



1 Shift of seed mass and fruit type spectra along longitudinal gradient: high 2 water availability and growth allometry

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11 **Abstract.** Propagule traits vary among communities along geographical gradients such as longitude, but the
12 mechanisms that underlie these variations remain unclear. This study aims to explore seed mass variation patterns of
13 different community types along a longitudinal gradient and their underlying variation mechanisms by involving an
14 in-depth analysis on the variation of seed mass, fruit type spectra, growth forms and dispersal mode spectra in Inner
15 Mongolia and northeastern China. Plant community characterization and seed collection were conducted in 26 sites
16 spreading over five vegetation types and covering 622 species belonging to 66 families and 298 genera. We found
17 there are significantly declining trend for mean seed mass, vertebrate-dispersed species richness and fleshy-fruited
18 species richness along a longitudinal gradient from forests to desert grasslands. However, we also found the lowest
19 average seed mass and the smallest proportion of species dispersed by vertebrates occurring at typical grasslands in the
20 five communities. The variations of average seed mass display high congruent with transition of growth forms. The
21 selection for these propagule attributes is driven mainly by climatic factors such as precipitation, temperature, soil
22 moisture and evaporation, as well as by internal biotic factors such as growth forms, canopy coverage and leaf area. A
23 hypothesis was provided that environmental factors and botanical traits that favor greater water availability lead to
24 emergence (or speciation) of species with large seeds or fleshy fruits with high water content. Due to greater water



25 availability and increasing leaf area, much more photosynthate and allometric growth then ultimately increase the
26 community average seed mass along rising longitude (or declining latitude or elevation). Phylogenetic signal or
27 diversity are not found to be involved into the effect on the patterns. A novel mechanistic framework and model are
28 provided to expound seed variation among species or communities.

29

30 **1 Introduction**

31 Seed traits have great impact on plants' competitive ability, fitness, fecundity and reproduction. Therefore, studying
32 seed mass variations and their mechanism is crucial for understanding plant's ecological strategy and resource
33 acquisition (Zanne et al., 2014) as well as deep-time origin and evolution of seed attributes. Being a relatively stable
34 biological trait, seed mass is controlled by an appointed gene (Adamskia et al., 2009; Wang et al., 2014), while
35 retaining a certain degree of plasticity being affected by the surrounding environment (Baker, 1972). Therefore, an
36 individual plant's seed size is a combined result of its taxonomic group's evolutionary history and of immediate
37 selective pressures of the local environment (Westoby et al., 2002; Moles et al., 2005a). Furthermore, as an important
38 aspect in the reproductive biology of plants, seed mass is evolutionarily associated with and corresponds to other plant
39 traits, relating to plant habits, life history such as growth forms (Moles et al., 2005a), stature and canopy sizes (Venable,
40 1992; Leishman and Westoby, 1994; Moles et al., 2005a), dispersal modes (Greene and Johnson, 1993), leaf area (Díaz
41 et al., 2016) and plant longevity (Telenius and Torstesson, 1991), as well as to anatomical traits of flowers and fruits
42 (Primack, 1987).

43 Numerous works show that seed mass varies along environmental gradients such as latitude, elevation and
44 longitude owing to environmental variations in temperature and precipitation and canopy coverage both among and
45 within communities (Moles et al., 2007) and several mechanisms are proposed to explain such seed mass variation
46 gradients or patterns, for example, temperature (Moles et al., 2014), light (or solar radiation) (Murray et al., 2004;
47 Demalach and Kadmon, 2018), soil resource availability (Demalach and Kadmon, 2018), growth forms (Moles et al.,
48 2005b), dispersal modes (Moles and Westoby, 2003), soil pH (Tautenhahn et al., 2008) etc. However, a deep
49 understanding of the factors that underlie these major biogeographical variations is missing (Demalach and Kadmon,



2018), especially at a continental scale along longitude. Previous work suggested that community-level average seed mass tends to decrease towards higher latitudes and elevations (Moles et al., 2007). These trends can be explained by shifts in habitat type, plant growth form spectra, seed disperser assemblage (Moles and Westoby, 2003), solar radiation and metabolic expenditure (Murray et al., 2003; 2004) and NPP (Bu et al., 2007; Guo et al., 2010) along latitudinal and elevational gradients. Additionally, species that prefer shaded habitats and late successional stages generally tend to have larger seeds than those in open arid habitats or earlier successional stages (Baker, 1972; Salisbury, 1974; Foster and Janson, 1985; Hallett et al., 2011; Moles and Westoby, 2006), indicating a strong effect of high water availability on seed mass owing to low evaporation under close canopy coverage. Longitudinal variations of seed mass has been discussed among species with a single genus (Murray et al., 2003; 2004); however, there are few studies that focus on how community-level variations of seed mass (especially across species) correspond with other plant traits along longitudinal gradients, because of the difficulty to predict variations of comprehensive environmental factors arising from complex topography. Average seed mass is expected to decrease with declining longitude due to gradually less rainfall from forests to desert ecosystems (Murray et al., 2003; 2004). Here we present a study of community-level variations in seed mass in correspondence to position in the continent (relative to the sea) across Inner Mongolia and northeastern China, to identify the longitudinal pattern and discuss the mechanisms that may underlie them.

Previous works emphasize the role of high light acquisition and allometric growth in shaping seed mass variation through model prediction and experiment testing (Demalach and Kadmon, 2018; Demalach et al., 2019), and in this article we emphasize the importance of high water availability and allometric growth for speciation and colonization of species with large seeds due to environmental factors and biological traits. Allometry of biomass growth and size-asymmetry of light competition became the drivers of seed mass variation owing to soil resource availability and ultimate productivity heterogeneity along soil resource gradient (surely including water gradient). As we know, primary production of communities increases across an increasing water gradient (Bai et al., 2008). This article presents a novel mechanistic framework that integrates previous theory and hypotheses (related to climate, phylogeny, water conduction systems and other traits related to water balance) to evaluate seed mass variation among species or communities (Figure 1).



75 The objectives of this study are to explore seed mass variation patterns of different community types along a
76 longitudinal gradient and seed mass variation mechanisms. First, we test whether community-level seed mass declines
77 from forests to deserts and what drives the patterns by identifying correlations between average seed mass and
78 precipitation and temperature. Second, we test whether species richness and growth form display similar variations as
79 seed mass, because growth forms are the key determinant of seed mass (Moles et al., 2005b). Third, we test whether
80 seed mass variations are significantly associated with growth forms, fruit types and dispersal modes in order to know
81 whether woody species combine larger seed or fleshy-fruited species. Fourth, we expound whether these patterns can
82 be simply explained by phylogeny, latitude and elevation. Finally, we construct a general hypothesis for seed mass
83 evolution based on our results and conclusions. In addition, like most plant functional traits, seed size and fruit water
84 content are also considered to be related to phylogenetic history (Griffiths and Lawes, 2006; Norden et al., 2012).
85 These traits are often strongly phylogenetically conserved, so phylogenetic distances need to be considered when
86 examining trait variation patterns and their correspondence to environmental variables (Griffiths and Lawes, 2006; Yu
87 et al., 2017). Therefore, we also took into account the effect of phylogenetic signal or diversity on the seed mass
88 distribution patterns in our analysis.

