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Carabid community structure in northern China grassland ecosystems - Does local habitat drive species richness, species composition and functional diversity?

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Background: Increasing land-use and climate change are two major drivers of grassland degradation worldwide. In China grasslands account for more than 40% of the national land. Most carabid beetles are active on the ground and are therefore particularly sensitive to changes in local habitat characteristics.

Methods: We investigated the influence of vegetation (plant biomass, coverage, density, height and species richness), soil (bulk density, above ground litter, moisture and temperature) and climate (humidity, precipitation and temperature) on carabid community structure (species richness, species composition and functional diversity - measured as body size and movement diversity) in three types of grasslands in northern China: desert, typical and meadow steppes. We used Canonical Correspondence Analysis to investigate the role of habitat characteristics on species composition and multiple linear regressions to investigate the responses of species richness and functional diversities.

Results: We found that carabid community structure was strongly influenced by local habitat characteristics and particularly by climatic factors. Carabids of the desert steppe responded less to habitat characteristics than those inhabiting the medium and typical steppes. Temperature had a strong positive effect on carabid assemblage characteristics effect in the desert steppe. Plant biomass, density and height were the best vegetational predictors. Soil characteristics had weak effects.

Discussion: Carabid responses to environmental characteristics varied among grassland types, which warns against generalizations and indicates that management programs should be considered at grassland scale. Carabid community structure is strongly influenced by climatic factors, and can be therefore particular sensitive to the ongoing climate change.

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Carabid community structure in northern China

2 grassland ecosystems – Does local habitat drive

3 species richness, species composition and functional

4 diversity?

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ABSTRACT

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- 22 Background: Increasing land-use and climate change are two major drivers of grassland
- 23 degradation worldwide. In China grasslands account for more than 40% of the national land.
- 24 Most carabid beetles are active on the ground and are therefore particularly sensitive to changes
- 25 in local habitat characteristics.
- 26 Methods: We investigated the influence of vegetation (plant biomass, coverage, density, height
- and species richness), soil (bulk density, above ground litter, moisture and temperature) and
- 28 climate (humidity, precipitation and temperature) on carabid community structure (species
- 29 richness, species composition and functional diversity measured as body size and movement
- 30 diversity) in three types of grasslands in northern China: desert, typical and meadow steppes. We
- 31 used Canonical Correspondence Analysis to investigate the role of habitat characteristics on
- 32 species composition and multiple linear regressions to investigate the responses of species
- 33 richness and functional diversities.
- 34 **Results:** We found that carabid community structure was strongly influenced by local habitat
- 35 characteristics and particularly by climatic factors. Carabids of the desert steppe responded less
- 36 to habitat characteristics than those inhabiting the meadow and typical steppes. Temperature had
- 37 a strong positive effect on carabid assemblage characteristics, except in the desert steppe. Plant



- 38 biomass, density and height were the best vegetational predictors. Soil characteristics had weak
- 39 effects.
- 40 **Discussion:** Carabid responses to environmental characteristics varied among grassland types,
- 41 which warns against generalizations and indicates that management programs should be
- 42 considered at grassland scale. Carabid community structure is strongly influenced by climatic
- 43 factors, and can be therefore particular sensitive to the ongoing climate change.

44 45

INTRODUCTION

- 46 The decrease of biodiversity is one of the most important worldwide concerns (Wagner, 2018;
- 47 Willig & Presley, 2018). As well as other major biomes, grasslands are experiencing strong
- 48 pressures from human activities, triggering the need for conservation plans (Batáry et al., 2008;
- 49 Jellinek et al., 2014). In China, where grasslands account for more than 40% of the national land
- 50 (Kang et al., 2007; Ren et al., 2008), increasing land-use for human activities and climate change
- are the two major drivers of grassland degradation (Lü et al., 2011).
- 52 Because most of carabid beetles (Coleoptera: Carabidae) are active on the ground, these insects
- 53 may be particularly vulnerable to changes in soil and vegetational characteristics that occur with
- 54 grassland degradation. It is well known that carabid assemblages are strongly influenced by
- 55 habitat structure, especially as reflected by vegetation and soil characteristics (Koivula. et al.,
- 56 1999; Brose, 2003; Taboada et al., 2008), being particular sensitive to anthropogenic alterations
- 57 (Rainio & Niemelä, 2003; Koivula, 2011). For these reasons, carabid distributional patterns and
- community structure can be strongly affected by land use changes (Eyre et al., 2003; Eyre &
- 59 Luff, 2004; Kotze et al., 2011
- 60 For example, soil bulk density (an indicator of soil structure, also used to estimate soil
- 61 compaction, Rabot et al., 2018), and soil moisture, two environmental characteristics that are
- altered by human activities, are key factors for carabid ecology. Kagawa & Maeto (2014)
- showed that the abundance of some species is associated with different degrees of soil moisture,
- 64 whereas Magura, Tóthmérész & Elek (2003) reported that soil compaction negatively influences
- 65 carabid activities, such as eggs laying and digging into the soil during aestivation and
- 66 hibernation.
- 67 Carabids can be also impacted by the amount of litter on the soil (Magura, Tóthmérész & Elek,
- 68 2003) since it modulates both soil moisture and temperature (Xiao et al., 2014), improves soil
- 69 fertility and increases food availability (Koivula et al., 1999; Magura, Tóthmérész & Elek, 2005).
- 70 It has been observed that leaf litter increases the number of carabids through increasing habitat
- 71 heterogeneity, producing favorable microsites and allowing a separated vertical distribution in
- 72 the litter layer which may lead to decrease intra- and inter- specific competition (Magura,
- 73 Tóthmérész & Elek, 2003). Another soil characteristic that is particular relevant for carabids is
- 74 the soil temperature (Hiramatsu & Usio, 2018; Robinson et al., 2018) because this physical
- 75 parameter influences various species-specific temperature-dependent performances (Merrick &
- 76 Smith, 2004).



