

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

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

area, much more photosynthate (photosynthesis production) and allometric growth then ultimately increase the biome average seed mass from west to east. Phylogenetic signal or diversity are not found to be significantly involved into the effect on the patterns. A novel mechanistic framework and mathematical model are provided to expound seed variation among species or biomes.

1 Introduction

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

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

50 at a continental scale along longitude. Previous work suggested that community-level average seed mass tends to
51 decrease towards higher latitudes and elevations (Moles et al., 2007). These trends can be explained by shifts in habitat
52 type, plant growth form spectra, seed disperser assemblage (Moles and Westoby, 2003), solar radiation and metabolic
53 expenditure (Murray et al., 2003; 2004) and NPP (Bu et al., 2007; Guo et al., 2010) along latitudinal and elevational
54 gradients. Additionally, species that prefer shaded habitats and late successional stages generally tend to have larger
55 seeds than those in open arid habitats or earlier successional stages (Baker, 1972; Salisbury, 1974; Foster and Janson,
56 1985; Hallett et al., 2011; Moles and Westoby, 2006), indicating a strong effect of high water availability on seed mass
57 owing to low evaporation under close canopy coverage. Longitudinal variations of seed mass has been discussed
58 among species with a single genus (Murray et al., 2003; 2004); however, there are few studies that focus on how
59 community-level variations of seed mass (especially across species) correspond with other plant traits along
60 longitudinal gradients, because of the difficulty to predict variations of comprehensive environmental factors arising
61 from complex topography. In this region average seed mass is expected to decrease with declining longitude due to
62 gradually less rainfall from forests to desert ecosystems (Murray et al., 2003; 2004). Here we present a study of
63 community-level variations in seed mass in correspondence to position in the continent (relative to the sea) across
64 Inner Mongolia and northeastern China, to identify the longitudinal pattern and discuss the mechanisms that may
65 underlie them.

66 Previous works emphasize the role of high light acquisition and allometric growth (a growth pattern in which
67 different parts of an organism grow at defined rates) in shaping seed mass variation through model prediction and
68 experiment testing (Demalach and Kadmon, 2018; Demalach et al., 2019), and in this article we emphasize the
69 importance of high water availability and allometric growth for speciation and colonization of species with large seeds
70 due to environmental factors and biological traits. Allometry of biomass growth and size-asymmetry of light
71 competition became the drivers of seed mass variation owing to soil resource availability and ultimate productivity
72 heterogeneity along soil resource gradient (surely including water gradient). As we know, primary production of
73 communities increases across an increasing water gradient (Bai et al., 2008). This article presents a novel mechanistic
74 framework that integrates previous theory and hypotheses (related to climate, phylogeny, water conduction systems

75 and other traits related to water balance) to evaluate seed mass variation among species or communities.

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

90

91 **2 Methods**

92 **2.1 Study sites and plant community characterization**

93 The study area is located in continental arid Inner Mongolia plateau, where vegetation types shift from broad-leaved
94 deciduous forest to typical grassland and finally to desert (from east to west, respectively), due to a gradual increase in
95 sunshine duration (from 3000 to 3200h/y) and intensity (from 586×10^4 to 796×10^4 KJ/m²) and decrease in rainfall
96 (from 780.6 to 29 mm) (Table 1). The study was carried out in 26 sites along this gradient, extending between
97 longitude 100°E ~ 124°E (about 2864 km distance between the westernmost and easternmost sites) and 41°N ~ 44° N
98 in Inner Mongolia and northeastern China (Table 1).

99 Different sampling designs were used in different habitat types, owing to differences in vegetation structure and

density. Within each forest plot, 6 quadrats of 10×10 m 2 were selected at random in undisturbed or slightly disturbed (at least in recent several years) areas. For shrub communities and herbaceous communities, 3 quadrats of 5×5 m 2 and at least 8 quadrats 1×1 m 2 were investigated, respectively. Species composition (species number and number of individuals per species) were recorded. The geographical positions (latitude, longitude and elevation) were measured by wireless GPS logger (HOLUX Technology Inc., Taiwan). Other physiographic factors such as grade of slope, slope aspect and micro-topography were recorded. The vegetation types were determined based on the dominant species and information referenced from the classification system of Chinese vegetation (Editorial Committee for Vegetation of China, 1980). Data of temperature and precipitation as well as other climatic factors were retrieved from the Wordclim database (<http://www.worldclim.org/> version1.4) using R raster package (R Core Team, 2017): average values per site were obtained from interpolations of observed data during the period between 1950 and 2000. Two climatic variables, mean annual temperature (MAT) and mean annual precipitation (MAP) were used to analyze the relationship between seed mass and the climate along the geographical gradient (Table 1).

112

113 **2.2 Seed collection and characterization**

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

125 Dispersal modes were assigned for all 622 species, based on ornamentation and appendages on fruits and seeds.
126 The dispersal modes of each species were confirmed by referring the Kew Gardens (Howe and Smallwood, 1982) and
127 literature collection from northwest China (Liu et al., 2014). For some species, dispersal modes were confirmed with
128 empirical analysis according to morphological features of their diaspores, and the dispersal modes represent how seeds
129 move from the parent plant to the soil surface. Each species was treated as having a single dispersal mode, reflecting
130 their principal dispersal agents (PDA) (Leishman and Westoby 1994; Butler et al., 2007): wind-adapted (279 species,
131 with wings, hairs or a pappus), vertebrate-adapted (66 species, with an aril or fleshy fruits), ant-adapted (195 species,
132 with an elaiosome), unassisted (70 species, no obvious morphological structure) and adhesion-adapted (12 species,
133 with hooks, spines or bards).

134

135 **2.3 Fruit types and other plant traits**

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

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

145

146 **2.4 Soil moisture measurement**

147 The soil moisture of top 10-cm depth was measured gravimetrically by oven-drying the samples at 105°C for 24 hours
148 in 12 sites of typical grasslands and desert grasslands. Five soil samples were collected from each sites on July 10-17,
149 2014, 21 days after rainfall.

150

151 **2.5 Data analysis**

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

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

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

175 (including both linear and quadratic terms) and the phylogenetic diversity measure PD as independent variables, we
176 built a linear model using R package stats (R Core Team, 2018).