89

90 **2 Methods**

91 **2.1 Study sites and plant community characterization**

92 The study area is located in continental arid Inner Mongolia plateau, where vegetation types shift from broad-leaved
93 deciduous forest to typical grassland and finally to desert (from east to west, respectively), due to a gradual increase in
94 sunshine duration and intensity and decrease in rainfall (from 780.6 to 29 mm) (Table 1). The study was carried out in
95 26 sites along this gradient, extending between longitude 100°E ~ 124°E (about 2864 km distance between the
96 westernmost and easternmost sites) and 41°N ~ 44° N in Inner Mongolia and northeastern China (Table 1).

97 Different sampling designs were used in different habitat types, owing to differences in vegetation structure and
98 density. Within each forest plot, 6 quadrats of 10×10 m² were selected at random in undisturbed or slightly disturbed
99 (at least in recent years) areas. For shrub communities and herbaceous communities, 3 quadrats of 5×5 m² and at least



100 8 quadrats $1 \times 1 \text{ m}^2$ were investigated, respectively. Species composition (species number and number of individuals per
101 species) were recorded. The geographical positions (latitude, longitude and elevation) were measured by wireless GPS
102 logger (HOLUX Technology Inc., Taiwan). Other physiographic factors such as grade of slope, slope aspect and
103 micro-topography were recorded. The vegetation types were determined based on the dominant species and
104 information referenced from the classification system of Chinese vegetation (Editorial Committee for Vegetation of
105 China, 1980). Data of temperature and precipitation as well as other climatic factors were retrieved from the Wordclim
106 database using R raster package: average values per site were obtained from interpolations of observed data during the
107 period between 1950 and 2000. Two climatic variables, mean annual temperature (MAT) and mean annual
108 precipitation (MAP) were used to analyze the relationship between seed mass and the climate along the geographical
109 gradient (Table 1).

110

111 **2.2 Seed collection and characterization**

112 Mature seeds were collected for each species observed in each site at the start of natural dispersal season (from June to
113 October) during the years 2008-2014. Seeds of each species were collected from at least three mother individuals in
114 the same stand and mixed together to avoid bias caused by maternal effects. Seeds were allowed to air-dry to a
115 constant mass in the laboratory before being weighed. For each plant species, seed mass was calculated as the average
116 values of 5 to 100 (even to 1000) seeds, depending on seed size and availability, and at least three repeated
117 measurements were conducted for each species. Seed mass was measured to microgram precision on a PB303 balance
118 (Mettler, Toledo). Seeds that were likely to be inviable (unusually small seeds that contained abnormal looking
119 embryos or that appeared hollow) were subjectively excluded before the measurement. For some species with
120 caryopsis, achene and utricle, dry mass of entire propagules was weighed. Structures such as delicate wings and
121 pappus (or hairs) strictly associated with wind dispersal were removed and the spine was retained before weighing the
122 seeds.

123 Dispersal modes were assigned for all 622 species, based on ornamentation and appendages on fruits and seeds.
124 The dispersal modes of each species were obtained from the Kew Gardens (Howe and Smallwood, 1982) and literature



125 reference collection from northwest China (Liu et al., 2014). For some species, dispersal modes were confirmed with
126 empirical analysis according to morphological features of their diaspores, and the dispersal mode represents seeds from
127 the parent plant to the soil surface. Each species was treated as having a single dispersal mode, reflecting their
128 principal dispersal agents (PDA) (Leishman and Westoby 1994; Butler et al., 2007): wind-adapted (279 species, with
129 wings, hairs or a pappus), vertebrate-adapted (66 species, with an aril or fleshy fruits), ant-adapted (195 species, with
130 an elaiosome), unassisted (70 species, no obvious morphological structure) and adhesion-adapted (12 species, with
131 hooks, spines or bards).

132

133 **2.3 Fruit types and other plant traits**

134 Fruits were classified as fleshy if they were described in the flora as berries, drupes, pomes, rose hips, multiple fruits
135 and pepos or as possessing fleshy pericarp or succulent tissue in general (including arils) (Yu et al., 2017). Accordingly,
136 capsules, achenes, nuts, caryopses, legumes, follicles, pods, cremocarps, utricles, samaras and schizocarps were
137 classified as non-fleshy (dry) fruits. Some species (e.g., *Vitex nengudo* var. *heterophylla*) that were described to be
138 fleshy-fruited in related local flora were reclassified as dry-fruited owing to very low water content.

139 Species life-history information is drawn primarily from the Flora of China and based on our yearly field
140 observations. Species in the flora were grouped into the following five major growth-form categories: trees (12
141 species), shrubs (65 species), subshrubs (20 species), lianas (15 species), perennials (400 species) and annuals (110
142 species).

143

144 **2.4 Soil moisture measurement**

145 The soil moisture of top 10-cm depth was measured gravimetrically by oven-drying the samples at 105° C for 24 hours
146 in 12 sites of typical grasslands and desert grasslands. Five soil samples were collected from each sites on July 10-17,
147 2014, 21days after rainfall.

148

149 **2.5 Data analysis**



150 Seed mass, longitude and precipitation were log-transformed before analysis to meet the normality and
151 homoscedasticity assumptions of linear regression models. In order to ensure that any observed seed mass variation
152 along the longitudinal gradient is independent of latitude and elevation, general linear models (GLM) were employed.
153 Seed mass and other plant traits were treated as the dependent variable in all analyses with latitude, longitude and
154 climatic variables entered into models as independent variables.

155 The proportions and species richness of plants with various seed mass and fruit types in different communities
156 were compared using analysis of variance (ANOVA). ANOVA was also used to compare average seed mass between
157 different growth forms, different community types, different fruit types and dispersal types. The GLM procedure was
158 used to examine the explanatory power of community types, dispersal types, longitude, precipitation and temperature
159 on seed mass. All analyses were performed with R-3.3.3 (R Core Team, 2018). By use of the function `commonality` in
160 the R package `yhat` (Nimon et al., 2013), we take the log-transformed seed size as dependent variable, life forms,
161 vegetation types, dispersal modes and latitude as independent variables, exploring predictive power of each variables.

162 For the 620 species (two gymnosperm species were excluded owing to their low relatedness with most of
163 angiosperm species), a supertree was constructed using the software `PhyloMatic` (Webb et al., 2008). The phylogenetic
164 backbone was based on the APG III tree (R20120829, <http://phylodiversity.net/phyloMatic/>). We quantified the
165 strength of phylogenetic conservatism and tested the phylogenetic signal in seed mass using Pagel's λ (Pagel, 1999)
166 and Blomberg's K (Blomberg et al., 2003) calculated using the 'phylosig' function in the package 'phytools' v0.2-1 (R
167 Foundation, Vienna, Austria) (Revell, 2012). A λ or K of 0 indicates no phylogenetic signal (Pagel, 1999; Panchen et
168 al., 2015). Regression analyses were conducted between phylogenetic signal and longitude across the sites in five
169 community types. Using the phylogenetic tree with branch length, we calculated the phylogenetic diversity using the
170 measure PD, which was defined as the minimum total length of all the phylogenetic branches required to span a given
171 set of taxa on the phylogenetic tree (Faith, 1992). Taking mean seed mass as dependent variable and longitude
172 (including both linear and quadratic terms) and the phylogenetic diversity measure PD as independent variables, we
173 built a linear model using R package `stats` (R Core Team, 2018).

174 We considered the relations between the number of species with fleshy fruits and longitude, the number of



175 families, number of genera, and the phylogenetic diversity PD. Since there are strong correlations between the latter
176 four variables ($r > 0.67$, $p < 0.001$), they cannot be used in the same model. Therefore, we built four models. Each took
177 one of the four variables as the independent variable and the number of species with fleshy fruits as dependent variable.
178 A generalized linear regression model with Poisson family was fitted using R package stats (R Core Team, 2017). In
179 the model, we also included $\log(\text{number of species})$ as offset.

