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6 **Carabid community stability is enhanced by carabid diversity but reduced by aridity in**
7 **Chinese steppes**

8
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18
19 **ABSTRACT**

20 Carabids (Coleoptera, Carabidae) are an important arthropod component of grassland ecosystems,
21 where they are involved in many important ecosystem services. Grasslands are the most widespread
22 ecosystems in China, where they are under increasing degradation that turn productive grasslands
23 into desert. We studied the relationships between carabid community stability and various
24 community parameters (richness, diversity, dominance, evenness, and proportion of the most
25 dominant species) in three types of steppes characterized by a different degree of aridity (desert,
26 typical and meadow) in northern China. Carabid community stability was lowest in the most arid
27 environment (i.e. the desert steppe). In the less arid steppe (i.e. the meadow steppe) stability was
28 correlated positively with richness, diversity, and equitability, and negatively with dominance and
29 proportion of the most abundant species. This supports the diversity hypothesis (i.e. that high levels
30 diversity lead to higher levels of stability, possibly by increasing niche complementation) and
31 falsifies the mass ratio hypothesis (i.e. that ecosystem processes, and hence their stability, are
32 strongly influenced by the most dominant species). Current transformation of productive grasslands
33 into arid lands will reduce carabid community stability and this might compromise ecosystem
34 functioning even at moderate levels of degradation, as observed in the typical steppe.

35

36 **Key words:** Carabidae; Grasslands; Community stability; Degradation; Diversity-stability
37 correlation; Mass ratio hypothesis; Steppes

38 **1. Introduction**

39 The Eurasian steppe is the largest temperate grassland type in the world. With over 13 million km²,
40 this biome accounts for some 8% of the Earth land (Wesche and Treiber, 2012). Steppes are the
41 most widespread ecosystems in China, where they cover more than 40% of the national land, thus
42 being of immense ecological and socio-economic importance (Kang et al., 2007; Ren et al., 2008).
43 Chinese steppes are sensitive to degradation due to climate change and land-use intensification
44 (namely overgrazing and conversion to croplands) which are rendering both grassland biodiversity
45 and local human populations highly vulnerable (Lü et al., 2011; Werger and van Staalduinen, 2012).
46 The contribution of climate change and human activities to grassland degradation is almost
47 equilibrium (47.9% vs 46.4%) (Zhou et al., 2017). Thus, following the classification of Salafsky et
48 al. (2008), the main threats can be assigned to the categories “Agriculture and aquaculture” and
49 “Climate change and severe weather”. Additional factors of grassland degradation in China are
50 unregulated collection of fuel (“Energy production and mining) and medicinal plants (“Biological
51 resource use”), drought (“Climate change and severe weather”), locust attacks and rodent activities
52 (“Invasive and other problematic species and genes”) (see Zhou et al., 2017). These degradation
53 processes will have serious impacts at both local and global levels. At the local scale, Gao et al
54 (2009) reported that intense grazing pressure and drought stress in grasslands significantly impact
55 vegetation species composition and community structure, thus lowering biodiversity. The negative
56 effects on vegetation lead to rapid wind erosion with major impacts on soil structure, making soils
57 drier and with less litter (Akiyama, and Kawamura, 2007). At the global level, grassland
58 degradation is turning highly productive grasslands into barren land and desert. During the period
59 from the 1980s to 2011, more than 90% of available native grassland has degraded, and moderate
60 desertification and salinization has affected 50% of the total grassland in China (Wu et al., 2019).
61 The maintenance of ecosystem services requires community stability, which, in turn, seems to be
62 associated with diversity (Báez and Collins, 2008; Gamfeldt et al., 2008; Zavaleta et al., 2010;
63 Isbell et al., 2011). In fact, plant ecologists proposed two main mechanisms explaining community
64 stability: the diversity hypothesis and the mass ratio hypothesis. Proponents of the diversity
65 hypothesis claim that greater levels of diversity promote stability by stabilizing community
66 fluctuations, because a higher diversity implies more niche complementarity and hence a better use
67 of the resources (Cottingham et al., 2001; Ives and Carpenter, 2007; Isbell et al., 2011; Cardinale et
68 al., 2012; De Mazancourt et al., 2013; Loreau and De Mazancourt, 2013; Gross et al., 2014; Tilman
69 et al., 2014). By contrast, according to the mass ratio hypothesis, ecosystem processes, and hence
70 their stability, are strongly influenced by the most dominant species (Hillebrand et al., 2008; Sasaki
71 and Lauenroth, 2011; Hallett et al., 2014; Yang et al., 2017; Valone and Balaban-Feld, 2018). Since

72 plant diversity seems to be connected with ecosystem productivity (Loreau et al., 2001; Mittelbach
73 et al., 2001; Jiang et al., 2009; but see also Huston et al., 2000), researches on community stability
74 have been focused on plant communities, whereas studies on animal communities are relatively less
75 abundant (McArdle et al., 1990; Thibaut et al., 2012; Blüthgen et al., 2016).

76 Carabid beetles (Coleoptera Carabidae) are widely used in ecological (Rainio and Niemelä, 2003;
77 Koivula, 2011; Kotze et al., 2011; Heino et al., 2019) and conservation studies (Desender et al.,
78 2010; Borchard et al., 2014; Liu et al., 2014) because their communities are distinctly influenced by
79 environmental characteristics such as vegetation type and structure and soil properties (Brose, 2003;
80 Magura et al., 2003; Harvey et al., 2008; Schaffers et al., 2008; Worthen and Merriman, 2013; Zou
81 et al., 2013; Kagawa and Maeto, 2014; Xiao et al., 2014; Liu et al., 2016; Spake et al., 2016).
82 Carabids constitute the most abundant ground dwelling insects in grassland ecosystems, where they
83 play important roles in soil formation and structure, energy flow and nutrient cycling, participate to
84 pest regulation and seed dispersion, and serve as food for insectivorous animals (Araujo et al., 2012;
85 Zhang et al., 2015; Lessard-Therrien et al., 2018; Li X. et al., 2018).

