Response to the referees

We thank the two reviewers for their valuable comments. According to their suggestions, we revised our article, and the revision details are as follows.

Referee 2

1）To make the novel mechanistic framework that you present more prominent from the beginning, rather than introducing it towards the end,

We had adjusted the position of the mechanistic framework from the discussion to the beginning (introduction) of the article.

2）…and implement a modelling approach that could disentangle these mechanistic processes rather than base results purely on correlations.

According to referee's suggestions, 1) we revised the mechanistic framework, supplementing new information; 2) we implemented a model that disentangle how the seed mass improved with water increment in discussion. 3) Four references were added. 4) Abstract was revised again.

3）Additionally, figure captions should be improved, indicating more clearly what is shown and why (related to which question), so that they can stand by themselves without having to read the whole results section.

We had improved each figure caption in this article according to the referee's suggestions.

Referee 1

1） We revised our article again.

In addition, some small mistakes were corrected, for instances, fair to hair, in line 386.

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

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Abstract. Propagule traits vary among biomes along geographical gradients such as longitude, but the mechanisms that underlie these variations remain unclear. This study aims to explore seed mass variation patterns of different biome~~s~~ types along a longitudinal gradient and their underlying variation mechanisms by involving an in-depth analysis on the variation of seed mass, fruit type spectra, growth forms and dispersal mode spectra in Inner Mongolia and northeastern China. Plant ~~community~~ biome characterization and seed collection were conducted in 26 sites spreading over five vegetation ~~ty~~types and covering 622 species belonging to 66 families and 298 genera. We found there are significantly declining trend for mean seed mass, vertebrate-dispersed species richness and fleshy-fruited species richness along a longitudinal gradient from forests to desert grasslands in the study region. However, we also found the lowest average seed mass and the smallest proportion of species dispersed by vertebrates occurring at typical grasslands in the five biomes. The variations of average seed mass display high congruent with transition of growth form spectra~~spectra~~. The selection for these propagule attributes is driven mainly by climatic factors such as precipitation, temperature, soil moisture and evaporation, as well as by internal biotic factors such as growth forms, canopy coverage and leaf area. A hypothesis was provided that environmental factors and botanical traits that favor greater water availability lead to emergence (or speciation) of 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. ~~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 mass 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 of 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~~ and canopy coverage~~ both among and within communities (Moles et al., 2007) and several ecological factors ~~mechanisms~~ 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 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 availibility 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. In this region 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 (a growth pattern in which different parts of an organism grow at defined rates) ~~(a growth pattern in which different parts of an organism grow at defined rates)~~ 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~~ (Figure1)~~.

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

2 Methods

2.1 Study sites and plant community characterization

The study area is located in continental arid Inner Mongolia plateau, where vegetation types shift from broad-leaved deciduous forest to typical grassland and finally to desert (from east to west, respectively), due to a gradual increase in sunshine duration (from 3000 to 3200h/y) and intensity (from 586×10^4 to 796×10^4 KJ/m^2) and decrease in rainfall (from 780.6 to 29 mm) (Table 1). ~~due to a gradual increase in sunshine duration (3000-3200h/y) and intensity (586×10^4~~

~~- 796×10^4 KJ/m^2) and decrease in rainfall (from 780.6 to 29 mm) (Table 1).~~ The study was carried out in 26 sites along this gradient, extending between longitude 100°E ~ 124°E (about 2864 km distance between the westernmost and easternmost sites) and 41°N ~ 44° N in Inner Mongolia and northeastern China (Table 1).

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 m² were selected at random in undisturbed ~~Within each forest plot, 6 quadrats of 10×10 m² were selected uniformly at random in undisturbed~~ or slightly disturbed ~~- (at least in recent several years)~~ areas (at least in recent several years). For shrub communities and herbaceous communities, 3 quadrats of 5×5 m²and at least 8 quadrats 1×1 m²were 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. ~~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).

2.2 Seed collection and characterization

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

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

2.3 Fruit types and other plant traits

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

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

2.4 Soil moisture measurement

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

2.5 Data analysis

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

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

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

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

3 Results

3.1 Seed mass variations along the longitudinal gradient

Although the majority of species had medium-sized seeds (Figure 1), variations among all species were great. There were considerable differences in average seed mass and seed spectra among the five biome types (Figure 1). Forests have the largest average seed mass (23.45 ± 18.34 mg) and both typical grasslands (4.75 ± 3.93 mg) and sparse forests (4.45 ± 1.18 mg) have the lowest average seed mass. ~~There were considerable differences in average seed mass and~~

~~seed spectra among the five community types (Figure 1). Forests have the largest average seed mass (23.45±18.34 mg) and both typical grasslands (4.75±3.93 mg) and sparse forests (4.45 ± 1.18 mg) have the lowest average seed mass.~~ Average seed mass of forests is significantly greater than that of the sparse forests (F = 12.13, $p = 0.0253$), and deserts are remarkably larger (20.12 ± 8.26 mg) than desert grasslands (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 grasslands. The average seed mass of typical grasslands is significantly smaller than that of desert grasslands (F = 11.92, $p = 0.0025$), while there is no significant difference between average seed mass of typical grasslands and sparse grasslands (F = 0.019, $p = 0.892$).

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

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

3.3 Seed mass relations to growth forms, seed dispersers and fruit types

Average seed mass of trees was significantly larger than that of shrubs (F = 12.2, $p = 0.000$), shrubs had larger seeds than perennials (F = 59.57, $p = 0.000$), and average seed mass of perennials was larger than that of annuals (F = 4.932, $p = 0.0268$~~) (~~, Figure 2).

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

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

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

3.4 Seed mass relations to environmental variables

Average seed mass was minimum at approximately 112 degrees longitude where typical grasslands occur (Figure 3). However, phylogenetic diversity (PD) was not a significant explanatory variable ($p > 0.8$) (Figure 3). Linear regression model shows that there is no significant decreasing trend from forests to deserts along declining longitude ($F = 2.289$, $p = 0.143$) in the study area. If the westernmost sample site (Ejinaqi) is excluded, seed mass significantly decrease inland ($R^2 = 0.2434$, $F = 7.398$, $p = 0.012$).

Significant negative relationships were found between seed mass and MAT ($R^2 = 0.1752$, $p = 0.01915$) and elevation ($R^2 = 0.1221$, $p = 0.0449$) across all sample sites, but no significant relationships were found between seed 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 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 ($p < 0.05$) and soil moisture significantly decrease with declining longitude from typical to desert grasslands in the study area.

3.5 Species richness and proportion of fleshy fruited species

Among the five biome types, ~~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 the lowest proportion (1.00 ± 1.49) (Figure ~~5~~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 ~~5~~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 MAT ($R^2 = 0.0414$, $p = 0.9416$).

