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1 **Phylogeny and ecological processes influence grass coexistence at different spatial**
2 **scales within the steppe biome**

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17

18 **Author contribution statement** HL and CPO designed research; HL, GJ and ML
19 performed research; HL, RPF and DY analyzed data; HL wrote the initial manuscript, all
20 authors contributed to revisions.

21

22

23 **Abstract**

24 Phylogenetic analyses are essential for disentangling how environmental filtering and
25 competition determine species coexistence across spatial scales. Inner Mongolia steppe
26 has strong environmental gradients, but how the phylogenetic relatedness of co-occurring
27 species and phylogenetic signals of functional traits change across spatial scales remain
28 unclear. We investigated the phylogenetic structure of grass assemblages along
29 environmental gradients from regional to local scales, and measured functional traits
30 within assemblages. We compared phylogenetic signals of plant traits between the same
31 numbers of species randomly selected from the regional pool and species observed at the
32 local scale, did phylogenetic principal component analysis to infer the main factors
33 driving species coexistence, and examined the key plant trait-environment relationships
34 across the phylogeny to reveal ecological adaptation mechanisms. Regionally, grass
35 species were phylogenetically clustered with contrasting climate preferences. With
36 decreasing spatial scales, species richness declined, changing from phylogenetically
37 clustered to overdispersed, and phylogenetic signals of plant traits became weaker. At the
38 local scale, grass assemblages were structured by soil water content and neighbor density,
39 and the trait-environment relationships were less clear than those at the regional scale.
40 This study demonstrated that at smaller scales, co-occurring grass species in the steppe
41 tended to be more phylogenetically overdispersed, and that phylogenetic signals of plant
42 functional traits became weaker with increasing abiotic and biotic interactions. Our
43 findings contributed evidence for understanding species coexistence and maintenance at
44 scales spanning regional to local communities in the East Asia steppe biome.

45

46 **Keywords** Inner Mongolian steppe, phylogenetic niche conservatism, plant functional trait,
47 Poaceae, scale dependence.

48 **Introduction**

49 The phylogenetic structure of species coexistence in different spatial units (Kraft and
50 Ackerly 2010; Swenson et al. 2006; Trisos et al. 2014) or in different ecosystems
51 (Kunstler et al. 2012; Swenson 2013) is basic information that is essential for
52 understanding species assemblage patterns and the underlying processes (Weber et al.
53 2017). It is likely to change across spatial scales because the dominant processes that
54 structure communities are different when spatial scale shifts (Cavender-Bares et al. 2018;
55 Mouquet et al. 2012). When the spatial scale is sufficiently large, species are more likely
56 to be phylogenetically clustered (co-occurred species are more closely related than the
57 random expectation), due to larger species pools, geographic separation and climatic
58 restrictions (Swenson et al. 2007; Webb et al. 2002). Also the importance of species
59 interactions in determining the phylogenetic structure is relaxed at the large spatial scale
60 compared to small scale because plant individuals tend to interact only with their nearest
61 neighbors (Uriarte et al. 2010; Wiegand et al. 2017). At smaller spatial scales,
62 phylogenetic overdispersion (co-occurring species tend to be more distantly related than
63 the random expectation) or a random species assemblage might occur, and in some cases
64 phylogenetic clustering might also be observed such as the clustering of *C₄*
65 *Andropogoneae* in burned grasslands (Forrestel et al. 2014). Therefore, continuous
66 species sampling across the geographical gradients could help to elaborate phylogenetic
67 patterns in terms of different ecological processes and to determine the scale at which the
68 phylogenetic patterns shift.

69 However, the linkage between phylogenetic patterns and ecological processes is
70 complex, and strongly associates with species strategies in the trait-based context (Cadotte
71 2017; Gerhold et al. 2015; Mayfield and Levine 2010). For example, if closely related
72 species have similar fitness with advantageous functional traits, they can coexist through

73 competition and lead to phylogenetic clustering, which is often attributed to
74 environmental filtering (HilleRisLambers et al. 2012; Kunstler et al. 2012; Mayfield and
75 Levine 2010). Conversely, if critical functional traits that adapt to the environment and
76 influence distributions are convergent across co-occurring species, this environmental
77 filtering can also cause phylogenetic overdispersion, which often indicates competition
78 exclusion (Cavender Bares et al. 2004; Kraft et al. 2007). Furthermore, the relative
79 contributions of environmental filtering and competition are expected to be strongly scale-
80 dependent (Wiegand et al. 2017). Thus, it is fundamental to consider both phylogenetic
81 structures and functional traits in studying species assemblages across spatial scales.

82 Phylogeny reveals the past dispersal and evolutionary patterns (Donoghue 2008;
83 Swenson 2013; Wiens 2018), and studies that only consider ecological processes will lose
84 the historical information. Recent plant community studies on functional traits also
85 suggest that different phylogenetic structures might depend on whether the functional
86 traits of coexisting species are convergent or divergent (Wilcox et al. 2018; Zhang et al.
87 2018). On one hand, the determinate functional traits of coexisting species may be
88 phylogenetically conserved (closely related species are more similar, i.e. phylogenetic
89 niche conservatism, PNC) (Wiens and Graham 2005). On the other hand, these traits
90 could also arise through convergent evolution in unrelated groups (Webb et al. 2002).
91 Therefore, phylogenetic tests on the key functional traits in species assemblages (Pavoine
92 et al. 2011) can predict how different lineages respond differently to global changes, and
93 thus how new distribution patterns are formed (Edwards and Smith 2010). It can also
94 reveal more clearly the underlying species assemblage rules (Weber et al. 2017), and/or
95 even macroevolution patterns such as the role of diversification (Cavender-Bares et al.
96 2018; Gerhold et al. 2015) and dispersal (Wiens 2018).

97 To gain insights into the interplay of phylogenetic patterns, ecological processes and
98 functional traits on species coexistence, especially to integrate results across spatial scales,
99 we chose the Inner Mongolian steppe as our study object. It covers a large area, and is the
100 main component of Mid-Asian temperate grasslands, with gradually increasing altitude
101 and decreasing temperature and precipitation from east to west. The low (120 - 460 mm)
102 mean annual precipitation (MAP) in the steppe makes it important to explore species
103 distribution patterns in relation to restricted water availability. At the regional scale,
104 studies have reported productivity (Bai et al. 2008), biodiversity (Zhang 1998) and
105 species distribution (Pyankov et al. 2000) along climatic gradients, but no literature has
106 yet carried out phylogenetic analyses of plant ecophysiological traits and species
107 coexistence mechanisms in this steppe biome. However, such studies could not only test
108 the theories about how phylogeny and ecological processes structure assemblages, but
109 also are extremely important to understand this fragile biome, where species composition
110 might change under future climatic changes such as greater drought incidence.

111 We comprehensively sampled the grass species pool of the Inner Mongolian steppe,
112 investigating how species were filtered across different spatial scales. Here we refer to the
113 regional, intermediate and local scales by reference to the whole area of Inner Mongolia,
114 the administrative county and the field site scales, respectively (Fig. 1). We then selected
115 local habitats with contrasting soil water gradients, and directly measured
116 ecophysiological traits of all coexisting grasses, including plant functional traits related
117 with water and nutrient use, soil water and nitrogen content, and neighbor density. To
118 infer the main factors driving species coexistence in Poaceae assemblages, we used
119 phylogenetic principal component analysis (PPCA) and analyzed how the functional traits
120 associated with environmental gradients against the phylogenetic background. Our
121 hypotheses are: (H1) Phylogenetic structure of co-occurring species will be more

122 clustered at regional and intermediate spatial scales than that at local scale. (H2)
123 Phylogenetic signals in functional traits and environmental variables become weaker at
124 the local scale. (H3) Based on phylogenetic principal component analysis, both
125 environmental filtering and competition will affect species coexistence at the local scale.
126 (H4) Based on phylogenetic general linear models, the relationships between functional
127 traits and environmental variables persist across scales.