86 The aim of the present paper is to investigate the relationships between carabid community structure
87 and stability in grasslands characterized by different vegetation settings. In particular, we tested: (1)
88 if carabid community stability is better explained by the diversity hypothesis or the mass ratio
89 hypothesis; and (2) if carabid community stability and diversity vary among grasslands
90 characterized by different levels of aridity. Drought is known to decrease local plant species
91 richness and hence ecosystem stability (De Boeck et al., 2018; García-Palacios et al., 2018). By
92 comparing ecosystems with different levels of aridity, we tested here if carabid community diversity
93 and stability are also reduced by increasing drought.

94

95 **2. Materials and methods**

96

97 **2.1. Study area and experimental design**

98 The study was conducted in the Ningxia region (northern China), in an area comprised between
99 36°N and 38°N and between 105°E and 108°E, where three types of grassland ecosystems (desert,
100 typical and meadow steppes; Kang et al., 2007; Zhao et al., 2018; Li C. et al., 2019) are present.
101 These three steppes are mainly characterized by different levels of aridity: the desert steppe is the
102 most arid environment (with annual precipitation between 150 and 250 mm), the meadow steppe is
103 the less arid (with annual precipitation around 450 mm), and the typical steppe has an intermediate
104 condition (with annual precipitation around 350 mm) (Kang et al., 2007; Tsafack et al., 2019).

105 Data on carabid abundance were gathered from 90 sampling sites. We adopted a stratified sampling

106 design, with a different number of trapping sites among grassland types to reflect their within-
107 ecosystem variability. To avoid possible autocorrelation problems, sampling sites were separated by
108 at least 150 m. Based on the prevailing vegetation, each site was then assigned to one of the three
109 grassland types:

110 (1) Desert steppe (15 sites), with vegetation mainly represented by drought-tolerant species such as
111 *Agropyron mongolicum*, *Artemisia desertorum*, *A. blepharolepi* and *Stipa* spp.

112 (2) Typical steppe (45 sites), with natural patches of grass (*Stipa bungeana*, *S. grandis*, *Artemisia*
113 *frigida*, *Thymus mongolicus*, *Heteropappus altaicus* and *Potentilla acaulis*), associated with cut
114 grasses used as fire belts and crops.

115 (3) Meadow steppe (30 sites), with *Festuca brachyphylla*, *Stipa bungeana*, *Artemisia frigida* and
116 *Achnatherum splendens*.

117 At each sampling site, five pitfall traps (separated by at least five meters from each other) were used.
118 Pitfall traps consisted of 7.15-cm diameter plastic cups, sunk in the ground with the cup-lip level
119 with the soil surface. Each trap was filled with 60 mL of a mixture of tap water and vinegar (8%),
120 sugar (4%) and 70% alcohol (4%). Sampling was done from May to September 2017. During the
121 sampling period, pitfall traps were put down once a month in mid-month, and left in the field for 72
122 h prior to collection. Thus, we collected 25 samples (5 pitfall traps × 5 sampling dates) for each site,
123 for a total of 2,250 samples. Further details about study area and data collection can be found in
124 Tsafack et al. (2019). For each site, we pooled the data from the traps active in the same period and
125 calculated species abundance as the average among the five sampling dates.

126

127 **2.2. Methods for determining the diversity and stability of carabid communities**

128 Stability of carabid communities was determined by using the inverse of the coefficient of variation,
129 $ICV = \mu/\sigma$, where μ is the average relative abundance of all carabid species in one particular site
130 over time and σ is the standard deviation for the average relative abundance of all carabid species in
131 that site over time (Sasaki and Lauenroth, 2011; Yang et al., 2011; Valone and Balaban-Feld, 2018).
132 Because no single index can adequately describe all aspects of community structure (Magurran,
133 2004; Battisti and Contoli, 2011), we used a combination of them that reflects richness, diversity,
134 dominance and evenness.

135 To express richness, we used *Chao-1* (bias-corrected form) estimator and Margalef richness index.
136 *Chao-1* uses the species occurrences throughout the samples to estimate the total number of species
137 on the basis of the number of singletons and doubletons:

138

139 $Chao-1 = S + F_1(F_1 - 1) / (2(F_2 + 1))$,

140

141 where S is the observed number of species, F_1 is the number of singleton species and F_2 is the
142 number of doubleton species. Comparative analyses of the behaviour of various nonparametric
143 estimators showed that *Chao-1* performed best in estimating the true species numbers on the basis
144 of collected samples (see, for example, Hortal et al., 2006; Fattorini, 2013).

145 The Margalef richness index:

146

$$147 \quad Mg = (S - 1)/\ln(n),$$

148

149 where n is the number of collected individuals. This index seems to have a good discriminant ability
150 (Yeom and Kim, 2011), but is strongly influenced by the sampling size and effort (Magurran, 2004).

151 To take into account relative abundances, we used the Shannon-Wiener index H' :

152

$$153 \quad H' = -\sum \frac{n_i}{n} \ln\left(\frac{n_i}{n}\right),$$

154

155 where n_i is the abundance of species i and n is the overall abundance. H' ranges from 0 (one species
156 dominates the community completely) to high values for communities with many species, each with
157 similar number of individuals. H' has its foundations in information theory and represents the
158 uncertainty about the identity of an unknown individual (Morris et al., 2014). By combining
159 richness and evenness, this index is considered particularly effective in encapsulating different
160 aspects of diversity into a single value (Hayek and Buzas, 2010).