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

183

184 **3 Results**

185 **3.1 Seed mass variations along the longitudinal gradient**

186 Although the majority of species had medium-sized seeds (Figure 1), variations among all species were great. There
187 were considerable differences in average seed mass and seed spectra among the five biome types (Figure 1). Forests
188 have the largest average seed mass (23.45 ± 18.34 mg) and both typical grasslands (4.75 ± 3.93 mg) and sparse forests
189 (4.45 ± 1.18 mg) have the lowest average seed mass. Average seed mass of forests is significantly greater than that of
190 the sparse forests ($F = 12.13$, $p = 0.0253$), and deserts are remarkably larger (20.12 ± 8.26 mg) than desert grasslands
191 (10.08 ± 2.34 mg) ($F = 6.914$, $p = 0.0466$), being nearly 4.2-fold decline in average seed mass from deserts to typical
192 grasslands. The average seed mass of typical grasslands is significantly smaller than that of desert grasslands ($F =$
193 11.92 , $p = 0.0025$), while there is no significant difference between average seed mass of typical grasslands and sparse
194 grasslands ($F = 0.019$, $p = 0.892$).

195

196 **3.2 Variation of species richness, growth form spectra and abundance along the longitudinal gradient**

197 There are declining trends for herbaceous species richness and canopy coverages from forests to desert along
198 decreasing longitudinal gradient in this region (Table 2). Typical steppe was found to have the lowest woody species
199 richness and highest herbaceous abundance in five community types (Table 2).

200
201 **3.3 Seed mass relations to growth forms, seed dispersers and fruit types**
202 Average seed mass of trees was significantly larger than that of shrubs ($F = 12.2, p = 0.000$), shrubs had larger seeds
203 than perennials ($F = 59.57, p = 0.000$), and average seed mass of perennials was larger than that of annuals ($F = 4.932,$
204 $p = 0.0268$, Figure 2).

205 Seeds that are dispersed by vertebrates ($232.09 \pm 823.98\text{mg}$) were significantly larger than those dispersed by
206 wind ($2.46 \pm 6.23 \text{ mg}$) ($F = 238.2, p < 0.0001$), ants ($3.56 \pm 10.03 \text{ mg}$) ($F = 17.73, p < 0.0001$), and those with
207 unassisted dispersal ($7.42 \pm 12.08 \text{ mg}$, $F=17.73, p=0.000$) and adhesive dispersal ($5.07 \pm 8.12 \text{ mg}$, $F = 17.73, p <$
208 0.0001 , Table 3).

209 Average seed mass of species with fleshy fruits ($40.15 \pm 110.41 \text{ mg}$) were significantly greater than that with dry
210 fruits ($26.58 \pm 286.97 \text{ mg}$) for the whole 622 species pool ($F = 18.61, p = 0.0125$), for the five community types
211 (Figure 2, SP 1) and for each sites (SP 2, Figure 2).

212 Seed mass is weakly negatively correlated with leaf area ($R^2 = 0.063, p = 0.005$) and not significantly correlated
213 with SLA across all sampled species ($R^2 = 0.006, p = 0.195$). SLA is significantly related with leave area ($R^2 = 0.160,$
214 $p < 0.001$).

215
216 **3.4 Seed mass relations to environmental variables**

217 Average seed mass was minimum at approximately 114 degrees longitude where typical grasslands occur (Figure 3).
218 However, phylogenetic diversity (PD) was not a significantly explanatory variable ($p > 0.8$) (Figure 3). Linear
219 regression model shows that there is no significant decreasing trend from forests to deserts along declining longitude
220 ($F = 2.289, p = 0.143$) in this region. If the westernmost sample site (Ejinaqi) is excluded, seed mass significantly
221 decrease inland ($R^2 = 0.2434, F = 7.398, p = 0.012$).

222 Significant negative relationships were found between seed mass and MAT ($R^2 = 0.1752, p = 0.01915$) and
223 elevation ($R^2 = 0.1221, p = 0.0449$) across all sample sites, but no significant relationships were found between seed
224 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

through desert grassland to typical grassland, average seed mass had significantly negative relationship with longitude ($R^2 = 0.232, p = 0.012$) and MAP ($R^2 = 0.48, p = 0.00015$), while across 20 sample sites from typical steppe to forests average seed mass had significantly positive relationship with longitude ($R^2 = 0.232, p = 0.012$) and MAP ($R^2 = 0.48, p = 0.00015$). Average seed mass was found to just be weakly positive relationship with MAT both from desert through desert grassland to typical grassland and from typical grassland to the forests ($R^2 = 0.09207, p = 0.08665$). According to above analysis, MAP should be crucial environmental drive factor for seed mass variation.

In addition, average seed mass is significantly related with soil moisture ($R^2 = 0.8259, p = 0.0017$) and soil moisture significantly decrease with declining longitude from typical to desert grasslands ($R^2 = 0.6019, p = 0.0018$).

3.5 Species richness and proportion of fleshy fruited species

Among the five community types, forests have the highest number (7.44 ± 1.26) and proportion (28.05 ± 6.16) of fleshy fruited species, while desert grasslands have the lowest number (0.06 ± 0.097) and typical grasslands have the lowest proportion (1.00 ± 1.49) (Figure 4). Fleshy fruited species richness ($F = 22.25, p = 0.00919$) and proportion ($F = 18.61, p = 0.0125$) in sparse forests are significantly smaller than those in forests. The desert has higher fleshy fruited species richness ($F = 6.081, p = 0.0239$) and proportion ($F = 24.9, p < 0.0001$) than desert grasslands. Sparse forests have remarkably higher fleshy fruited species richness ($F = 281.3, p = 0.000$) and proportion ($F = 78.6, p = 0.0009$) than typical grasslands (Figure 4).

