

1 **Long term experimental drought alters community plant trait variation, not trait**
2 **means, across three semiarid grasslands**

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21 **Abstract**

22 *Background and Aims* Grasslands are expected to experience droughts of
23 unprecedented magnitude and duration in this century. Plant traits can be useful for
24 understanding community and ecosystem responses to climate extremes. Few studies,
25 however, have investigated the response of community-scale traits to extreme drought
26 on broad spatial/temporal scales, with even less research on the relative contribution
27 of species turnover *vs.* intraspecific trait variation to such responses.

28 *Methods* We experimentally removed ~66% of growing season rainfall for three years
29 across three semi-arid grasslands of northern China and tracked changes in
30 community functional composition, defined as the community mean and variation of
31 several leaf economic traits.

32 *Results* Community trait variations were more sensitive to drought than community
33 trait means, which suggests this component of functional composition may be a better
34 indicator of initial community drought responses than trait values themselves. The
35 greatest change in trait variation was observed at the high aridity site and was driven
36 largely by intraspecific trait variability. Apart from specific leaf area, trait variability
37 increased with increasing aridity across sites, largely due to species turnover.

38 Variations in soil moisture and fertility likely mediated the responses of community
39 trait variations to water stress.

40 *Conclusions* These results highlight the importance of measuring community trait
41 variability in response to drought and support the well-documented pattern of
42 increased community drought sensitivity of more arid ecosystems.

- 43 **Keywords:** climate change, plant functional traits, grasslands, intraspecific trait
- 44 variability, species turnover

45 **Introduction**

46 Plant traits are useful proxies of plant strategies for coping with biotic and abiotic
47 stress (Bruehlheide *et al.*, 2018, He *et al.*, 2018, Wright *et al.*, 2004). When the
48 appropriate traits are measured at the community level, they have the potential to
49 greatly improve predictions of ecosystem responses to environmental change
50 (Bruehlheide *et al.*, 2018, Griffin-Nolan *et al.*, 2018a, Suding *et al.*, 2008).
51 Quantification of community functional composition (*i.e.*, community plant trait
52 means and variation) is therefore expected to provide valuable insights into
53 community assembly processes in response to climate change (Bruehlheide *et al.*,
54 2018, Cornwell & Ackerly, 2009, Grime, 2006). The magnitude and frequency of
55 extreme climatic events, such as summer drought, are projected to increase in arid and
56 semiarid ecosystems with climate change (Dai, 2011, Handmer *et al.*, 2012); however,
57 few studies assess the response of functional composition to climate extremes at broad
58 spatial and temporal scales.

59 Extreme drought can act as an environmental filter, whereby only certain trait
60 combinations confer survival/fitness leading to trait convergence and a reduction in
61 the trait diversity at the community level (Cornwell & Ackerly, 2009). Shifts in
62 functional composition may be due to species turnover (*i.e.*, species migration) and/or
63 intraspecific variation (*i.e.*, phenotypic plasticity or shifts in genotypic composition)
64 (Albert *et al.*, 2010). Quantifying the relative contribution of each of these processes
65 is critical to a mechanistic understanding of how drought alters community functional
66 composition (Ackerly & Cornwell, 2007, Lepš *et al.*, 2011, Violle *et al.*, 2012).

67 Precipitation manipulation experiments and observations along aridity gradients are
68 two approaches to determine the short- and long-term impacts of water-limitation on
69 community functional composition, respectively (Elmendorf *et al.*, 2015, Knapp *et*
70 *al.*, 2018, Luo *et al.*, 2011, Yuan *et al.*, 2017). Experimental approaches allow
71 ecologists to study shifts in functional composition following short-term precipitation
72 change (Dunne *et al.*, 2004, Sandel *et al.*, 2010), while natural aridity gradients allow
73 for studies on community assembly processes in response to long-term water
74 limitation (Elmendorf *et al.*, 2015, Hewitt *et al.*, 2007). Previous drought experiments
75 have been performed at a single site, with the implicit assumption that the responses
76 can represent the entire ecosystem type (Cherwin & Knapp, 2012); However,
77 community responses to climate extremes can vary greatly among different sites, even
78 within the same ecosystem (*i.e.*, grasslands) (Griffin-Nolan *et al.*, 2018b, Grime *et al.*,
79 2000, Luo *et al.*, 2018). Thus, coordinated distributed experiments across multiple
80 sites with contrasting climatic conditions are needed to accurately predict the
81 responses of plant communities to drought (Cherwin & Knapp, 2012).