161 As measures of dominance we used Simpson (D) index:

162

$$163 \quad D = \sum \left(\frac{n_i}{n}\right)^2,$$

164

165 which represents the probability that two randomly chosen individuals belong to the same species
166 (see Morris et al., 2014 for details). The inverse of Simpson index provides a good estimate of
167 diversity at relatively small sample sizes and, in essence, it captures the variance of the species
168 abundance distribution (Magurran, 2004). D increases when diversity in the community decreases.

169 Finally, as a measure of evenness we used Pielou's index (J) of equitability, which is the ratio
170 between H' and the logarithm of species richness. This index measures the evenness with which

171 individuals are divided among the species present, and is constrained between 0 (one species
172 dominates the community completely) and 1 (all species are equally abundant).

173

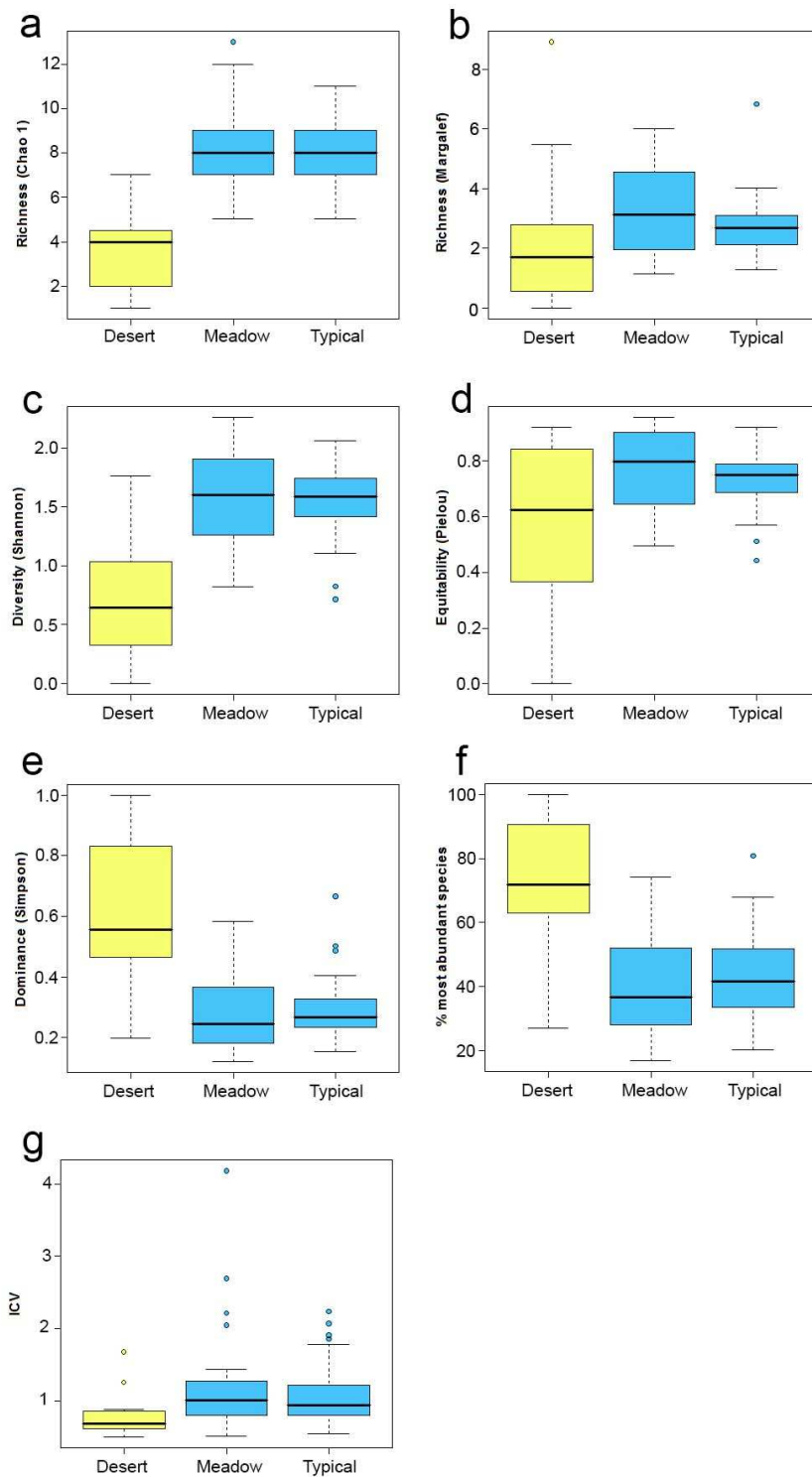
174 **2.3. Statistical analysis**

175 Data were checked for deviations from normality and homogeneity of the variances using the
176 Shapiro test and the Bartlett test, respectively. Logarithmic and arcsin transformations were used
177 when appropriate. Differences in the values for the indices of diversity and the stability of carabid
178 communities of the three compared ecosystems were evaluated by analysis of variance (ANOVA)
179 followed by Newman–Keuls tests for multiple comparisons (Wang et al., 2019) using sites as
180 replicates. Because of the possible non linearity of relationships, Spearman’s rank coefficients were
181 used to determine the correlation between the relative abundance of the most dominant species and
182 community stability, as well as the relationships among the indices of diversity, dominance and
183 equitability and community stability. In all test, significance was set at $P = 0.05$. All statistical
184 analyses were performed in R (version 3.5.3).