180

181 **3 Results**

182 **3.1 Seed mass variations along the longitudinal gradient**

183 Although the majority of species had medium-sized seeds (Figure 1), variations among all species were great. There
184 were considerable differences in average seed mass and seed spectra among the five community types (Figure 2).
185 Forests have the largest average seed mass (23.45 ± 18.34 mg) and both typical grasslands (4.75 ± 3.93 mg) and sparse
186 forests (4.45 ± 1.18 mg) have the lowest average seed mass, being nearly 5-fold decline in average seed mass from
187 forests to typical grasslands. Average seed mass of forests is significantly greater than that of the sparse forests
188 ($F=12.13$, $p=0.0253$), and deserts are remarkably larger (20.12 ± 8.26 mg) than desert grasslands (10.08 ± 2.34 mg)
189 ($F=6.914$, $p=0.0466$), being nearly 4.2-fold decline in average seed mass from deserts to typical grasslands. The
190 average seed mass of typical grasslands is significantly smaller than that of desert grasslands ($F=11.92$, $p=0.0025$),
191 while there is no significant difference between average seed mass of typical grasslands and sparse grasslands
192 ($F=0.019$, $p=0.892$).

193

194 **3.2 Seed mass relations to other plant traits**

195 Average seed mass of trees was significantly larger than that of shrubs ($F=12.2$, $p=0.000$), shrubs had larger seeds than
196 perennials ($F=59.57$, $p=0.000$), and average seed mass of perennials was larger than that of annuals ($F=4.932$,
197 $p=0.0268$) (Figure 3). From forests to grasslands, wooden species richness displayed a declining trend along
198 decreasing longitude (Table 2).

199 Seeds that are dispersed by vertebrates (232.09 ± 823.98 mg) were significantly larger than those dispersed by



200 wind (2.46 ± 6.23 mg) ($F=238.2$, $p < 0.0001$), ants (3.56 ± 10.03 mg) ($F=17.73$, $p < 0.0001$), and those with unassisted
201 dispersal (7.42 ± 12.08 mg) ($F=17.73$, $p=0.000$) and adhesive dispersal (5.07 ± 8.12 mg) ($F=17.73$, $p < 0.0001$) (Table 3).

202 Seed mass is weakly negatively correlated with leaf area ($R^2 = 0.063$, $p = 0.005$) and not significantly correlated
203 with SLA across all sampled species ($R^2 = 0.006$, $p = 0.195$). SLA is significantly related with leaf area ($R^2 = 0.160$,
204 $p < 0.001$).

205

206 3.3 Seed mass relations to environmental variables

207 Average seed mass was minimum at approximately 112 degrees longitude where typical grasslands occur (Figure 4).
208 However, phylogenetic diversity (PD) was not a significant explanatory variable ($p > 0.8$) (Figure 4). Linear regression
209 model shows that there is no significant decreasing trend from forests to deserts along declining longitude ($F = 2.289$,
210 $p = 0.143$). If the westernmost sample site (Ejinaqi) is excluded, seed mass significantly decrease inland ($R^2 = 0.2434$,
211 $F = 7.398$, $p = 0.012$).

212 Significant negative relationships were found between seed mass and MAT ($R^2 = 0.1752$, $p = 0.01915$) and
213 elevation ($R^2 = 0.1221$, $p = 0.0449$) across all sample sites, but no significant relationships were found between seed
214 mass and latitude ($R^2 = -0.028$, $p = 0.576$) and MAP ($R^2 = -0.008$, $p = 0.380$). Across 23 sample sites from desert
215 through desert grassland to typical grassland, average seed mass had significantly negative relationship with longitude
216 ($R^2 = 0.232$, $p = 0.012$) and MAP ($R^2 = 0.48$, $p = 0.00015$), while across 20 sample sites from typical steppe to forests
217 average seed mass had significantly positive relationship with longitude ($R^2 = 0.232$, $p = 0.012$) and MAP ($R^2 = 0.48$, p
218 $= 0.00015$). Average seed mass was found to just be weakly positive relationship with MAT both from desert through
219 desert grassland to typical grassland and from typical grassland to the forests ($R^2 = 0.09207$, $p = 0.08665$). According
220 to above analysis, MAP should be crucial environmental drive factor for seed mass variation.

221 In addition, average seed mass is significantly related with soil moisture ($p < 0.05$) and soil moisture significantly
222 decrease with declining longitude from typical to desert grasslands.

223

224 3.4 Species richness and proportion of fleshy fruited species



225 Average seed mass of species with fleshy fruits (40.15 ± 110.41 mg) were significantly greater than that with dry fruits
226 (26.58 ± 286.97 mg) ($F = 18.61$, $p = 0.0125$) for the whole species pool (622 species), for the five community types
227 (Figure 3, SP 1) and for each sites (SP 2) (Figure 4).

228 Among the five community types, forests have the highest number (7.44 ± 1.26) and proportion (28.05 ± 6.16) of
229 fleshy fruited species, while desert grasslands have the lowest number (0.06 ± 0.097) and typical grasslands the lowest
230 proportion (1.00 ± 1.49) (Figure 6). Fleshy fruited species richness ($F = 22.25$, $p = 0.00919$) and proportion ($F = 18.61$,
231 $p = 0.0125$) in sparse forests are significantly smaller than those in forests. The desert has higher fleshy fruited species
232 richness ($F = 6.081$, $p = 0.0239$) and proportion ($F = 24.9$, $p < 0.0001$) than desert grasslands. Sparse forests have
233 remarkably higher fleshy fruited species richness ($F = 281.3$, $p = 0.000$) and proportion ($F = 78.6$, $p = 0.0009$) than
234 typical grasslands (Figure 6).

235

236 **3.5 Fleshy fruited species relations to environmental factors**

237 Fleshy fruited species richness was significantly associated with longitude ($R^2 = 0.1691$, $p = 0.02113$) and MAP (R^2
238 $= 0.4749$, $p = 0.0000$) across the 26 sample sites. Significantly positive correlation existed between the proportions of
239 species with fleshy fruits and MAT ($R^2 = 0.1172$, $p = 0.0486$), while the correlation with elevation ($R^2 = 0.0938$, $p =$
240 0.0703) and longitude ($R^2 = 0.0831$, $p = 0.0832$) was weak. In addition, there were no significant relationships between
241 proportions of fleshy fruited species and latitude ($R^2 = -0.0396$, $p = 0.8272$) as well as MAP ($R^2 = -0.0389$, $p = 0.8009$),
242 and no strong relationships between fleshy fruited species richness and latitude ($R^2 = 0.0408$, $p = 0.8899$) as well as
243 MAT ($R^2 = 0.0414$, $p = 0.9416$).

244 From desert through desert grassland to typical grassland, significantly positive correlations were found between
245 richness of fleshy fruited species and longitude ($R = 0.3466$, $p = 0.0019$) and MAP ($R^2 = 0.284$, $p = 0.0052$), while there
246 were no significant correlations between proportion of fleshy fruited species and MAT ($R^2 = 0.1295$, $p = 0.0513$). From
247 typical grassland to the forests, remarkable correlations occurred between proportion of fleshy fruited species and
248 longitude ($R^2 = 0.324$, $p = 0.00418$) and MAP ($R^2 = 0.324$, $p = 0.00418$), however no significant relationships were
249 found between MAT and proportion ($R^2 = -0.0519$, $p = 0.9065$) and species richness ($R^2 = -0.0522$, $p = 0.93$) of fleshy



250 fruited plants. The number of species with fleshy fruits increased with longitude ($p = 0.022$) and number of families (p
251 $= 0.005$), but correlations with number of genera and phylogenetic diversity were not significant ($p = 0.056$ and 0.058
252 respectively) (Figure 5, c-d).