From desert through desert grassland to typical grassland, significantly positive correlations were found between richness of fleshy fruited species and longitude (R = 0.3466, $p= 0.0019$) and MAP ($R^2 = 0.284$, $p = 0.0052$), while there were no significant correlations between proportion of fleshy fruited species and MAT ($R^2 = 0.1295$, $p = 0.0513$). From typical grassland to the forests, remarkable correlations occurred between proportion of fleshy fruited species and longitude ($R^2 = 0.324$, $p = 0.00418$) and MAP ($R^2 = 0.324$, $p = 0.00418$), however no significant relationships were found between MAT and proportion ($R^2 = -0.0519$, $p=0.9065$) and species richness ($R^2 = -0.0522$, $p = 0.93$) of fleshy fruited plants. The number of species with fleshy fruits increased significantly with longitude ($p = 0.022$, Figure 5 a) and number of families ($p = 0.005$, Figure 5 b), but correlations with number of genera and phylogenetic diversity were not significant ($p = 0.056$ and 0.058 respectively) (Figure ~~4~~5~~,~~ c~~e~~, ~~-d~~d).

3.7 Phylogenetic signals and their shift along longitudinal gradient

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

4 Discussion

4.1 Variation of seed mass spectra and environmental factors

There is strong and consistent effect of community type (along a longitudinal gradient) on seed mass (Figure 1, Figure 3). The average seed mass displays a significantly declining trend along decreasing longitude from forests to typical grasslands and then to some sites in desert grasslands in this region (Figure 3)~~The average seed mass displays a significantly declining trend along decreasing longitude from forests to typical grasslands and then to some sites in desert grasslands in this study (Figure 3), showing congruent distribution patterns to plant growth form spectra variation (Table 2)~~. In these sites, average seed mass was found to have significantly positive relationship with MAP and weakly positive relationship with MAT. The combined effects of precipitation and temperature may be, to some extent, most important to certain vegetation syndromes such as high seed mass and high fruit water content (Moles et al., 2014). High water availability potentially can produce high assimilation products and high temperature (in normal range of plant growth) can increase water availability. ~~The combined effects of precipitation and temperature may be, to some extent, most important to certain vegetation syndromes such as high seed mass and high fruit water content (Moles et al., 2014). High water availability potentially can produce high assimilation products and high temperature (in normal range of plant growth) can increase water availability.~~

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

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

With increasing MAP, richness of wind dispersed species decreased (S3, S4) in the study region. The proportion of vertebrate dispersed species in typical grasslands was the lowest in comparison to other communities (S4). The patterns of seed dispersal syndromes observed in this study are congruent with previous findings in Australia's subtropics (Butler et al., 2007). Biotic dispersal agents exert a strong selective pressure on angiosperm species with various seed size in Inner Mongolian plateau, as evidenced by the evolution of a wide range of adaptations for animals (such as ants, birds, squirrels) dispersal. ~~(such as ants, birds, squirrels) dispersal.~~

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

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

4.3 Ecological and evolutionary drivers of seed mass variations

A consistent combination was found between possession of fleshy fruits and heavier seeds when comparing seed mass among clades with fleshy and non-fleshy fruits (Figure 2, S1, S2). The results were largely in agreement with previous findings (Eriksson et al., 2000; Butler et al., 2007; Bolmgren and Eriksson, 2010). A possible explanation may be that woody species have larger internal water surpluses and photosynthate to invest in their seeds and fruits as mentioned above. Accordingly, formation of seed mass may also be related to plant resource acquisition and allocation strategies or to allometric growth of plant apparatus (Weiner, 2004; Price et al., 2007; Demalach and Kadmon, 2018).

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 (Figure 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 the 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~~ in plants is becoming unfavorable with increase of evaporation westwards (Table 1).

In previous studies, soil moisture was found to not correlate with the relative abundance of fleshy-fruited species due to low temperature on water availability constraints (Yu et al., 2017). As we know, seed plants employ two main strategies to increase water use efficiency: one is to take up more water through strong root systems and the other is reducing water loss through low evapotranspiration. In our study, canopy coverage decreases from forests to sparse forests and then to grasslands and desert grasslands (Table 2), leads to gradual reduction in fleshy-fruited or large-seeded species richness (Figure ~~5~~4, Table 2). However, since fleshy fruits have high water content and thus inquire higher plant internal water content (Yu et al., 2017), we suggest the correspondence of seed size and fruit water content imply that some species evolved to contain more water or photosynthate in multiple body parts. Furthermore, CO$_2$ concentration is generally the same everywhere although there is some small variation during growth seasons (Wang et al., 2002), ~~although there is some small variation during growth seasons (Wang et al., 2002),~~ its impact on seed mass variation patterns should be expelled. Solar radiation variation is not very large along longitude (see site description) especially among typical grasslands, desert grasslands and deserts with similar elevation, therefore, its effect on seed mass variation is very small, moreover, since light is not a limited factor for growth in northern China according to our observation. Variation trend of sunshine hours or light intensity are contrary to that of rainfall amount along longitude. Only when water remain sufficient, strong light may favor plant growth and increase seed mass. For example, combination of much more belowground water with more sunshine hours or higher light intensity in Erjina may increase its average seed mass, and this may be responsible for larger seed mass in desert than in some sites of desert grasslands. ~~Solar radiation variation is not very large along longitude (see site description) especially among~~

~~typical grasslands, desert grasslands and deserts with similar elevation, therefore, its effect on seed mass variation is very small, moreover, since light is not a limited factor for growth in northern China according to our observation. Variation trend of sunshine hours or light intensity are contrary to that of rainfall amount along longitude. Only when water remain sufficient, strong light can favor plant growth and increase seed mass.~~ Therefore, combined with previous results of other studies, we deduce that drivers of seed mass spatial distribution patterns include temperature, rainfall, solar radiation, soil moisture and nutrients, leaf area, canopy coverage and their interactions, however, high water availability in plant body may be the most vital driving factor in shaping seed mass spatial distribution patterns. ~~For example, combination of much more belowground water with more sunshine hours or higher light intensity in Erjina may increase the average seed mass, and this may be responsible for larger seed mass in desert than in some sites of desert grasslands. Therefore, combined with previous results of other studies, we deduce that drivers of seed mass spatial distribution patterns include temperature, rainfall, solar radiation, soil moisture and nutrients, leaf area, canopy coverage and their interactions, however, high water availability in plant body may be the most vital driving factor in shaping seed mass spatial distribution.~~ 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 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:

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

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

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 (St/n), n is number of species in a community, C_{i1} is the allometric growth coefficient (or allocation portion to seeds)~~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 (St/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. St 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 to affect and what extent will be ~~done~~ conducted 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 ~~five communities~~signal ~~and~~ 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 environment affects seed mass 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).~~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. As mentioned above, combination of much more belowground water with more sunshine hours or higher light intensity in Erjina may increase seed mass and shape the present seed mass variation patterns in this region. ~~As mentioned above, combination of much more belowground water with more sunshine hours or higher light intensity in Erjina can increase seed mass and may be the other ecological factors for the present seed mass patterns.~~ Moreover, ecological scale and environmental heterogeneity often affects results of functional traits along biogeographical gradients, so further study may be necessary in larger scale (or large investigation area) to identify the results of this article.