82 We experimentally reduced growing season precipitation (66% reduction) within
83 three grassland sites along an aridity gradient in northern China and tracked changes
84 in functional composition (*i.e.*, community trait means and variation). We focus on
85 four leaf economic traits, namely specific leaf area (SLA), leaf dry matter content
86 (LDMC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC), all of
87 which reflect plant performance and fast *vs.* slow strategies for coping with limiting
88 resources (Reich, 2014, Wright *et al.*, 2004). We test the following hypotheses: (1)

89 community-level trait mean and variation will decrease in response to experimental
90 drought and with increasing aridity due to environmental filtering; (2) the response of
91 community functional composition to experimental drought will differ from the
92 spatial trends observed along the natural aridity gradient with the response driven
93 primarily by species turnover at a spatial scale (aridity gradient) and intra-specific
94 trait variation at a temporal scale (experimental drought); and (3) community
95 functional composition will be more sensitive to experimental drought with increasing
96 aridity (Huxman *et al.*, 2004).

97 **Materials and methods**

98 Experimental sites

99 In 2014, we selected three sites that represent much of the east-west extent of the arid
100 and semi-arid grasslands of northern China (Figure S1a). All experimental plots for
101 each site were established across areas with homogeneous soils and uniform
102 vegetation to exclude the potential influence of small-scale heterogeneity. The three
103 sites, as part of the ‘Extreme Drought in Grassland Experiment’ (EDGE)
104 (<http://edge.biology.colostate.edu/EDGEchina.html>) vary in plant species composition
105 as well as climatic and edaphic properties (Table 1). The low aridity site, located at
106 the Inner Mongolia Grassland Ecosystem Research Station (116°33'E, 43°32'N),
107 receives about 346 mm of mean annual precipitation (MAP) and has a mean annual
108 temperature (MAT) of 1.9 °C. The medium aridity site, located in Sheila MuRen
109 (111°53'E, 41°47'N), is drier and hotter than the low aridity site (MAP=251 mm;
110 MAT=4.5 °C). The high aridity site, located at the Urat Desert-Grassland Research

111 Station (106°58'E, 41°25'N), receives an average of 175 mm of precipitation annually
112 and is the hottest of the three sites (MAT=5.6 °C) (see Table 1 for more detailed
113 information about each site).

114 Experimental treatments

115 In the summer of 2015, drought was imposed at each site using large rainout shelters
116 (Figure S1b), which reduced each precipitation event by 66% for the entire growing
117 season (May to August) – this is roughly equivalent to a 50% reduction in annual
118 precipitation. The experimental design was a randomized complete block design with
119 six replications, and treatments were applied during three consecutive years (2015-
120 2017). The 12 (6 m× 6 m) plots (control and drought) were randomly assigned with at
121 least 2 m between plots. Each plot was hydrologically isolated from the surrounding
122 soil matrix by aluminum flashing installed to a depth of 1 m around the perimeter. In
123 the center of each plot, one 16 m² (4 m× 4 m) subplot was established with a 1 m
124 buffer with the edge of the sampling plots and adjacent treatment subplots. Rainfall
125 was passively removed from drought plots to maintain the frequency and timing of
126 natural rainfall events (Knapp *et al.*, 2016) using roofs composed of strips of clear
127 polycarbonate plastic (Beijing Plastics Research Institute, Beijing, China). Untreated
128 control subplots were also trenched yet lacked rainout shelters and received ambient
129 precipitation. The drought shelters were 0.5 m and 2 m above the ground at the lowest
130 and highest point, respectively, which allowed for air circulation and prevented
131 microclimatic changes. The shelters had minimal shading effects (<10% reduction in
132 photosynthetically active radiation) and are known to have little influence on

133 ecosystem functions in grasslands. Species richness, diversity and evenness were
134 similar between control and treatment plots at each site prior to imposing
135 experimental drought (Luo *et al.*, 2018). Soil moisture was measured at 0-10 cm
136 (>70% of root biomass allocated to this soil layer, Matthew and others 2001) every
137 hour from May through August in 2016 and 2017 (PG-110, Jingchuang Electronic
138 Technology Co., Handan, China) with measurements averaged to produce daily mean
139 values at each site. Identical protocols were used across all three sites to avoid
140 confounding results from methodological differences (Smith *et al.*, 2017). Further
141 details on the experimental design can be found in Luo *et al.* (2018).

