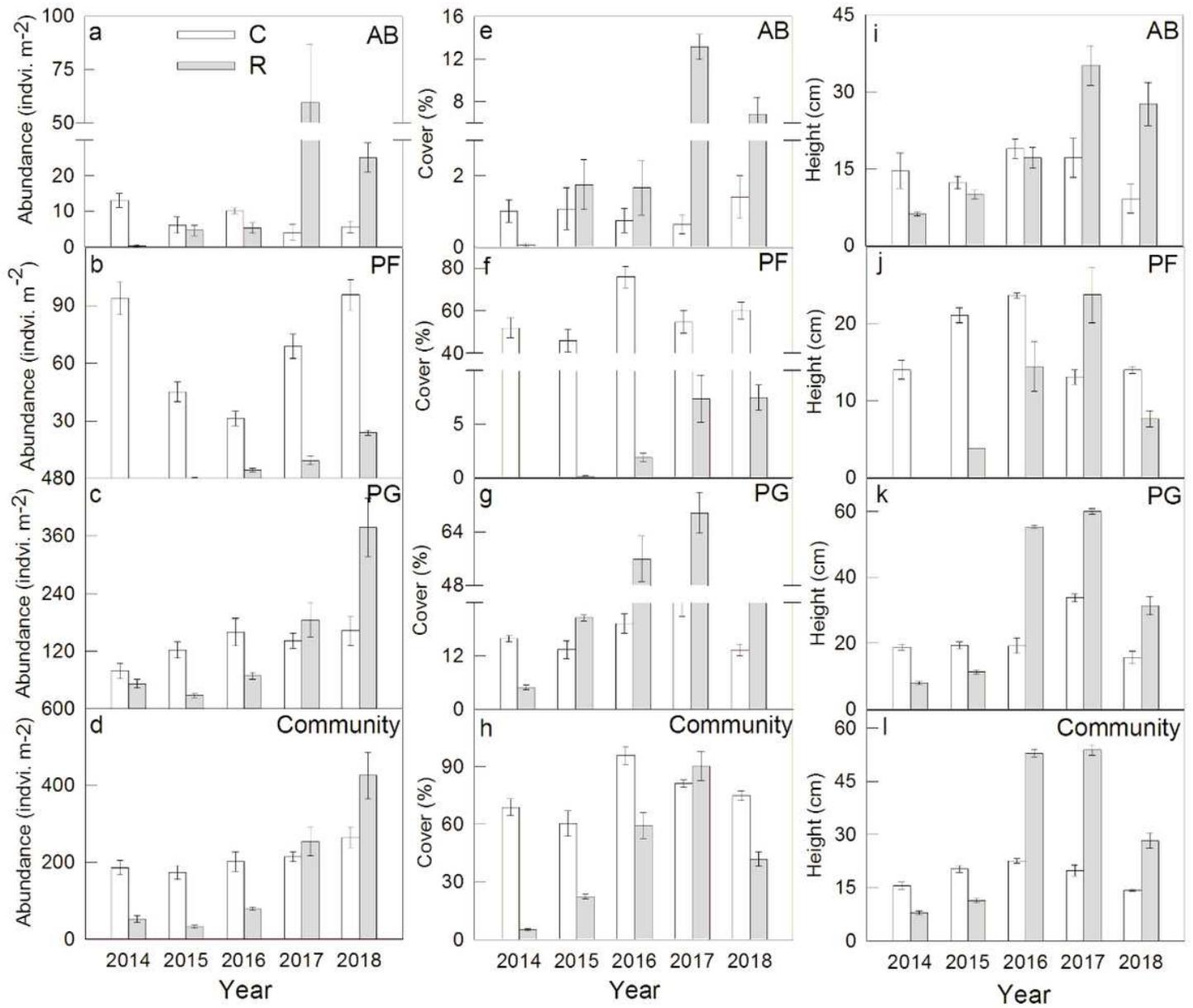


Figure 1

Mean values (\pm SE) of abundance, cover, and height for annuals and biennials (AB), perennial grasses (PG), perennial forbs (PF), and the entire plant community under control (C) and restoration (R) treatments.