5 Conclusions

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

Author contributions

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

Acknowledgements

This study was funded by the National Natural Science Foundation of China (No. 40771070，41171041) and Beijing Natural Science Foundation (No. 5092015).

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TABLE 1 Information geographic positions and environmental factors in 26 sampling sites in Inner Mongolia plateau and Northeastern China (MAP: mean annual precipitation, MAT: mean annual temperature, *K*-value: phylogenetic signal values, the small the values, the weak the signals. Evaporation: the change process of evaporating from a liquid to a vapor. Vegetation types: Deserts-DS, Desert grasslands-DG, Typical grasslands-TG, Sparse forest-SF, Forests-FR)~~**TABLE 1** Information geographic positions and environmental factors in 21 sampling sites in Inner Mongolia 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	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	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

~~MAP: mean annual precipitation, MAT: mean annual temperature, K-value: phylogenetic signal values, the small the values, the weak the signals. Evaporation: the change process of evaporating from a liquid to a vapor. Vegetation types: Deserts (DS), Desert grasslands (DG), Typical grasslands (TG), Sparse forest (SF), Forests (FR).~~

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

Ecosystem types	**Sites**	**Woody species**		**Herbaceous species**		**Abundance**	**Canopy coverages**
		Richness	Percentage	Richness	Percentage		
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

~~Ecosystem types~~	~~Sites~~	~~Woody~~		~~Herbaceous~~		~~Abundance~~	~~Canopy coverages~~
		~~Richness~~	~~Percentage~~	~~Richness~~	~~Percentage~~		
~~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~~

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**	**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

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

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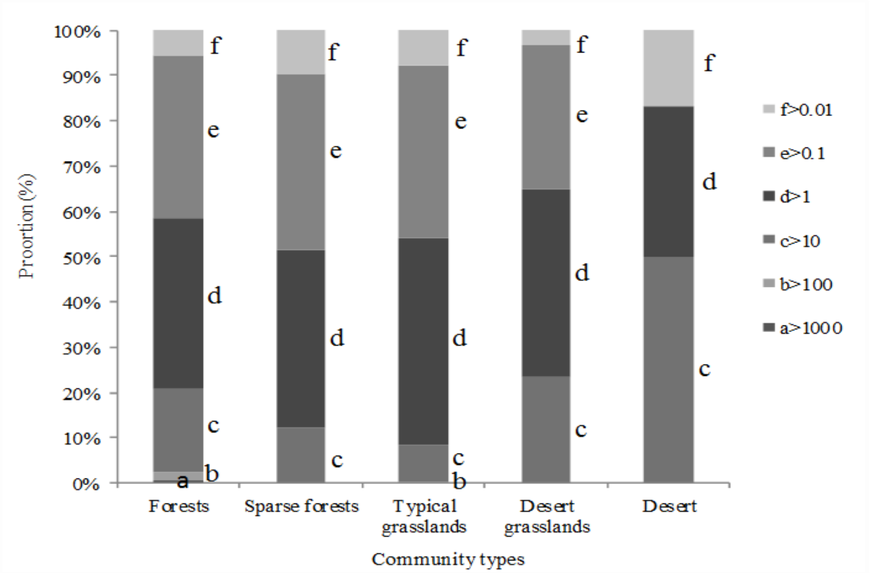
~~Total~~	~~50.12±172.09~~	~~622~~	~~100~~

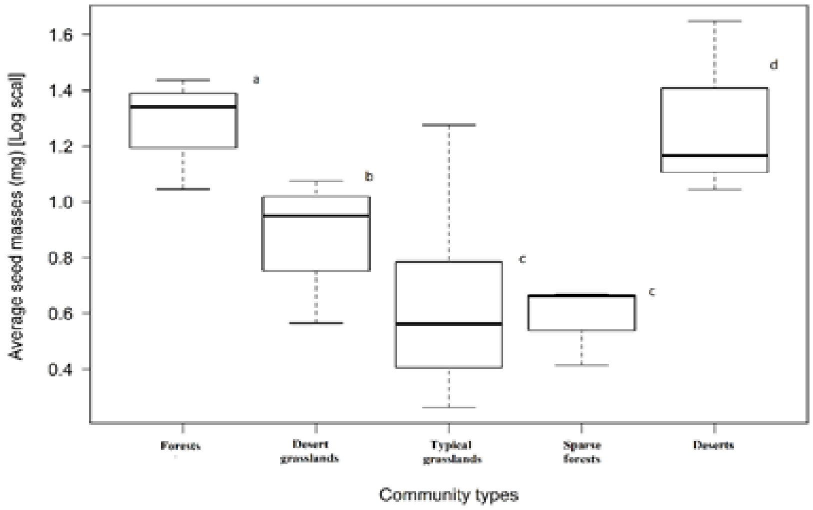
FIGURE 1 Seed mass spectra vary among five community types in Inner Mongolia and proportions of larger seeds (A) and average seed mass decline from forests to desert grasslands along decreasing longitude in the region but increase in deserts (Average seed mass bearing the same letter are not significantly different at $p < 0.05$, B)

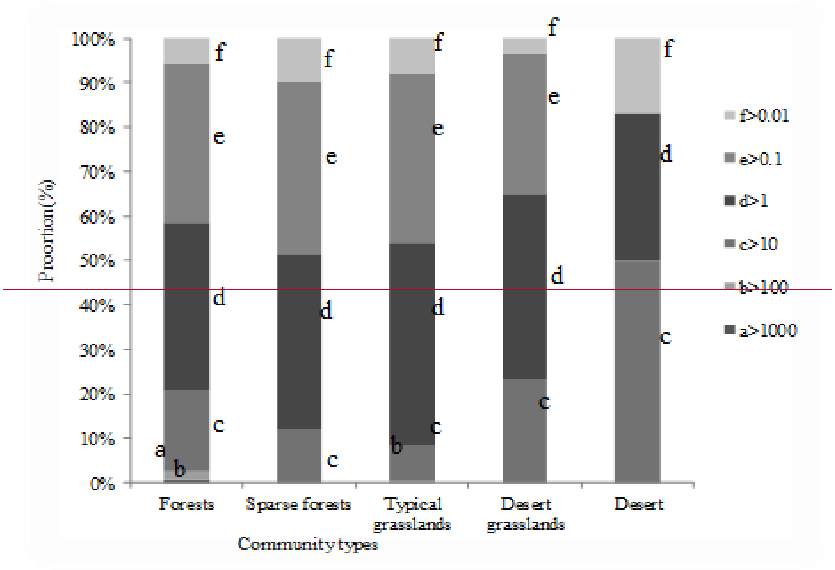


~~**FIGURE 1**~~

~~Seed mass spectra varied among five community types in Inner Mongolia and proportions of larger seeds and average seed mass decline from forests to desert grasslands along decreasing longitude but increase in deserts (Average seed mass bearing the same letter are not significantly different at $p < 0.05$)~~