142 Growing season precipitation (GSP) varied at each site over the three-year study
143 period but was within the expected climatic range (approx. 50th percentile of historic
144 amounts) (Figure S2). Also note that, at the high aridity site, GSP was below the
145 normal season precipitation values in 2015 and 2017 (Figure S2). In each year, the
146 drought treatment reduced rainfall close to the 10th percentile of an estimated
147 probability function calculated from 32-year record of GSP for the low aridity site and
148 44-year records for the medium and high aridity sites (Figure S2). Soil moisture was
149 greatly reduced by the imposed drought but effects on soil and air temperature, and
150 relative humidity were minimal (Luo *et al.*, 2018). The drought treatment reduced
151 mean soil moisture by 33%, 38%, and 30% at the low, medium, and high aridity site,
152 respectively, during 2016-2017 growing seasons (Figure S3).

153 Community sampling

154 Plant community composition was surveyed from a 2 m×2 m permanent plot at the

155 beginning and middle of the growing season (June and August, respectively) during
156 each year of the 4-year study (1 year of pre-treatment, 3 years of treatment). The 2 m
157 ×2 m permanent species composition plot was divided into four 1m ×1 m sub-plots,
158 and aerial coverage (to the nearest 1%) of each sub-plot was recorded. Aboveground
159 net primary production (ANPP) was measured during peak biomass (early August) in
160 each treatment year by clipping all aboveground plant parts of all species in two 0.25-
161 m² quadrats located adjacent to the permanent plot. Simultaneously, leaves were
162 collected from all species in another two separate 0.25 m² quadrats during each
163 treatment year for plant trait measurements. Three recently emerged and fully
164 expanded leaves were collected from three sun-exposed individuals of each species
165 per plot and traits were measured following standard protocols (Pérez-Harguindeguy
166 *et al.*, 2013). Biomass and trait values were averaged across the quadrats for each plot.
167 The harvested species cumulatively represented 90% (or more) of total plant coverage
168 in each plot. Rare species were not sampled unless enough leaf material was available
169 for each trait measurement. Further details on the sampled species can be found in
170 supporting information.

171 We focus on four leaf economic traits expected to be involved in drought filtering
172 and niche differentiation in our study. Plant SLA and LDMC are useful traits related
173 to plant economics, including plant responses to water stress (Reich, 2014, Wright *et*
174 *al.*, 2004). Plant LNC and LPC are not often related to plant responses to water;
175 however, they are linked with plant economics and highly predictive of ecosystem
176 functions such as aboveground net primary productivity (ANPP) (Wright *et al.*, 2004;

177 Luo *et al.*, 2015, 2018). Leaf area was measured using Image J
178 (<https://imagej.nih.gov/ij/>) after fully rehydration. Leaf dry weight was measured after
179 drying all the leaves at 65°C for 48 hr to calculate both SLA (m² kg⁻¹) and LDMC (mg
180 g⁻¹) following standardized protocols (Garnier *et al.*, 2001). Then, these leaves were
181 ground for measurements of leaf chemistry. We measured LNC (mg g⁻¹) using an
182 elemental analyzer (2400II CHN elemental analyzer, Perkin-Elmer, USA) and LPC
183 (mg g⁻¹) using inductively coupled plasma atomic emission spectrometry (OPTIMA
184 3000 DV, Perkin Elmer, USA) after H₂SO₄-H₂O₂ digestion.

185 After removing the litter layer, one composite soil core (0-10 cm depth) was
186 obtained from five randomly selected locations in each of the two quadrats of each
187 plot, using a soil gauge (2.5 cm diameter). Subsamples of each soil sample were used
188 to quantify gravimetric soil water content. Subsamples were air-dried, ground and
189 filtered through a 1 mm sieve (NM200, Retsch, Haan, Germany). Soil organic carbon
190 and total nitrogen content were measured using an elemental analyzer (2400II CHN
191 elemental analyzer, Perkin-Elmer, USA). Soil carbon: nitrogen (C:N) ratios were
192 estimated and used to explore the indirect effects of drought on community functional
193 composition through changes in soil fertility.

194 Data analysis

195 For each sampled plot, community-level trait variability, defined as the degree of
196 dissimilarity in traits among all species in a community, was quantified for each of the
197 four traits separately. Community trait variation, the coefficient of variation of trait
198 values, was calculated as the ratio of community trait standard deviation (σ) to the

199 community trait mean (t); with $t = \frac{\sum_{i=1}^S ti}{S}$ and $\sigma = \sqrt{\frac{\sum_{i=1}^S (ti-t)^2}{S}}$, where ti is the trait
200 values of species i , and S is the total number of species in the community plot. All
201 species are weighted equally in trait variation calculation, thus changes in the measure
202 of community-level trait variability are driven by species presence or absence,
203 reflecting responses of species turnover to environmental changes (Jung *et al.*, 2010;
204 Mason *et al.*, 2012). Trait variability is minimized when all resident species have
205 similar trait values and is maximized when trait values are dispersed and clustered
206 along the trait axis.