128

129 **Materials and methods**

130 **Study area**

131 The Inner Mongolian Autonomous Region (IMAR) in China covers an area of 1.2 million
132 km², of which 66% is natural grasslands. The Inner Mongolian steppe biome has a strong
133 east-west altitude (230~1400 m) and climatic gradients (Fig. 1). The mean annual
134 temperature (MAT) ranges from -1.7 to 8.6 °C, and the mean annual precipitation (MAP)
135 from 120 to 460 mm, ~70-80% of which coincides with peak temperature during the
136 growing season (May to September).

137 There are 88 counties in total in the IMAR, each with a fully documented species pool,
138 which allowed us to investigate species filtering into smaller areas. In the middle of the
139 steppe, we chose the Hunshandake sandland within the Zhenglan county for the local scale
140 study (Fig. 1). Our local field site is located in the Hunshandake sandland, where around
141 27 km² land area has been fenced since 2001 to exclude livestock for vegetation recovery
142 and environmental protection. Data for 1960~1999 from the local meteorological bureau
143 showed a temperate arid and semi-arid climate, with MAT, average January and average
144 July temperatures of 1.8°C, -17.9°C and 18.7°C, respectively. The MAP is 378 mm,
145 fluctuating from 150 to 450 mm, 64% of which concentrated in the growing season.

146 The four main habitat types at the local field site are moving dune, fixed dune, lowland
147 meadow and wetland. There are strong increasing gradients of soil water content, soil
148 nitrogen contents and species density in each habitat along the gradient from moving dune
149 to wetland ([Appendix S1](#)).

150

151 **Data collection at the regional scale**

152 We assembled three datasets for the Inner Mongolian grasses:

153 (1) Records of 265 Poaceae species from the Flora of Inner Mongolia (Editorial
154 Committee on Flora Intramongolica 1998), including culm height, leaf length and width,
155 flowering date, leaf type (flat and/or folded/rolled, use “folded” hereafter), and county-
156 scaled occurrences for each species ([Appendix S2 Table S1](#)). Folded leaf is an important
157 adaptation strategy of grass species to avoid drought and its occurrence differs among
158 grass subfamilies (Liu and Osborne 2014). The taxonomy was based on Grass Genera of
159 the World (Watson 1992 onwards). There are six subfamilies of Poaceae in Inner
160 Mongolia: the largest, Pooideae, accounted for nearly 80% of the total species, the second
161 and third largest subfamilies, Panicoideae and Chloridoideae, had 35 and 21 species,
162 respectively ([Appendix S3](#)).

163 (2) Geographical and climatic information for 88 counties of the IMAR for 1971~2000,
164 including temperature, precipitation, area and population for each county (China
165 Meteorological Data Sharing Service System 2005, Standard climate dataset for
166 international exchange on Chinese surface weather stations 1971-2000.
167 <http://data.cma.cn/site/index.html>; [Appendix S2 Table S2](#)). Based on the species
168 distribution table ([Appendix S2 Table S3](#)), we calculated species richness and proportions
169 of each subfamily/tribe for each county, and arithmetic means of the climatic values
170 associated with the county-scaled distribution for each species, including mean growing

171 season (May to September) temperature (MGT) and precipitation (MGP). We tested
172 phylogenetic structures of co-occurring species in each county (Appendix S2 Table S4).
173 (3) For each species in Inner Mongolia, we calculated species water requirement
174 (Editorial Committee on Flora Intramongolica 1998) (Appendix S2 Table S1). We
175 assigned a numerical score to each plant ecological tolerance describing water availability,
176 giving equal weighting to the extremes (Hydrophyte = 5, Helophyte = 4, Mesophyte = 3,
177 Xerophyte = 1), resulting in a continuous sequence of values for each species. These four
178 values were summarized as a range “water range” and a mean “water score” for each
179 species (Osborne and Freckleton 2009). This “water score” was positively related with
180 MGP (regional scale) and soil water content (local scale), supporting the consistency of
181 species water requirements across spatial scales (Appendix S1 Figure S2).

182

183 **Sampling and measurements at the local scale**

184 To investigate community structure in the Hunshandake sandland, we carried out field
185 surveys and measurements in July and August, 2010. First, three sites (each ~0.3 km²)
186 were chosen from each of the four habitats (moving dune, fixed dune, lowland meadow
187 and wetland), with 12 sites in total. At each site, we collected all distinguishable grass
188 species for identification. Second, we randomly sampled three individuals for each
189 species from each habitat, apart from two rare and one early season species, where only
190 two individuals were available. We sampled 147 individuals of 32 Poaceae species in total.

191 For each individual, we dug the soil from the surface down to 30 cm depth (30 cm
192 covers the main root distribution layer due to the shallow roots of most grass species),
193 measuring the water content of three layers (0~10, 10~20 and 20~30 cm) using a soil
194 moisture probe (ThetaKit type TK3; Delta-T Devices Ltd, Cambridge, UK), then took soil
195 samples separately. We then ground dried soil samples with a ball mill (Mixer Mill MM

196 200; Retsch, Haan, Germany), and measured total soil nitrogen through Kjeldahl
197 determination on an Auto Distillation Unit (Kejeltec™ 2200; FOSS, Denmark). To
198 quantify the biotic environment, we recorded relative species abundance (assessed by
199 Drude's scale), together with neighbor number (within a 30cm radius), distance to the
200 nearest neighbor and the height of the tallest neighbor.

201 Functional traits can explain and predict the dramatic variations in species abundances
202 and compositions (Adler et al. 2014), therefore we selected traits to reflect life history
203 strategies of each species, including plant growth (e.g. culm and leaf sizes, root depth),
204 resource acquisition (e.g. leaf nutrient concentration, stomatal pore area index) and abiotic
205 stress adaptation (e.g. folded leaf and midday water potential). We directly measured
206 culm height, leaf height, leaf length and width, and the number of living leaves per tiller,
207 and referenced root depths for each species from a previous study (Chen 1986), with five
208 missing species measured by completely excavating their roots in the field. During soil
209 moisture measurements, we took roots connected to the aboveground culms to ensure they
210 were from the same species. After carefully washing and sieving, we scanned a part of the
211 fine roots (diameter < 1mm) on a flatbed scanner (PhantomF60; Microtek, Shanghai,
212 China) to calculate specific root length (SRL).

213 From 12:00 to 14:00 on sunny days, we cut one or two young mature leaves at the
214 ligule for each individual to measure midday water potential using a psychrometer
215 (PSYPRO; Wescor, Utah, USA) with C-30 Sample Chambers. We calibrated the
216 psychrometer beforehand in an air-conditioned laboratory (25°C) with a series of standard
217 NaCl solutions. To keep the samples at a stable temperature (~25°C) under strong sunlight,
218 we used an insulated ice box with a thick towel separating ice packs and sample chambers.
219 We scanned leaf samples after measurements and imported both leaf and root images into
220 ImageJ (Abramoff et al. 2004) to obtain leaf area and root length (Kimura et al. 1999).

221 We calculated specific leaf area (SLA) and specific root length (SRL) after weighing the
222 oven dried (65°C, 24h) samples. We ground dried leaf samples using a ball mill
223 (Tissuelyser, Retsch, Qiagen GmbH, Germany), and determined leaf carbon and nitrogen
224 concentrations and stable isotope ratios using a stable isotope ratio mass spectrometer
225 (PDZ Europa 20-20; PDZ Europa Ltd, Cheshire, UK).