185

186 **3. Results**

187 Significant differences in diversity, dominance, equitability, and stability of carabid communities
188 were detected among the three investigated grasslands (Figure 1, Table 1).



189

190 **Fig. 1.** Boxplots (median, interquartile range, range and outliers) of (a) Chao-1 estimated richness,
 191 (b) Margalef richness, (c) Shannon-Wiener diversity, (d) Pielou equitability, (e) Simpson
 192 dominance, (f) proportion of the most abundant species and (g) stability ICV index in carabid
 193 communities of the three grassland ecosystems in Northern China.

194

195 **Table 1.** Results of the Analysis of Variance for differences in proportion of the most abundant

196 species, species richness (Chao-1 estimates and Margalef index), diversity (Shannon-Wiener index),
 197 equitability (Pielou index), dominance (Simpson index), and stability (ICV index), in carabid
 198 communities of three grassland ecosystems in Northern China. Values of proportion of the most
 199 abundant species were arcsin-transformed; values of Margalef index and ICV index were log₁₀-
 200 transformed. SS = Sum of Squares, DF = Degrees of Freedom, MS = Mean Square, F = F-ratio, P =
 201 probability. P values ≤ 0.05 are in bold.

202

	SS	DF	MS	F	P
Proportion of the most abundant species					
Type of steppe	5933.8	2	2966.9	27.919	<0.0001
Error	9245.3	87	106.3		
Chao-1 estimated richness					
Type of steppe	263.1	2	131.6	41.000	<0.0001
Error	278.4	87	3.2		
Margalef richness					
Type of steppe	0.365	2	0.183	6.477	0.002
Error	2.453	87	0.028		
Shannon diversity					
Type of steppe	8.784	2	4.392	33.120	<0.0001
Error	11.537	87	0.133		
Pielou equitability					
Type of steppe	0.492	2	0.246	8.604	<0.0001
Error	2.488	87	0.029		
Simpson dominance					
Type of steppe	1.450	2	0.725	34.747	<0.0001
Error	1.815	87	0.0209		
ICV					
Type of steppe	0.239	2	0.119	4.281	0.017
Error	2.426	87	0.028		

203

204 In particular, using the Newman-Keuls test, Chao-1, Margalef, Shannon-Wiener, and Pielou indexes
 205 were significantly lower in the desert steppe compared to the other grasslands (Table 2). By contrast,
 206 Simpson index was significantly higher in the desert steppe than in the other grasslands (Table 2).

207
 208 **Table 2.** Results of Newman–Keuls tests for multiple comparisons following the ANOVAs of
 209 Table 1. P values ≤ 0.05 are in bold.

	P (Desert vs Typical)	P (Desert vs Meadow)	P (Typical vs Meadow)
Proportion of the most abundant species	<0.0001	<0.001	0.582
Chao-1 estimated richness	<0.0001	<0.001	0.862
Margalef richness	0.004	<0.001	0.322
Shannon diversity	<0.001	<0.001	0.767
Pielou equitability	<0.001	<0.002	0.631
Simpson dominance	<0.001	<0.001	0.861
ICV	0.016	0.005	0.456

211
 212
 213 The relative abundance of the most dominant species was significantly higher in the desert steppe
 214 than in the other grasslands (Figure 1, Tables 1, 2), whereas stability showed a reverse pattern
 215 (Figure 2, Tables 1, 2). The relative abundance of the most dominant species was significantly
 216 negatively correlated with community stability in the meadow steppe, but not in the desert and
 217 typical steppes (Table 3).

218 In the meadow steppe, stability was significantly positively correlated with Margalef, Shannon-
 219 Wiener, and Pielou indexes (a positive correlation with Chao-1 was marginally not significant)
 220 (Table 3). By contrast, Simpson index had a significantly negative correlation with stability (Table
 221 3). No significant correlations were detected for the desert and the typical steppe (Table 3).

222
 223 **Table 3.** Spearman rank coefficient between stability (ICV index) proportion of the most abundant
 224 species, richness (Chao-1 estimated and Margalef index), diversity (Shannon-Wiener index),
 225 equitability (Pielou index), and dominance (Simpson index) in carabid communities of three
 226 grassland ecosystems in Northern China. P values ≤ 0.05 are in bold.

227

	Spearman coefficient	P
Desert		
Proportion of the most abundant species	0.371	0.174
Chao-1 estimated richness	-0.278	0.316
Margalef richness	-0.273	0.326
Shannon diversity	-0.328	0.233
Pielou equitability	-0.252	0.364
Simpson dominance	0.335	0.223
Meadow		
Proportion of the most abundant species	-0.546	0.002
Chao-1 estimated richness	0.327	0.078
Margalef richness	0.526	0.003
Shannon diversity	0.547	0.002
Pielou equitability	0.587	0.001
Simpson dominance	-0.564	0.001
Typical		
Proportion of the most abundant species	-0.141	0.355
Chao-1 estimated richness	0.122	0.424
Margalef richness	0.184	0.225
Shannon diversity	0.165	0.278
Pielou equitability	0.138	0.367
Simpson dominance	-0.217	0.153

228

229 **4. Discussion**

230 Our study indicates that the stability of carabid communities was lower in the most arid ecosystem,
 231 i.e, the desert steppe, whereas the meadow and the typical steppes had similar values. This indicates
 232 that the drought of the three grassland types influences diversity and stability of their carabid
 233 communities.