- 77 Vegetation composition and diversity also impact carabid community structure (Koricheva et al.,
- 78 2000; Brose, 2003; Schaffers et al., 2008; Zou et al., 2013; Pakeman & Stockan, 2014; Ng et al.,
- 79 2018a) and functional diversity (Liu et al., 2014; Pakeman & Stockan, 2014; Spake et al., 2016;
- 80 Magura, 2017), because plants provide both shelter and food, directly (for herbivores) and
- 81 indirectly (by providing prey for predators).
- 82 Within local environmental characteristics, in addition to vegetation and soil characteristics,
- 83 climate plays an important role in carabid ecology. Temperature influences flight, speed of
- 84 digestion, fecundity and also larval survival (Thiele, 1977; Butterfield, 1996; Lövei &
- 85 Sunderland, 1996), and Rainio & Niemelä (2003) showed that ambient temperature and humidity
- 86 were the two main abiotic factors influencing carabid species. Carabid community structure may
- 87 be also positively impacted by precipitation through the responses of plants to this factor.
- 88 Because plant diversity and biomass increase with increasing precipitation (Yan et al., 2015),
- 89 sites with more rainfall should provide more habitat diversity and food for carabids.
- 90 Knowing carabid community responses to climatic, soil and vegetational characteristics in
- 91 grassland ecosystems is of pivotal importance to adopt conservation measures to cope with
- 92 grassland degradation due to land use and climate change. This is not only particularly
- 93 compelling for environmental conservation in China, where grasslands play important roles in
- 94 servicing the ecological environment and socio-economics (Kang et al., 2007), but may also
- 95 provide important insights into insect conservation in grassland ecosystems worldwide,
- 96 especially in the light of ongoing desertification processes.
- 97 In this study, we aimed at investigating the influence of habitat characteristics on the structure of
- 98 carabid communities in different types of grasslands in China that reflect a gradient of aridity
- 99 from most arid to most humid: desert steppe, typical steppe, and meadow steppe (Kang et al.,
- 100 2007). For this, we considered twelve environmental variables including five vegetational
- 101 characteristics (plant biomass, coverage, density, height and species richness), four soil factors
- 102 (bulk density, above ground litter, moisture and temperature) and three climatic factors
- 103 (humidity, precipitation and temperature). We investigated carabid responses to these factors at
- regional scale and at grassland type-level by considering three assemblage characteristics:
- species richness, species composition and functional diversity (measured as body size and
- 106 movement diversity).
- We expect that species richness should increase with rainfall, humidity and temperature, at the
- regional scale and in the three grassland types, except for the desert steppe, for which we
- postulate a negative relationship, because of the very high temperatures that are recorded there.
- We expect that plant biomass, coverage, density, height and richness should promote carabid
- richness. Sites with higher values of plant biomass, coverage, density, height and richness are
- expected to be more productive and to offer a higher variety of microhabitats and food resources.
- The effects should be stronger in the desert steppe, where vegetation is sparse and less varied.
- than in the other grassland types. We also predict that soil bulk density should have a negative
- impact on species richness, because higher soil compaction should affect negatively some
- carabid activities. We expect that the aboveground litter and moisture should positively impact



- 117 carabid richness, independently from the grassland type, because water is a limiting factor in all the study grasslands. We also expect that soil temperature should influence positively carabid 118 richness in the meadow and typical steppes (because the range of temperature in these grassland 119 types are likely to encompass different species preferences), but negatively in the desert steppe 120 121 (where high temperatures may be intolerable for most species). At regional scale, we expect that carabid richness are influenced positively by litter and moisture, and negatively by soil 122 temperature (because of the negative impact of the highest temperatures recorded in the desert 123 124 steppe). We expect that climatic factors, and in particular temperature are the most important drivers of 125 species composition both at the regional scale and for the three grassland types. We also expect 126 that all vegetation and soil factors are important predictors of carabid community composition at 127 the regional scale, but their relative importance should vary according to the grassland type. 128 129 because the different grassland types have different environmental characteristics. We expect 130 that climatic factors are important predictors of functional diversity at the regional scale and for the three grassland types. However, we also expect the different environmental conditions of the 131 three grassland types should lead to the presence of species assemblages with functional
- 132 diversity influenced by different factors. In particular, as small body size is a characteristic of
- 133
- carabid beetles that inhabit severe environments, probably because of depauperate food 134
- availability (Blake et al., 1994; Lövei & Magura, 2006; Hiramatsu & Usio, 2018), we expect to 135
- have a lower functional diversity in the desert steppe. 136

137 138

MATERIALS & METHODS

- Study areas and sampling design 139
- The study was carried out in the Ningxia region, northern China. We selected three sampling 140
- 141 areas representing the three main ecosystems of the region: desert steppe, typical steppe, and
- meadow steppe (Figs. 1 and 2). 142
- The desert steppe area is located in Eastern Ningxia, Yanchi county (37°59'13"N 107°05'42"E). 143
- 144 This area is characterized by a cold, semi-arid continental monsoonal climate zone (Liu et al.,
- 2015), with an average annual temperature of 8.3 °C (-8°C in January, 22 °C in July), and 145
- 146 average annual precipitation of around 200 mm (Kang et al., 2007). The vegetation is
- 147 characterized by typical drought tolerant plant species, such as Agropyron mongolicum,
- Artemisia desertorum, Artemisia blepharolepi and Stipa spp. The typical steppe area is located in 148
- southern Ningxia, Guyuan County, near the Natural Reserve of the Yunwu Mountain. This area 149
- is characterized by a continental monsoon climate. Average annual temperature is 5.7°C (-22 °C 150
- in January, 28°C in August) and annual rainfall is 350 mm (Kang et al., 2007). The top of the 151
- mountain (36°12'16"N 106°24'37" E) was characterized by grass vegetation crossed by patches 152
- of cut grasses that serve as fire belts. The natural vegetation on the top of the mountain included 153
- 154 Stipa bungeana, Stipa grandis, Artemisia frigida, Thymus mongolicus and Heteropappus
- altaicus. The bottom of the mountain (36°15'6"N 106°23'5" E) is occupied by crop fields and 155
- natural vegetation including Stipa bungeana, Artemisia frigida, Thymus mongolicus and 156



- Potentilla acaulis. We selected in this area three sectors: the first and second sectors were 157 located on the top of the mountain, in natural patches of grass vegetation and in fire belts, 158 respectively; the third sector was selected at the bottom of the mountain. The meadow steppe 159 area is located in Western Ningxia, Haiyuan county, near the Nanhua mountain. This area is 160 161 characterized by a semi-humid climate, with an annual temperature of 7 °C (-7 °C in January, 20°C in July), and average annual precipitation of 450 mm (Kang et al., 2007). Within this area, 162 we selected two sampling sectors to reflect different vegetation types. The first sector 163 (36°26'50"N - 105°38'24"E) was located at the south-west side of the mountain peak (2600 m) 164 165 and was dominated by several species of the genus of Festuca, principally the alpine fescue Festuca brachyphylla. The second sector (36°25'13" N – 105°36'41"E) was located at the bottom 166 of the mountain peak (1800 m) and its vegetation was dominated by Stipa bungeana, Artemisia 167 frigida and Achnatherum splendens. 168 In total, we selected 15 sampling sites in the desert steppe, 45 sites (15 sites per sector) in the 169 typical steppe and 30 sites in the meadow steppe (15 sites per sector). Sites were separated by at 170 171 least 150 m from each other. At each sampling site, five pitfall traps were placed at a distance of least five m from each other. Pitfall traps were made of plastic cups (diameter: 7.15 cm, depth: 9 172 173 cm) dug into the ground and filled with 60 ml of an attractant solution (vinegar, sugar, 70% alcohol and water in the following proportion: 2:1:1:20). Pitfall traps were left one timper 174 month at the mid-month, from May to September 2017, and collected three days after. In total, 175 we used 2,250 pitfall traps (90 sampling sites \times 5 pitfall traps \times 5 sampling dates). Prior to 176 analyses, we pooled the data from the five pitfall traps of each sampling, because soil and 177 178 vegetation characteristics were observed at the sampling site level. Trap content was sorted in the 179 laboratory and carabids identified to species level and assigned to trophic categories (herbivores 180 vs. predators). All material is preserved in the insect collections of the School of Agriculture of Ningxia University. 181 182 Vegetation and soil characteristics 183 At each sampling site, we set up one quadrat frame of 0.25 m² to record plant dry biomass (PB, 184 g/m²), cover (PC, % of soil covered by plants), density (PD, number of plants per m²), height 185 (PH, average, cm) and species diversity, expressed as richness (PSD). Near the quadrat frames 186 187 we collected samples of aboveground litter to measure litter dry mass (SL, g/m²) and samples of soil (10 cm depth) to measure soil moisture (SM, %) and bulk density (SBD, g/cm3). SM was 188 189 estimated using the thermo-gravimetric method also known as oven dry method (Majumdar, 2001): SM = $[(W_2-W_3)/(W_3-W_1)] \times 100$ where W_1 is the weight of the empty aluminum box (g); 190 191 W_2 is weight of the box + soil sample (g) and W_3 is the weight of the box and oven dry soil (g).
- 192 SBD was estimated using the ring knife method (Bi, Zou & Zhu, 2014), using the formula SBD
- 192 SDD was estimated using the ring kine method (B), Zou & Zhu, Zo14), using the formula SDL
- 193 = $(W_r \times 100)/(V_r \times (100 + SM))$ where W_r is the weight of the soil in the ring knife; V_r is the ring
- knife volume and SM is the soil moisture. We also measured soil temperature (ST, 10 cm depth)
- using a portable multiparametric probe TRS-II (Zhejiang Tuopu Instrument Co. Ltd. China;
- accuracy of ± 0.5 °C). Monthly mean values of humidity (Hum); precipitation (Prec) and