226 According to the leaf economic spectrum, photosynthetic capacity is one of the most
227 important axes in plant life history strategies, and is closely related with stomatal
228 conductance (Wright et al. 2004). For dried leaf samples, to estimate stomatal
229 conductance and photosynthetic potential, stomatal pore area index (SPI) was calculated
230 based on stomatal morphological traits, on the assumption that stomata would open
231 completely at their maximum photosynthetic rate (Franks and Beerling 2009). We made
232 dental putty (President Plus-light body, Coltène/Whaledent Ltd., Burgess Hill, West
233 Sussex, UK) impressions from the rehydrated leaf samples, and prepared microscope
234 slides of both adaxial and abaxial surfaces using nail polish imprints of the impressions.
235 We observed slides under an inverted microscope equipped with a digital camera (Leica
236 Laborlux S, Wetzlar, Germany) and an image analysis system (Leica Quantimet 500 Q
237 win software). From each peel, we randomly chose three images as replicates and
238 measured: guard cell length (GL) and width of the guard cell pair (SW), the stomatal
239 density (SD) and SPI (a dimensionless index of stomata pore area per lamina area), where
240 $SPI = SD \cdot GL^2$ (Sack et al. 2003).

241

242 **Phylogenetic trees**

243 We constructed phylogenetic trees for the 265 species (76 genera) of Poaceae in the Flora
244 of Inner Mongolia by integrating published phylogenies. First, we used a large
245 phylogenetic tree of over 3000 Poaceae species as a framework (Edwards et al. 2010),

246 then extracted 110 matched species from it after accounting for synonymies (Clayton
247 2002 onwards). Second, we comprehensively searched published phylogenies for
248 different genera and identified 60 more species (10 genera) (Appendix S3 Table S5). We
249 assembled all the 60 species (10 small trees) into the 110-species tree, using function
250 bind.tree in the R (<https://www.r-project.org>) package ape (Paradis et al. 2004), such that
251 a 170-species tree (species for which DNA sequence data were measured) was used in the
252 following phylogenetic tests (Appendix S3 Figure S4 tree A). Finally, we added 58 more
253 species by replacing their congeners' positions based on the phylogeny from Edwards et
254 al. (2010) using species name replacement (Appendix S3). Due to the potential
255 uncertainty of this 238-species tree, we only used it as a phylogenetic background (all
256 species in the region) in the sampling test (Table 1), and used the 170-species tree for all
257 the phylogenetic models. We also compared our phylogenetic tree with the latest
258 phylogenetic work on Poaceae (Soreng et al. 2017), finding that the two phylogenetic
259 trees were consistent with each other.

260 There were 88 species recorded in the Zhenglan county, and 32 of them were found in
261 the four habitats within the field sites. Corresponding phylogenetic trees of each of the 88
262 counties and the 32-species tree were extracted from the 170-species tree for the
263 phylogenetic analyses in each case (Appendix S3 Figure S4 tree BC).

264

265 **Statistical analysis**

266 Based on the strong climatic gradients in the steppe, we firstly analyzed the relationship
267 between species richness of different phylogenetic lineages and climatic conditions at the
268 regional scale, to see if different lineages have different climatic niches. For example, if a
269 dominant lineage occurred more in dry areas, it generally will lead to a phylogenetically

270 clustered pattern in dry areas due to niche conservatism (Wiens and Graham 2005). In this
271 case, it is simple and direct to link biogeographical with phylogenetic perspectives.

272 For hypothesis (H1), to analyze phylogenetic structure across spatial scales, net
273 relatedness index (NRI) was used as a standardized index based on the mean phylogenetic
274 distance (MPD) of species co-occurring in an assemblage. NRI is defined as $(\text{rndMPD} - \text{MPD}) / \text{sdrndMPD}$, where MPD was calculated from the phylogenetic tree of the regional
275 species pool, rndMPD and sdrndMPD were the average and standard deviation of MPDs
276 obtained from a null model by reshuffling the species tips 9999 times across the same
277 phylogenetic tree (Faith 1992). NRI indicates whether co-occurring species in one
278 assemblage are phylogenetically clustered ($\text{NRI} > 0$) or overdispersed ($\text{NRI} < 0$) (Webb et
279 al. 2002). Many studies have also calculated the nearest taxon index (NTI), but NTI
280 focuses on specific differences and is more sensitive to tree topology than NRI (Letcher
281 2010). Here we tried to compare among different trees and communities, thus only NRI
282 was calculated using the R package picante.

284 Phylogenetic signal measures the statistical dependence among species' trait values
285 based on their phylogenetic relationships. For binary variables, we used Fritz and Purvis's
286 D to calculate phylogenetic signals (Fritz and Purvis 2010). D measures the sum of
287 changes in estimated nodal values of a binary trait along edges in a phylogeny. To
288 calibrate for phylogenetic size, observed D is compared with simulated D values using the
289 same phylogeny under two models: Brownian threshold model and phylogenetic
290 randomness, in order to set points of 0 and 1, respectively. $D < 0$ indicates a highly
291 phylogenetically conserved trait, while $D > 1$ suggests a phylogenetically overdispersed
292 trait. Although species occurrence in each county (a binary variable, 1 and 0) is not a trait,
293 we interpreted its phylogenetic signal as a niche similarity measurement of local species
294 filtered from a larger species pool. If local species are more closely related than expected

295 by chance, it represents the influences of biogeographic or climatic heterogeneity on
296 species distributions and local diversification (Levin 1993).

297 For hypothesis (H2), to test ecophysiological traits, Pagel's λ was used based on a
298 Brownian model of quantitative trait evolution (Pagel 1999). The extent to which traits
299 evolve by random drift from a common ancestor gives a λ value between 0 and 1, where λ
300 = 1 indicates strong phylogenetic dependence, while $\lambda = 0$ implies no phylogenetic
301 dependence (Freckleton et al. 2002). Our interpretation of conservatism here is that high λ
302 values indicate that traits of closely related species are more similar than expected by
303 chance (Cooper et al. 2010). Both D and λ were calculated using the R package caper.

304 Furthermore, to test whether the λ values for quantitative traits differed significantly
305 between the 170 (regional) and 32 (local) species samples, we used a randomization
306 method by drawing 1000 random samples of 32 species from the 170-species phylogeny
307 and calculated the average λ value. The results were compared with those obtained from
308 the real assemblage. If the observed λ were lower than the average λ based on random
309 samples, we interpreted this as a scale-dependent decline in PNC at the local scale (32
310 species) compared with the regional scale (170 species).

311 For hypothesis (H3), to distinguish the driving factors in determining species
312 distributions within local assemblages, phylogenetic principal component analysis (PPCA)
313 was used (Felsenstein 1985). Data were log-transformed to meet the requirement of a
314 normal distribution. PPCA was carried out using the `phyl.pca` function in the R package
315 `phytools`. The variables for each of the 32 species in the Hunshandak sand were divided
316 into two groups, 10 environmental variables and 17 plant traits. Since the 32 species
317 scattered among the four habitats with a contrasting water gradient ([Appendix S1](#)), we
318 expected that both the driving environmental variables and plant intrinsic traits should be
319 related with water availability, absorption and consumption.

320 For hypothesis (H4), the key traits that distinguished species at the local scales
321 detected by PPCA were used to analyze plant-environment relationships. Phylogenetic
322 general linear models (PGLM) were used, based on the same functions in estimating λ
323 values in the R package caper. Currently PGLM is the best suitable method to test
324 correlations between trait pairs, other methods such as phylogenetic independent contrast
325 (PIC) is an extreme case of PGLM when phylogenetic signal λ is set to one.