234 The fact that low values of diversity metrics characterize arid steppes does not imply that these
 235 communities have a low conservation value. In fact, these ecosystems, exactly for their instability
 236 and harsh conditions, host some highly specialized species, some of which might be of conservation
 237 concern. To contrast the increasing degradation in soil and vegetation characteristics, and to make

238 economically productive arid lands, there are many projects in China that include the creation of
239 irrigation channels, sand barriers to fix the drifting sand, and plantations of shrubs, trees and grass,
240 which anchor sand and bring economic benefits to local farmers (Xie and Wittig, 2004; Zhu et al.,
241 2013; Huang et al., 2018; Zhao et al., 2018; Li Z. et al., 2019). This might have unexplored
242 consequences on the conservation of species associated with these environments. For example,
243 Battisti and Contoli (2011) pointed out that, at the landscape level, high values of diversity indices
244 in agro-ecosystems may hide a qualitatively poor species assemblage inhabiting these landscapes,
245 mostly composed of non-native and/or synanthropic species of low conservation concern.

246 Since increasing degradation in soil and vegetation characteristics are turning highly productive
247 grasslands into arid lands (Christensen et al., 2004; Angerer et al., 2008), our study indicates that
248 this process will also lead to a decrease in community stability. This phenomenon is most probably
249 caused by the significantly decreased diversity and evenness of carabid communities with
250 increasing degree of degradation, because high levels of diversity can minimize community
251 fluctuations through the ecological niche complementation (Cottingham et al., 2001; Ives and
252 Carpenter, 2007; De Mazancourt et al., 2013; Loreau and De Mazancourt, 2013).

253 We also found positive correlations of diversity and evenness with the corresponding stability of
254 carabid communities in the meadow steppe, whereas dominance had a negative correlation with
255 stability in this ecosystem. This suggests that high levels of diversity lead to higher levels of
256 complementary resource use via niche complementation (Cottingham et al., 2001; Ives and
257 Carpenter, 2007; De Mazancourt et al., 2013; Loreau and De Mazancourt 2013). Our study also
258 showed a low correlation between richness and the corresponding stability of carabid communities.
259 Thus, diversity and evenness, rather than richness, were the most important drivers of stability of
260 carabid communities, as also found by Wang et al. (2019) for plant communities in the Northern
261 Tibet Plateau.

262 The meadow steppe did not differ significantly from the typical steppe for diversity, evenness and
263 dominance values, yet the typical steppe did not show any correlation between these community
264 parameters and stability, as also found for the desert steppe. Thus, the typical steppe is similar to the
265 meadow steppe in terms of diversity, evenness and dominance, but it is similar to the desert steppe
266 in terms of diversity-stability relationships. This suggests that ecosystem stability can be
267 compromised even when values of diversity decline only slightly as it is in typical steppe.

268 We found a significantly negative correlation between the relative abundance of the most dominant
269 species and the corresponding stability of carabid communities in the meadow steppe. As postulated
270 by Wang et al. (2019), this can be due to the fact that the stability of communities decreases with
271 increasing degree of degradation (aridification in the case of our grasslands), but the relative

272 abundance of the most dominant species increases with increasing degree of degradation. This is in
273 turn a reflection that with increasing aridity there is an increase in the dominance of the very few
274 species able to survive in harsh conditions (Tsafack et al., 2019). Thus, our results support the
275 diversity hypothesis (Cottingham et al., 2001; Ives and Carpenter, 2007; De Mazancourt et al., 2013;
276 Loreau and De Mazancourt, 2013) rather than the mass ratio hypothesis (Grime, 1998; Hillebrand et
277 al., 2008; Valone and Balaban-Feld, 2018). In conclusion, our study indicates that more arid
278 conditions reduce community stability by decreasing diversity and favouring the dominance of few
279 species.

280 In this study we investigated community stability and diversity among three ecosystems with
281 different aridity levels that are indicative of what can be expected under increasing degradation.
282 Future research should be addressed: (1) to investigate possible gradients in the distribution of
283 carabid populations within each grassland type under different levels of degradation, and (2) and to
284 assess if carabids have a significant effect on grassland plant diversity and stability.

285

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293

294 **Author contribution**

295 SF conceived, designed this study, managed the assembly of the data set, designed and performed
296 the statistical analyses and drafted the manuscript. LBD designed and performed the statistical
297 analyses, and drafted the manuscript. NT managed the assembly of the data set, contributed
298 reagents, materials and analysis tools and drafted the manuscript. YX conceived and designed the
299 experiments and contributed reagents, materials and analysis tools. XW conceived and designed the
300 experiments, performed the experiments, and contributed reagents, materials and analysis tools.