- 197 temperature (Temp) were recorded from the meteorological stations of each county. Range, mean and standard deviation for the aforementioned environmental variables are given in Table 198 199 S1. 200 201 Species characteristics We expressed functional diversity with reference to two aspects: dispersal power and body size. 202 For dispersal (FD-Movement), we used the following morphometric traits, under the assumption 203 that longer and more robust legs facilitate beetle movements on the ground: (1) length (from 204 apex to coxa) and (2) maximum width of metafemurs, (3) length of metatibiae, (4) length of 205 206 metatarsi and (5) presence of wing. For body size (FD-Size), we used: (1) width of the head, (2) pronotum maximum width and (3) pronotum maximum height. A ese traits were used to 207 compute a total functional diversity (FD-Total). Measurements were done using a digital caliper 208 (precision to 0.01 mm, Stainless Hardened). For species with more than 50 collected individuals, 209 210 we measured 50 specimens (14 species); for other species, we measured a variable number of 211 individuals depending on their abundance (11 species). 212 213 Data analysis We assessed the species richness using the individuals-based rarefaction method implemented in 214 the "iNEXT" library of R (Hsieh, Ma & Chao, 2016). The input matrix was based on species 215 abundances (total number of individuals of each sample site). 216 For each trait we calculated functional diversity indices using Rao's quadratic entropy, which 217 expresses the sum of the dissimilarities in the trait space among all possible pairs of species 218 219 weighted by species relative abundances (Rao, 1982; Botta-Dukát & Wilson, 2005). High functional divergence should indicate a high degree of niche differentiation (Mason et al., 2005). 220 To express functional diversity based on multiple traits, we calculated species dissimilarities 221 with the commonly used Gower distance (Pavoine et al., 2009; Laliberté & Legendre, 2010). 222 223 Calculations were done using the package "StatMatch" and the function "melodic" in R (de Bello et al., 2016). 224 Differences in species richness and functional diversity between the three grassland types were 225 tested using one-way Analyses of Variance (ANOVA, with type I of SS) followed by post hoc 226 227 Tukey tests. The effects of vegetation, soil and climate characteristics on beetles rarefied 228 richness and functional diversity were investigated using multiple linear regressions. To select 229 the best model, we used the Second-Order Akaike Information criterion (AICc) as recommended 230 by Burnham & Anderson (2002). The best model was that with the highest Akaike weight (Wi). The relative importance of a variable was assessed as the sum of the Akaike weights (Σ Wi) that 231 included the given variable. The lower the Wi for models that excluded a given variable, the 232 233 more important the variable (Burnham & Anderson, 2002). Analyses were done using the package "MuMIn" in R (Bartoń, 2018). 234
- The effects of vegetation, soil and climate characteristics on beetle community structure were investigated using Canonical Correspondence Analysis (CCA) with abundance data. This



237 technique was particularly appropriate to our data because it deals well with the double-zero problem which characterizes community compositional data (Legendre & Gallagher, 2001) and 238 does not try to display all variation in the data, but only the part that can be explained by the 239 constraints (Oksanen et al., 2015). Permutation tests (999 permutations) were ran to assess model 240 241 significance. The sum of the canonical eigenvalues was used as a measure of the variability in the response variables explained by predictors. The importance of predictors was preliminarily 242 assessed by using the variance inflation factor (VIF). A high VIF (>10) indicates that the 243 predictor is strongly dependent on others and does not carry independent information (Oksanen 244 et al., 2015). Analyses were conducted in R using the package "vegan" (Dixon, 2009; Oksanen et 245 al., 2015). We used the function "step" to determine the best model and the most important 246 predictors in each CCA. 247

248249

RESULTS

250 We collected a total of 6,873 individuals belonging to 25 carabid species (Table 1). Overall, 18 251 species were predators and 7 were herbivores (6 herbivores and 6 predators in the desert steppe, 4 herbivores and 14 predators in the typical steppe, and 4 herbivores and 15 predators in the 252 meadow steppe). Range, mean and standard deviation of rarefied richness, FD-Total, FD-253 Movement and FD-size are given in Table S2. The desert steppe was the grassland type with the 254 lowest values of rarefied species richness and the three measures of functional diversity, whereas 255 no significant differences were found between the meadow and the typical steppe (Fig. 3). 256 Climate predictors had strong effects on carabid species richness (Table 2). At least two climate 257 predictors were significant at regional scale and for each of the three grassland types. Humidity 258 (Hum) was positively related to species richness in desert and typical steppe. Precipitation (Prec) 259 had a positive effect on richness at regional scale and in the meadow steppe, but a negative effect 260 261 in the desert steppe. Temperature (Temp) had a positive effect on richness at regional scale, in the meadow and in the typical steppes. At regional scale bulk density (SBD) and soil temperature 262 (ST) had negative effects and litter dry mass (SL) a positive effect, whereas none of the soil 263 predictors was significant when the three grassland types were analyzed separately None of the 264 vegetation predictors were important to explain species richness in the meadow steppe. In the 265 266 typical steppe, plant dry biomass (PB), plant cover (PC) and plant density (PD) had positive 267 effects. Plant species diversity (PSD) had a negative effect in the desert steppe. At the regional scale, the most important vegetation predictor was PD, with a positive effect. 268 In all CCAs, all predictors had VIFs<10, meaning that they are independent (Table S3). At 269 270 regional scale (Fig. 4a, Table 3), the total variance explained by CCA was 22%, with the first two axes accounting for 55% of the explained variance. Constraints were significant (F = 8.81, p 271 =0.01) and all predictors were retained in the selection procedure (Table S4). However, the first 272 axis showed that PB, soil moisture (SM), ST and Temp were the most important variables, with 273 274 SM and ST acting in opposite directions. In the desert steppe community (Fig. 4b, Table 3), CCA explained 40% of total variance, with the first two axes accounting for 56% of the explained 275 276 variance. Constraints were not significant (F = 1.53, p = 0.07), with only humidity and