3.6 Fleshy fruited species relations to environmental factors

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

250 MAT ($R^2 = 0.0414$, $p = 0.9416$).

251 From desert through desert grassland to typical grassland, significantly positive correlations were found between
252 richness of fleshy fruited species and longitude ($R = 0.3466$, $p = 0.0019$) and MAP ($R^2 = 0.284$, $p = 0.0052$), while
253 there were no significant correlations between proportion of fleshy fruited species and MAT ($R^2 = 0.1295$, $p = 0.0513$).
254 From typical grassland to the forests, remarkable correlations occurred between proportion of fleshy fruited species
255 and longitude ($R^2 = 0.324$, $p = 0.00418$) and MAP ($R^2 = 0.324$, $p = 0.00418$), however no significant relationships were
256 found between MAT and proportion ($R^2 = -0.0519$, $p = 0.9065$) and species richness ($R^2 = -0.0522$, $p = 0.93$) of fleshy
257 fruited plants. The number of species with fleshy fruits increased with longitude ($p = 0.022$) and number of families (p
258 = 0.005; Figure 5, a-b), but correlations with number of genera and phylogenetic diversity were not significant (p =
259 0.056 and 0.058, respectively) (Figure 5, c-d).

260

261 **3.7 Phylogenetic signals and their shift along longitudinal gradient**

262 Most phylogenetic signals (k values) are weak (from 0.234 to 0.688, $p > 0.05$) for the five biome types and for most
263 sample plots except Naimanqi (1.928, $p < 0.05$) in early-successional stage. No significant relationships are found
264 between phylogenetic signals (k values) and longitude across 26 sample sites ($R = 0.0403$, $p = 0.8596$). Both from
265 desert (to desert grasslands) to typical grasslands ($R = 0.047$, $p = 0.9123$) and from typical grasslands to the forests (R
266 = 0.0401, $p = 0.6382$), phylogenetic signals were not related to longitude for the five community types.

267

268 **4 Discussion**

269 **4.1 Variation of seed mass spectra and environmental factors**

270 There is strong and consistent effect of community type (along a longitudinal gradient) on seed mass (Figure 1, Figure
271 3). The average seed mass displays a significantly declining trend along decreasing longitude from forests to typical
272 grasslands and then to some sites in desert grasslands in this region (Figure 3). In these sites, average seed mass was
273 found to have significantly positive relationship with MAP and weakly positive relationship with MAT. The combined
274 effects of precipitation and temperature may be, to some extent, most important to certain vegetation syndromes such

275 as high seed mass and high fruit water content (Moles et al., 2014). High water availability potentially can produce
276 high assimilation products and high temperature (in normal range of plant growth) can increase water availability.

277 In this study average seed mass of each biome displays congruent distribution patterns to plant growth form spectra
278 variation (Table 2, Figure 1). General linear models (GLMs) revealed significant relationships between seed mass and
279 each of the variables predicted to influence the longitudinal gradient in seed mass: plant growth form (99.76%),
280 vegetation types (99.01%) and seed dispersal syndrome (99.88%), as the each variable reflects different profiles of
281 biome syndromes, not being independent effect factors to the seed mass. Such patterns have previously been attributed
282 mostly to a correspondence of seed mass to plant growth form and seed dispersal syndrome, which themselves are
283 driven by climatic and environmental variations (Moles et al. 2005a; Moles et al. 2007). In Inner Mongolia, typical
284 grasslands are often composed mainly of grasses (many of which are biennial and perennial) that are small-seeded
285 (Figure 2), whereas trees and lianas that dominate forests and shrubs that dominate deserts have the largest seeds
286 (Figure 2). Large seeds were proved to be often associated with woody growth forms (Salisbury, 1942; Baker, 1972;
287 Silvertown, 1981; Mazer, 1989; Jurado et al., 1991; Elenius and Torstensson 1991; Leishman and Westoby, 1994;
288 Moles et al., 2005a; Moles et al., 2005b). This pattern is often attributed to woody plants' better capability to take up
289 (Schenk and Jackson, 2002; Li et al., 2002; Qi et al., 2019) and store resources and to buffer effects of environmental
290 variations on seed size (Weiner, 2004; Moles et al., 2005a), or to reduced evaporation for understory species (Yu et al.,
291 2017). Surely, woody species, on average, having larger leaves, can produce more photosynthate to invest in seeds
292 (Díaz et al., 2016).

293 It is possible that larger seeds are more common in drought-prone habitats most likely because they allow
294 seedlings to establish large root systems early, with a better chance of surviving drought (Baker, 1972; Salisbury, 1974).
295 In this study, desert grassland and desert ecosystems are found to be dominated by shrubs that often possess larger
296 seeds (Figure 2). In Inner Mongolian Plateau these species are seldom exposed to strong interspecific competition or
297 shading that make the plants invest more in propagules than in vegetative apparatus for competitive strength (Bai et al.,
298 2008). In addition, relatively high species richness and the highest number of species occurred in this typical steppe
299 grassland (Table 2), and in contrast, desert steppe had very low species richness and number of individuals (abundance)

300 (Table 2).

301 With increasing MAP, richness of wind dispersed species decreased (SP3, SP4). The proportion of vertebrate
302 dispersed species in typical grasslands was the lowest in comparison to other communities (S4). The patterns of seed
303 dispersal syndromes observed in this study are congruent with previous findings in Australia's subtropics (Butler et al.,
304 2007). Biotic dispersal agents exert a strong selective pressure on angiosperm species with various seed size in Inner
305 Mongolian plateau, as evidenced by the evolution of a wide range of adaptations for animals (such as ants, birds,
306 squirrels) dispersal.

307

308 **4.2 Variation of fruit type spectrum and associations of seed mass with fruit types**

309 Fleshy fruited species richness significantly corresponded to gradual changes of climate, especially for MAP (Table 1).
310 The smallest proportion of fleshy fruited species occurred in typical grasslands and desert grasslands (Figure 3), at the
311 middle zone of Inner Mongolia. Previous findings showed that fleshy fruited species were often associated with shaded
312 habitats, mature forests, tropical forests, regions with lower elevations and woody life form (summarized in Yu et al.,
313 2017), indicating high canopy coverage and low evaporation (Figure 6). The increasing prevalence of canopy coverage
314 (Table 2, Figure 4) with increasing fleshy-fruited species is probably related to the prominence of species with larger
315 seeds in such habitats. Previous hypotheses suggest that fleshy fruit evolution is related to water availability and the
316 ineffectiveness of wind-assisted dispersal beneath a dense canopy (Butler et al., 2007; Yu et al., 2017). The reduced
317 dispersal capability following from an increase in seed mass may be counterbalanced by evolution of traits mediating
318 seed dispersal by animals, such as fleshy fruits. Alternatively, increasing water availability may promote the evolution
319 of species with fleshy fruits (Yu et al., 2017) and large seeds.