326

327 **Results**

328 **H1: Phylogenetic structure of grass assemblages across spatial scales**

329 The three largest monophyletic lineages (subfamilies) of Poaceae in the Inner Mongolian
330 steppe showed distinct patterns along the regional climatic gradients from east to west
331 (Fig. 2). With increasing MGT, species richness of Pooideae dropped significantly, while
332 that of Chloridoideae and Panicoideae slightly increased (Fig. 2a). However, at higher
333 MGP, species richness of Chloridoideae decreased while that of Panicoideae increased,
334 and species richness of Pooideae varied widely (Fig. 2bc). Among the monophyletic
335 lineages in Pooideae, species richness of Aveneae and Stipeae had positive and negative
336 relationships with MGP, respectively (Fig. 2d), but all the others showed no associations.
337 General linear models with county area as an additive factor confirmed that sampling area
338 had no significant effects on these relationships.

339 Across spatial scales, the sampling distribution of the 170-species across the 238-
340 species showed a phylogenetically clustered trend ($\text{NRI} > 0$ and $D = 0.44$; Table 1). This
341 was mainly due to the lack of DNA sequence data for native Chinese species in several
342 large genera like Festuca, Poa, Roegneria and Stipa (Appendix S3 Figure S4 tree A). The
343 88-species pool of the Zhenglan county showed phylogenetic overdispersion against the
344 regional species pool represented by the 238-species tree ($\text{NRI} < 0$, $D = 0.84$; $P < 0.05$ for

345 D = 1), but phylogenetic clustering against the 170-species tree (NRI > 0, D > 1, [Table 1](#);
346 [Appendix S3 Figure S4 tree B](#)). However, 32 out of 88 counties in the IMAR were
347 phylogenetically clustered, most of these formed a contiguous cropland-grassland border
348 area, dominated by species from Paniceae, Eragrostideae, Triticeae, Bromeae and
349 Aveneae ([Appendix S2 Table S4](#)). The 32-species local assemblage in the Hunshandake
350 sandland also showed phylogenetically overdispersed patterns within either the 238- or
351 170-species tree (NRI < 0 ns, D values ns from 1, [Table 1](#); [Appendix S3 Figure S4 tree C](#)).
352 For the four habitats, species assemblages showed no patterns from NRI values, but were
353 phylogenetically overdispersed based on D values (all D ns from 1; [Table 1](#)).

354

355 **H2: Phylogenetic signals in plant traits and environmental variables across spatial** 356 **scales**

357 At the regional scale, significant phylogenetic signals were detected for most of the traits
358 ([Table 2](#)). Morphological traits, flowering start and end date showed λ values from 0.29 to
359 0.95 (P < 0.05 for both $\lambda = 0$ and 1), although leaf shape had λ around 0. Measures of
360 environmental niches (water score, MGT and MGP) showed phylogenetic signals (λ from
361 0.14 to 0.92; P < 0.05 for both $\lambda = 0$ and 1), with the exception of water range.

362 For the traits measured at both regional and local scales, random selection models of
363 32 species from the 170-species dataset showed λ values lower than those for the full
364 regional sample of species (except water range), but higher than those for the full local
365 species sample (except culm height) ([Table 2](#)). Of the traits measured only at the local
366 scale, specific root length (SRL), stomatal density, guard cell length, stomatal width and
367 leaf $\delta^{13}\text{C}$ showed phylogenetic signals. Meanwhile, no phylogenetic signals were detected
368 in either biotic or abiotic factors except the tallest neighbour ($\lambda = 0.48$, P < 0.01 for both λ
369 = 0 and 1), water score and SWC ($\lambda = 0.21$ and 0.39, but both P ns for $\lambda = 0$) ([Table 2](#)).

370

371 **H3: PPCA results at the local scale**

372 PPCA on environmental variables showed that local species distributions were separated
373 first by abiotic factors, and then biotic factors (Table 3a). Three principal components (PC)
374 together explained 77% of the variance. The first PC indicated soil nitrogen content (SNC)
375 of three soil layers and soil water content (SWC) of the 20-30cm soil layer (positive
376 loadings). The second PC showed neighbor density, relative abundance and tallest
377 neighbor (negative loadings). The third PC was tallest neighbor, SWC of the first layer
378 (positive loadings), and SNC of the first and second layers (negative loadings).

379 For the whole set of morphological traits, three PCs explained 68% of the variance,
380 indicating that leaf morphology, stomatal and rooting traits were three axes that
381 distinguished species (Table 3b). The first PC included leaf length and width, single leaf
382 area and mass (negative loadings). The second PC was mainly from stomatal width, SLA
383 (negative loadings) and root depth (positive loadings). The third PC corresponded to
384 guard cell length and width (negative loadings), and stomatal density (positive loadings).

385 Water-related traits were plotted across the phylogenetic tree (Appendix S4). It was
386 hard to discern patterns for culm and leaf size, except two extreme values in Stipeae.
387 However, larger but less dense stomata were seen in Pooideae compared with other
388 subfamilies (Appendix S4, column 1 to 4). Meanwhile, there was no phylogenetic signal
389 in leaf water potential, which was inversely associated with culm height (Appendix S4,
390 column 5). Both neighbor density and SWC showed high values in Poae and Aveneae,
391 without overall phylogenetic dependences (Appendix S4, column 6 and 7).

392

393 **H4: Phylogeny-based trait-environment relationships**

394 Phylogenetic models of trait-environment relationships did not show consistent patterns at
395 the regional and local scales (Table 4).

396 Regionally, culm height unexpectedly decreased with increasing MGT, although the
397 variance explained was low. Morphological traits had significant positive relationships
398 with both MGP and water score, and water score (habitat-scale measurements) was better
399 in explaining variance (Table 4a). Since all the regressions had low explanatory power,
400 and all λ values were greater than zero (0.16 to 0.80, $P < 0.05$ for both $\lambda = 0$ and 1), the
401 three morphological traits were not explained well by environmental variables, but
402 depended on phylogeny.

403 At the local scale, most models showed no patterns, only SWC explained variance in
404 culm height and SRL, and neighbor density explained variance in culm height and root
405 depth. The λ values of models were similar to those for the univariate analysis, and were
406 only higher for culm height and stomata related traits (Table 4b). Results were also
407 insensitive to whether SWC was averaged over the whole profile or taken from the
408 surface layer only. No trends were found for leaf traits with increasing SWC or neighbor
409 density, but there were significant positive relationships between culm height, SRL and
410 SWC (Fig. 3ab), and between culm height, root depth and neighbor density (Fig. 3cd).

411

412 Discussion

413 H1: Scale dependence within the steppe: from phylogenetic clustering to 414 overdispersion

415 At the regional scale, Poaceae species in the steppe biome indicated phylogenetically
416 clustered patterns, which was consistent with the global picture (Edwards and Smith 2010;
417 Hartley 1950; Liu et al. 2012; Visser et al. 2014), and patterns in other regions, such as
418 Australia (Hattersley 1992), North America (Taub 2000), Mongolia (Pyankov et al. 2000)

419 and South Africa (Visser et al. 2012). Pooideae had more species in low MGT areas with
420 an early flowering date, indicating its cold tolerant strategy (Vigeland et al. 2013).
421 Chloridoideae occurred more in drier habitats than Panicoideae, which was supported by
422 our previous findings that shorter height and narrower leaves, denser and smaller stomata,
423 and smaller seeds, better adapt Chloridoideae to low water availability (Liu et al. 2012).
424 Different climatic niches of the main grass lineages indicated phylogenetic niche
425 conservatism (Wiens and Graham 2005), emphasizing the importance of phylogeny in
426 understanding species geographical distributions. Specifically, the contrasting responses
427 to climatic gradients of different Poaceae lineages in our study might indicate their
428 different distribution patterns under future global changes (Edwards and Smith 2010).