277 temperature being included in the final model after the selection procedure (Table S4). In the 278 typical steppe community (Fig. 4c, Table 3), CCA explained 37% of total variance, with the first two axes accounting for 68% of the explained variance. Constraints were significant (F = 9.74, p. 279 =0.01), and the final model included PB (as the most important variable), PC, PD, SL, Hum, 280 281 Prec and Temp (Table S4). In the meadow steppe community (Fig. 4d, Table 3), CCA explained 25% of total variance, with the first two axes accounting for 65% of the explained variance. 282 Constraints were significant (F = 3.38, p = 0.01), with PB, plant height (PH), SL, Hum and Temp 283 being retained in the final model. PH and Temp were the most important variables (Table S4). 284 Finally, the regional scale and the desert steppe biplots showed that the herbivorous Amara 285 species tended to cluster together and to be associated with ST (at the regional scale) and Hum 286 (in the desert) (Fig. 4a, 4b). In the typical steppe and meadow, there were fewer herbivores (4) 287 species) and they were scattered with no clear association with any driver (Fig. 4c, 4d). 288 289 The response of functional diversity to habitat characteristics (vegetation, soil, and climate) 290 differed among grassland types (Table 4). At regional scale, five predictors showed significant effects on FD-Total: PB (negative), PH (positive), SBD (negative), Prec and Temp (positive). In 291 the desert steppe only two predictors had significant effects: PD (negative) and SL (positive). In 292 the typical steppe, only the climate characteristics Hum and Temp were important and both had 293 positive effects. Similarly to the regional scale, in the meadow steppe, PB and PH had negative 294 and positive effects, respectively. PD and ST were also important predictors of meadow FD-295 Total, both with a positive effect. Within climate variables, Hum (negatively) and Prec 296 (positively) were the best predictors of FD-Total. The response of FD-Movement (Table S5) was 297 similar to that of FD-Total, except in the meadow steppe, where the effect of PD was 298 insignificant. At regional scale, four predictors showed significant effects on FD-Size (Table S6): 299 SBD (negatively) and PH, Hum and Temp (positively). In the desert steppe, three variables 300 influenced FD-Size: Hum (positively), Prec (negatively) and PSD (negatively). In the typical 301 steppe, Hum, Temp (positively) and SL (negatively) showed significant effects on FD-Size. In 302 303 the meadow steppe, important predictors where PD, PH, ST and Temp (all positively).

304 305

DISCUSSION

306 In accordance with our predictions, we found a positive relationship between carabid richness 307 and temperature. Temperature is known as a major predictor of species richness for several organisms (e.g., Allen, Brown & Gillooly, 2002; Peters et al., 2016; Yu et al., 2016), and it is an 308 important factor in the life-cycle of most carabid species (Thiele, 1977). The lack of any 309 310 influence of temperature on carabid richness in the desert steppe is consistent with our prediction that in this environment higher temperatures can be intolerable for most species. Moreover, in 311 this environment, differences between day and night temperatures are much more pronounced 312 than in the other grassland types, a source of variation which is not included in our measures, but 313 which might be important for carabids. 314 As expected, rainfall is also a major predictor of species richness at the regional scale and in the

As expected, rainfall is also a major predictor of species richness at the regional scale and in the meadow. By contrast, we found no effect in the typical steppe and a negative effect in the desert



317 steppe. Rainfall drives many ecological processes and may influence shelter sites and food resources used by carabids (Morecroft et al., 2004). The unexpected negative effect of rainfall 318 observed in the desert steppe may be due to two causes. First, it is possible that this environment 319 hosts species that are particularly adapted to arid conditions, and are therefore negatively 320 321 affected by rainfall. Second, our sampling area in the arid steppe is surrounded by many industries, and Thiele (1977) mentioned that carabids are highly vulnerable to polluted rainfall. 322 Thus, it is possible that rainfall was locally polluted by industry emissions that negatively 323 affected carabids richness, but we do not have data to test this hypothesis. 324 325 We found a strong positive effect of humidity on carabid species richness in desert and typical 326 steppes (which is an accordance with our hypothesis), but not in the meadow steppe and at regional scale. This lack of influence of humidity may be due to the fact that carabids have 327 variable preferences for humidity (Thiele, 1977). Our hypothesis that vegetation characteristics 328 329 should be positively related to carabid species richness was partially supported at regional scale 330 and in the typical steppe, but not in the desert and meadow steppes. In the typical steppe carabid species richness was positively related to plant biomass, cover and density. Rahman et al. (2015) 331 hypothesized that vegetation cover might accelerate the establishment of carabid communities 332 because it provides living space and modifies the microclimate to create a heterogeneous and 333 stratified microenvironment supporting different carabid species. We think that these 334 explanations can be also applied to plant biomass and density in our study. By contrast, plant 335 species diversity was not an important predictor of carabid species richness in our study system. 336 and, contrary our expectations, we found a negative relationship between plant and carabid 337 richness in the desert steppe. This result contrasts with previous studies reporting that a higher 338 339 plant species richness implies more diverse food resources, thus allowing the presence of species with different feeding preferences (Byers et al., 2000; Brose, 2003). However, this hypothesis 340 may be straightforward for phytophagous insects, whereas most carabid species are predators, so 341 they can be influenced by plant diversity only indirectly (for example, if a higher plant diversity 342 supports a higher diversity of prey). In fact, several studies report a lack of significant 343 relationships or even negative correlations between plant and arthropod diversity (see Zou et al., 344 2013). An increased plant diversity may actually promote an increase in herbivores; a higher 345 diversity and/or abundance of herbivores, however, can represent an increase in food sources and 346 347 niches for other predators (such as spiders), thus increasing the overall competition levels and consequently reducing the overall diversity of carabids. 348 Contrary to our expectation, plant height did not influence carabid species richness. Plant height 349 might enhance arthropod diversity by adding vertical strata in species niches, thus decreasing the 350 overall competition. The lack of significant effects suggests that this is not important for 351 carabids, probably because most of them are ground dwelling insects that do not separate their 352 niches using a differential vertical distribution. Contrary to our expectation, soil characteristics 353 were poor predictors of species richness in the three grassland types, but they were important at 354 355 the regional scale. Thus, we suspect that these contrasting results may be due to the low 356 variability in soil data sets within grasslands types. As expected, bulk density (which increases