207 Repeated-measures linear mixed models were applied to examine the effects of
208 experimental treatment (control *vs.* drought) on community trait mean and variation,
209 with treatment as fixed factors and block as a random factor for each site separately in
210 each year. The community trait mean and variation at the three sites were compared
211 using one-way ANOVAs, with Duncan's Test as the post-hoc test for multiple
212 comparisons in each year.

213 Changes in community-level trait variability in response to drought is attributable
214 to either species turnover (*i.e.*, species presence/absence) and/or intraspecific variation
215 in trait values. The relative contribution of species turnover (C_{turn}) *vs.* intraspecific
216 trait variation (C_{intra}) to the drought response of community-level trait variability was
217 calculated as: $C_{\text{turn}} = H_{\text{dr}^*} - H_{\text{co}}$, and $C_{\text{intra}} = H_{\text{dr}} - H_{\text{dr}^*}$, where H_{dr} and H_{co} are the
218 observed community trait variation in drought and control plots, respectively, and H_{dr^*}
219 is community trait variation recalculated in drought plots using species trait values
220 from control plots within each block (Jung *et al.*, 2014). We used these same methods

221 to calculate C_{turn} and C_{intra} of trait variability trends along the natural aridity gradient
222 (Kichenin *et al.*, 2013). We recalculated H_{dr^*} from the species in the control plots at
223 each site, but now using the mean species trait values in the control plots across all
224 three sites under the hypothesis of a lack of intraspecific variation (Kichenin *et al.*,
225 2013).

226 Linear mixed effects models were used to assess the relationship between
227 community trait variation and both soil fertility (*i.e.*, soil C:N ratio) and moisture
228 content. Across sites, mixed effects models included soil fertility or moisture as fixed
229 effects with block, site, and year as random effects. Within sites (*i.e.*, experimental
230 drought), random effects included only block and year.

231 Data were tested for normality using the Kolmogorov-Smirnov test and for equality
232 of error variance using Levene's test. As all the data met model assumptions, we used
233 untransformed data for statistical analyses. All statistical analyses were performed
234 using the *lme* function in the *nlme* package of R software (v3.2.3, R Core Team,
235 2015).

236 **Results**

237 Experimental drought significantly altered community trait variation, particularly at
238 the high aridity site (Figure 1). Surprisingly, the loss/addition of species due to
239 following three years of drought (Table S1 and Figure 2) did not impact community
240 mean trait values (Figure S4). Community trait variation varied considerably along
241 the natural aridity gradient with trait-specific trends ($p < 0.05$; Figure 1). While
242 community mean SLA remained constant (Figure S4), SLA variation decreased

243 generally with increasing aridity ($p < 0.05$; Figure 1), indicating that species are more
244 likely to converge upon a mean value of SLA in arid sites. Community mean LDMC
245 decreased with increasing aridity ($p < 0.05$; Figure S4), yet trait variation increased
246 ($p < 0.05$; Figure 1), possibly due to unequal reductions among species (Figure 2).
247 Community means and variations for both LNC and LPC increased with increasing
248 aridity ($p < 0.05$; Figures 1 and S4), due to unequal increases among species along the
249 aridity gradient (Figure 2).

250 Both species turnover (*i.e.*, species presence-absence) and intraspecific trait
251 variation played a key role in driving community trait variation at each site (Table 2).
252 For community trait variation, species turnover had a more important role than
253 intraspecific trait variation at the low and medium aridity site, while intraspecific trait
254 variability played a more important role at the high aridity site (Table 2). Moreover, in
255 many cases, intraspecific trait variation explained about 100% of the variability in
256 community trait variation in response to experimental drought at the high aridity site
257 (Table 2). Along the natural aridity gradient, intraspecific trait variation only
258 explained about 10% of the variability in community trait variation across sites (Table
259 2).

260 Soil moisture and fertility were significantly correlated with the variation of certain
261 traits, depending on site. At the low aridity site, variation in SLA was positively
262 correlated with soil water content ($p = 0.007$), while community variation in LNC was
263 negatively correlated with soil C:N ratio ($p = 0.023$; Figure 3). At the medium aridity
264 site, variations of community SLA and LDMC were significantly and positively

265 correlated with soil water content ($p=0.002$ and 0.021 , respectively), while variation
266 of community LPC was negatively correlated to soil water content ($p=0.001$; Figure
267 3). Variations of community SLA and LPC were negatively ($p=0.06$) and positively
268 ($p=0.02$) correlated with soil C:N ratio at the medium aridity site, respectively (Figure
269 3). At the high aridity site, community variation in LNC and LPC were both
270 negatively correlated with soil moisture content (both $p<0.001$; Figure 3) and with
271 soil C: N ratio ($p<0.01$; Figure 3). Again, at the high aridity site, community variation
272 in LDMC was positively correlated with soil C:N ratio ($p=0.025$ and 0.012 ,
273 respectively).