429 With decreasing spatial scales, co-occurring species in the steppe ecosystem shifted
430 from phylogenetically clustered to overdispersed patterns (Table 1). Our results agreed
431 with other community-scale studies showing phylogenetic overdispersion, as in oak
432 communities across the US (Cavender-Bares et al. 2018) and English meadows
433 (Silvertown et al. 2006), but contrasted with the phylogenetic clustering observed for
434 other plant communities at small scales (Forrestel et al. 2014; Prinzing et al. 2008). One
435 possible explanation for the phylogenetic overdispersion of grass assemblages at smaller
436 scales in our results was interspecific interactions, such as competition, because at large
437 spatial scales, biotic interactions are less important in structuring communities, causing
438 overdispersion to diminish as reported in previous work on oaks across spatial scales
439 (Cavender-Bares et al. 2018). It was also notable that at intermediate scale of Zhenglan
440 and other counties, grass assemblages could be either phylogenetic overdispersed or
441 clustered depending on different species pools. This indicated the important role of
442 species pool in determining phylogenetic structures, and suggested that county could be
443 the spatial scale at which the phylogenetic pattern of grass assemblages started to shift.

444

445 **H2: Weaker phylogenetic signals in functional traits and environmental variables**

446 As expected, phylogenetic signals in the same traits tested at regional scale became
447 weaker at intermediate and local scales. The simulated random draw from the regional
448 dataset also produced higher λ values of these traits than the observed dataset, verifying a
449 scale-dependent decline in PNC at the local scale compared with the regional scale (Table
450 2). PNC is generally caused by stabilizing selection within the same climate zone or at the
451 regional scale (Donoghue 2008), but smaller spatial scales restricted not only the species
452 pool but also the trait variation. This tends to weaken the phylogenetic signals of traits,
453 either through the narrower phylogenetic range caused by environmental filtering, or the
454 tendency towards convergence caused by competitive exclusion, leading to the
455 phylogenetic overdispersion of co-occurring species (Webb et al. 2002). For example,
456 grass species have a wide global range of MAT (-20~40 °C) and MAP (10~810 mm), but
457 the narrow range of both MAT (-2~9 °C) and MAP (100~500 mm) in the Inner Mongolia
458 steppe constrained both co-occurring species and their trait variability.

459 Of the traits only measured at the local scale, we used a number of ecophysiological
460 traits that have not been commonly tested in previous studies on species coexistence.
461 However, the phylogenetic signals of these traits were very weak within habitats (Table 2).
462 The loss of phylogenetic signals is potentially due to: (1) lowered species richness at
463 smaller scales, where the phylogenetically overdispersed pattern will weaken the
464 statistical power to detect phylogenetic signals; (2) Other functional traits fluctuated over
465 time like leaf water potential, so that they might also be unrepresentative of long-term
466 species values for the phylogenetic tests; (3) The sensitivity of phylogenetic tests among
467 species could be reduced by using average values across the four habitats. Phenotypic
468 plasticity and the ability to extract limiting resources from the environment determine the

469 niche breadth of each species, and crucially affect interactions among and within species
470 (Genung et al. 2012). In our data, some species were exclusively in one habitat, indicating
471 strong, specific environmental adaptations, while others had wide niche breadths.
472 Therefore, phylogenetic niche conservatism in traits alone was insufficient to explain
473 species distribution, and environmental factors had to be added at the small spatial scales
474 (Wiegand et al. 2017).

475 However, for traits that still retained phylogenetic signals at smaller scales, the
476 divergences among major lineages might have contributed to species coexistence, since
477 our previous work found that separate phylogenetic tests on the two largest C₄ subfamilies
478 would weaken the strong phylogenetic signals for the whole dataset (Liu et al. 2012). In
479 this study, leaf $\delta^{13}\text{C}$ had strong phylogenetic signals due to the large difference in CO₂
480 discrimination between C₃ and C₄ species (Farquhar et al. 1989), and the clustering of C₄
481 photosynthesis into particular lineages (Grass Phylogeny Working Group II 2012; Sage
482 and Monson 1999).

483

484 **H3: Environmental drivers for species assemblage at local scales**

485 The SWC and SNC in deeper soil layers were the best predictors of species distribution
486 across the four habitats, suggesting that water and nitrogen at depth are most important for
487 sorting species in semiarid steppes (Sala et al. 1992), in agreement with previous studies
488 in the same area of Inner Mongolia based on soil water and nutrient measurements for 102
489 communities (Song and Guo 2007). Environmental filtering could sort species into
490 different niches, increase species coexistence through the complementary use of water and
491 nutrient resources (Cardinale 2011). The complementarity is also related to neighbor-
492 related indices and leaf morphology in our data, emphasizing the importance of
493 competition intensity. Phylogenetic overdispersion of grass species at the local scale was

494 confirmed by niche complementarity of species in the same genus using different
495 strategies to cope with neighbors (Gubsch et al. 2011). For example, in the wetland,
496 *Puccinellia macranthera* has a very dense population and tall culms in or around water;
497 but its congener, *Puccinellia hauptiana*, is tiny and dispersed near water margins. Unlike
498 plant trait hierarchy-driven interactions in tree communities (Kunstler et al. 2012), we
499 argue that strong correlations between biotic and abiotic factors, as well as trait variation
500 are all involved in differentiating niche gradients in this semi-arid region (Table 3).

501

502 **H4: Weaker functional trait-environment relationships**

503 Regionally, trait-environment relationships were influenced more by phylogenetic
504 background than the same tests both at the global (Liu et al. 2012) and the intermediate
505 scales (Table 4). This scale dependence supported the idea that phylogeny and
506 environment both play roles in species distribution (Webb et al. 2002). Within the region,
507 morphological traits correlated better with water availability than MGT/MGP, suggesting
508 that species growth was associated more closely with habitat wetness than regional
509 precipitation (Appendix S1). Meanwhile, these positive trait-environment relationships
510 became weaker at smaller spatial scales, implying that more environmental factors must
511 be invoked to explain variance in plant traits (Table 4). Specifically, positive relationships
512 between culm height and SWC suggested more aboveground growth with more soil water,
513 while SRL increased with SWC indicated that with more water availability, species
514 tended to use a resource acquisitive strategy with a high root surface area per unit
515 investment (Eissenstat 1991). Culm height and root depth increased with neighbor density
516 showing the importance of above- and below-ground competition in understanding
517 species coexistence (Kraft et al. 2015).

518

519 **Conclusions**

520 This study has demonstrated that co-occurring grass species in the steppe biome tend to
521 be more phylogenetically overdispersed, and phylogenetic signals of plant
522 ecophysiological traits become weaker at smaller spatial scales. At the local scale, abiotic
523 and biotic interactions are tested to be more important than the regional scale, at which
524 scale other processes such as dispersal limitation might be more determinant. Our findings
525 contribute to the understanding of species coexistence and maintenance at scales spanning
526 regional to local communities in the East Asia steppe biome.

527

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536

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538

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721

722 **Electronic supplementary material** The online version of this article contains
723 supplementary material, which is available to authorized users.