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- 357 with soil compaction) was negatively related to species richness. The negative relationship between bulk density and carabid richness might be due to the fact that soil compaction makes 358 difficult egg laving and digging into the soil (see Magura, Tóthmérész & Elek, 2003). Soil 359 surface temperature was negatively related to species richness at the regional scale, which may 360 361 be explained by the fact that the highest temperatures recorded in our study system are those of the desert steppe, a grassland type with overall low carabid richness. Surprisingly, moisture did 362 not impact carabid richness in the three grassland types, nor at the regional scale, which suggests 363 that most of the species occurring in the study area are not hygrophilous. 364 In accordance with our hypothesis, we found that climatic factors, and in particular temperature. 365 366 were the most important variables in predicting the variability in carabid species composition. both at regional scale and for grassland types, except for the desert steppe, for which these 367 factors had a limiting explanatory power. Temperature has been reported as the most important 368 environmental factor for carabid communities (Eyre et al., 2005; Ernst & Buddle, 2015; Yu et 369 370 al., 2016), and our results support this conclusion. Previous research found that vegetation and soil characteristics are also important drivers of carabid species composition (Holmes, Boyce & 371 Reed, 1993; Perner & Malt, 2003; Schaffers et al., 2008; Gioria et al., 2010; Birkhofer et al., 372 2015; Liu et al., 2016; Vogels et al., 2017; Ng, et al., 2018b). As expected, we found that at 373 regional scale all vegetation and soil factors were important predictors of carabid community 374 composition. Particularly, we found that herbivorous species at the regional scale tend to be 375 positively influenced by soil temperature, a possible consequence of their smaller size (see Tseng 376 et al., 2018). 377 On the other hand, carabid communities of different grassland types are influenced by different 378 379 vegetation and soil characteristics. Some vegetation and soil characteristics are important for the typical and meadow steppe carabids, but not for desert steppe community. These results indicate 380 that different grassland types host different carabid communities that are influenced in different 381 ways by different vegetation and soil characteristics, and that virtually of them concur to 382 383 generate the overall patterns that emerge when the three grassland types are considered simultaneously. 384 Plant height has been reported as an important factor influencing carabid assemblages in 385 peatlands (Holmes, Boyce & Reed, 1993), whereas the possible influence of plant biomass 386 387 remained unknown. In our study, plant biomass and plant height were the only important vegetational characteristics for the meadow carabid community, whereas all vegetational 388 characteristics except plant height were important for the typical steppe. Thus, plant biomass was 389 the common best vegetation predictor for both these grassland types, suggesting that ecosystem 390 productivity (for which plant biomass may be a proxy) is an important driver of carabid 391 392 assemblage composition. Within soil characteristics, the aboveground litter was the only important predictor of species 393
- Within soil characteristics, the aboveground litter was the only important predictor of species composition in the typical and meadow steppes. Previously evidence of the role of the amount of litter in carabid species composition has been reported in forests (Magura, Tóthmérész & Elek,



396 2003; Vician et al., 2018) and our study indicates that this soil characteristic may be important also in other ecosystems. 397 None of the vegetation characteristics had an important influence in the carabid species 398 composition of the desert steppe, even though half of the species collected in this grassland type 399 400 were herbivores. These results are in contrast with a previous study in an arid region of the northwestern China (Liu et al., 2016), where height and cover of shrubs were important 401 predictors of predator species composition, and shrub cover and herbaceous species richness 402 were important predictors of herbivorous species richness. We can hypothesize that the lack of 403 influence of any vegetation and soil characteristics on the carabid composition in our desert 404 405 steppe may reflect the fact that most of these parameters have relatively similar values (as shown by their relatively small ranges and standard deviations) through the sampling sites, compared to 406 the typical and meadow steppes. In other words, the desert steppe was environmentally quite 407 homogeneous, and thus there was too little variation in vegetation and soil characteristics among 408 409 sampling sites to generate assemblages that can be differently influenced by these factors. Climate factors were the most important variables to explain the overall functional diversity at 410 regional scale, in the typical and in the meadow steppes, but not in the desert steppe, where no 411 climatic variable was identified to have a significant effect. Looking at the different components 412 of functional diversity in desert steppe, however, it is interesting to note that humidity and 413 temperature (positively), and precipitation (negatively) influenced FD-Size. This suggests that 414 higher humidity values tend to select large-sized species, possibly because an increase of 415 humidity is related to soft soil conditions, higher food resources and diverse shelter and 416 417 hibernation places necessary for large species, whereas increasing rainfall tends to select small-418 sized species that constitute the major part of the local species pool in this type of grassland. As regards the overall functional diversity, humidity acts in a contrasting way in the typical 419 steppe (positively) and in the meadow steppe (negatively), which explains the lack of effects at 420 the regional scale. We found parallel results with FD-Movement. This suggests that high 421 422 humidity favors species with homogenous traits and tends to select slow species in the meadow steppe, while favoring species with heterogenous traits and high mobile traits in typical steppe. 423 Precipitation was important in the meadow and at regional scale (but not in the typical steppe). 424 whereas temperature was important at regional scale and in the typical steppe (but not in the 425 426 meadow). Even close in term of climate factors, meadow and typical steppes harbor different functional species pool which respond differently to climate factors. This difference may be 427 attributed to the physiological needs of the different species pool, of each grassland. To our 428 knowledge, this study is the first to investigate the relation between carabid functional diversity 429 and climate factors in grasslands. 430 431 Plant biomass had a negative effect on FD-Total and FD-Movement, whereas plant height had a positive effect on all the three measures of functional diversity, both at regional scale and in the 432 meadow steppe. Thus, larger and more mobile species were associated with higher plants, while 433 434 small-sized and less mobile species were associated with higher amount of biomass. It is possible 435 that higher biomass produces a higher quantity of debris, which hinders the movement of larger



436 species, while situations in which there are high but sparser plants are favorable to large predators, for which higher plants may host a higher variety of prey. 437 Other vegetational characteristics impacted carabid functional diversity weakly. Plant density 438 had a positive influence on FD-Total in the meadow steppe (through body size traits), and a 439 440 negative influence in the desert steppe (though movement traits). Thus, in the desert steppe, denser vegetation limits the occurrence of more mobile species, whereas larger species are 441 favored by higher plant density in the meadow. It is possible that in the desert steppe, where 442 vegetation is more scattered, more sedentary species, which tend to remain near to patches of 443 high plant density (where they can find more easily food, shelter, water, lower temperatures and 444 445 less exposition to solar radiation), are favored. By contrast, in the more favorable and homogeneous conditions of the meadow, high plant density promotes the presence of large sized 446 species, possibly indicating that these species may find there a refuge against predators and/or 447 the preferred microclimate conditions supported by dense vegetation, as also found by Martins 448 449 da Silva et al. (2017). In line with our hypothesis, high bulk density (which was the only important soil predictor of 450 functional diversity at regional scale) decreased functional diversity. Other important soil 451 variables were soil litter (through FD-Movement) in desert steppe and temperature in meadow 452 steppe. Since in arid environments, most invertebrates are detritivorous, larger quantities of litter 453 may indicate a higher abundance of prey, which may attract more carabid species with higher 454 ability to move. A general trend is that warmer soils tend to select small sized species (Tseng et 455 al., 2018), but in soft soil, like in meadow steppe, the rise of soil temperature favor both larger 456 and high mobile species. This may be attributed to the fact that temperature moderates predation 457 458 effects (Chase, 1996). Thus, larger and higher mobile species will be selected at the expense of small-size species which can less compete during predation. 459