(A)


1.6
1.4
1.2
1.0
0.8
0.6
0.4
Average seed masses (mg) [Log scal]
a
b
c
c
d
Forests
Desert grasslands
Typical grasslands
Sparse forests
Deserts
Community types


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proortion(%)
f
e
d
c
a
b
Forests
Sparse forests
Typical grasslands
Desert grasslands
Desert
Community types
f>0.01
e>0.1
d>1
c>10
b>100
a>1000

(B)

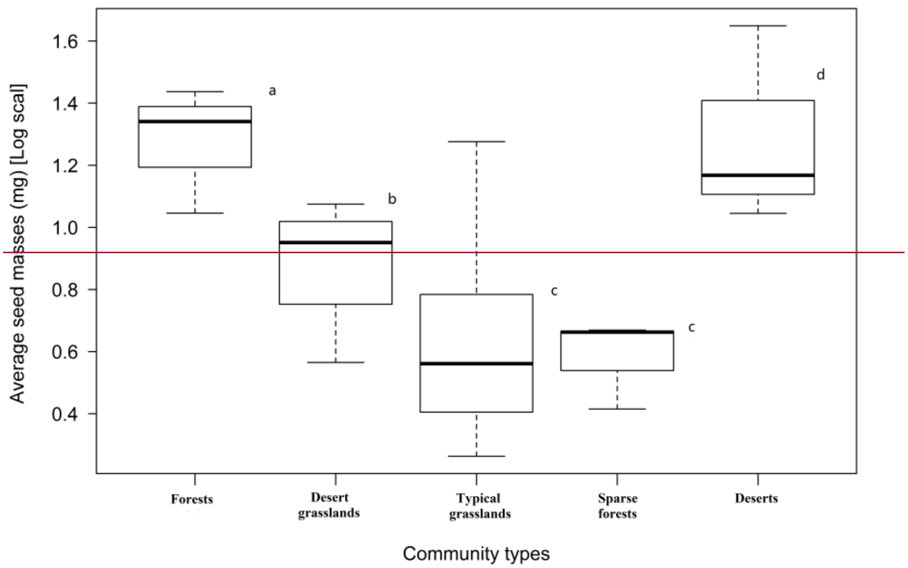
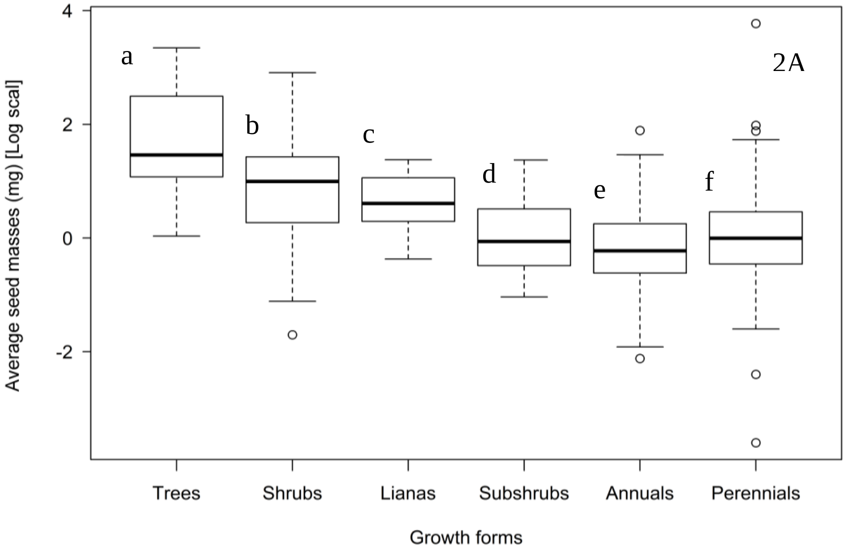
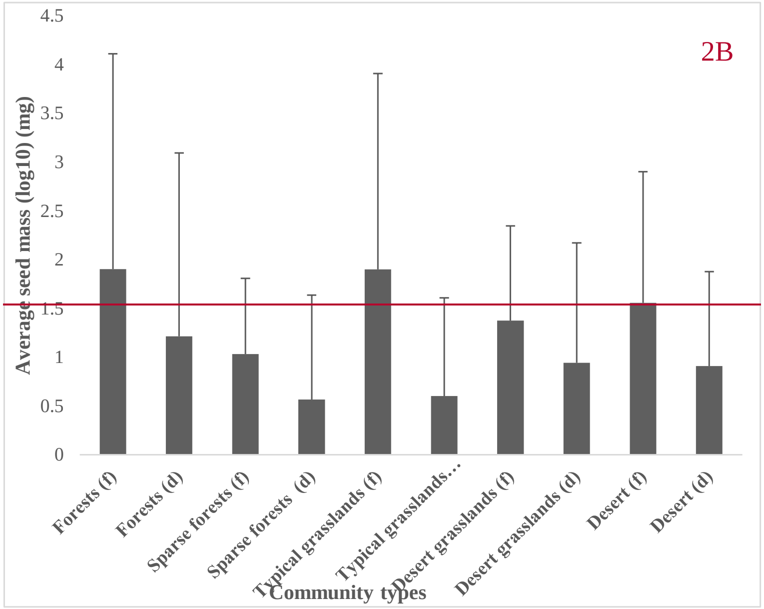


FIGURE 2 Trees (12 species) have largest average seed mass, followed by shrubs (65 species), lianas (15 species), subshrubs (20 species), perennial herbs (396 species) and annuals (110 species) (2A) (Average seed mass bearing the different letter are significantly different at $p < 0.05$). Average seed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



2A
Average seed masses (mg) [Log scal]
4
2
0
-2
a
b
c
d
e
f
Trees
Shrubs
Lianas
Subshrubs
Annuals
Perennials
Growth forms



2B
Average seed mass (log10) (mg)
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
Forests (f)
Forests (d)
Sparse forests (f)
Sparse forests (d)
Typical grasslands (f)
Typical grasslands…
Desert grasslands (f)
Desert grasslands (d)
Desert (f)
Desert (d)
Community types