724

725 **Appendix S1** Environmental gradients and the consistency of water availability across
726 spatial scales

727 **Appendix S2** Poaceae species list with morphological traits, habitat, biogeographic data
728 and species occurrence in the 88 counties in Inner Mongolia. County-level phylogenetic
729 signals and phylogenetic structure were also reported

730 **Appendix S3** A phylogenetic tree of 238 Poaceae species in Inner Mongolia, showing
731 species filtered across spatial scales

732 **Appendix S4** A phylogenetic tree of 32 Poaceae species at the local scale (Hunshandake
733 sandland), with species abundance in four habitats and main variables mapped across the
734 tree based on PPCA results

735

736 **Tables**

737 **Table 1** Phylogenetic analyses for grass species occurrences filtered from the regional
 738 (238 and 170 species pools) to the intermediate (88 species) and then local (32 species)
 739 scales in the Inner Mongolian steppe. The 238-species phylogenetic tree is an overall
 740 species pool; it merged the 170-species tree that was strictly constructed based on DNA
 741 data and another 58 congeners. Sample size (n), D and P values for D = 0 and 1 are
 742 reported. Level of significance: * P < 0.05; ** P < 0.01; *** P < 0.001; ns, not significant.
 743 SR, species richness; NRI, net relatedness index. C, phylogenetically clustered; O,
 744 phylogenetically overdispersed

	SR	NRI	P	Pattern	n	D	P _(D=0)	P _(D=1)	Pattern
Filtered from 238 spp. tree									
170 spp. in the region	170	0.63	ns	C	238	0.44	***	***	C
88 spp. in the county	88	-1.93	ns	O	238	0.84	***	*	O
32 spp. in the local field	32	-4.82	ns	O	238	1.03	***	ns	O
Filtered from 170 spp. tree									
88 spp. in the county	88	0.10	ns	C	170	1.12	***	ns	O
32 spp. in the local field	32	-2.03	ns	O	170	0.70	*	ns	O
Filtered from 32 spp. tree									
5 spp. in the moving dune	5	-1.07	ns	O	32	1.20	***	ns	O
10 spp. in the fixed dune	10	0.04	ns	C	32	1.28	***	ns	O
21 spp. in the meadow	21	-1.26	ns	O	32	0.88	*	ns	O
12 spp. in the wetland	12	2.14	ns	C	32	0.77	*	ns	O

746 **Table 2** Phylogenetic signals in plant functional traits, abiotic and biotic environmental
747 variables for grasses in the Inner Mongolian steppe at both regional and local scales.
748 Random selection models give the mean \pm SD of λ values based on 1000 random
749 selections of 32 species from the regional dataset. Data are natural logged in tests except
750 those with †. Sample size (n), λ and P values for both $\lambda = 0$ and 1 are reported. Level of
751 significance: * P < 0.05; ** P < 0.01; *** P < 0.001; ns, not significant. SLA, specific
752 leaf area; SRL, specific root length; DNN, distance to the nearest neighbor; MGT, mean
753 growing season (May to September) temperature; MGP, mean growing season
754 precipitation

	Regional scale				Random selection models	Local scale (n = 32)		
	n	λ	P ($\lambda = 0$)	P ($\lambda = 1$)	λ	λ	P ($\lambda = 0$)	P ($\lambda = 1$)
Culm height (cm)	166	.83	***	***	.37 \pm .01	.51	**	**
Leaf length (cm)	159	.95	***	***	.48 \pm .01	.36	ns	***
Leaf width (mm)	154	.78	***	***	.56 \pm .01	.00	ns	***
Leaf mass (g)						.07	ns	***
Leaf number per tiller						.00	ns	***
SLA (cm ² g ⁻¹)						.19	ns	***
Root depth (cm)						.13	ns	***
SRL (cm g ⁻¹)						.41	*	***
Flat leaf (%) †	127	.39	ns	ns		.00	ns	***
Folded leaf (%) †	75	.43	ns	ns		.14	ns	***
Flowering start †	135	.29	***	***	.18 \pm .01	.00	ns	*
Flowering end †	135	.50	***	***	.43 \pm .01	.34	ns	*
Leaf nitrogen content (%)						.26	ns	***
Leaf $\delta^{15}\text{N}$ (‰)						.00	ns	***
Leaf carbon content (%)						.23	ns	***
Leaf $\delta^{13}\text{C}$ (‰)						.78	***	ns
Leaf water potential (MPa)						.12	ns	***
Stomatal density (mm ⁻²)						.46	***	***
Guard cell length (μm)						.56	***	***
Stomatal width (μm)						.43	*	***

Stomatal pore index						.14	ns	***
Water range	166	.00	ns	***	.09±.01	.00	ns	***
Water score	166	.92	***	***	.31±.01	.21	ns	***
MGT (°C)	165	.24	**	***	.12±.01	.00	ns	***
MGP (mm y ⁻¹)	165	.14	*	***	.11±.01	.00	ns	***
Soil water content (%)						.39	ns	***
Soil nitrogen content (%)						.00	ns	***
Relative abundance						.00	ns	***
Neighbour density (m ⁻²)						.09	ns	***
DNN (cm)						.15	ns	***
Tallest neighbour (cm)						.48	**	***

756 **Table 3** Principal component (PC) loadings for phylogenetic PCA (PPCA) on (a)
 757 environmental variables and (b) plant functional traits of grasses at the local scale
 758 (Hunshandak sandland). SWC1-2-3, soil water content from 0-10, 10-20, 20-30 cm layers;
 759 SNC1-2-3, soil nitrogen content from 0-10, 10-20, 20-30 cm layers; ND, neighbour
 760 density; RA, relative abundance; TN, tallest neighbour; NN, nearest neighbour distance;
 761 LL, leaf length; LA, leaf area; LM, leaf mass; LW, leaf width; SW, stomatal width; RD,
 762 root depth; LC, leaf carbon content; GL, guard cell length; SD, stomatal density. For each
 763 PC, the first four variables with highest loadings are in bold

(a) PPCA on environmental variables				(b) PPCA on morphological traits			
Variable	PC1	PC2	PC3	Variable	PC1	PC2	PC3
n = 10				n = 17			
SNC3	0.886	0.137	0.226	LL	-0.957	0.108	-0.064
SNC2	0.81	0.174	0.418	LA	-0.947	0.01	-0.095
SNC1	0.803	-0.122	0.435	LM	-0.932	0.193	-0.123
SWC3	0.752	0.165	-0.353	LW	-0.891	-0.3	0.105
ND	0.478	-0.788	0.05	Abxial SW	-0.185	-0.8	-0.396
RA	0.09	-0.774	-0.114	RD	-0.425	0.751	-0.142
TN	0.201	-0.547	-0.619	SLA	0.377	-0.659	0.199
NN	-0.581	0.533	0.006	LC	-0.435	-0.581	0.001
SWC1	0.553	0.468	-0.546	Abxial GL	-0.104	-0.149	-0.876
SWC2	0.722	0.442	-0.286	Adxial SD	-0.681	0.072	0.595
				Adxial GL	-0.516	-0.155	-0.468
				Adxial SW	-0.185	-0.8	-0.396
Total	40.92	23.09	13.18		38.74	18.49	10.44
variance (%)							
Cumulative	40.92	64.01	77.19		38.74	57.23	67.67
variance (%)							

765 **Table 4** Phylogenetic general linear models (PGLM) of relationships between plant
766 functional traits and environmental variables for grasses in (a) the whole Inner Mongolia
767 region and (b) the local scale (Hunshandak sandland). Sample size (n), F, P and λ values,
768 slopes and R^2 are listed. All data are natural-logged for standardization. Slopes and F
769 values with significant fits are in bold. CH, culm height; LL, leaf length; LW, leaf width;
770 water, water score; SWC, soil water content; ND, neighbor density; SNC, soil nitrogen
771 content; LM, leaf mass; LA, leaf area; RD, root depth; GL, guard cell length; SW, stomatal
772 width

(a) Regional scale	n	λ	$P_{(\lambda=0)}$	$P_{(\lambda=1)}$	F^P	slope	R^2
CH ~ MGT	161	.18	*	***	7.9^{**}	-1.43	.04
LL ~ MGT	155	.77	***	***	1.25 ^{ns}	-.66	.002
LW ~ MGT	149	.47	*	***	.59 ^{ns}	-.59	.003
CH ~ MGP	161	.16	*	***	1.88^{**}	.50	.058
LL ~ MGP	155	.73	***	***	5.08[*]	.41	.026
LW ~ MGP	149	.42	**	***	8.35^{**}	.65	.047
CH ~ water	162	.43	*	***	2.63^{***}	.39	.11
LL ~ water	155	.80	***	***	22.66^{***}	.50	.12
LW ~ water	151	.48	*	***	42.80^{***}	.76	.22