301 All authors contributed to the interpretation of the results and approved the final draft.

302

303 **Competing interests statement**

304 Authors have no competing interests to declare.

305

306 **References**

- 307 Akiyama, T., Kawamura, K., 2007. Grassland degradation in China: Methods of monitoring,
308 management and restoration. *Grassl. Sci.* 53, 1–17.
- 309 Angerer, J., Han, G., Fujisaki, I., Havstad, K., 2008. Climate change and ecosystems of Asia with
310 emphasis on inner Mongolia and Mongolia. *Rangelands* 30, 46–51.
- 311 Araujo, P.I., Yahdjian, L., Austin, A.T., 2012. Do soil organisms affect aboveground litter
312 decomposition in the semiarid Patagonian steppe, Argentina? *Oecologia* 168, 221–230.
- 313 Báez, S., Collins, S.L., 2008. Shrub invasion decreases diversity and alters community stability in
314 Northern Chihuahuan Desert plant communities. *PLoS One* 3, e2332.
- 315 Battisti, C., Contoli, L., 2011. Diversity Indices as ‘Magic’ Tools in landscape planning: a
316 cautionary note on their uncritical use. *Landsc. Res.* 36, 111–117.
- 317 Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., Fischer, M., Hölzel, N.,
318 Klaus, V.H., Kleinebecker, T., Tschapka, M., Weisser, W.W., Gossner, M.M., 2016. Land use
319 imperils plant and animal community stability through changes in asynchrony rather than
320 diversity. *Nat. Commun.* 7, 10697.
- 321 Borchard, F., Buchholz, S., Helbing, F., Fartmann, T., 2014. Carabid beetles and spiders as
322 bioindicators for the evaluation of montane heathland restoration on former spruce forests.
323 *Biol. Conserv.* 178, 185–192.
- 324 Brose, U., 2003. Bottom-up control of carabid beetle communities in early successional wetlands:
325 mediated by vegetation structure or plant diversity? *Oecologia* 135, 407–413.
- 326 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,
327 Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B.,
328 Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on
329 humanity. *Nature* 486, 59–67.
- 330 Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z., 2004. Vulnerability of the Asian Typical
331 Steppe to Grazing and Climate Change. *Clim. Change* 63, 351–368.
- 332 Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal
333 variability of ecological systems. *Ecol. Lett.* 4, 72–85.
- 334 De Boeck, H.J., Bloor, J.M.G., Kreyling, J., Ransijn, J. C. G., Nijs, I., Jentsch, A., Zeiter, M., 2018.
335 Patterns and drivers of biodiversity–stability relationships under climate extremes. *J. Ecol.*
336 106, 890–902.
- 337 De Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., Haegeman, B.,
338 Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey,
339 B.J., Loreau, M., 2013. Predicting ecosystem stability from community composition and

340 biodiversity. *Ecol. Lett.* 16, 617–625.

341 Desender, K., Dekoninck, W., Dufrêne, M., Maes, D., 2010. Changes in the distribution of carabid
342 beetles in Belgium revisited: Have we halted the diversity loss? *Biol. Conserv.* 143, 1549–
343 1557.

344 Fattorini, S., 2013. Faunistic knowledge and insect species loss in an urban area: the tenebrionid
345 beetles of Rome. *J. Insect Conserv.* 17, 637–643.

346 Gamfeldt, L., Hillebrand, H., Jonsson, P.R., 2008. Multiple functions increase the importance of
347 biodiversity for overall ecosystem functioning. *Ecology* 89, 1223–1231.

348 Gao, Y.Z., Giese, M., Han, X.G., Wang, D.L., Zhou, Z.Y., Brueck, H., Lin, S., Taube, F., 2009.
349 Land use and drought interactively affect interspecific competition and species diversity at the
350 local scale in a semiarid steppe ecosystem. *Ecol. Res.* 24, 627–635.

351 García-Palacios, P., Gross, N., Gaitán, J., Maestre, F. T., 2018. Climate mediates the biodiversity–
352 ecosystem stability relationship globally. *Proc. Natl. Acad. Sci. U.S.A.* 115 (33), 8400–8405.

353 Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Polley, H.W., Reich, P.B., van
354 Ruijven, J., 2014. Species richness and the temporal stability of biomass production: a new
355 analysis of recent biodiversity experiments. *Am. Nat.* 183, 1–12.

356 Hallett, L.M., Hsu, J.S., Cleland, E.E., Collins, S.L., Dickson, T.L., Farrer, E.C., Gherardi, L.A.,
357 Gross, K.L., Hobbs, R.J., Turnbull, L., Suding, K.N., 2014. Biotic mechanisms of community
358 stability shift along a precipitation gradient. *Ecology* 95, 1693–1700.

359 Harvey, J.A., van der Putten, W.H., Turin, H., Wagensaar, R., Bezemer, T.M., 2008. Effects of
360 changes in plant species richness and community traits on carabid assemblages and feeding
361 guilds. *Agric. Ecosyst. Environ.* 127, 100–106.

362 Hayek, L-A., Buzas, M., 2000. Surveying natural populations, quantitative tools for assessing
363 biodiversity. Columbia University Press, New York.

364 Heino, J., Alahuhta, J., Fattorini, S., Schmera, D., 2019. Predicting beta diversity of terrestrial and
365 aquatic beetles using ecogeographical variables: insights from the replacement and richness
366 difference components. *J. Biogeogr.* 46, 304–315.

367 Hillebrand, H., Bennett, D.M., Cadotte, M.W., 2008. Consequences of dominance: a review of
368 evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510–1520.

369 Hortal, J., Borges, P.A.V., Gaspar, C., 2006. Evaluating the performance of species richness
370 estimators: sensitivity to sample grain size. *J. Anim. Ecol.* 75, 274–287.

371 Huang, Z., Liu, Y., Cui, Z., Fang, Y., He, H., Liu, B.-R., Wu, G.-L., 2018. Soil water storage deficit
372 of alfalfa (*Medicago sativa*) grasslands along ages in arid area (China). *Field Crops Res.* 221,
373 1–6.