253

254 **3.6 Phylogenetic signals and their shift along longitudinal gradient**

255 Most phylogenetic signals (k values) are weak (from 0.234 to 0.688, $p > 0.05$) for the five community types and for
256 most sample plots except Naimanqi (1.928, $p < 0.05$) in early-successional stage. No significant relationships are found
257 between phylogenetic signals (k values) and longitude across 26 sample sites ($R = 0.0403$, $p = 0.8596$). Both from
258 desert (to desert grasslands) to typical grasslands ($R = 0.047$, $p = 0.9123$) and from typical grasslands to the forests (R
259 $= 0.0401$, $p = 0.6382$), phylogenetic signals were not related to longitude for the five community types. Positive
260 relationships between longitude and number of families or species with fleshy fruits are significant ($p = 0.022$ and
261 0.005 respectively, Figure 5), and number of species and families with fleshy fruits increased as longitude increased.
262 However, relationships between number of genera or genetic diversity and longitude are not significant ($p = 0.056$ and
263 0.058), respectively (Figure 4).

264

265 **4 Discussion**

266 **4.1 Variation of seed mass spectra and environmental factors**

267 There is strong and consistent effect of community type (along a longitudinal gradient) on seed mass (Figure 2, Figure
268 4). The average seed mass display a significantly declining trend along decreasing longitude from forests to typical
269 grasslands and then to some sites in desert grasslands (Figure 4), however, mean seed masses increased from typical
270 grasslands to desert grasslands and desert ecosystems and then to forests (Figure 2), showing congruent distribution
271 patterns to plant growth forms (Table 2). MAT and MAP may be responsible for the results because of the significant
272 relationships between seed mass and MAT and MAP across 26 or 23 sample sites respectively (see results). This
273 indicates that climatic control of vegetation trait distribution in Inner Mongolia is not only by temperature but also by
274 precipitation (Moles et al., 2014). The combined effects of precipitation and temperature may be, to some extent, most



275 important to certain vegetation syndromes such as seed mass and fruit water content. High water availability
276 potentially can produce high assimilation products and high temperature (in normal range of plant growth) can increase
277 water availability.

278 General linear models (GLMs) revealed significant relationships between seed mass and each of the variables
279 predicted to influence the longitudinal gradient in seed mass: plant growth form (99.76%), vegetation types (99.01%)
280 and seed dispersal syndrome (99.88%). Such patterns have previously been attributed mostly to a correspondence of
281 seed mass to plant growth form and seed dispersal syndrome, which themselves are driven by climatic and
282 environmental variations (Moles et al. 2005a; Moles et al. 2007). In Inner Mongolia, typical grasslands are often
283 composed mainly of grasses (many of which are biennial and perennial) that are small-seeded (Figure 3), whereas trees
284 and lianas that dominate forests and shrubs that dominate deserts have the largest seeds (Figure 3). Large seeds were
285 proved to be often associated with woody growth forms (Salisbury, 1942; Baker, 1972; Silvertown, 1981; Mazer, 1989;
286 Jurado et al., 1991; Elenius and Torstensson 1991; Leishman and Westoby, 1994; Moles et al., 2005a; Moles et al.,
287 2005b). This pattern is often attributed to woody plants' better capability to take up (Schenk and Jackson, 2002; Li et
288 al., 2002; Qi et al., 2019) and store resources and to buffer effects of environmental variations on seed size (Weiner,
289 2004; Moles et al., 2005a), or to reduced evaporation for understory species (Yu et al., 2017). Surely, woody species,
290 on average, having larger leaves, can produce more photosynthate to invest in seeds (Díaz et al., 2016).

291 It is possible that larger seeds are more common in drought-prone habitats most likely because they allow
292 seedlings to establish large root systems early, with a better chance of surviving drought (Baker, 1972; Salisbury, 1974).
293 In this study, desert grassland and desert ecosystems are found to be dominated by shrubs that often possess larger
294 seeds (Figure 3). These species are seldom exposed to strong interspecific competition or shading in Inner Mongolian
295 Plateau (Bai et al., 2008). In addition, relatively high species richness and the highest number of species occurred in
296 this typical steppe grassland (Table 2), and in contrast, desert steppe had very low species richness and number of
297 individuals (abundance) (Table 2).

298 With increasing MAP, richness of wind dispersed species decreased (S3, S4). The proportion of vertebrate
299 dispersed species in typical grasslands was the lowest in comparison to other communities (S4). The patterns of seed



300 dispersal syndromes observed in this study are congruent with previous findings in Australia's subtropics (Butler et al.,
301 2007). Biotic dispersal agents exert a strong selective pressure on angiosperm species with various seed size in Inner
302 Mongolian plateau, as evidenced by the evolution of a wide range of adaptations for animal dispersal.

303

304 **4.2 Variation of fruit type spectrum and associations of seed mass with fruit types**

305 Fleshy fruited species richness significantly corresponded to gradual changes of climate, especially for MAP (Table 1).
306 The smallest proportion of fleshy fruited species occurred in typical grasslands and desert grasslands (Figure 4), at the
307 middle zone of Inner Mongolia. Previous findings showed that fleshy fruited species were often associated with shaded
308 habitats, mature forests, tropical forests, regions with lower elevations and woody life form (summarized in Yu et al.,
309 2017), indicating high canopy coverage and low evaporation (Fig.6) (Yu et al., 2017). The increasing prevalence of
310 fleshy-fruited species with increasing canopy coverage (Table 2) is probably related to the prominence of species with
311 larger seeds in such habitats. Previous hypotheses suggest that fleshy fruit evolution is related to water availability and
312 the ineffectiveness of wind-assisted dispersal beneath a dense canopy (Butler et al., 2007; Yu et al., 2017). The reduced
313 dispersal capability following from an increase in seed mass may be counterbalanced by evolution of traits mediating
314 seed dispersal by animals, such as fleshy fruits. Alternatively, increasing water availability may promote the evolution
315 of species with fleshy fruits (Yu et al., 2017) and large seeds.

316

317 **4.3 Ecological and evolutionary drivers of seed mass variations**

318 A consistent combination was found between possession of fleshy fruits and heavier seeds when comparing seed mass
319 among clades with fleshy and non-fleshy fruits (Figure 3, S1, S2). The results were largely in agreement with previous
320 findings (Eriksson et al., 2000; Butler et al., 2007; Bolmgren and Eriksson, 2010). A possible explanation may be that
321 woody species have larger internal water surpluses and photosynthate to invest in their seeds and fruits. Accordingly,
322 formation of seed mass may also be related to plant resource acquisition and allocation strategies or to allometric
323 growth of plant apparatus (Weiner, 2004; Price et al., 2007; Demalach and Kadmon, 2018).