320

321 **4.3 Ecological and evolutionary drivers of seed mass variations**

322 A consistent combination was found between possession of fleshy fruits and heavier seeds when comparing seed mass
323 among clades with fleshy and non-fleshy fruits (Figure 2, SP1, SP2). The results were largely in agreement with
324 previous findings (Eriksson et al., 2000; Butler et al., 2007; Bolmgren and Eriksson, 2010). A possible explanation

325 may be that woody species have larger internal water surpluses and photosynthate to invest in their seeds and fruits.
326 Accordingly, formation of seed mass may also be related to plant resource acquisition and allocation strategies or to
327 allometric growth of plant apparatus (Weiner, 2004; Price et al., 2007; Demalach and Kadmon, 2018).

328 As a result of evolution for high water availability, large seeds are often associated with low latitude (Moles et al.,
329 2003) and low elevation (Bu et al., 2007), or with shaded habitats such as northern slopes (Csontos et al., 2004) and
330 closed vegetation (Mazer, 1989; Hammond and Brown, 1995) and with late successional stages (Hammond and Brown,
331 1995). All those phenomena indicate that seed mass may be related to low evaporation and high water availability in
332 plants (Figure 6). We suggest that, as an ecological strategy, the derivation and evolution of species with large seeds
333 may be due to improved water accommodation in plants by strong resource acquisition ability (such as having strong
334 water absorbing root system and advanced water conductive ability) or water retention ability (such as habituating
335 shaded environment or developing small, thick leaves and hair or waxiness on leaf to prevent water loss) (Baker, 1972;
336 Fonseca et al., 2000). Plant species have evolved various ecological strategies to match their environments (Laughlin,
337 2014). These strategies are manifested in many plant organs and traits. In the present study, seed mass is strongly
338 connected with other biological characteristics such as plant dispersal ability (SP 4, Table 3), fruit types and growth
339 forms. For example, there is rising trend in average leaf area (Wright et al., 2004) and water-conducting conduits
340 (Wheele et al., 2007; Zanne et al., 2014) along increasing longitude (or declining latitude and elevation). Seed mass
341 also is sure to be coordinated with conducting issues of plant apparatus (Wheele et al., 2007; Zanne et al., 2014).
342 Anatomical structures of lots of species indicated that the species with large seeds or fleshy fruits often have wide and
343 long vessel elements that can provide much more water (Carlquist, 1975; Zimmermann, 1983). As suggested before,
344 seed mass also is likely to be a result of co-evolution among various organs that determine plant responses to changing
345 abiotic factors (Díaz and Cabido, 1997; Sandel et al., 2010).

346 In light of growth allometry theory, average seeds mass variation should converge with community total biomass
347 (Demalach and Kadmon, 2018). Evidently, spatial distributions of community-level seed mass and NPP consistency
348 correspond (Moles and Westoby, 2003; Murray et al., 2003; Griffiths and Lawes, 2006; Chen et al., 2007; Chen et al.,
349 2011). In Inner Mongolia ANPP (aboveground net primary production) and RUE (rain-use efficiency) increased indeed

350 in space across different communities or ecosystems with increasing MAP eastwards (Bai et al., 2008), showing
351 similar variation trend with the average seed mass of the biomes. Both soil moisture and soil nutrient (total N) was
352 found to decrease significantly in Inner Mongolia from east to west (Liu et al., 2017), showing similar variation trend
353 with ANPP and seed mass. Moreover, water retention of plants is becoming unfavorable with increase of evaporation
354 westwards (Table 1).

355 In previous studies, soil moisture was found to not correlate with the relative abundance of fleshy-fruited species
356 due to low temperature on water availability constraints (Yu et al., 2017). As we know, seed plants employ two main
357 strategies to increase water use efficiency: one is to take up more water through strong root systems and the other is
358 reducing water loss through low evapotranspiration. In our study, canopy coverage decreases from forests to sparse
359 forests and then to grasslands and desert grasslands (Table 2), leads to gradual reduction in fleshy-fruited or
360 large-seeded species richness (Figure 5, Table 2). However, since fleshy fruits have high water content and thus inquire
361 higher plant internal water content (Yu et al., 2017), we suggest the correspondence of seed size and fruit water content
362 imply that some species evolved to contain more water or photosynthate in multiple body parts. Furthermore, CO₂
363 concentration is generally the same everywhere although there is some small variation during growth seasons (Wang et
364 al., 2002), its impact on seed mass variation patterns should be expelled. Solar radiation variation is not very large
365 along longitude (see site description) especially among typical grasslands, desert grasslands and deserts with similar
366 elevation, therefore, its effect on seed mass variation is very small, moreover, since light is not a limited factor for
367 growth in northern China according to our observation. Variation trend of sunshine hours or light intensity are contrary
368 to that of rainfall amount along longitude. Only when water remain sufficient, strong light may favor plant growth and
369 increase seed mass. For example, combination of much more belowground water with more sunshine hours or higher
370 light intensity in Erjina may increase its average seed mass, and this may be responsible for larger seed mass in desert
371 than in some sites of desert grasslands. Therefore, combined with previous results of other studies, we deduce that
372 drivers of seed mass spatial distribution patterns include temperature, rainfall, solar radiation, soil moisture and
373 nutrients, leaf area, canopy coverage and their interactions, however, high water availability in plant body may be the
374 most vital driving factor in shaping seed mass spatial distribution patterns. According to growth allometry, a fraction of

photosynthate, coming from each increment of temperature, rainfall, soil moisture and nutrients, leaf area, canopy coverage, is considered to be allocated to seeds. In addition, biological structures (such as fair or waxiness on leaf or fruits to prevent water loss), that favor water retention in plant body would also be useful in increasing seed mass or fruit water content.