- 374 Huston, M. A., Aarssen, L.W., Austin, M.P., Cade, B.S., Fridley, J.D., Garnier, E., Grime, J.P.,
375 Hodgson, J., Lauenroth, W.K., Thompson, K., Vandermeer, J.H., Wardle, D.A., Hector, A.,
376 Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A.,
377 Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J.,
378 Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H.,
379 O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M.,
380 Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E., Terry, A.C., Troumbis, A.Y., Woodward,
381 F.I., Yachi, S., Lawton, J.H., 2000. No consistent effect of plant diversity on productivity.
382 *Science* 289, 1255a.
- 383 Isbell, F.I., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen,
384 M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau,
385 M., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477, 199–202.
- 386 Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. *Science* 317, 58–62.
- 387 Jiang, L. Wan, S. Q., Li, L. H., 2009. Species diversity and productivity: why do results of
388 diversity-manipulation experiments differ from natural patterns? *J. Ecol.* 97, 603–608.
- 389 Kagawa, Y., Maeto, K., 2014. Ground beetle (Coleoptera: Carabidae) assemblages associated with
390 a satoyama landscape in Japan: the effects of soil moisture, weed height, and distance from
391 woodlands. *Appl. Entomol. Zool.* 49, 429–436.
- 392 Kang, L., Han, X., Zhang, Z., Sun, O.J., 2007. Grassland ecosystems in China: review of current
393 knowledge and research advancement. *Philos. Trans. R. Soc. B Biol. Sci.* 362, 997–1008.
- 394 Koivula, M., 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera,
395 Carabidae) reflecting environmental conditions. *ZooKeys* 100, 287–317.
- 396 Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M., Lovei, G.,
397 Mossakowski, D., Noordijk, J., Paarmann, W., Pizzoloto, R., Saska, P., Schwerk, A., Serrano,
398 J., Szyszko, J., Taboada Palomares, A., Turin, H., Venn, S., Vermeulen, R., 2011. Forty years
399 of carabid beetle research in Europe – from taxonomy, biology, ecology and population
400 studies to bioindication, habitat assessment and conservation. *ZooKeys* 100, 55–148.
- 401 Lessard-Therrien, M., Humbert, J.-Y., Hajdamowicz, I., Stańska, M., van Klink, R., Lischer, L.,
402 Arlettaz, R., 2018. Impacts of management intensification on ground-dwelling beetles and
403 spiders in semi-natural mountain grasslands. *Agric. Ecosyst. Environ.* 251, 59–66.
- 404 Li, C., Li, Y., Li, G., Wang, C., Li, B., 2019. Environmental change and human activity in the
405 northeastern part of the North China Plain during early MIS-2. *J. Asian Earth Sci.* 170, 96–
406 105.
- 407 Li, X., Liu, Y., Duan, M., Yu, Z., Axmacher, J.C., 2018. Different response patterns of epigeic

- 408 spiders and carabid beetles to varying environmental conditions in fields and semi-natural
409 habitats of an intensively cultivated agricultural landscape. *Agric. Ecosyst. Environ.* 264, 54–
410 62.
- 411 Li, Z., Schneider, R.L., Morreale, S.J., Xie, Y., Li, J., Li, C., Ni, X., 2019. Using woody organic
412 matter amendments to increase water availability and jump-start soil restoration of desertified
413 grassland soils of Ningxia, China. *Land Degrad. Dev.* 30, 1313–1324.
- 414 Liu, J.-L., Li, F.-R., Sun, T.-S., Ma, L.-F., Liu, L.-L., Yang, K., 2016. Interactive effects of
415 vegetation and soil determine the composition and diversity of carabid and tenebrionid
416 functional groups in an arid ecosystem. *J. Arid Environ.* 128, 80–90.
- 417 Liu, Y., Duan, M., Zhang, Xuzhu, Zhang, Xin, Yu, Z., Axmacher, J.C., 2014. Effects of plant
418 diversity, habitat and agricultural landscape structure on the functional diversity of carabid
419 assemblages in the North China Plain. *Insect Conserv. Diver.* 8, 163–176.
- 420 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston,
421 M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Biodiversity and ecosystem
422 functioning: Current knowledge and future challenges. *Science* 294, 804–808.
- 423 Loreau, M., De Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of
424 underlying mechanisms. *Ecol. Lett.* 16, 106–115.
- 425 Lü, Y., Fu, B., Wei, W., Yu, X., Sun, R., 2011. Major Ecosystems in China: Dynamics and
426 Challenges for Sustainable Management. *Environ. Manage.* 48, 13–27.
- 427 Magura, T., Tóthmérész, B., Elek, Z., 2003. Diversity and composition of carabids during a forestry
428 cycle. *Biodivers. Conserv.* 12, 73–85.
- 429 Magurran, A. E., 2004. *Measuring Biological Diversity*. Wiley-Blackwell, Oxford.
- 430 McArdle, B.H., Gaston, K.J., Lawton, J.H., 1990. Variation in the Size of Animal Populations:
431 Patterns, Problems and Artefacts. *J. Anim. Ecol.* 59, 439–454
- 432 Mittelbach, G. G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig,
433 M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species
434 richness and productivity? *Ecology* 82, 2381–2396.
- 435 Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C.,
436 Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S.,
437 Rillig, M.C., 2014. Choosing and using diversity indices: insights for ecological applications
438 from the German Biodiversity Exploratories. *Ecol. Evol.* 4, 3514–3524.
- 439 Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers.*
440 *Conserv.* 12, 487–506.
- 441 Ren, J.Z., Hu, Z.Z., Zhao, J., Zhang, D.G., Hou, F.J., Lin, H.L., Mu, X.D., 2008. A grassland

442 classification system and its application in China. *Rangel. J.* 30, 199–209.

443 Salafsky, N., Salzer, D., Stattersfield, A., Hilton-Taylor, C., Neugarten, R., Butchart, S., Collen, B.
444 Cox, N., Master, L.L., O'Connor, S., Wilkie, D.. 2008. A standard lexicon for biodiversity
445 conservation: unified classifications of threats and actions. *Conserv. Biol.* 22, 897-911.