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CONCLUSIONS

Our study indicates that carabid community structure and functioning in grasslands are strongly influenced by climatic factors, and can be therefore particular sensitive to the ongoing climate change. We found, however, that responses of carabid communities to climate and other factors vary according to the grassland type, which warns against generalizations. Carabid responses to vegetation and soil characteristics also varied among grassland types, which indicates that management programs should be considered at grassland scale. Responses of carabid community in meadow steppe were close to that observed at regional scale, which means that the meadow steppe is the grassland with less constraints, whereas responses in desert steppe were very different from that at regional scale, which means that this type of grassland is that with the stronger constraints for carabids. Local habitat characteristics of the desert steppe seem to act as a strong filter favoring small-sized and less mobile species. Restrictive climatic conditions in desert steppe constitute a barrier for the occurrence of species and therefore strongly shape carabid species assemblages in this environment. Given the currently increasing aridification processes, we can hypothesize that in the future carabid communities will be progressively more



- similar to those of the desert steppe, and will be therefore represented by assemblages of fewer
- and generally smaller sized species, reinforcing the urgent need to put in place conservation
- 478 policies.

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Figure 1(on next page)

Study area and sampling sites

The inset in panel (a) shows the location of the study area in China. Panel (b) shows the 15 sampling points in desert steppe. Panel (c) shows the 45 samplings points in the three sectors of the meadow steppe (orange dots: sampling points in fire belts on mountain top; dark dots: sampling points in natural patches on mountain top; white dots: sampling points in the mountain bottom). Panel (d) shows the 30 sampling points in the two sectors of the meadow steppe (green dots: south-west side; blue dots: mountain bottom).

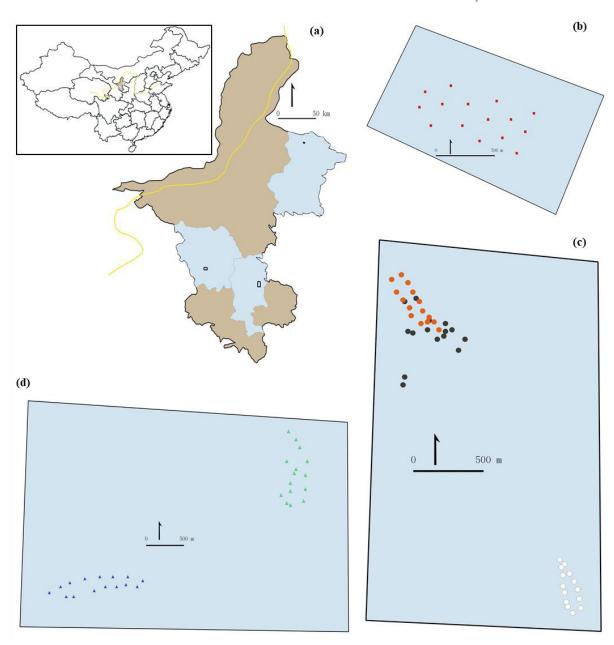




Figure 2(on next page)

The three types of grasslands investigated in this study

(a) desert steppe; (b) meadow steppe, (c) typical steppe

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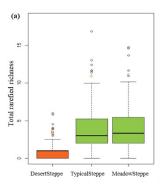


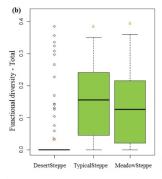
Carabid community structure

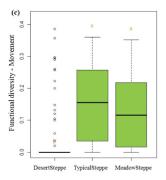
(a) total rarefied richness, (b) total functional diversity, (c) functional diversity for movement traits, (d) functional diversity for size traits in three different grasslands: desert, meadow, and typical steppes. Same letter/ color indicate non-significant differences according to Tukey tests after ANOVA. Number of sampled individuals: 6873 at regional level, 338 in the desert steppe, 4206 in the typical steppe and 2329 in the meadow steppe

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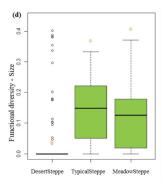


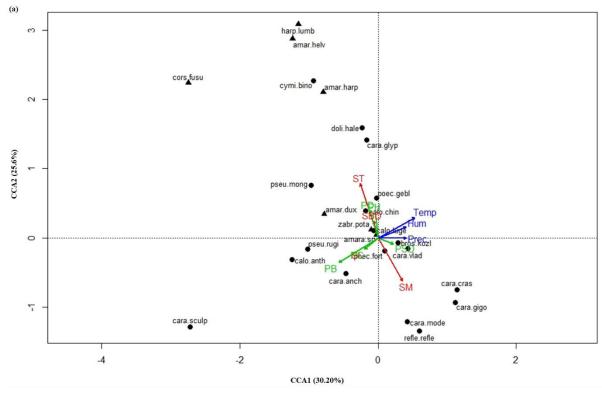


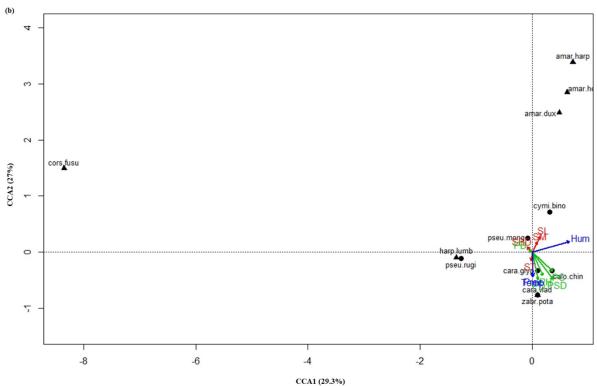
Figure 4(on next page)

Canonical Correspondence Analysis (CCA)