274 The spatial patterns in trait variation observed along the aridity gradient were also
275 partially explained by soil moisture and fertility. Community SLA variation was
276 positively correlated with soil water content ($p=0.002$), while community variation in
277 LDMC and LPC were both negatively correlated with soil water content ($p=0.019$ and
278 0.029 , respectively; Figure 3). Community variations in LDMC, LNC and LPC were
279 all positively correlated with soil C:N ratio along the aridity gradient ($p<0.05$; Figure
280 3).

281 **Discussion**

282 Ecosystem responses to climate extremes are in part driven by the functional
283 composition of plant communities. Thus, understanding the drought sensitivity of
284 community-scale plant traits may improve predictions of ecosystem responses to
285 climate change. Here, three years of experimental drought had no effect on
286 community trait means and had variable effects on trait variability, especially at the

287 most arid site (Figures 1 and S4). This difference implies that community functional
288 responses to drought are not only reflected in the average trait values, but also in the
289 variation and distribution of traits (Benedetti-Cecchi, 2003), with variability perhaps
290 responding more rapidly to climate extremes than community means. Further
291 assessments of community-level trait variability may thus increase the detection of
292 environmental filtering and improve model predictions of vegetation dynamics in
293 response to climate change. Variable effects of drought on trait variability can be
294 attributed to differences in the relative contribution of intraspecific trait variability and
295 species turnover.

296 The highest absolute differences in community trait variation between control and
297 drought plots were found at the driest site, suggesting that species trait distributions
298 are more sensitive to drought in drier *vs.* moister environments. This result is
299 consistent with our hypothesis, and in line with many previous studies which suggest
300 that ecosystem properties, such as plant productivity (Huxman *et al.*, 2004), CO₂ flux
301 (Hoover *et al.*, 2014) and plant species richness (Cleland *et al.*, 2013), are more
302 sensitive to drought in arid ecosystems. One potential explanation for this differential
303 sensitivity could be the greater contribution of intraspecific trait variation to the
304 functional response of the high aridity site compared to the other sites (Table 2). The
305 stability of community-level trait variability is driven by both species turnover/re-
306 ordering and intraspecific trait variability (Lepš *et al.*, 2011, Violle *et al.*, 2012). The
307 extent to which populations of species can adjust trait values (either through
308 phenotypic plasticity or shifts in genotypic abundance) can determine whether they

309 are out-competed by other species with more environmentally suitable traits (*i.e.*,
310 lower SLA with decreased soil moisture). Species composition has been shown to be
311 insensitive to rainfall manipulation in some arid sites (Tielbörger *et al.*, 2014), which
312 may explain why species turnover contributed less to the functional response
313 observed at the high aridity sites. Trait adjustments of certain species along with
314 survival of other species incapable of adjustment led to increased trait variation. It is
315 worth noting, however, that trait variation was calculated using presence/absence data,
316 thus, any change in abundance of species unable to acclimate to drought (*i.e.*, trait
317 plasticity) was not captured in these calculations.

318 Contrary to our hypothesis, we did not observe a decline in trait variability towards
319 a limited set of trait values in response to experimental drought. This may simply be
320 because our drought treatments did not cause significant species loss across all sites.
321 Moreover, functional traits do not respond to resource limitation in the same way
322 (especially not for every species), thus, it is not surprising that convergence did not
323 occur for all traits simultaneously. Additionally, hydraulic traits and/or traits related to
324 plant phenology or reproductive strategy (*e.g.*, onset of flowering) may have been
325 more responsive to drought treatments (Anderegg *et al.*, 2016, Reich, 2014, Nogueira
326 *et al.*, 2018). Across sites, we did observe convergence towards a common community
327 SLA (*i.e.*, decreased variability) with increasing aridity, largely due to species
328 turnover.