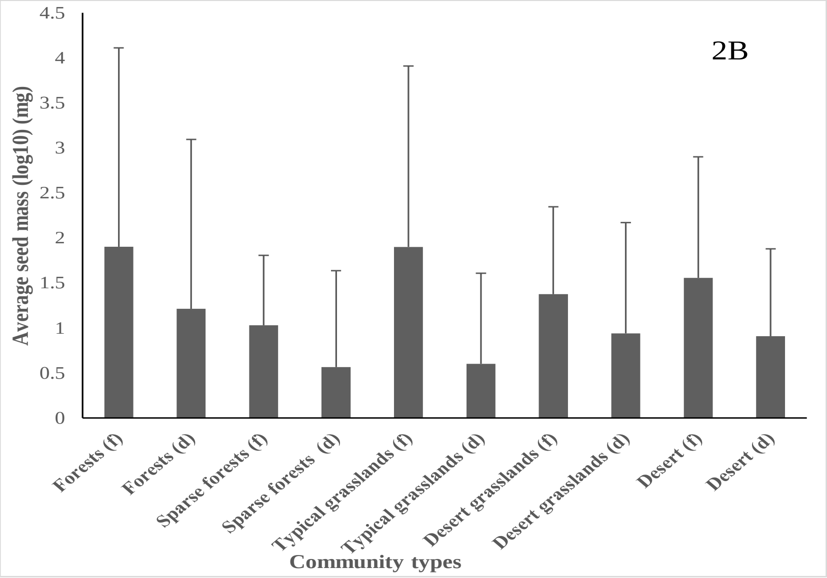
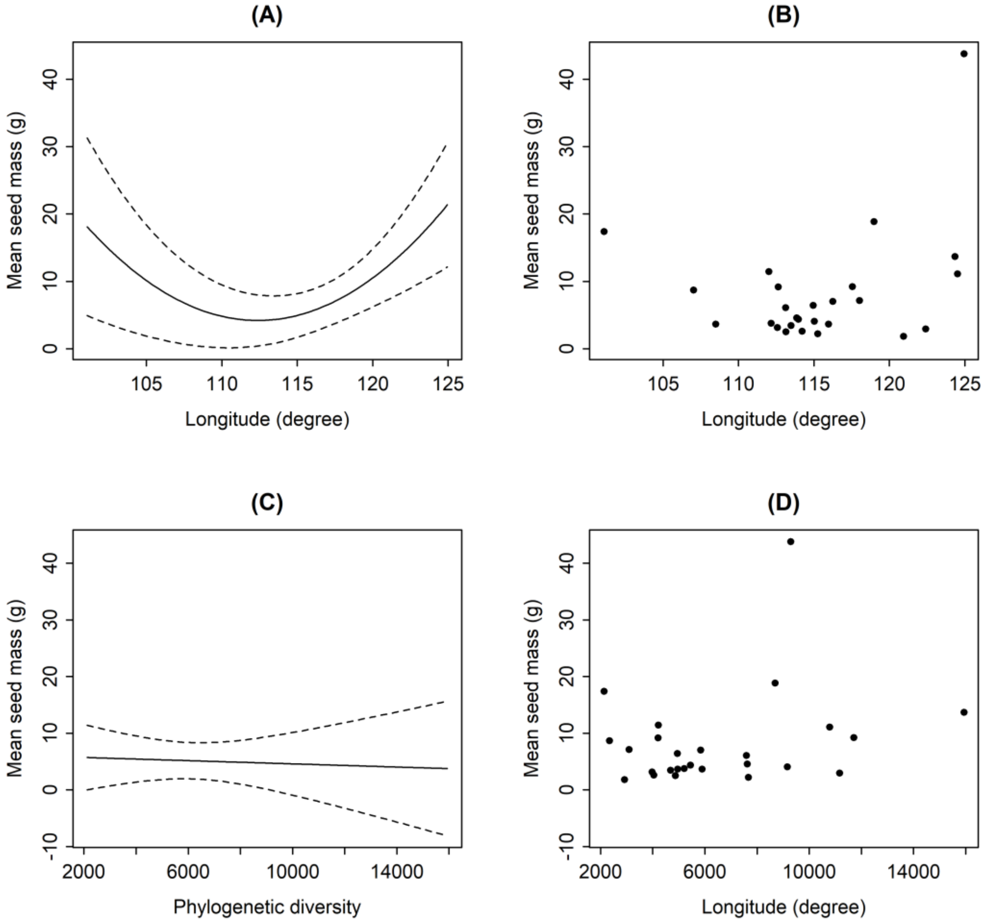
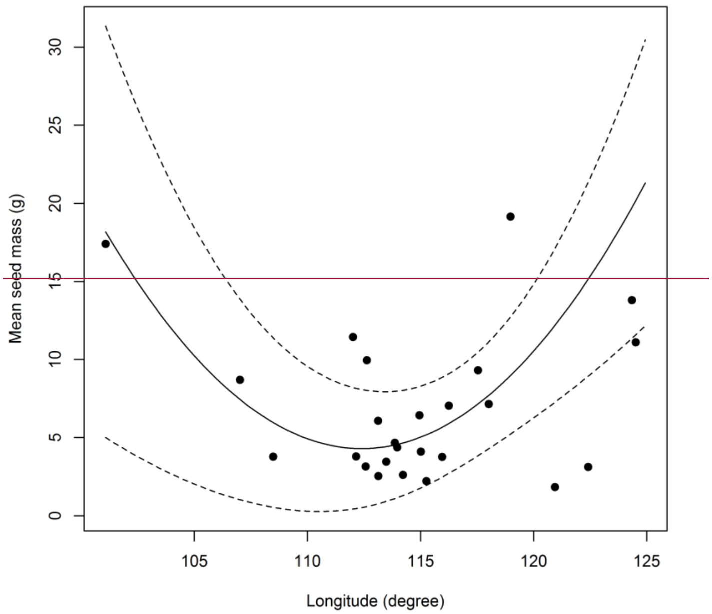


FIGURE 3 Relationships between average seed mass of communities and longitude (A, B) and phylogenetic diversity (C, D). Average seed mass declines as longitude rises and it reaches its bottom at around 114 degrees, and after that it increases. But average seed mass do not have significant relationships with phylogenetic diversity (p>0.05)~~**FIGURE 3** Average seed mass of communities in 26 sampling sites (except sites of deserts) decline along rising longitude and no significant relationships occur between seed mass and phylogenetic diversity~~


(A)
Mean seed mass (g)
0
10
20
30
40
105
110
115
120
125
Longitude (degree)
(B)
Mean seed mass (g)
0
10
20
30
40
105
110
115
120
125
Longitude (degree)
(C)
Mean seed mass (g)
-10
0
10
20
30
40
2000
6000
10000
14000
Phylogenetic diversity
(D)
Mean seed mass (g)
-10
0
10
20
30
40
2000
6000
10000
14000
Longitude (degree)


Mean seed mass (g)
0
5
10
15
20
25
30
105
110
115
120
125
Longitude (degree)