324 As a result of evolution for high water availability, large seeds are often associated with low latitude (Moles et al.,



2003) and low elevation (Bu et al., 2007), or with shaded habitats such as northern slopes (Csontos et al., 2004) and closed vegetation (Mazer, 1989; Hammond and Brown, 1995) and with late successional stages (Hammond and Brown, 1995). All those phenomena indicate that seed mass may be related to low evaporation and high water availability in plants (Fig.6). We suggest that, as an ecological strategy, the derivation and evolution of species with large seeds may be due to improved water accommodation in plants by strong resource acquisition ability (such as having strong water absorbing root system and advanced water conductive ability) or water retention ability (such as habituating shaded environment or developing small, thick leaves and hair or waxiness on leaf to prevent water loss) (Baker, 1972; Fonseca et al., 2000). Plant species have evolved various ecological strategies to match their environments (Laughlin, 2014). These strategies are manifested in many plant organs and traits. In the present study, seed mass is strongly connected with other biological characteristics such as plant dispersal ability (SP 4, Table 3), fruit types and growth forms. For example, there is rising trend in average leaf area (Wright et al., 2004) and water- conducting conduits (Wheele et al., 2007; Zanne et al., 2014) along increasing longitude (or declining latitude and elevation). Seed mass also is sure to be coordinated with conducting issues of plant apparatus (Wheele et al., 2007; Zanne et al., 2014). Anatomical structures of lots of species indicated that the species with large seeds or fleshy fruits often have wide and long vessel elements that can provide much more water (Carlquist, 1975; Zimmermann, 1983). As suggested before, seed mass also is likely to be a result of co-evolution among various organs that determine plant responses to changing abiotic factors (Díaz and Cabido, 1997; Sandel et al., 2010).

In light of growth allometry theory, average seeds mass variation should converge with community total biomass (Demalach and Kadmon, 2018). Evidently, spatial distributions of community-level seed mass and NPP consistency correspond (Moles and Westoby, 2003; Murray et al., 2003; Griffiths and Lawes, 2006; Chen et al., 2007; Chen et al., 2011). In Inner Mongolia ANPP (aboveground net primary production) and RUE (rain-use efficiency) increased indeed in space across different communities or ecosystems with increasing MAP eastwards (Bai et al., 2008), showing similar variation trend with average seed mass. Both soil moisture and soil nutrient (total N) was found to decrease significantly in Inner Mongolia from east to west (Liu et al., 2017), showing similar variation trend with ANPP and seed mass. Moreover, water retention of plants is becoming unfavorable with increase of evaporation westwards (Table



350 1).

351 In previous studies, soil moisture was found to not correlate with the relative abundance of fleshy-fruited species
352 due to low temperature on water availability constraints (Yu et al., 2017). As we know, seed plants employ two main
353 strategies to increase water use efficiency: one is to take up more water through root systems and the other is reducing
354 water loss through evapotranspiration. In our study, canopy coverage decreases from forests to sparse forests and then
355 to grasslands and desert grasslands (Table 2), leads to gradual reduction in fleshy-fruited or large-seeded species
356 richness (Fig.1, Table 2). However, since fleshy fruits have high water content and thus inquire higher plant internal
357 water content (Yu et al., 2017), we suggest the correspondence of seed size and fruit water content imply that some
358 species evolved to contain more water or photosynthate in multiple body parts. Furthermore, CO₂ concentration is
359 generally the same everywhere although there is some small variation during growth seasons, its impact on seed mass
360 variation patterns should be expelled. Solar radiation is very similar along longitude especially among typical
361 grasslands, desert grasslands and deserts with similar elevation, its effect on seed mass variation should be partitioned
362 out. Therefore, combined with previous results of other studies, we deduce that drivers of seed mass spatial distribution
363 patterns include temperature, rainfall, solar radiation, soil moisture and nutrients, leaf area, canopy coverage and their
364 interactions, however, high water availability in plant body may be the most vital driving factor in shaping seed mass
365 spatial distribution. According to growth allometry, a fraction of photosynthate, coming from each increment of
366 temperature, rainfall, soil moisture and nutrients, leaf area, canopy coverage, is considered to be allocated to seeds. In
367 addition, biological structures (such as hair or waxiness on leaf to prevent water loss), that favor water retention in
368 plant body would also be useful in increasing seed mass or fruit water content.

369 Moreover, as suggested by previous works, transition between small and large seeds in response to environmental
370 variations should be genetically simple, involving suppression and re-expression of only a few genes (Wang et al.,
371 2014; Zanne et al., 2014). On basis of the above all, we suggested that transition between dry fruits and fleshy fruits in
372 response to environmental variations may also be genetically simple, involving suppression and re-expression of only a
373 few genes.

374 Generally, seed mass is quite phylogenetically conservative (Lord et al., 1995). However, in this study,



375 phylogenetic signal is weak across the 26 sites (Table 1) and the five communities and found to be little involved in the
376 relationships between seed mass and longitude, MAP and MAT. This proves that the environment affects seed mass in
377 the community context independent of phylogenetic constraints. The five communities are in middle or late
378 successional stages in which the main construction process is competitive exclusion rather than environmental filtering
379 (Norden et al., 2012).

380 A simple mechanistic model is provided to explain average (or total) seed mass variation between communities
381 for one species as following:

$$382 \quad S_a = 1/n \sum_{i=1}^n C_{i1} B_t \quad (C_{i1} < 1), \quad S_t = \sum_{i=1}^n C_{i1} B_t \quad (C_{i1} < 1)$$

$$383 \quad B_t = B_{id} + B_{i0} + B_l$$

384 S_a is average seed mass of a community for one species (Fig.2), S_t is the total seed mass of all species in a community,
385 n is number of species in a community, C_{i1} is the allometric growth coefficient (or allocation portion to seeds) that
386 differ among species. B_t is total biomass from photosynthate per species. B_{id} value is the biomass of photosynthate
387 related to water from conducting issues for one species, B_{i0} is the biomass of photosynthate related to water from other
388 approach (for instances, lessening evaporation), B_l is the biomass of photosynthate related to leaf area (Fig.1).

389 In additions, abundant groundwater in the desert ecosystem (Heihe river runs through Ejinaqi, the westernmost
390 sample plot in this study, here *Populus euphratica* sparse forest even develops around the river) may be responsible for
391 the “strange” patterns about distribution of average seed mass and fleshy fruited species found in this study. In this
392 study, we just measure the soil moisture of top 10cm which mainly influence growth of herbs, but for the growth of
393 shrubs and trees, rich soil water below the depth of 10 cm in some area of Ejinaqi also is useful. Moreover, ecological
394 scale and environmental heterogeneity often affects results of functional traits along biogeographical gradients, so
395 further study may be necessary in larger scale (or large area) to identify the results of this article.

396 **5 Conclusions**

397 Mean seed mass, seed dispersal spectra, fruit type spectra and plant growth forms of five community types vary
398 significantly along a longitudinal gradient, with the lowest average seed mass and the smallest proportion of species



399 dispersed by vertebrates occurring at the middle longitude (typical grasslands). The selection for these propagule
400 attributes is most likely to be driven by environmental factors such as precipitation, temperature, soil moisture, soil
401 nutrient and underground water, as well as many biological factors such as canopy coverage, plant morphologies and
402 life-spans, dispersal syndromes, densities of competing plants, and growth forms, however, water availability
403 potentials and growth-allometry may be key drivers of seed-mass variation along climatic gradients or resource
404 gradients. Larger seeded species may have evolved due to high water availability and more photosynthate. Our
405 findings have important implications in understanding origin and evolution of species with large seeds or fleshy fruits.
406 Further studies are needed to better understand the combined effects of climate, soil and evolutionary history on seed
407 mass variations among plants.