In order to understand variation mechanism of seed mass better, a simple mechanistic model is provided to trying explain quantitatively average (or total) seed mass variation between communities for one species as following:

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

$$B_t = B_{id} + B_{i0} + B_l$$

S_t is the total seed mass of all species in a community, S_a is the average seed mass per species taken from the total community (S_t/n), n is number of species in a community, C_{i1} is the allometric growth coefficient (or allocation portion to seeds) that differ among species. B_t is total biomass from photosynthate per species. B_{id} value is the biomass of photosynthate related to water from conducting issues for one species, B_{i0} is the biomass of photosynthate related to water from other approach (for instances, lessening evaporation), B_l is the biomass of photosynthate related to leaf area (Figure 6). As we know, ecological factors affecting S_t are numerous. S_t will be developed according to other sufficient data basis. For instances, seed developing time, sunshine duration and intensity and belowground water may affect B_t , however, how affect and what extent will be done further in the future to improve and perfect B_t .

Generally, seed mass is quite phylogenetically conservative (Lord et al., 1995). However, in this study, phylogenetic signal is weak across the 26 sites (Table 1) and the phylogenetic signal are found to be little involved in the relationships between seed mass and longitude, MAP and MAT in the five biomes. This proves that the environmental factors affect seed mass variation in the community context and phylogenetic constraints are not significant (Figure 3, 4). The five communities are in middle or late successional stages in which the main construction process is environmental filtering (effect) rather than competitive exclusion (Norden et al., 2012).

In additions, in this study we just measure the soil moisture of top 10cm which mainly influence growth of herbs, but for the growth of shrubs and trees, rich soil water below the depth of 10 cm in some area of Ejinaqi also is useful.

399 As mentioned above, combination of much more belowground water with more sunshine hours or higher light
400 intensity in Erjina may increase seed mass and shape the present seed mass variation patterns in this region. Moreover,
401 ecological scale and micro-environmental heterogeneity often affects results of functional traits along biogeographical
402 gradients, so further study may be necessary in larger scale (or large investigation area) to identify the results of this
403 article.

404 **5 Conclusions**

405 Mean seed mass, seed dispersal spectra, fruit type spectra and plant growth form spectra of five biome types vary
406 significantly along a longitudinal gradient, with the lowest average seed mass and the smallest proportion of species
407 dispersed by vertebrates occurring at the middle longitude (typical grasslands). The selection for these propagule
408 attributes is most likely to be driven by external and internal drivers (Figure 6), however, water availability potentials
409 and growth-allometry may be key drivers of seed-mass variation along climatic gradients or resource gradients. Larger
410 seeded species or species with fleshy fruits may have evolved due to much photosynthate or high water availability in
411 plants. Our findings can provide help in understanding origin and evolution of species with large seeds or fleshy fruits.

412

413 *Author contributions*

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

418

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422

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586 **TABLE 1** Information about geographic positions and environmental factors in 26 sampling sites in Inner
 587 Mongolia plateau and Northeastern China (MAP: mean annual precipitation, MAT: mean annual temperature, *K*-value:
 588 phylogenetic signal values, the small the values, the weak the signals. Vegetation types: Deserts-DS, Desert
 589 grasslands-DG, Typical grasslands-TG, Sparse forest-SF, Forests-FR) 

Number	Site names	Longitude	Latitude	Altitude (m)	MAP(mm)	MAT (°C)	<i>K</i> - 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	Erlianhaote	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	Zhengxiangbailqi	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	Linx	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

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593 **TABLE 2** Species richness (No./sample area) or percentages for woody plants and herbs (%) as well as abundance
 594 (individual/m²) and canopy coverages (%) in five ecosystem types

Ecosystem types	Sites	Woody		Herbaceous		Abundance	Canopy coverages		
		species		species					
		Richness	Percentage	Richness	Percentage				
Forests	Qingyuan	11±2	40.0±4.5	16±1	60.0±4.5	30±9	80-90		
Sparse forests	Sanggandalai	5±2	18.0±5.2	24±2	82.0±5.2	126±8	20-40		
Typical steppe	Sanggandalai	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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TABLE 3 Seed mass, species number and proportions of 5 dispersal types in the whole study area

Dispersal agent types	Seed mass (mg)	Species number	Occurrence proportion (%)
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

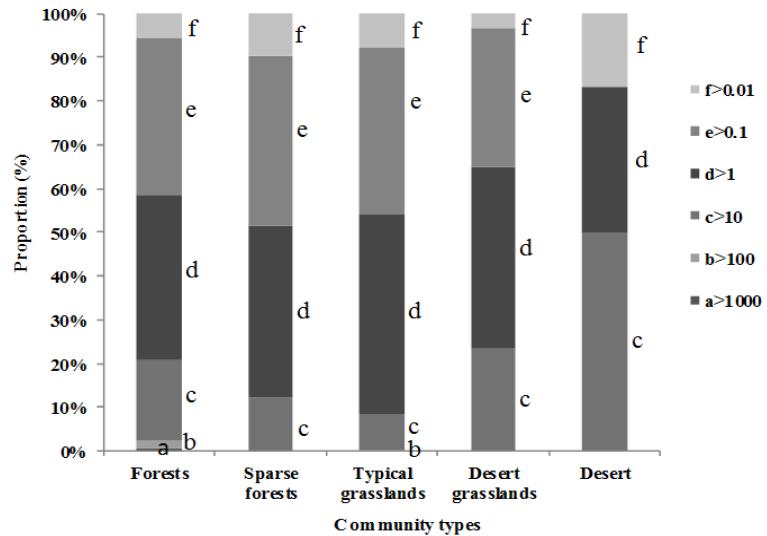
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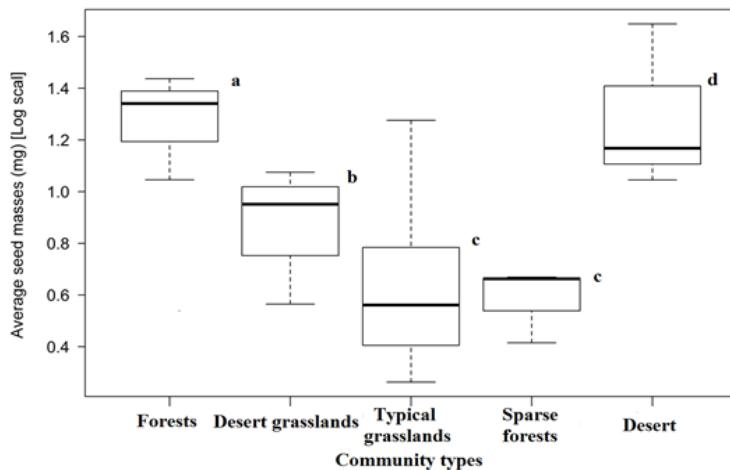
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602 **FIGURE 1** Seed mass spectra vary among five community types in Inner Mongolia (A) and proportions of larger
 603 seeds (A) and average seed mass (B) decline from forests to desert grasslands but increase in deserts (Average seed
 604 mass bearing the same letter are insignificantly different at $p > 0.05$) 