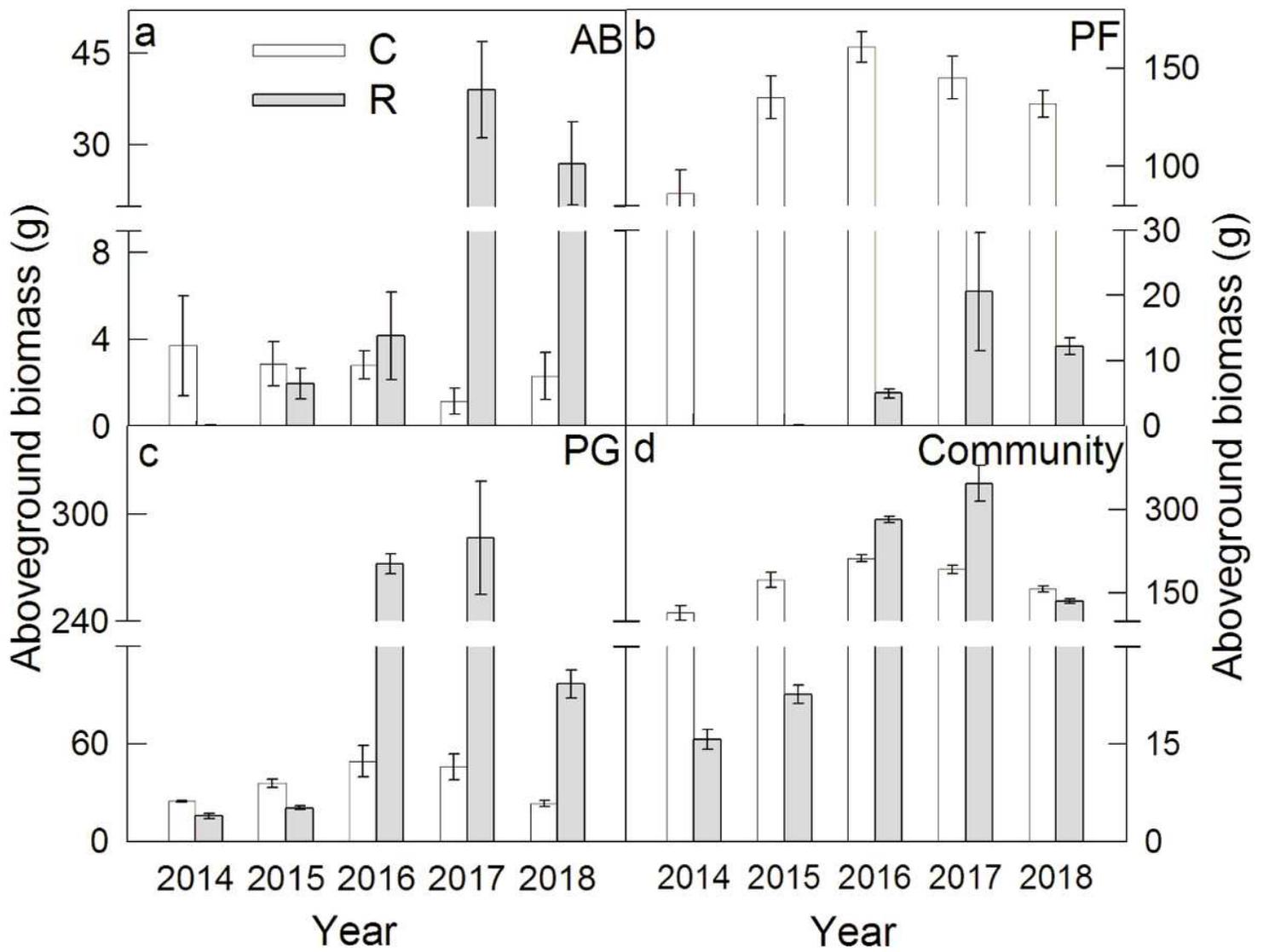


Figure 2

Mean values (\pm SE) of aboveground biomass for annuals and biennials (AB), perennial grasses (PG), perennial forbs (PF), and the entire plant community under control (C) and restoration (R) treatments.