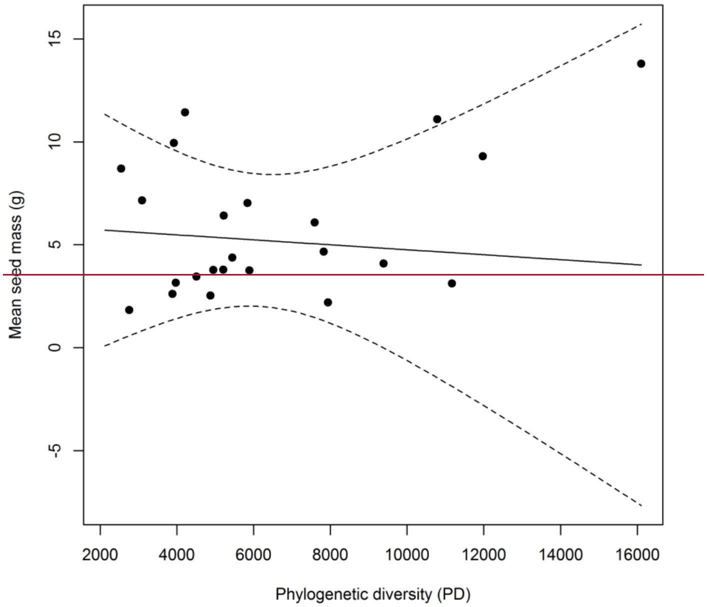
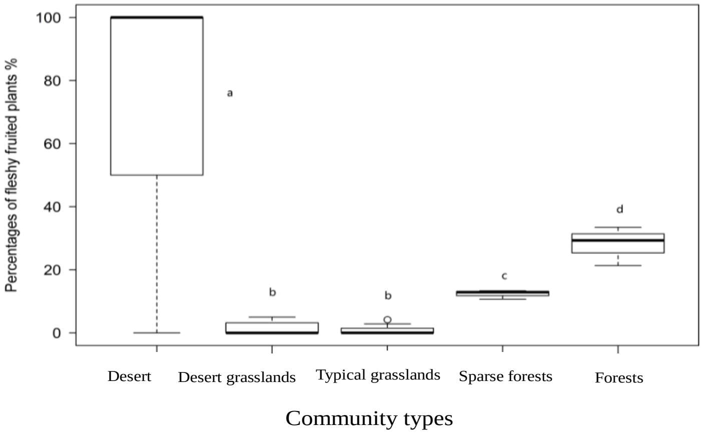
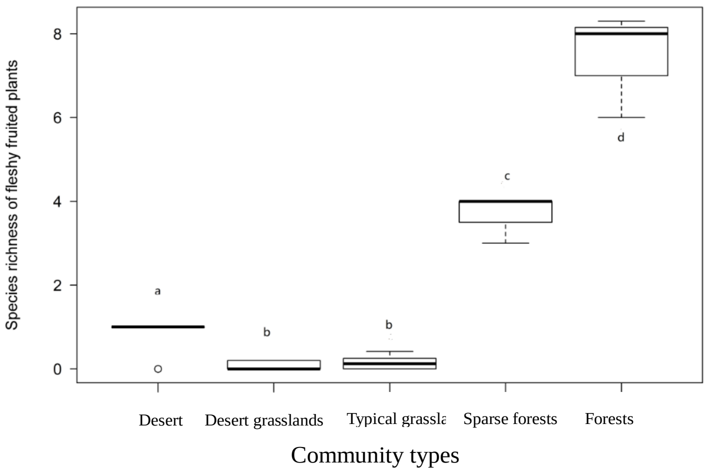

Mean seed mass (g)
-5
0
5
10
15
2000
4000
6000
8000
10000
12000
14000
16000
Phylogenetic diversity (PD)

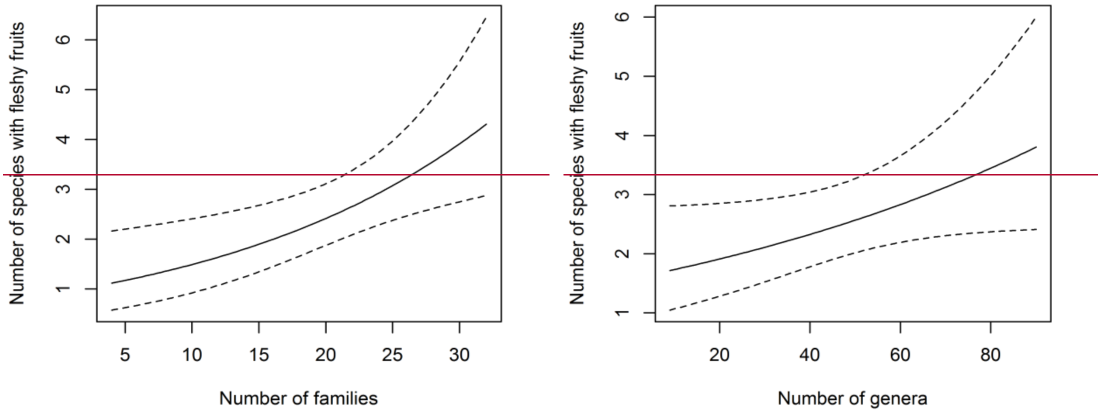
FIGURE 4 Proportions (A) and species richness (B) of plants with fleshy fruits decline gradually from forests through sparse forests to (typical and desert) grasslands, but increase in deserts (The same letter indicates difference is insignificant at $p < 0.05$)



(A)~~**FIGURE 4** Number of species with fleshy fruits rises in 23 sites (Ejinaqi, Wulatehouqi and Wulatezhongqi are not included) rises along increasing longitude and no significant relationships are found with phylogenetic diversity (families, genera and species)~~

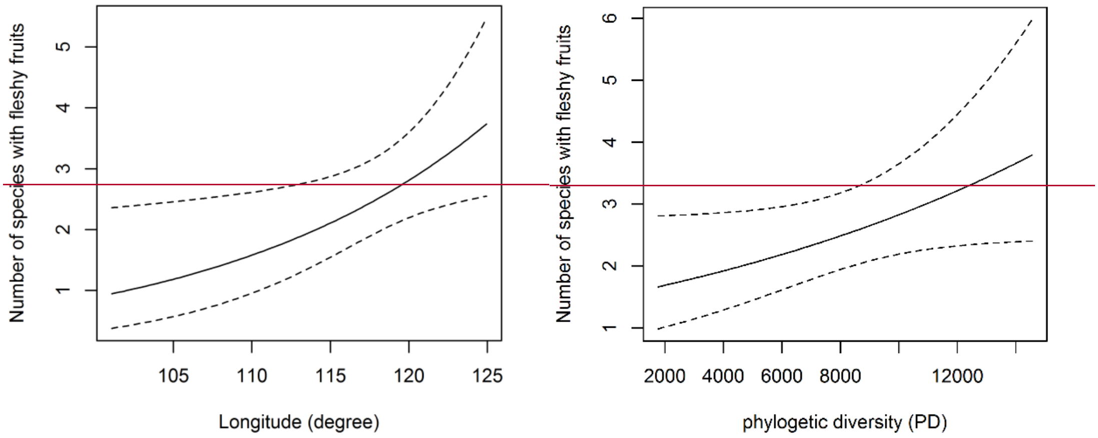

Species richness of fleshy fruited plants
0
2
4
6
8
a
b
b
c
d
Desert
Desert grasslands
Typical grassla
Sparse forests
Forests
Community types

(B)