408

409 *Author contributions*

410 S.L. Yu led data collection and analysis, conceived the idea and led manuscript writing. G.X. Wang and D.F. Li took
411 part in data collection and analysis. O. Katz assisted in manuscript writing. C.R. Liu carried out phylogenetic analysis.
412 QB Wang provided soil moisture data. M. Yue gave a critical revision suggestions on early draft. All authors
413 contributed critically to the drafts and gave final approval for publication.

414

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418

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589 **TABLE 1** Information geographic positions and environmental factors in 21 sampling sites in Inner Mongolia
 590 plateau and Northeastern China

Number	Site names	Longitude	Latitude	Altitude (m)	MAP(mm)	MAT (°C)	K- value	Evaporation (mm)	Vegetation types
1	Ejinaqi	101.0815	41.9520	942	29	8.9	0.774	3850	DS
2	Wulatehouqi	107.0160	41.0750	1137	136.8	7.9	0.647	3069	DG
3	Wulatezhongqi	108.4833	41.3002	1203	198.8	5.8	0.395	2500	DG
4	Erlanhaote	112.0108	43.7239	907	134.8	4.6	0.451	2700	DG
5	Suyouqi	112.6328	42.7662	1100	346.8	2.1	0.855	2700	DG
6	Chayouzhongqi	112.37	41.17	1737.3	223	3.2	0.383	2186	TG
7	Siziwangqi	112.1533	42.0780	1439	315.2	4	0.516	1900	TG
8	Wulanchabu	113.1244	41.0557	1392	350.1	4.7	0.512	2000	TG
9	Chayouhouqi	113.1358	41.5916	1499	318.8	4.3	0.430	2186	TG
10	Shangdu	113.4799	41.5415	1361	337.1	4.2	0.343	2020	TG
11	Xianghuangqi	113.8587	42.2400	1351	270.6	3.9	0.221	2250	TG
12	Huade	113.97	41.88	1483	311.9	3.2	0.483	2050	TG
13	Zhangbei	114.2200	41.3310	1413	383.7	3.6	0.450	1956	TG
14	Abagaqi	114.9481	44.0294	1153	238	1.9	0.291	1900	TG
15	Zhengxiangbaiqi	115.0138	42.2911	1389	351.2	2.8	0.274	1932	TG
16	Taipusiqi	115.2543	41.9875	1529	383.5	2.4	0.469	1879	TG
17	Lanqi	115.9547	42.6684	1315	359.6	2.5	0.313	1926	SF
18	Xilinhaote	116.2514	43.8036	1033	263.5	3	0.224	2100	TG
19	Keqi	117.5389	43.2250	1038	391.8	3.2	0.353	1600	TG
20	Linxi	118.02	43.6	923	369.5	5.2	0.365	1826	TG
21	Chifeng	118.9778	42.3060	568	370.2	7.8	0.376	1700	TG
22	Naimanqi	120.9421	42.9535	340	355.9	7.4	1.928	1979	TG
23	Kezuohouqi	122.4112	42.9017	251	414.9	6.8	0.395	1782	TG
24	Liaoyuan	124.3416	42.7950	240	604.2	7.1	0.338	1345	FR
25	Siping	124.5178	43.1757	243	622.6	5.8	0.491	797	FR
26	Qingyuan	124.9407	41.8513	682	780.8	6.2	0.538	1033	FR

591 Deserts: DS, Desert grasslands: DG, Typical grasslands: TG, Sparse forest: SF, Forests: FR.

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596 **TABLE 2** Species richness (No./sample area) or percentages for woody plants and herbs as well as abundance

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(individual/m²) in five ecosystem types

Ecosystem types	Sites	Woody richness/percentage	Herbaceous richness/percentage	Abundance	Canopy coverages (%)
Forests	Qingyuan	11±2/40.0±4.5	16±1/60.0±4.5	30±9	80-90
Sparse forests	Sanggendalai	5±2/18.0±5.2	24±2/82.0±5.2	126±8	20-40
Typical steppe	Sanggendalai	1±1/6.67±4.44	19±5/93.3±4.4	458±54	5-10
Desert grasslands	Erlianhaote	2±0/17.0±4.0	8±1/83.0±4.0	23±7	<5
Desert	Ejina	2±0/55.7±10.4	2±1/44.3±10.4	3±4	<5

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599

600 **TABLE 3** Seed masses, species number and proportions of 5 dispersal types in the whole study area

Dispersal agent types	Seed mass (mg)	Species number	Proportion in the whole (%)
Wind	2.46±6.23	279	44.86
Vertebrate	232.09 ± 823.98	66	10.61
Unassisted	7.42±12.08	70	11.25
Ants	3.56±10.03	195	31.35
Adhesive	5.07±8.12	12	1.93
Total	50.12±172.09	622	100

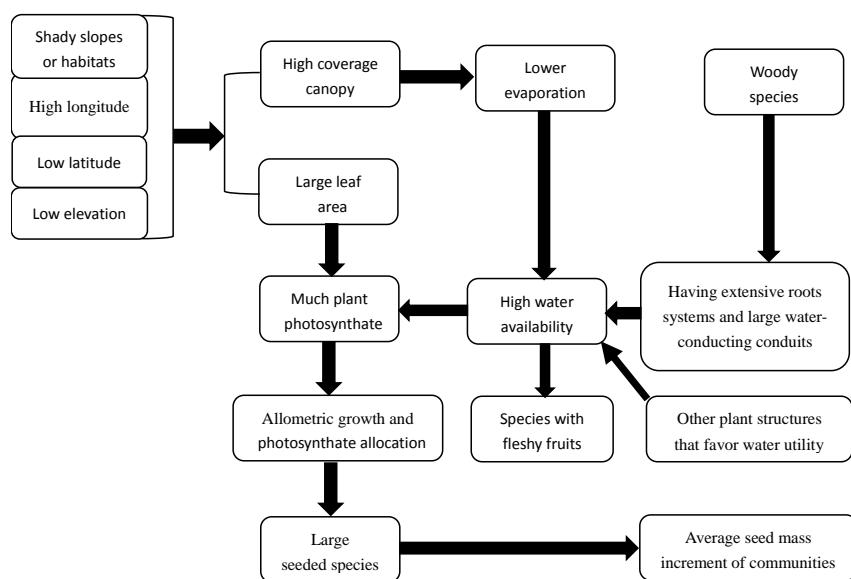
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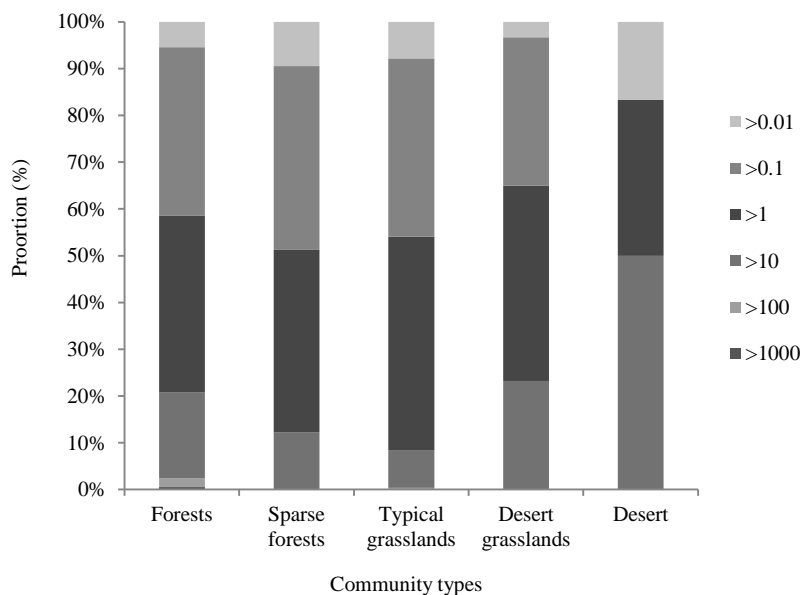
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FIGURE 1 Mechanistic frameworks of large seed formation and then community average seed mass increment process