329 Community responses to the drought treatment did not mirror spatial trends
330 observed along the aridity gradient. The discrepancies between the spatial and

331 temporal responses of communities and ecosystems to environmental change have
332 been observed in many climate change experiments (Blume-Werry *et al.*, 2016). For
333 example, Sandel *et al.* (2010) contrasts the trends in plant trait distributions along a
334 precipitation gradient with those observed in response to short-term water addition.
335 The response of plant community-level trait variability to experimental drought *vs.* a
336 spatial gradient in aridity is codetermined by species turnover and intraspecific trait
337 variation. This co-determination likely played a large role in the discrepancy between
338 spatial and temporal responses (Auger & Shipley, 2013, Smith, 2011). Indeed, 90% of
339 variability in trait variability along the natural gradient was determined by species
340 turnover whereas intraspecific trait plasticity played a larger role in within-site
341 responses (Table 2). Compared to the long-term influence of aridity, the drought
342 treatments imposed here reflect a novel environmental stress, which is more likely to
343 cause variable responses in functional composition. This explanation is supported by
344 the differential responses of community-level trait variability to experimental drought
345 among years, yet consistent trends along the natural aridity gradient throughout the
346 observational period (Figure 2).

347 Lastly, spatial differences in soil moisture and fertility likely played a role in
348 changes in functional composition observed here. Drought, and aridity more broadly,
349 can have indirect effects on community trait variability by reducing N-mineralization
350 rates and thus soil fertility (Bernard-Verdier *et al.*, 2012, Nogueira *et al.*, 2018). Here,
351 we show that differences in soil fertility between sites (*i.e.*, lower fertility with
352 increased aridity) at least partially drive the spatial trends in community trait

353 variability. Drought treatments had a similar influence on community trait variability;
354 however, spatial relationships between trait responses and soil moisture/fertility were
355 stronger than the within-site temporal models comparing drought and control plots
356 (Figure 3). The response of community-level trait variability to drought may converge
357 on trends observed along a natural gradient if the duration and/or intensity of drought
358 were to increase (Smith *et al.*, 2009). Long-term drought experiments are thus needed
359 to test whether species substitution and acclimation in drought plots will lead to
360 community shifts proportional to those observed along natural aridity gradients.

361 **Conclusion**

362 Long-term drought altered community trait variability with little effect on
363 community-level trait means. Trait variability, and functional diversity more broadly,
364 may thus be a better indicator of initial community drought responses than community
365 trait values themselves. Community-level trait variability generally remained constant
366 in response to drought at the low aridity sites and was more sensitive to drought at the
367 high aridity site. In contrast, community-level trait variability declined for SLA but
368 increased for the other traits along the aridity gradient. Thus, site-level responses to
369 drought do not mirror the trends observed along natural aridity gradients. While this
370 was not entirely unexpected, we urge caution when using broad aridity gradients to
371 make predictions concerning site-specific responses to drought.

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523

524 **Table 1** Climate, soil, and vegetative characteristics of the three study sites in arid and
 525 semiarid grasslands of northern China.

| | Low aridity site | Medium aridity site | High aridity site |
|---------------------------|---|--|---|
| General | | | |
| Latitude | 43°32'N | 41°47'N | 41°25'N |
| Longitude | 116°33'E | 111°53'E | 106°58'E |
| Grassland type | Typical steppe | Transition zone | Desert steppe |
| Climate | | | |
| MAP (mm) | 346 | 251 | 175 |
| GSP (mm) | 249 | 183 | 133 |
| MAT (°C) | 1.9 | 4.5 | 5.6 |
| Aridity index | 0.40 | 0.25 | 0.17 |
| Soil | | | |
| SOC (g kg ⁻¹) | 21.35 | 16.45 | 8.68 |
| STN (g kg ⁻¹) | 2.94 | 2.83 | 0.38 |
| Vegetation | | | |
| ANPP (g m ⁻²) | 133 | 55 | 23 |
| Dominant species | <i>S. grandis</i> and <i>L. chinensis</i> | <i>S. breviflora</i> and <i>L. chinensis</i> | <i>S. glareosa</i> and <i>Peganum harmala</i> |
| Species richness | 4.5 | 8.5 | 5.4 |

526 Note: All soil and vegetation characteristics (e.g., biomass and species richness) were calculated using the data from 2015-

527 2017 in control plots of the experiment. Climatic variables are calculated from a 32-year record (1982-2014) for the low

528 aridity site, and a 44-year record (1971-2014) for the medium and high aridity sites. MAP, mean annual precipitation; GSP,

529 growing season precipitation; MAT, mean annual temperature; SOC, soil organic carbon, STN, soil total nitrogen; ANPP,

530 aboveground net primary production. Species richness was calculated as the number of species. Aridity index was calculated

531 as the ratios of MAP to potential evapotranspiration (PET), with values closer to 0--denoting greater aridity.