Number of species with fleshy fruits
1
2
3
4
5
6
5
10
15
20
25
30
Number of families
Number of species with fleshy fruits
1
2
3
4
5
6
20
40
60
80
Number of genera

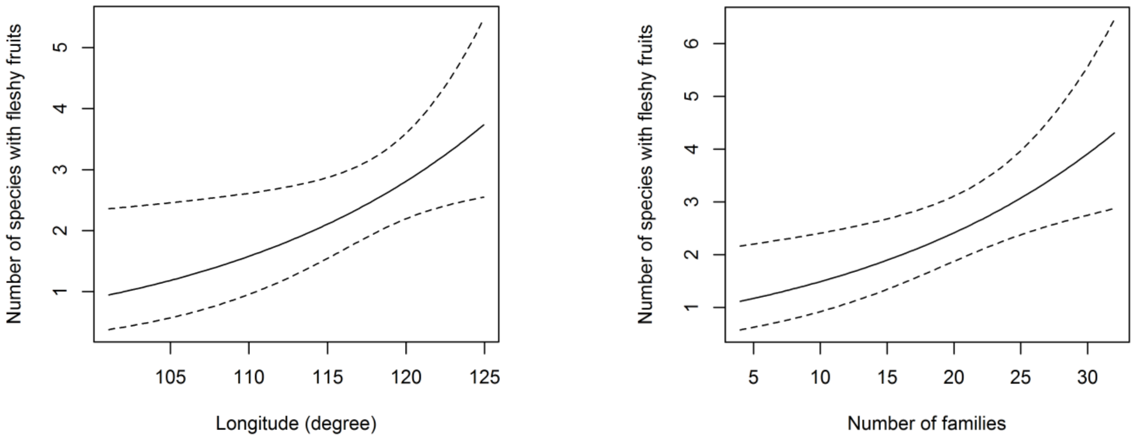
–

~~(a) (b)~~

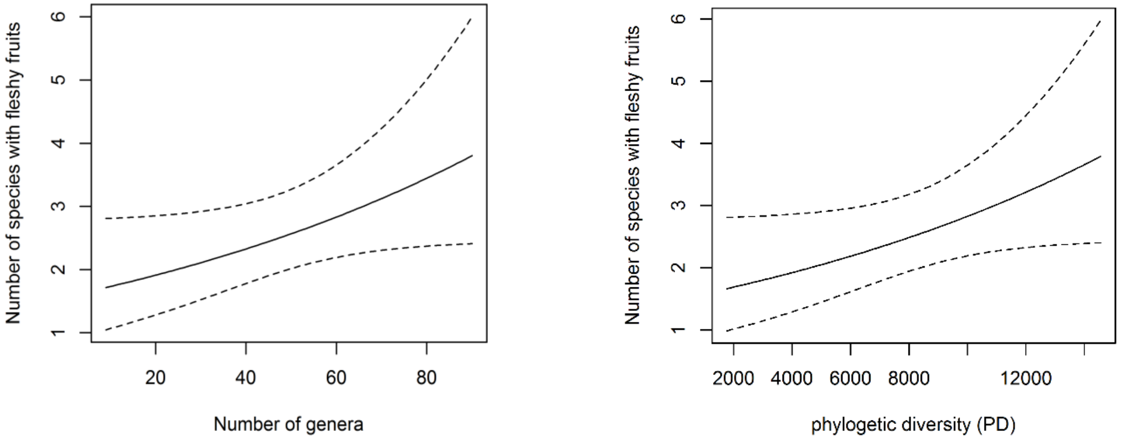


~~(c)~~ ~~(d)~~

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

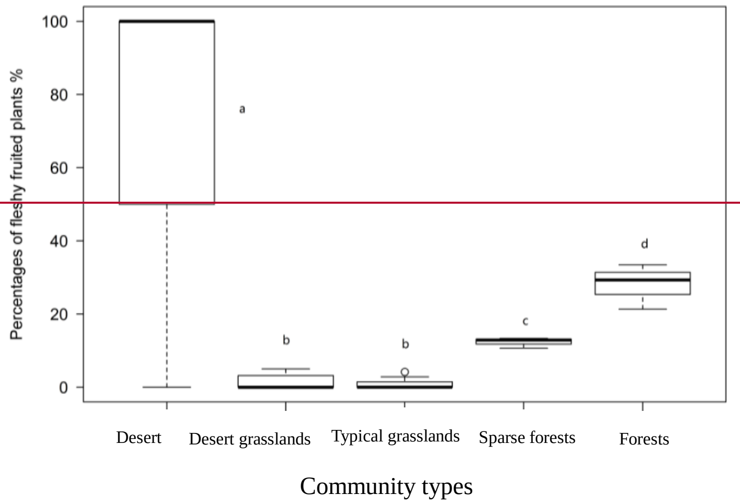


(a) (b)



(c) (d)

~~**FIGURE 5** Proportions and species richness of plants with fleshy fruits decline gradually from forests to desert grasslands, but increase in deserts (The sane letter indicates difference is insignificant at $p < 0.05$)~~


Percentages of fleshy fruited plants %
100
80
60
40
20
0
a
b
b
c
d
Desert
Desert grasslands
Typical grasslands
Sparse forests
Forests
Community types