773

(b) Local scale	n	λ	P		F^P		
			($\lambda=0$)	($\lambda=1$)	SWC	ND	SNC
CH ~ SWC+ND+SNC	32	.63	**	**	4.30[*]	6.22^{**}	1.64 ^{ns}
LL ~ SWC+ND+SNC	32	.35	ns	***	.01 ^{ns}	.52 ^{ns}	.04 ^{ns}
LW ~ SWC+ND+SNC	32	.00	ns	***	.81 ^{ns}	.05 ^{ns}	.15 ^{ns}
LM ~ SWC+ND+SNC	32	.00	ns	***	.01 ^{ns}	1.66 ^{ns}	.01 ^{ns}
LA ~ SWC+ND+SNC	32	.00	ns	***	.17 ^{ns}	.92 ^{ns}	.00 ^{ns}
SLA ~ SWC+ND+SNC	32	.00	ns	***	.56 ^{ns}	2.76 ^{ns}	.09 ^{ns}
RD ~ SWC+ND+SNC	32	.00	ns	***	1.64 ^{ns}	4.20[*]	.49 ^{ns}
SRL ~ SWC+ND+SNC	32	.37	ns	***	7.78^{**}	.16 ^{ns}	2.06 ^{ns}
SD ~ SWC+ND+SNC	32	.45	**	***	.99 ^{ns}	.03 ^{ns}	.04 ^{ns}
GL ~ SWC+ND+SNC	32	.66	***	***	1.68 ^{ns}	.37 ^{ns}	3.19 ^{ns}
SW ~ SWC+ND+SNC	32	.58	**	***	.08 ^{ns}	3.95 ^{ns}	.17 ^{ns}

774

775 **Figure legends**

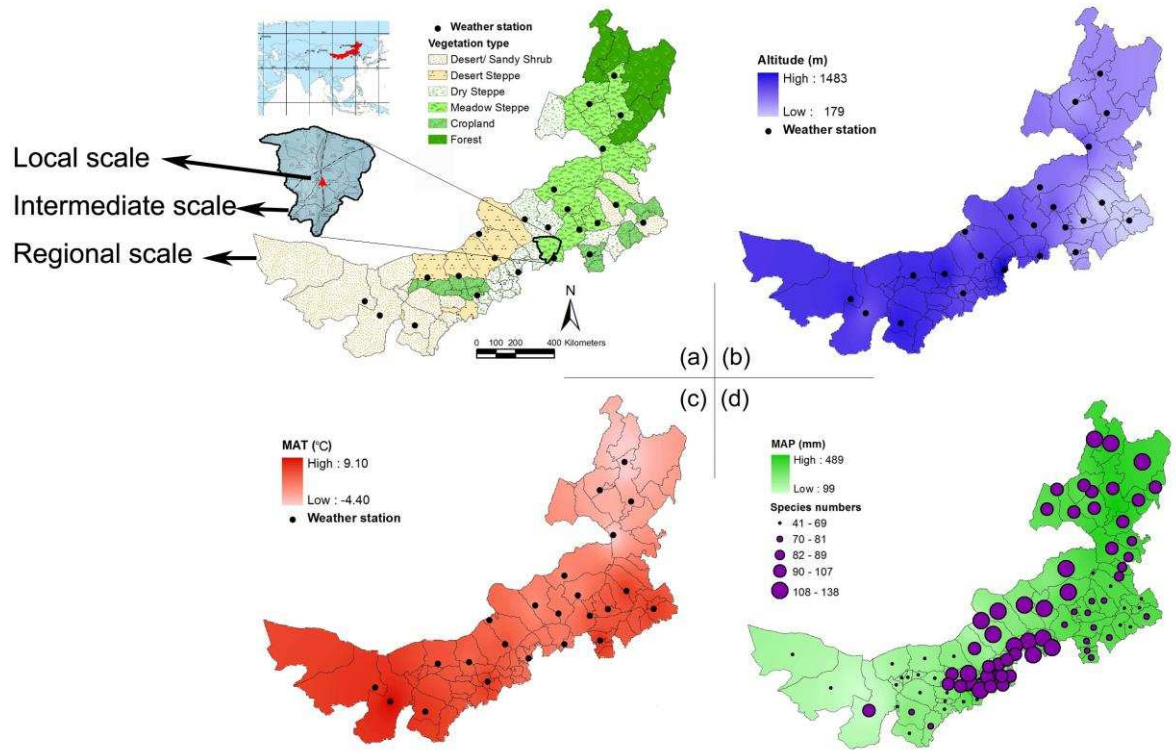
776 **Fig. 1** Map of the Inner Mongolian Autonomous Region (IMAR), China, showing spatial
777 and environmental gradients. (a) Main vegetation types of each county in IMAR,
778 intermediate (Zhenglan county) and local field site (Hunshandak sandland, the red triangle)
779 are labeled. (b) Altitude, (c) mean annual temperature (MAT), and (d) mean annual
780 precipitation (MAP) and grass species richness of each county across IMAR. See [Appendix](#)
781 [S1](#) for detailed environmental data. This figure is available in color in the online version of
782 the journal

783

784 **Fig. 2** Species richness of different grass lineages along the mean annual growth (a)
785 temperature and (b-c) precipitation gradients. Panel (b) is enlarged to show (c)
786 Chloridoideae and Panicoideae, and (d) tribes in Pooideae. In (d), Aveneae and Stipeae are
787 the only two of eight tribes in Pooideae that have significant regressions. In (a): Pooideae
788 (triangles), $y = -7.7 \cdot x + 189.8$, $F_{1,86} = 48.9$, $R^2 = 0.36^{***}$. In (b, c): Chloridoideae (black
789 dots), $y = -0.02 \cdot x + 14.0$, $F_{1,86} = 16.1$, $R^2 = 0.15^{***}$; Panicoideae (white dots), $y = 0.03 \cdot x +$
790 9.2 , $F_{1,86} = 4.4$, $R^2 = 0.31^{***}$. In (d): Aveneae (white squares) $y = 0.03 \cdot x + 4.6$, $F_{1,86} = 24.9$, R^2
791 $= 0.22^{***}$; and Stipeae (black squares), $y = -0.03 \cdot x + 17.2$, $F_{1,86} = 58.3$, $R^2 = 0.40^{***}$