532

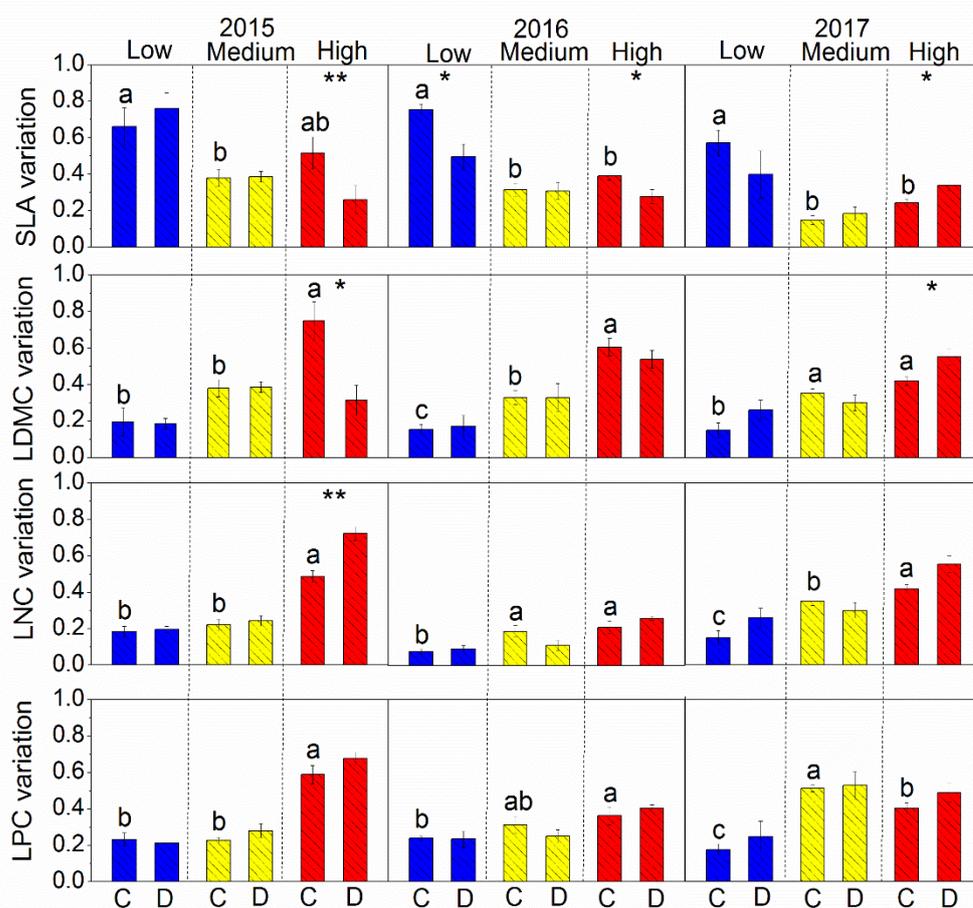
533 **Table 2** The relative contributions of species turnover and intraspecific trait variation
534 on changes in plant community trait variation under drought conditions within and
535 among three grassland sites along an aridity gradient over three years in northern
536 China. The contribution of intraspecific trait variation is given as a percent (%) for
537 community trait variation, while the remaining percent (not shown) represents the
538 contribution of species turnover. SLA, specific leaf area; LDMC, leaf dry matter
539 content; LNC, leaf nitrogen content; LPC, leaf phosphorus content.

| | Experiment manipulation | | | | | | | | | Gradient experiment | | |
|------|-------------------------|------|------|---------------------|------|------|-------------------|------|------|---------------------|------|------|
| | Low aridity site | | | Medium aridity site | | | High aridity site | | | 2015 | 2016 | 2017 |
| | 2015 | 2016 | 2017 | 2015 | 2016 | 2017 | 2015 | 2016 | 2017 | 2015 | 2016 | 2017 |
| SLA | 53 | 68 | 17 | 69 | 44 | 96 | 21 | 97 | 100 | 8 | 10 | 15 |
| LDMC | 46 | 18 | 5 | 47 | 49 | 23 | 59 | 55 | 100 | 20 | 10 | 7 |
| LNC | 58 | 20 | 46 | 70 | 9 | 38 | 20 | 87 | 100 | 6 | 18 | 14 |
| LPC | 57 | 67 | 37 | 52 | 20 | 53 | 61 | 85 | 100 | 7 | 7 | 8 |