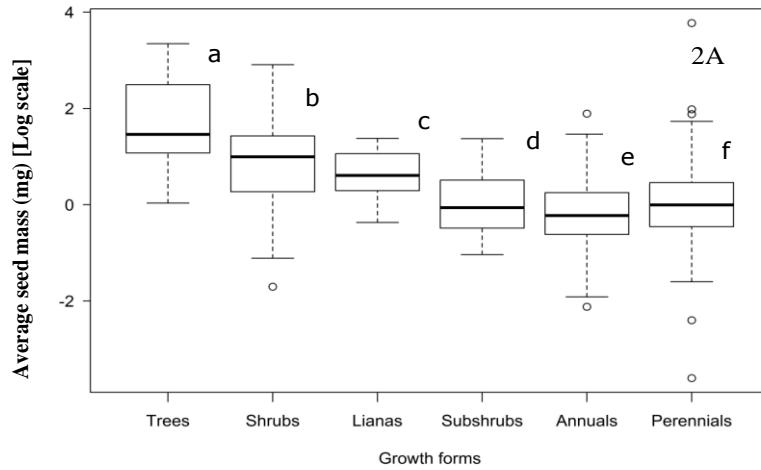


605 (A) 

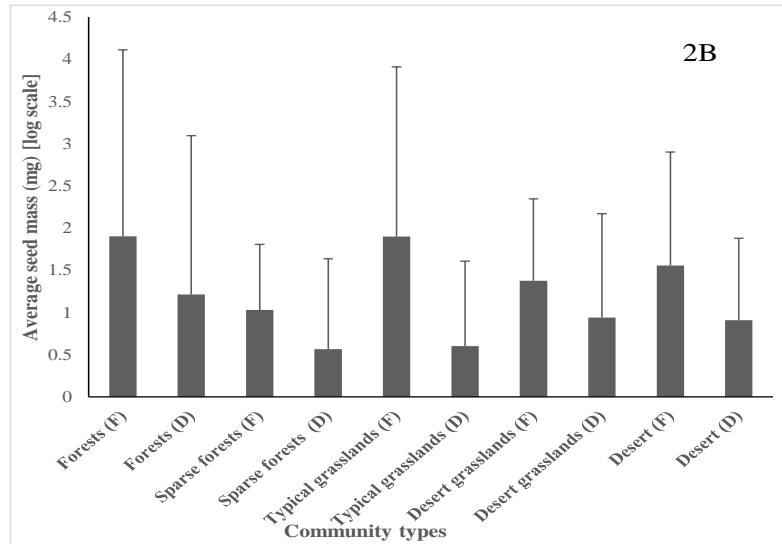


607 (B)

609 **FIGURE 2** Trees (12 species) have the largest average seed mass, followed by shrubs (65 species), lianas (15 species),
610 subshrubs (20 species), perennial herbs (396 species) and annuals (110 species) (2A) (Average seed mass bearing the
611 different letter are significantly different at $p < 0.05$). Average seed mass of fleshy fruits is larger than that of dry fruits
612 in each community type (2B) (F: fleshy fruits, D: dry fruits) 



613

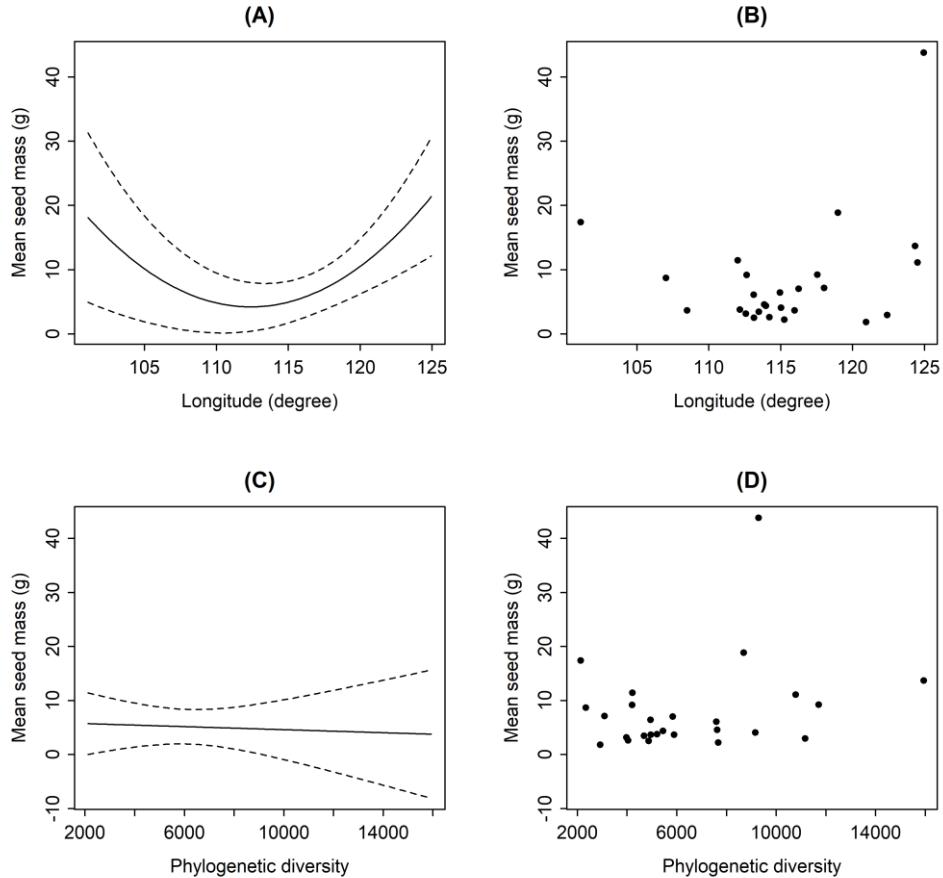


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616

617 **FIGURE 3** Relationships between average seed mass of communities and longitude (A, B) and phylogenetic diversity
 618 (C, D). Average seed mass declines as longitude rises and it reaches its bottom at around 114 degrees, and after that it
 619 increases. But average seed mass do not have significant relationships with phylogenetic diversity ($p>0.05$)
 620 