792

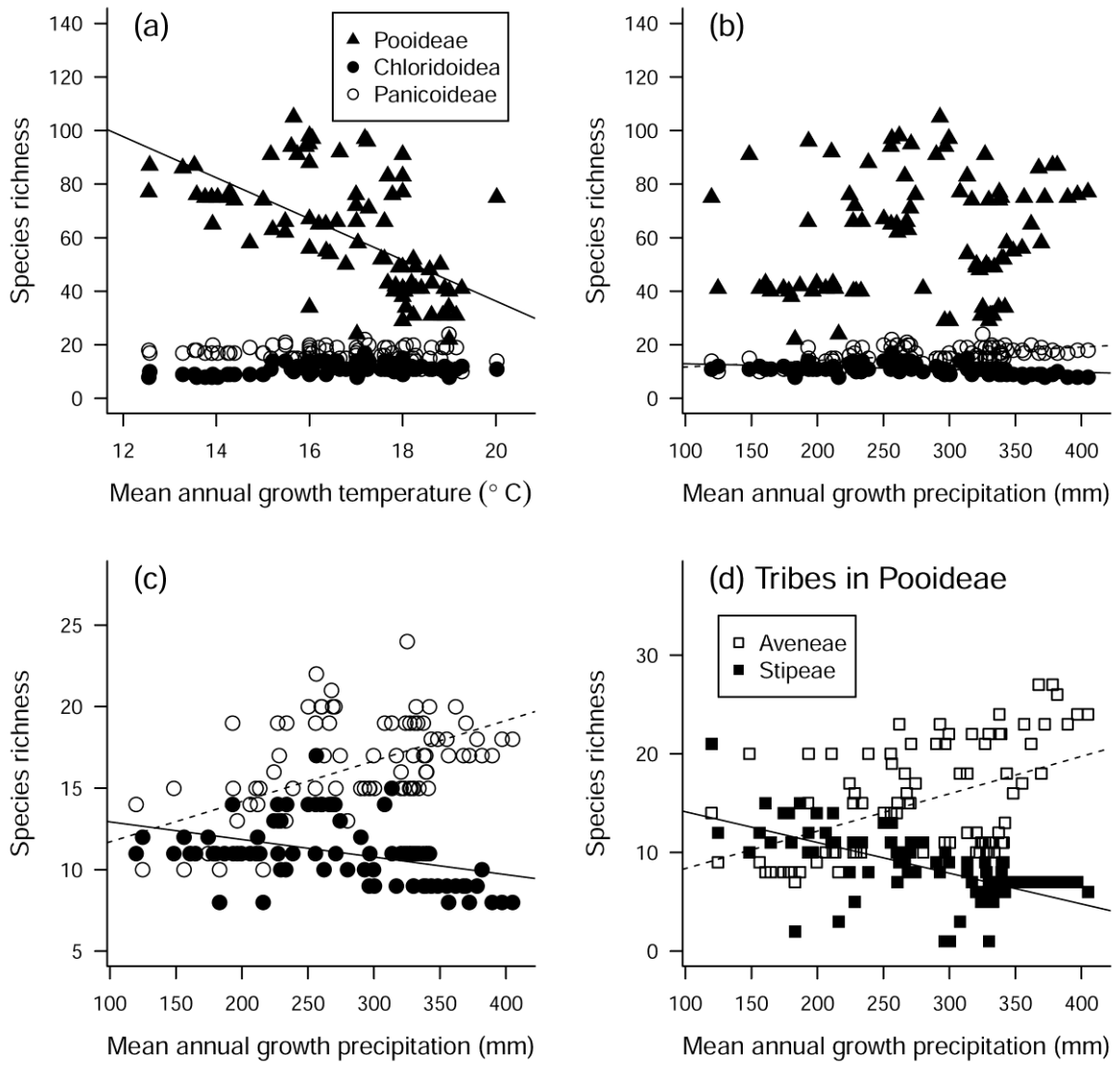
793 **Fig. 3** Relationships between plant functional traits and environmental factors based on the
794 models in Table 4. (a) culm height and (b) specific root length with soil water content; (c)
795 culm height and (d) root depth with neighbour density. Data are mean \pm SD. Subfamilies
796 are Pooideae (black dot), Panicoideae (white dot), Chloridoideae (white square) and
797 Arundinoideae (white triangle). Significant regressions based on PGLMs are (a): $y = 0.4 \cdot x$
798 $+ 2.6$, $F_{1,30} = 3.2$, $R^2 = 0.07^{ns}$; (b): $y = 0.4 \cdot x + 3.2$, $F_{1,30} = 7.9$, $R^2 = 0.18^{**}$; (c): $y = 0.3 \cdot x + 2.0$,
799 $F_{1,30} = 6.9$, $R^2 = 0.16^*$; and (d): $y = 0.29 \cdot x + 1.6$, $F_{1,30} = 3.7$, $R^2 = 0.08^*$



800

801 **Fig. 1**

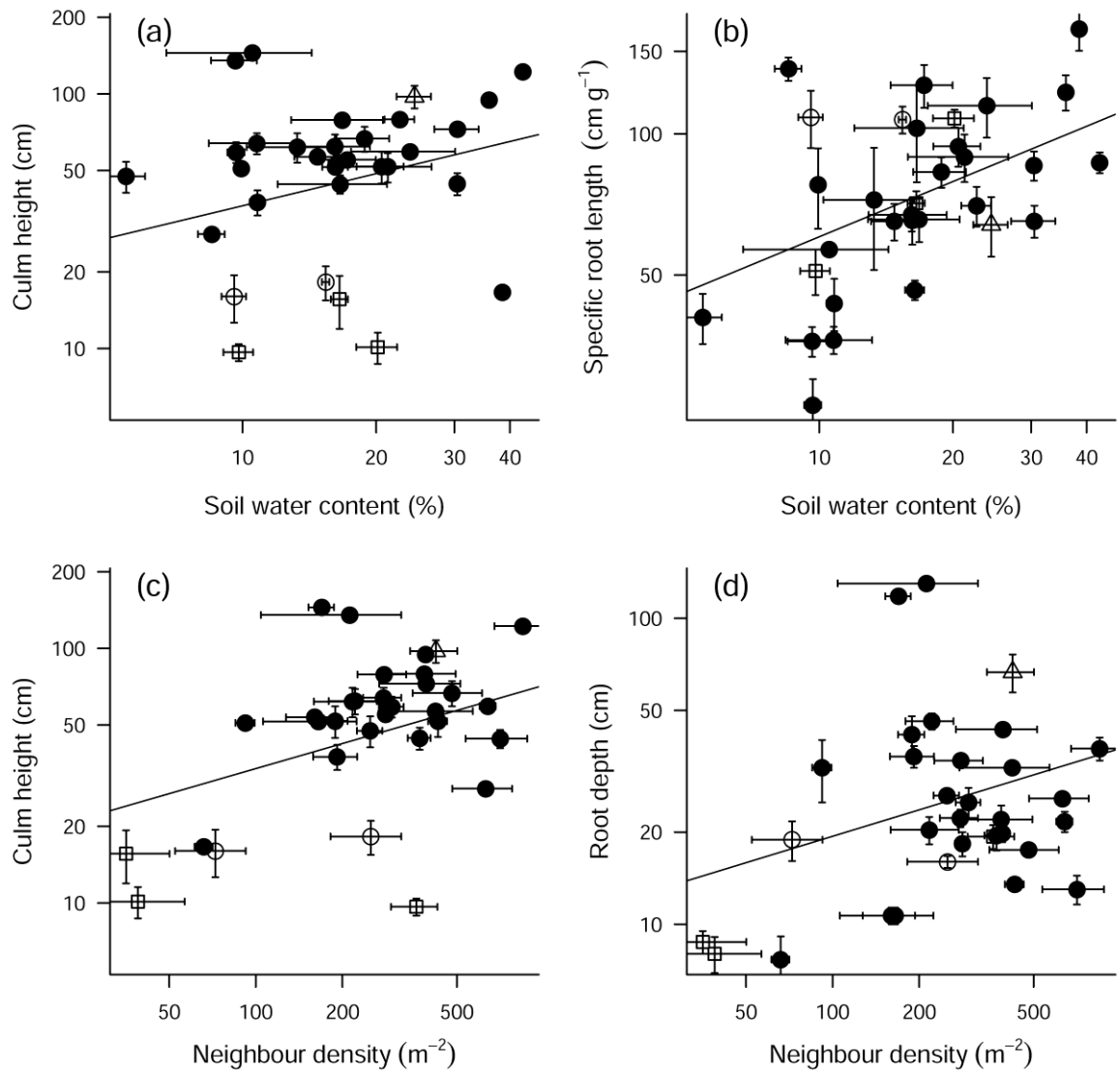
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803

804 **Fig. 2**

805



806

807 **Fig. 3**

808