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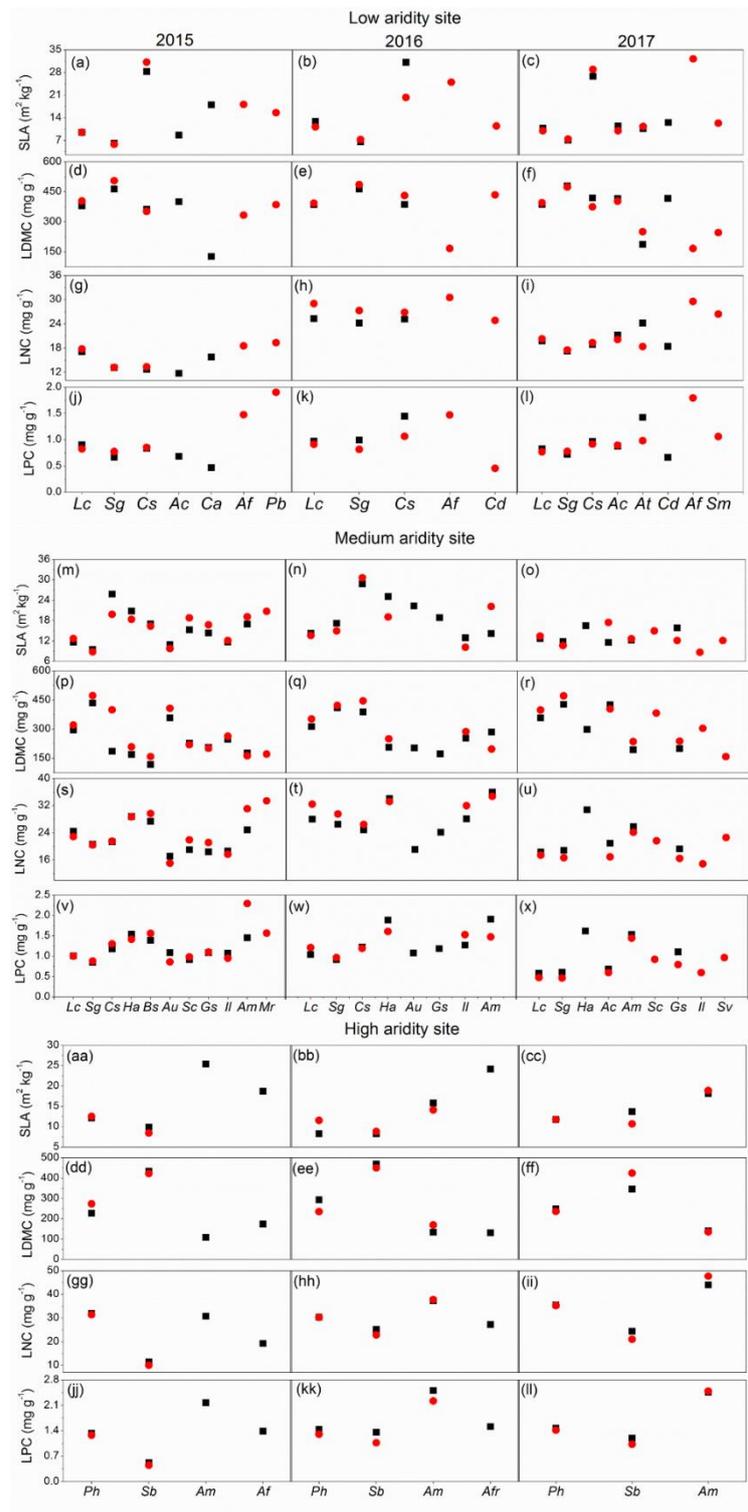
541

542 **Figure 1** Effects of drought (C, control; D, drought) and site (low, medium and high
 543 aridity site) on plant community trait variation during the treatment years (2015-
 544 2017). SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen
 545 content; LPC, leaf phosphorus content. Each bar represents the mean trait variation
 546 with error bars indicating standard errors calculated from replicate plots for each
 547 treatment. Different letters indicate significant differences among controls in different
 548 sites in each year at $p < 0.05$. Statistical significance of drought effect in each year is
 549 depicted as ** $p < 0.01$ and * $p < 0.05$.



550
 551

552 **Figure 2** Species trait means in control (black circle) and drought (red square) plots
553 during the treatment years (2015-2017) across three grassland sites along an aridity
554 gradient in northern China. SLA, specific leaf area; LDMC, leaf dry matter content;
555 LNC, leaf nitrogen content; LPC, leaf phosphorus content. Abbreviations for species
556 can be found in Table S1.



557

558 **Figure 2**

559 **Figure 3** Relationships between plant community trait variation and soil water
 560 content and fertility (soil C:N ratio) under drought conditions within and among three
 561 grassland sites along an aridity gradient during the treatment years (2015-2017). SLA,
 562 specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC,
 563 leaf phosphorus content. P -values and R^2 are shown for statistically significant
 564 regressions.
 565