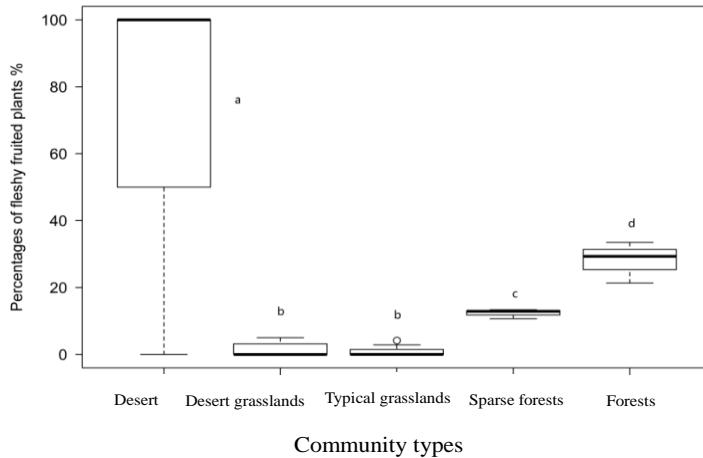
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622

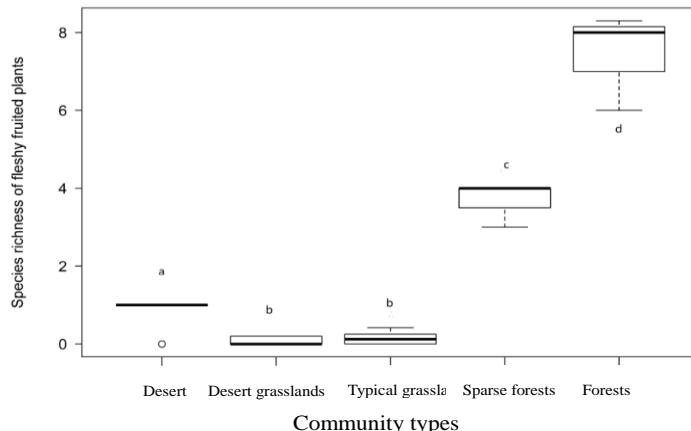
623

624

625 **FIGURE 4** Proportions (A) and species richness (B) of plants with fleshy fruits decline gradually from forests through
 626 sparse forests to (typical and desert) grasslands, but increase in deserts (The same letter indicates difference is
 627 insignificant at $p > 0.05$) 



(A)

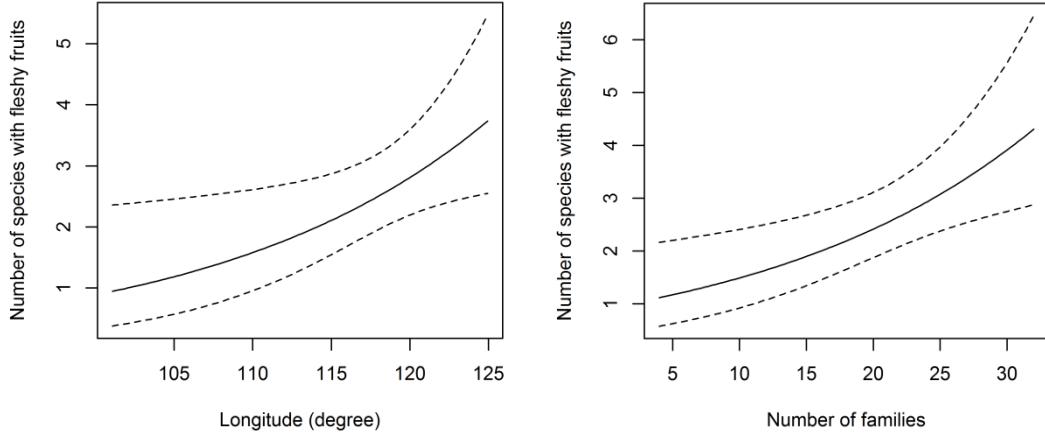


(B)

628

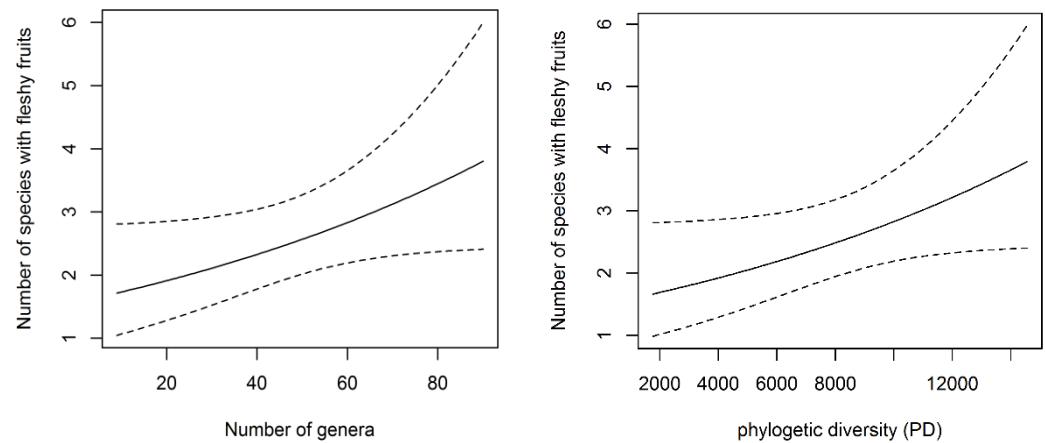
629

632 **FIGURE 5** Relationships between number of species with fleshy fruits and longitude (a), number of families and
633 genera (b, c) as well as phylogenetic diversity (d). Number of species with fleshy fruits increases as longitude increases.
634 But it does not have significant relationship with phylogenetic diversity ($p>0.05$)