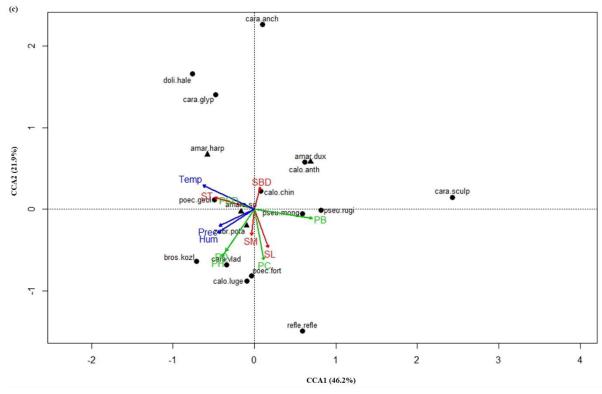
Plots showing relationships between species (● = predators, ▲ = herbivores; species abbreviations as in Table 1) and environmental variables (vegetation, green arrows. PB: Plant biomass, PC: Plant coverage, PD: Plant density, PH: Plant height, PSD: Plant species diversity; soil, red arrows: SBD: Bulk density, SL: Soil litter, SM: Soil moisture, ST: Soil temperature; and climate, blue arrows, Hum: Humidity, Prec: Precipitation, Temp: Temperature) at regional scale (a) and in the desert (b), typical (c) and meadow (d) steppes. See Table 1 for species names abbreviations

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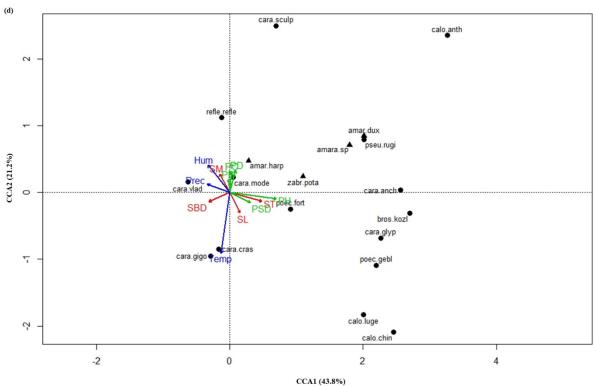




Table 1(on next page)

Carabid species, their trophic group (H: herbivores, P: predators) and abundances (total number of collected beetles in brackets).

Species name and trophic group	Species abbreviation	Regional scale (N=6873)	Grassland types Desert Steppe (N=338)	Typical Steppe (N=4206)	Meadow Steppe (N=2329)
Amara dux Tschitscherine, 1894. H	amar.dux	67	6	52	9
Amara harpaloides Dejean, 1828. H	amar.harp	11	7	3	1
Amara helva Tschitscherine, 1898. H	amar.helv	9	9	0	0
Amara sp. H	amara.sp	15	0	9	6
Broscus kozlovi Kryzhanovskij, 1995. P	bros.kozl	8	0	2	6
Calosoma anthrax Semenov, 1900. P	calo.anth	41	0	34	7
Calosoma chinense, Kirby, 1819. P	calo.chin	3	1	1	1
Calosoma lugens Chaudoir, 1869. P	calo.luge	11	0	9	2
Carabus anchocephalus Reitter, 1896. P	cara.anch	85	0	29	56
Carabus crassesculptus Kraatz, 1881. P	cara.cras	339	0	0	339
Carabus gigoloides Cavazzuti, 2000. P	cara.gigo	267	0	0	267
Carabus glyptoterus Fischer Von Waldheim, 1827. P	cara.glyp	886	252	587	47
Carabus modestulus Semenov, 1887. P	cara.mode	84	0	0	84
Carabus sculptipennis Chaudoir, 1877. P	cara.sculp	404	0	401	3
Carabus vladimirskyi Dejean, 1830. P	cara.vlad	2039	3	1212	824
Corsyra fusula Fischer Von Waldheim, 1820. H	cors.fusu	3	3	0	0
Cymindis binotata Fischer Von Waldheim, 1820. P	cymi.bino	19	19	0	0
Dolichus halensis Schaller, 1783. P	doli.hale	3	0	3	0
Harpalus lumbaris Mannerheim, 1825. H	harp.lumb	11	11	0	0
Poecillus fortipes Chaudoir, 1850. P	poec.fort	552	0	338	214
Poecillus gebleri Dejean, 1828. P	poec.gebl	1145	0	1134	11
Pseudotaphoxenus mongolicus (Jedlicka, 1953). P	pseu.mong	77	23	54	0
Pseudotaphoxenus rugupennis Faldermann, 1836. P	pseu.rugi	310	3	257	50
Reflexisphodrus reflexipennis Semenov, 1889. P	refle.refle	368	0	2	366
Zabrus potanini Semenov, 1889. H	zabr.pota	116	1	79	36



Table 2(on next page)

Results of multiple linear regressions between habitat characteristics and carabid rarefied richness at regional scale and for the three grassland types separately.

Model characteristics: d.f. = degree of freedom, logLik = Log-likehood, AICc = corrected Akaike Information Criterion, Δ AIC = delta AICc, Wi = Weight, r2 = coefficient of determination. Parameter estimates (\pm standard error), relative importance and *p-value* (in parentheses) are given for each predictor. ab indicates that the predictor is absent from the best model. Levels of significance: * = P<0.05, ** = P<0.01, *** = P<0.001. Predictors abbreviations: PB: Plant dry biomass, PC: Plant coverage, PD: Plant density, PH: Plant height, PSD: Plant species diversity (richness); SBD: Soil bulk density, SL: Soil litter, SM: Soil moisture, ST: Soil temperature; Hum: Humidity, Prec: Precipitation, Temp: Temperature.

		Dagianal asala	Grassland types					
		Regional scale	Desert steppe	Typical steppe	Meadow steppe			
	d.f.	11	5	7	7			
	logLik	-223.54	-20.80	-167.65	-99.15			
Model	AICc	469.79	53.32	349.86	213.21			
characteristics	ΔAIC	0.00	0.00	0.00	0.00			
	\mathbf{W}_{i}	0.06	0.04	0.03	0.01			
	r^2	0.31	0.54	0.35	0.44			
	PB	-0.05±0.03 (0.79; 0.088)	ab (0.18)	0.12 ±0.06* (0.64; 0.034)	-0.14 ±0.06* (0.61; 0.018)			
	PC	ab (0.43)	ab (0.30)	0.10±0.04* (0.90; 0.011)	ab (0.23)			
Vegetation	PD	0.05±0.02* (0.78; 0.033)	ab (0.47)	0.16±0.04*** (0.98; 0.000)	ab (0.42)			
	PH	ab (0.28)	ab (0.17)	ab (0.33)	ab (0.38)			
	PSD	0.04±0.03 (0.57; 0.123)	$-0.24 \pm 0.08** (0.79; 0.000)$	ab (0.25)	0.09±0.05 (0.42; 0.099)			
	SBD	-0.15 ±0.02*** (1; 0.002)	ab (0.20)	ab (0.43)	-0.10±0.045* (0.49; 0.041)			
G - 11	SL	0.10±0.28*** (0.94; 0.000)	ab (0.57)	ab (0.28)	ab (0.37)			
Soil	SM	ab (0.26)	ab (0.30)	ab (0.27)	ab (0.36)			
	ST	-0.10±0.03*** (1; 0.000)	ab (0.25)	ab (0.34)	ab (0.52)			
	Hum	0.05±0.03 (0.67; 0.103)	0.34±0.08*** (0.93; 0.000)	0.29±0.05*** (1; 0.000)	ab (0.38)			
Climate	Prec	0.12±0.03*** (1; 0.000)	-0.39±0.07*** (0.96; 0.000)	ab (0.48)	0.19±0.06*** (0.82; 0.001)			
	Temp	0.14±0.03*** (1; 0.000)	ab (0.24)	0.29±0.05*** (1; 0.000)	0.29±0.05*** (1; 0.000)			
	Intercept	1.48 ±0.02***(0.000)	0.45±0.07***	1.22 ±0.04***	1.27 ±0.05***			



Table 3(on next page)

Results of Canonical Correspondence Analysis. Percentage of variance explained and pvalue are given in parentheses.