446 Sasaki, T. & Lauenroth, W.K., 2011. Dominant species, rather than diversity, regulates temporal
447 stability of plant communities. *Oecologia* 166, 761–768.

448 Schaffers, A.P., Raemakers, I.P., Sýkora, K.V., ter Braak, C.J.F., 2008. Arthropod assemblages are
449 best predicted by plant species composition. *Ecology* 89, 782–794.

450 Spake, R., Barsoum, N., Newton, A.C., Doncaster, C.P., 2016. Drivers of the composition and
451 diversity of carabid functional traits in UK coniferous plantations. *For. Ecol. Manag.* 359,
452 300–308.

453 Thibaut, L.M., Connolly, S.R., Sweatman, H.P.A., 2012. Diversity and stability of herbivorous
454 fishes on coral reefs. *Ecology* 93, 891–901.

455 Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annu. Rev.*
456 *Ecol. Evol. Syst.* 45, 471–493.

457 Tsafack, N., Rebaudo, F., Wang, H., Nagy, D.D., Xie, Y., Wang, X., Fattorini, S., 2019. Carabid
458 community structure in northern China grassland ecosystems: Effects of local habitat on
459 species richness, species composition and functional diversity. *PeerJ* 6: e6197.

460 Valone, T.J., Balaban-Feld, J., 2018. Impact of exotic invasion on the temporal stability of natural
461 annual plant communities. *Oikos* 127, 56–62.

462 Wang, C., Wei, M., Wu, B., Wang, S., Jiang, K., 2019. Alpine grassland degradation reduced plant
463 species diversity and stability of plant communities in the Northern Tibet Plateau. *Acta Oecol.*
464 98, 25–29.

465 Werger, M.J.A., van Staalduinen, M.A., 2012. Eurasian Steppes. Ecological problems and
466 livelihoods in a changing world. Springer, Dordrecht.

467 Wesche, K., Treiber, J., 2012. Abiotic and Biotic Determinants of Steppe Productivity and
468 Performance – A View from Central Asia, in: Werger, M.J.A., van Staalduinen, M.A. (eds.),
469 Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World. Springer,
470 Dordrecht, pp. 3–43.

471 Worthen, W.B., Merriman, D.C.G., 2013. Relationships between Carabid Beetle Communities and
472 Forest Stand Parameters: Taxon Congruence or Habitat Association? *Southeast. Nat.* 12, 379–
473 386.

474 Wu, N., Liu, A., Wang, Y., Li, L., Chao, L., Guixiang Liu, L., 2019. An assessment framework for
475 grassland ecosystem health with consideration of natural succession: A case study in

476 Bayinxile, China. Sustainability, 11, 1096.

477 Xiao, W., Ge, X., Zeng, L., Huang, Z., Lei, J., Zhou, B., Li, M., 2014. Rates of Litter
478 Decomposition and soil respiration in relation to soil temperature and water in different-aged
479 *Pinus massoniana* forests in the Three Gorges reservoir area, China. PLoS One 9, e101890.

480 Xie, Y., Wittig, R., 2004. The impact of grazing intensity on soil characteristics of *Stipa grandis*
481 and *Stipa bungeana* steppe in northern China (autonomous region of Ningxia). Acta Oecol. 25,
482 197–204.

483 Yang, Z.L., van Ruijven, J., Du, G.Z., 2011. The effects of long-term fertilization on the temporal
484 stability of alpine meadow communities. Plant Soil 345, 315–324.

485 Yang, Z.L., Zhang, Q., Su, F.L., Zhang, C.H., Pu, Z.C., Xia, J.Y., Wan, S.Q., Jiang, L., 2017.
486 Daytime warming lowers community temporal stability by reducing the abundance of
487 dominant, stable species. Global Change Biol. 23, 154–163.

488 Yeom, D.-J., Kim, J. H., 2011. Comparative evaluation of species diversity indices in the natural
489 deciduous forest of Mt. Jeombong. For. Sci. Technol. 7, 68–74.

490 Zavaleta, E.S., Pasari, J.R., Hulvey, K.B., Tilman, G.D., 2010. Sustaining multiple ecosystem
491 functions in grassland communities requires higher biodiversity. Proc. Natl. Acad. Sci. USA
492 107, 1443–1446.

493 Zhang, Q., Wu, J., Sun, Y., Zhang, M., Mai, B., Mo, L., Lee, T.M., Zou, F., 2015. Do Bird
494 Assemblages Predict Susceptibility by E-Waste Pollution? A comparative study based on
495 species- and guild-dependent responses in China agroecosystems. PLoS One 10, e0122264.

496 Zhao, Z., Wei, J., Zhang, K., Li, H., Wei, S., Pan, X., Huang, W., Zhu, M., Zhang, R., 2018.
497 Asymmetric response of different functional insect groups to low-grazing pressure in Eurasian
498 steppe in Ningxia. Ecol. Evol. 8, 11609–11618.

499 Zhou, W., Yang, H., Huang, L., Chen, C., Lin, X, Hu, Z.J., Li, J., 2017. Grassland degradation
500 remote sensing monitoring and driving factors quantitative assessment in China from 1982 to
501 2010. Ecol. Indic. 83, 303–313.

502 Zhu, X., Li, Y., Li, M., Pan, Y., Shi, P., 2013. Agricultural irrigation in China. J. Soil Water
503 Conserv. 68, 147A-154A.

504 Zou, Y., Sang, W., Bai, F., Axmacher, J.C., 2013. Relationships between plant diversity and the
505 abundance and α -diversity of predatory ground beetles (Coleoptera: Carabidae) in a mature
506 Asian temperate forest ecosystem. PLoS One 8, e82792.

507