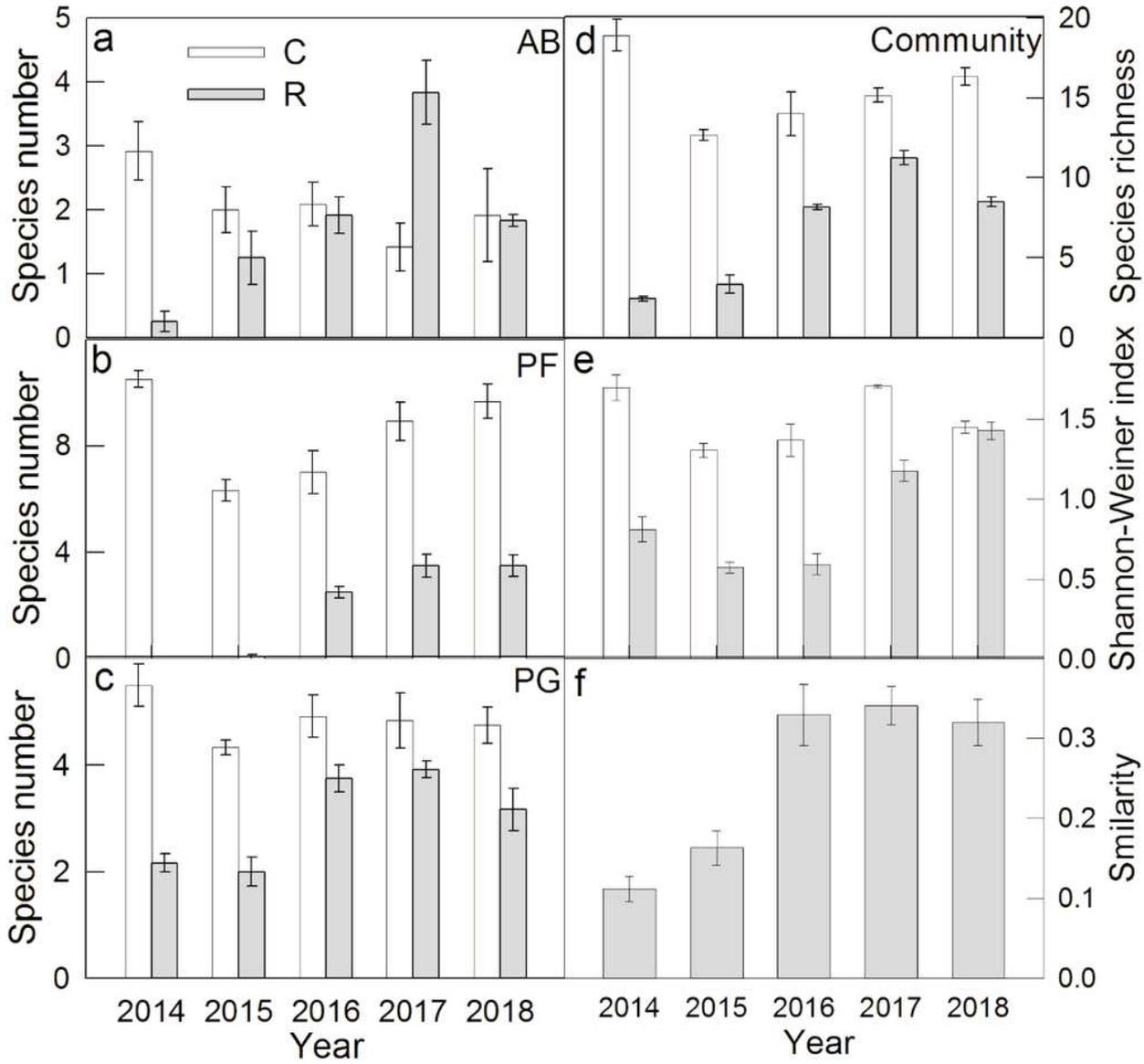


Figure 3

Mean values (\pm SE) of species number for annuals and biennials (AB), perennial grasses (PG), and perennial forbs (PF), and species richness and the Shannon-Weiner index for the plant community under control (C) and restoration (R) treatments, and similarity between control (C) and restoration (R) treatments from 2014 to 2018.