Levels of significance: * = P<0.05, ** = P<0.01, *** = P<0.001. Predictors abbreviations: PB: Plant dry biomass, PC: Plant coverage, PD: Plant density, PH: Plant height, PSD: Plant species diversity (richness); SBD: Soil bulk density, SL: Soil litter, SM: Soil moisture, ST: Soil temperature; Hum: Humidity, Prec: Precipitation, Temp: Temperature.

1	

		Regional sca	ile		Grassland Desert step	J 1		Typical sto	eppe		Me	eadow step	pe
	Total Constrained	1.6	69 (22.27)		1	.68 (39.65)		1	.22(37.48)		1	.13(25.26)	
Eigenvalues	CCA1	0.51 (30	.20; 0.001)	***	0.54	(26.96; 0.2	46)	0.56 (4	6.15; 0.001	(1) ***	0.49 (4	3.76; 0.00	!) ***
	CCA2	0.43 (25	.59; 0.001)	***	0.49	(29.34; 0.2	41)	0.27 (2	1.85; 0.001	(1) ***	0.24 (2	1.19; 0.00	!) ***
	CCA3	0.31 (18	.34; 0.001)	***	0.30	(17.79; 0.7	(04)	0.22	(17.66; 0.0	197)	0.16 (14.59; 0.00	2) **
Biplot scores													
for constraining		CCA1	CCA2	CCA3	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3	CCA1	CCA2	CCA3
variables													
	PB	-0.568	-0.357	0.172	-0.062	0.039	-0.599	0.708	-0.109	0.008	-0.020	0.195	0.396
	PC	-0.202	-0.164	0.671	0.368	-0.334	-0.257	0.115	-0.618	0.318	0.028	0.310	0.245
Vegetation	PD	-0.124	0.400	0.646	0.105	-0.490	-0.192	-0.352	-0.511	-0.090	0.089	0.332	0.429
	PH	-0.043	0.368	0.674	0.192	-0.414	-0.278	-0.400	-0.583	0.160	0.697	-0.097	0.624
	PSD	0.217	-0.085	-0.006	0.372	-0.482	0.189	-0.167	0.062	-0.124	0.309	-0.152	-0.104
	SBD	-0.066	0.243	-0.394	-0.089	0.093	-0.296	0.073	0.271	0.004	-0.311	-0.139	-0.317
	SL	-0.198	-0.159	0.352	0.148	0.285	-0.068	0.168	-0.470	0.182	0.156	-0.306	-0.357
Soil	SM	0.354	-0.621	0.101	0.092	0.188	-0.187	-0.037	-0.317	0.004	-0.151	0.275	-0.102
	ST	-0.258	0.782	0.259	-0.022	-0.147	0.003	-0.487	0.143	0.005	0.482	-0.132	0.391
	Hum	0.403	0.159	-0.023	0.663	0.193	0.229	-0.455	-0.290	-0.742	-0.324	0.412	0.708
Climate	Prec	0.407	-0.004	0.269	0.019	-0.417	-0.129	-0.431	-0.207	-0.305	-0.340	0.126	0.749
	Temp	0.531	0.287	0.011	0.010	-0.439	-0.108	-0.633	0.295	0.562	-0.130	-0.913	-0.051



Table 4(on next page)

Results of multiple linear regressions between habitat characteristics and carabid total functional diversity (FD-Total) at regional scale and for the three grassland types separately.

Model characteristics: d.f. = degree of freedom, logLik = Log-likehood, AICc = corrected Akaike Information Criterion, Δ AIC = delta AICc, Wi = Weight, r2 = coefficient of determination. Parameter estimates (\pm standard error), relative importance and *p-value* (in parentheses) are given for each predictor. ab indicates that the predictor is absent from the best model. Levels of significance: * = P<0.05, ** = P<0.01, *** = P<0.001. Predictors abbreviations: PB: Plant dry biomass, PC: Plant coverage, PD: Plant density, PH: Plant height, PSD: Plant species diversity (richness); SBD: Soil bulk density, SL: Soil litter, SM: Soil moisture, ST: Soil temperature; Hum: Humidity, Prec: Precipitation, Temp: Temperature.

		Danianal acala	Grassland types				
		Regional scale	Desert Steppe	Typical Steppe	Meadow Steppe		
	d.f.	7	5	4	9		
	logLik	361.90	42.66	217.91	161.41		
M - 1 - 1 - 1 4 i - ti	AICc	-709.50	-73.60	-427.62	-303.35		
Model characteristics	ΔAIC	0.00	0.00	0.00	0.00		
	W_i	0.05	0.02	0.02	0.01		
	r^2	0.20	0.37	0.31	0.43		
	PB	-0.01 ±0.01** (0.87; 0.007)	ab (0.23)	ab (0.24)	-0.03 ±0.01** (0.71; 0.001)		
	PC	ab (0.41)	ab (0.21)	ab (0.25)	-0.01±0.01 (0.53; 0.121)		
Vegetation	PD	ab (0.25)	-0.05±0.02** (0.80; 0.002)	ab (0.27)	0.02±0.01* (0.61; 0.048)		
	PH	0.02±0.01*** (1; 0.000)	ab (0.21)	ab (0.25)	0.03 ±0.01** (0.84; 0.002)		
	PSD	ab (0.28)	ab (0.29)	ab (0.31)	ab (0.25)		
	SBD	-0.02±0.01*** (1; 0.000)	ab (0.18)	ab (0.28)	ab (0.24)		
C .: 1	SL	ab (0.26)	0.04±0.02* (0.68; 0.033)	ab (0.39)	ab (0.46)		
Soil	SM	ab (0.27)	ab (0.22)	ab (0.26)	ab (0.26)		
	ST	ab (0.31)	-0.03±0.01 (0.41; 0.052)	ab (0.52)	0.03 ±0.01** (0.99; 0.002)		
	Hum	ab (0.31)	ab (0.44)	0.04±0.01*** (1; 0.000)	-0.02 ±0.01* (0.42; 0.032)		
Climate	Prec	0.02±0.01*** (0.98; 0.000)	ab (0.53)	ab (0.31)	0.03 ±0.01*** (0.69; 0.001)		
	Temp	0.01±0.01* (0.75; 0.038)	ab (0.24)	0.05±0.01*** (1; 0.000)	ab (0.67)		
	Intercept	0.14 ±0.00***	0.06 ±0.01***	0.16 ±0.01***	0.14 ±0.01***		