(a)

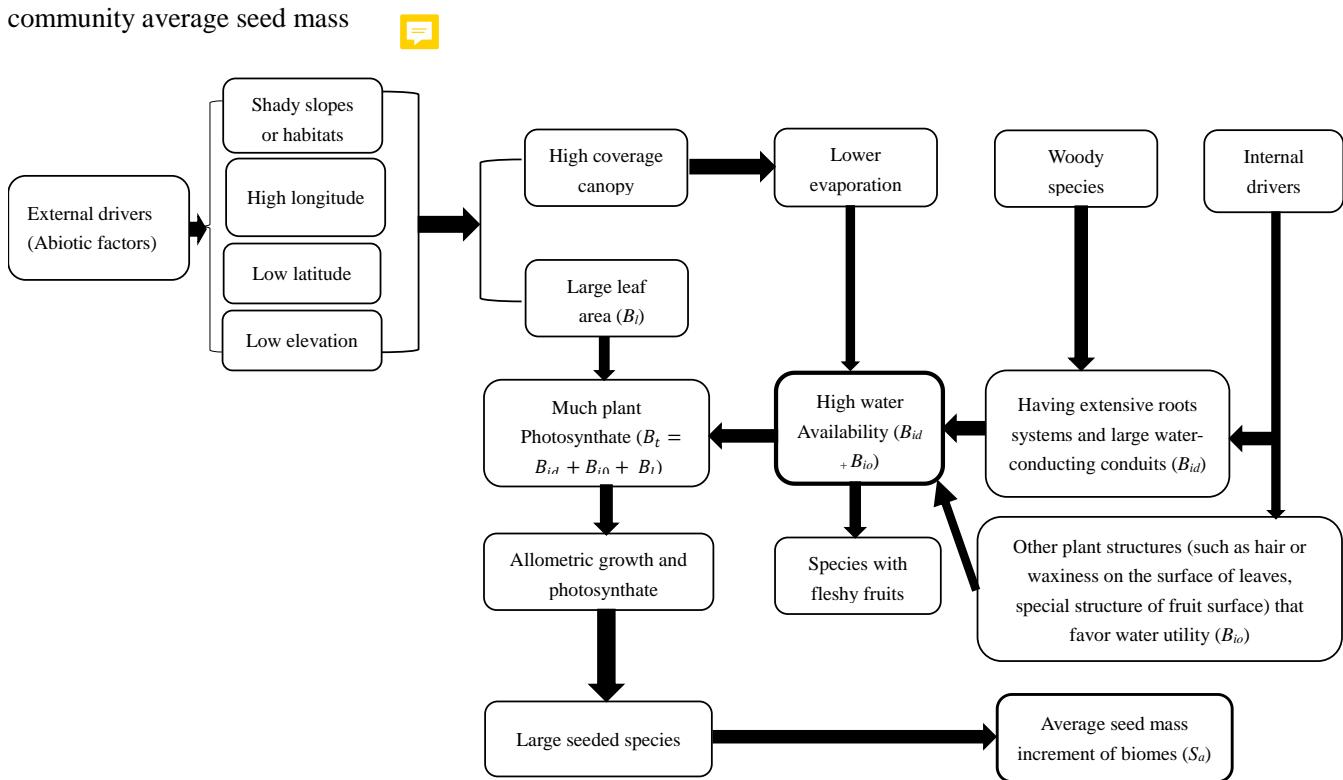
(b)



(c)

(d)

641 **FIGURE 6** Mechanistic frameworks of large seeded species formation and corresponding increment process of
 642 community average seed mass



Dear Anja Rammig,

Thank you very much for careful works! According to your opinions, we had revised those mistakes as following.

Shunli Yu

-
- 1) Table 1: Information about geographic.... of the 26 sampling sites... K-value: phylogenetic signal values with smaller values indicating a weaker signal.

In the caption of Table 1, you do not need to give a definition for evaporation. Please remove the sentence: Evaporation: the change process of evaporating from a liquid to a vapor.

We had removed the sentence: Evaporation: the change process of evaporating from a liquid to a vapor.

- 2) Table 3 last column, please revise and change to “Proportional occurrence”, is that correct?

We had changed “Proportion in the whole” into “Occurrence proportion” in Table 3 last column.

- 3) The text for the caption of Figure 1 is not clear, please revise.

We had revised the caption of Figure 1 and it had become “Seed mass spectra vary among five community types in Inner Mongolia (A) and proportions of larger seeds (A) and average seed mass (B) decline from forests to desert grasslands but increase in deserts (Average seed mass bearing the same letter are insignificantly different at $p > 0.05$)”.

- 4) Figure 1A, y-axis label, please change to “Proportion (%).”

We had changed “Proportion (%)” into “Proportion (%)” in y-axis label of Figure 1A.

- 5) The resolution of Fig. 1A and B is not very good, please improve.

We had improved resolution of Fig. 1A and B.

- 6) Caption of Figure 3, please revise: “... Average seed mass has a U-shape and declines with increasing longitude with lowest level at around 114 degrees. Average seed mass do not have significant relationships with phylogenetic diversity ($p>0.05$)....”. Please also correct x-axis labels in Fig. 3D, longitude values are different from A and B.

We had changed the caption into “Relationships between average seed mass of communities and longitude (A, B) and phylogenetic diversity (C, D). Average seed mass declines as

longitude rises and it reaches its bottom at around 114 degrees, and after that it increases. But average seed mass do not have significant relationships with phylogenetic diversity ($p>0.05$)”.

We also corrected x-axis labels in Fig. 3D as “Phylogenetic diversity”.

7) The text for the caption of Figure 6 is not clear, please revise.

We had revised the caption of Figure 6 and turned it into “Mechanistic frameworks of large seeded species formation and corresponding increment process of community average seed mass”.

8)

In addition, we had revised Fig.2A (for instances, scal to scale in y-axis, seed masses to seed mass) and Fig.2B (for instances, fleshy fruits, f to F, dry fruits, d to D).

We had revised Fig.4, for example, “insignificant at $p < 0.05$ ” to “insignificant at $p > 0.05$ ”.