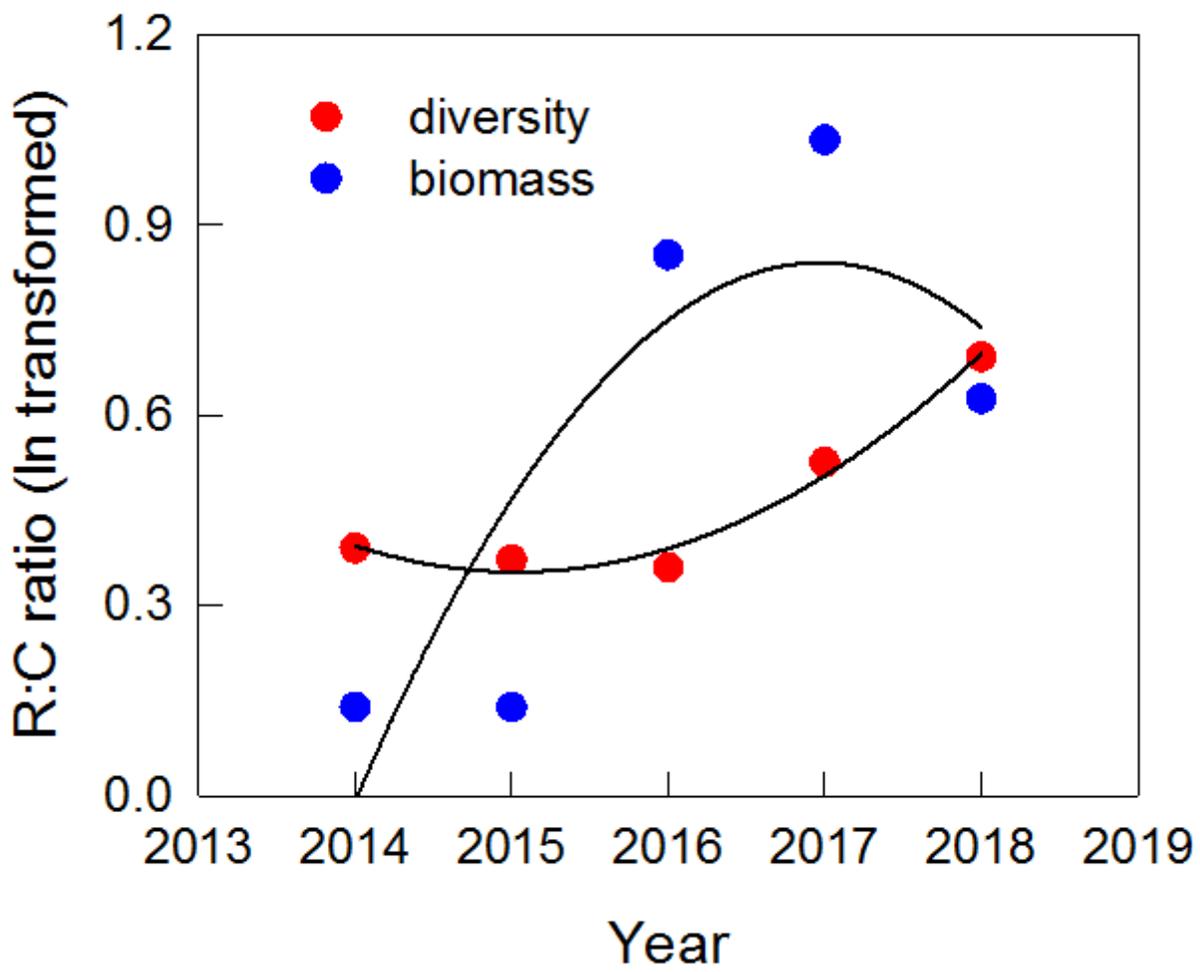


Figure 4

Temporal variation in the ratio of diversity and biomass between restoration (R) and control (C) treatments, 2014 to 2018.