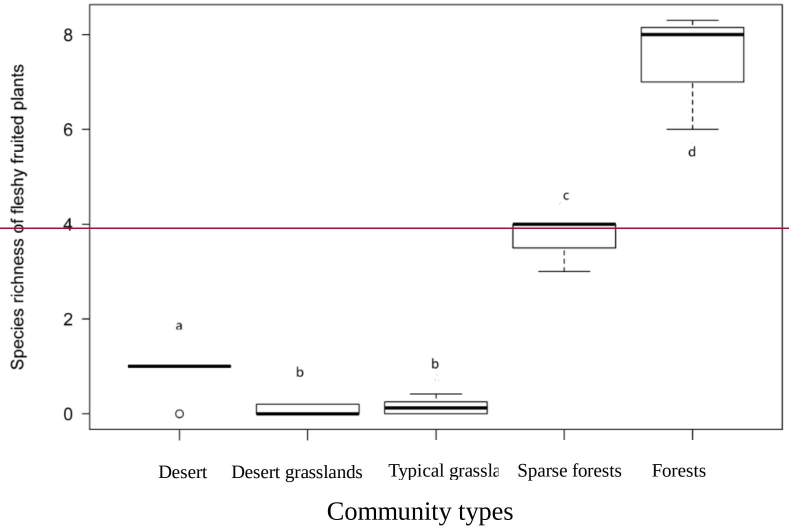
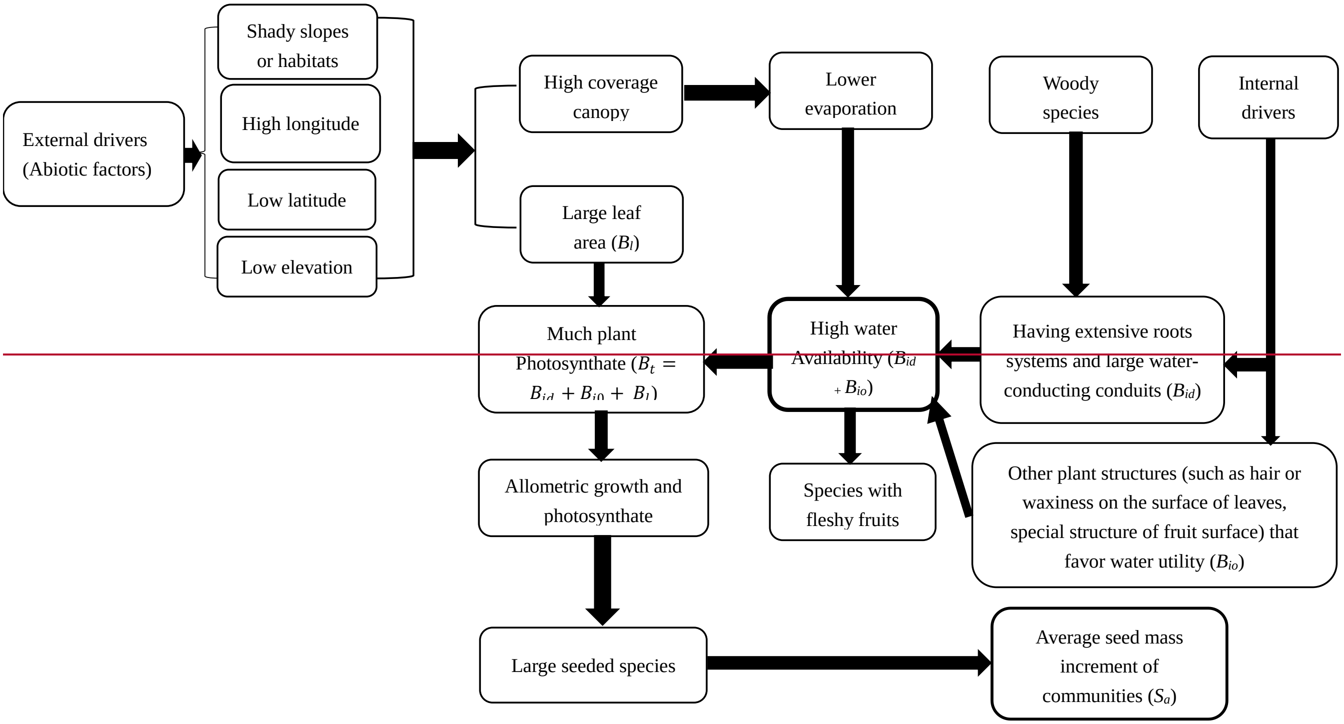
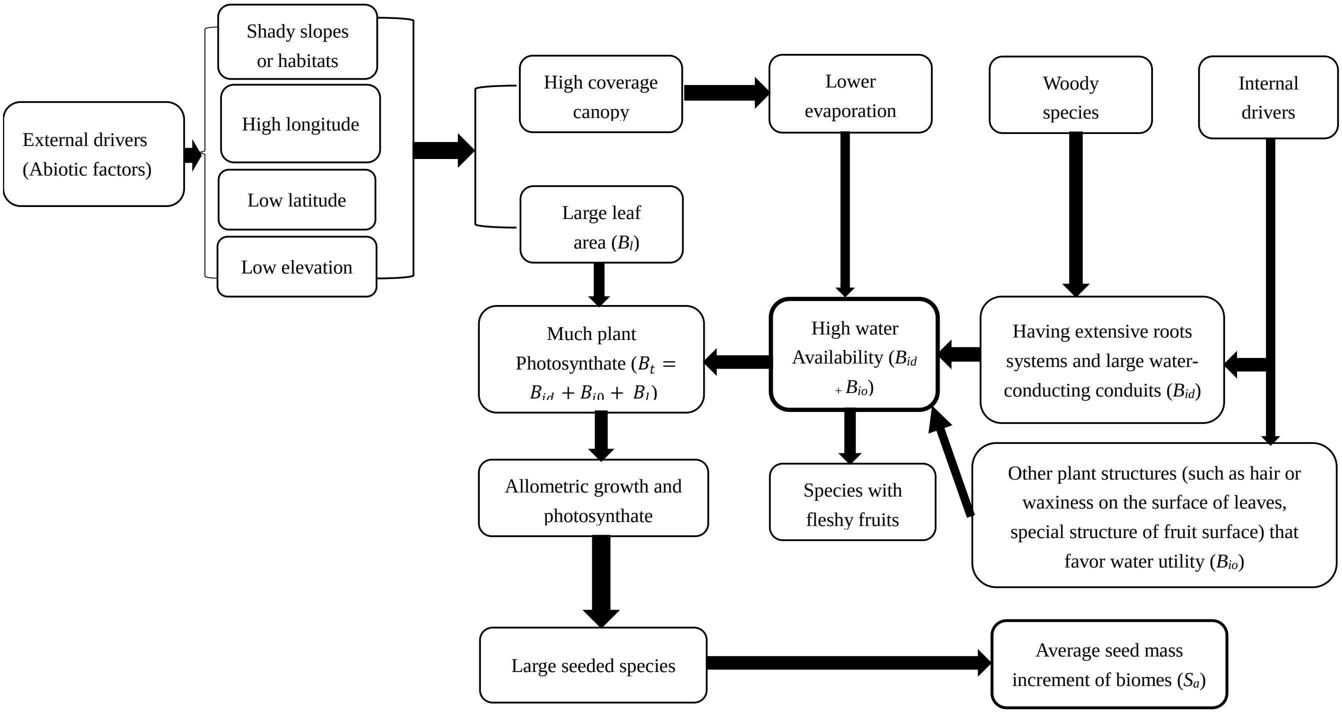

Species richness of fleshy fruited plants
8
6
4
2
0
a
b
b
c
d
Desert
Desert grasslands
Typical grassla
Sparse forests
Forests
Community types

FIGURE 6 Mechanistic frameworks of large seeded species formation and then biome average seed mass increment process~~**FIGURE 6** Mechanistic frameworks of large seed formation and then community average seed mass increment process~~




External drivers (Abiotic factors)
Shady slopes or habitats
High longitude
Low latitude
Low elevation
High coverage canopy
Large leaf area (B_l)
Lower evaporation
Woody species
Internal drivers
Much plant Photosynthate ($B_t = B_{id} + B_{io} + B_l$)
High water Availability ($B_{id} + B_{io}$)
Having extensive roots systems and large water-conducting conduits (B_{id})
Allometric growth and photosynthate
Species with fleshy fruits
Other plant structures (such as hair or waxiness on the surface of leaves, special structure of fruit surface) that favor water utility (B_{io})
Large seeded species
Average seed mass increment of biomes (S_a)