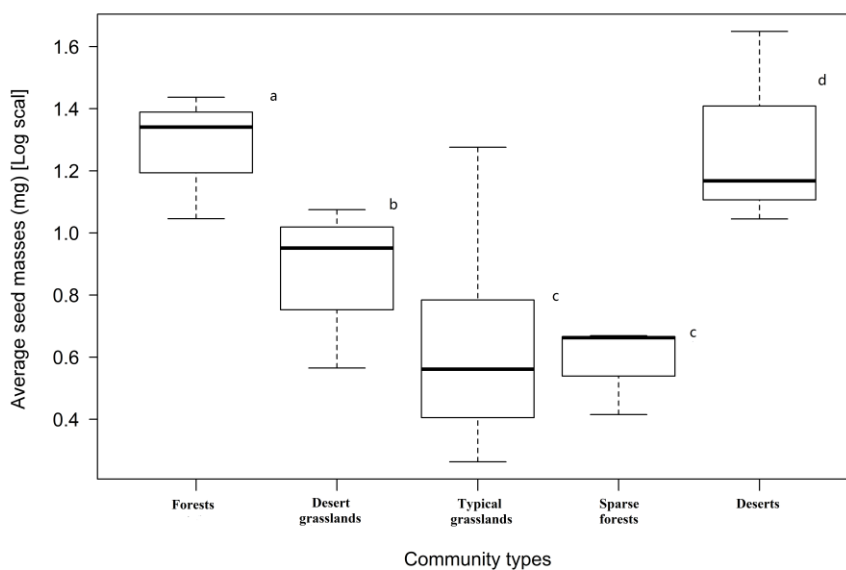




619 **FIGURE 2** Seed mass spectra varied among five community types in Inner Mongolia and proportions of larger seeds
620 and average seed mass decline from forests to desert grasslands along decreasing longitude but increase in deserts
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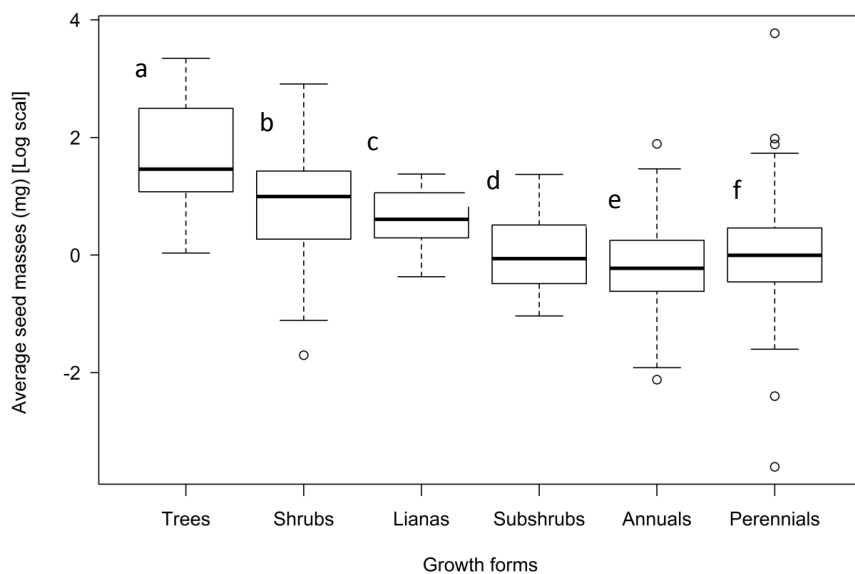
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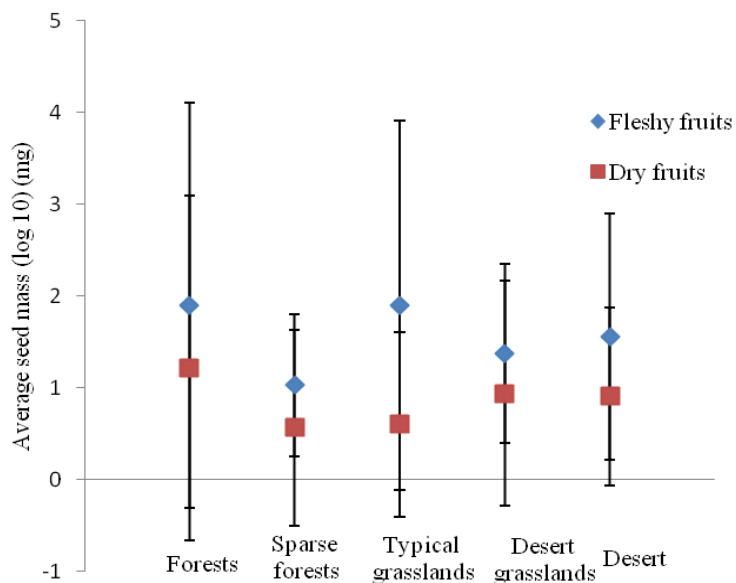
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624 **FIGURE 3** Trees (12 species) have largest average seed mass, followed by shrubs (65 species), lianas (15 species),
625 subshrubs (20 species), perennial herbs (396 species) and annuals (110 species). Average seed mass of fleshy fruits is
626 larger than that of dry fruits in each community type



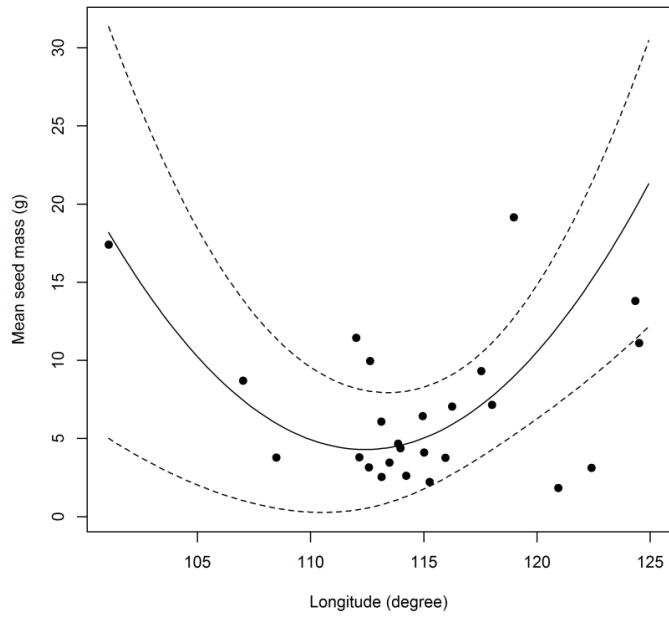
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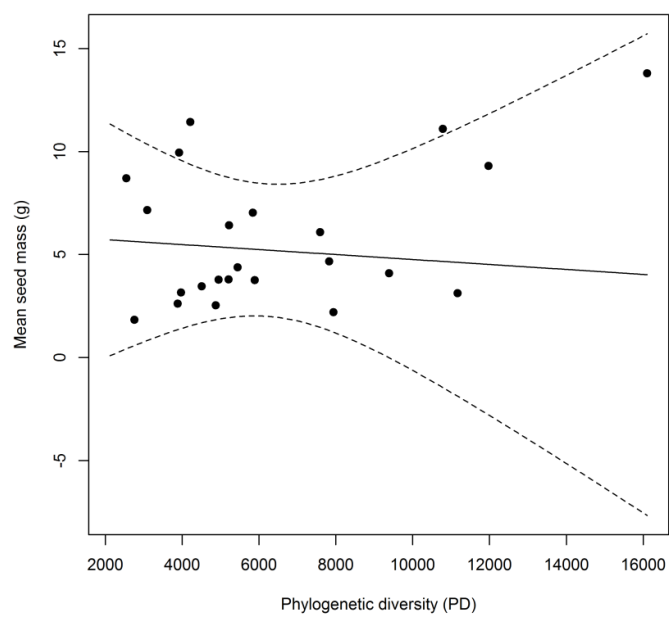
628