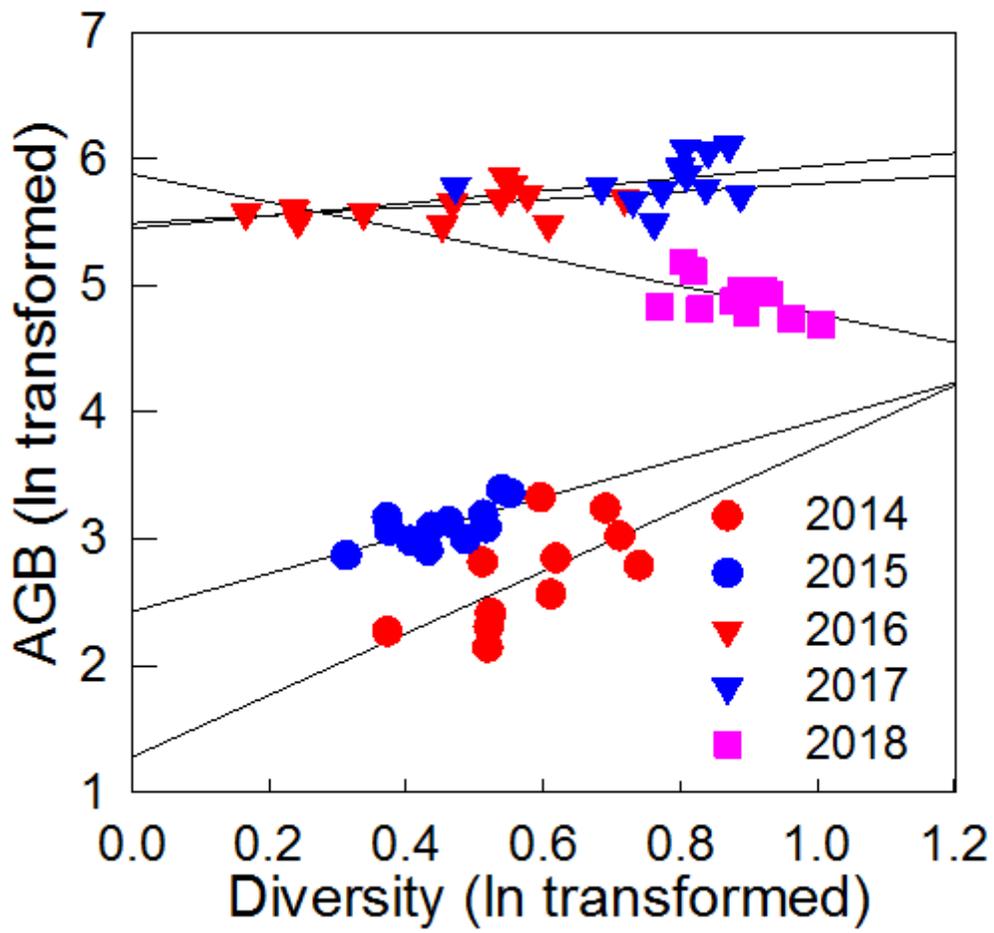


Figure 5

Temporal variation in the relationships between productivity and diversity in each year from 2014 to 2018.