629 **FIGURE 4** Average seed masses of communities in 26 sampling sites (except sites of deserts) decline along rising
630 longitude and no significant relationships occur between seed mass and phylogenetic diversity



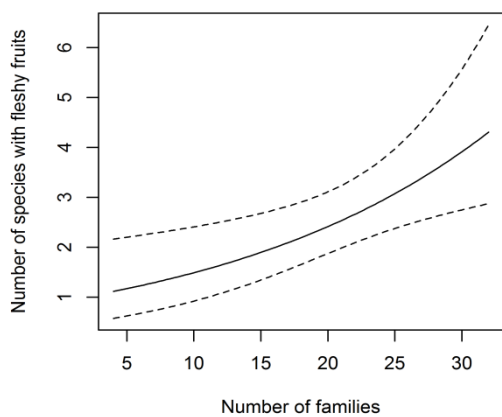
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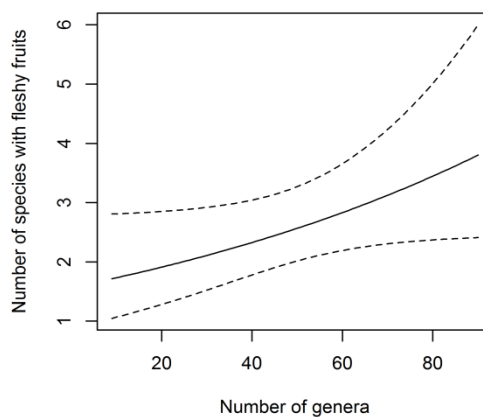


633 **FIGURE 5** Number of species with fleshy fruits rises in 23 sites (Ejinaqi, Wulatehouqi and Wulatezhongqi are not
634 included) rises along increasing longitude and no significant relationships are found with phylogenetic diversity
635 (families, genera and species)



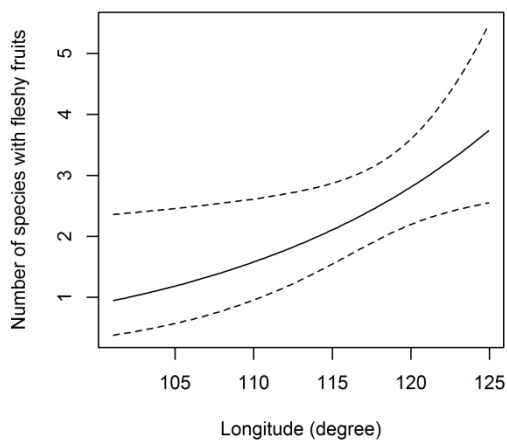
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(a)



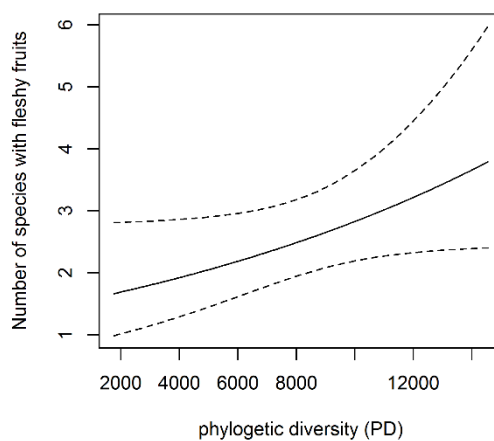
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(b)



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(c)



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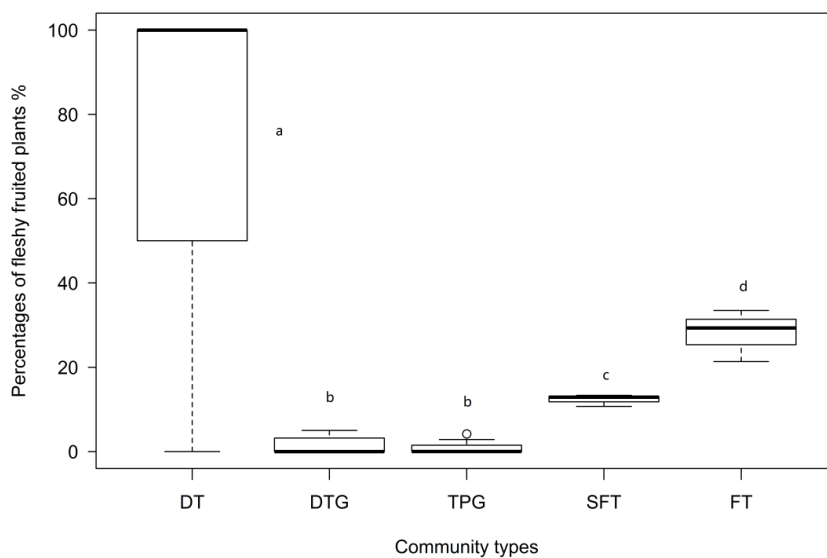
(d)

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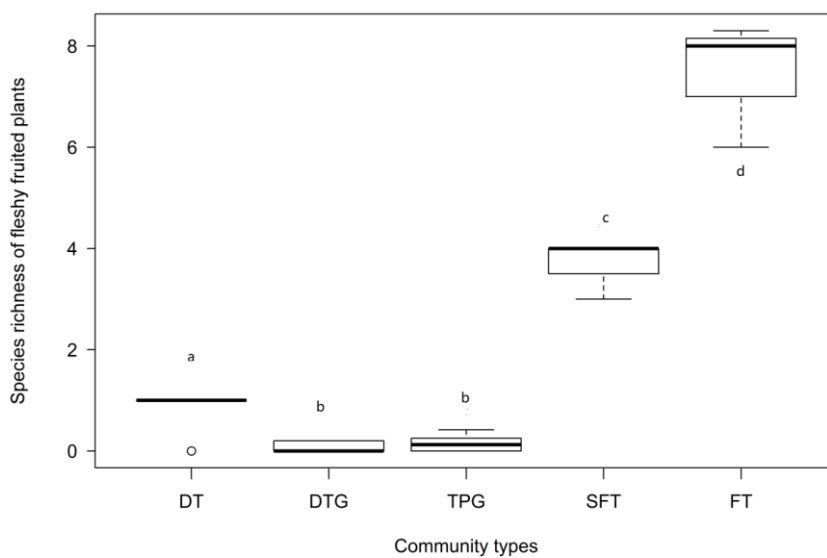
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642 **FIGURE 6** Proportions and species richness of plants with fleshy fruits decline gradually from forests to desert
643 grasslands, but increase in deserts (DT: deserts, DTG: desert grasslands, TPG: Typical grassland, SFT: Sparse forests,
644 FT: forests)



645



646