1 **Title:** Contemporary biodiversity pattern is affected by climate change at multiple temporal scales in

2 steppe on the Mongolian Plateau

3 **Running Title:** Climate change and plant biodiversity

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**Abstract**

Present and historical climate conditions jointly determine contemporary biodiversity patterns and

ecosystem functions. However, it remains unclear how contemporary climate and paleoclimate

changes together affect the three dimensions of biodiversity (i.e., taxonomic diversity, functional

diversity and phylogenetic diversity) and their relationship with ecosystem functions. Here, we

assess the impact of current climate, paleoclimate and its anomalies on contemporary biodiversity

and ecosystem functions. We estimated the taxonomic, functional and phylogenetic diversity of

grassland on the Mongolian Plateau using vegetation survey data and trait information. We then used

Random Forest and Structural Equation models to assess the relative importance of the present, the

Mid-Holocene and the Last-Glacial Maximum climate as well as paleoclimate changes as

determinants of diversity and aboveground biomass. Our results showed that paleoclimate changes

and modern climate jointly determined contemporary biodiversity patterns, while community

biomass was mainly affected by modern climate, namely the aridity index. Modern aridity and

temperature were two major influences on all three dimensions of biodiversity. Mid-Holocene

climate anomalies had a strong effect on species richness and phylogenetic diversity, while

functional diversity was mainly affected by temperature anomalies since the Last Glacial Maximum.

These findings suggest that contemporary biodiversity patterns may be affected by processes at

divergent temporal scales. Our results show that simultaneously exploring the response of the three

dimensions of biodiversity in different periods of climate change and the theoretical framework for

its impact on community biomass is helpful to provide a more comprehensive understanding of

patterns of biodiversity and its relationship with ecosystem functions.

**Keywords**

Aridity index, ecosystem functions, functional diversity, paleoclimate anomaly, phylogenetic

diversity, taxonomic diversity

**1. Introduction**

Global climate changes, such as increasing temperature and changing precipitation, are altering

biodiversity patterns at an unprecedented rate, and have serious consequences for ecosystem

functions related to biodiversity changes (Mottl et al., 2021; Nolan et al., 2018; Ye et al., 2019).

Ecosystem functioning associated with biodiversity, and contemporary diversity patterns and their

relationships may be regulated by modern climate, past climate and climate change (Fordham et al.,

2020; Eiserhardt et al., 2015; Svenning et al., 2015).

Ecosystem functions are strongly influenced by biodiversity (Isbell et al., 2011; Hooper et al.,

2005), but understanding the effects of different dimensions of biodiversity (i.e., taxonomic diversity,

functional diversity and phylogenetic diversity) on ecosystem functions is still a challenge in ecology

(Van Der Plas, 2019; Cadotte et al., 2008; Swenson, 2011). Traditionally, most studies of biodiversity

and ecosystem functions have predominantly focused on the relationship between taxonomic

diversity (i.e., species richness) and biomass or productivity. However, only considering taxonomic

diversity has the limitation that it may ignore important ecological processes such as the formation of

function traits or the evolutionary history of species (Flynn et al., 2011; Swenson, 2011). The

importance of taking into account other aspects of biodiversity, including functional diversity and

phylogenetic diversity, has increasingly been recognized. The effects of plant functional diversity on

ecosystem functioning are largely driven by variations in plant functional traits, such as adult plant

height and leaf size (Diaz et al., 2016). Phylogenetic diversity (PD) is a key driver of community

assembly and ecosystem functions (Srivastava et al., 2012; Cavender-Bares et al., 2009). Previous

research had shown that PD may be a better metric than species richness or functional diversity for

predicting plant biomass (Cadotte et al., 2008). Communities with higher PD have stronger

anti-interference ability because of their evolutionary potential to adapt to changing environmental

conditions. However, the role of multi-dimensional biodiversity in driving ecosystem functions in

response to climate change still needs further research. Elucidating the impacts of multi-dimensional

biodiversity on biomass in a changing world can deepen our understanding of the direct and indirect

effects of changes in climate and biodiversity on terrestrial ecosystems, and improve predictions of

the ecological consequences of global climate changes.

Changes in community biodiversity and composition caused by climate change have been

explored in various ecosystems (Avolio et al., 2021), including tropical forests in the Amazon

(Esquivel-Muelbert et al., 2019), alpine meadows on the Qinghai-Tibet Plateau (Liu et al., 2018a)

and a heterogeneous California grassland (Harrison et al., 2015). Dispersal limitation and

environmental filtering (i.e., climatic conditions and paleoclimate change) play an important role in

sorting species from the global species pool and in shaping large-scale diversity patterns (Kubota et

al., 2018; Liu et al., 2021). Many studies have found that climate changes in the Mid-Holocene and

the Quaternary interglacial period are the main driving factors of current species distribution,

functional traits and community phylogeny (Svenning and Skov, 2007b). The current patterns of

species richness and distribution of European flora are jointly affected by contemporary climatic

conditions and climate change during the Late Quaternary glacial-interglacial period (Svenning and

89    Skov, 2007a; Svenning and Skov, 2007b). Contemporary plant functional traits and composition are

90    highly sensitive to climate and influenced by climate from tens of thousands of years ago, with

91    important consequences for ecosystem functions (Blonder et al., 2018; Butler et al., 2017). For

92    example, in Europe patterns of plant functional diversity exhibited prominent glacial-interglacial

93    climate change imprints (Ordonez and Svenning, 2015; Ordonez and Svenning, 2017). This is partly

94    due to the non-random removal of functional combinations that may have occurred during the

95    Last-Glacial Maximum (LGM; ~21,000 years ago), increasing functional differences between native

96    and migratory species, leading to smaller and dispersed functional spaces (Ordonez and Svenning,

97    2017). Evidence derived from the fossil pollen sequence and ecological datasets has shown that the

98    acceleration of biodiversity changes began millennia ago, whereas vegetation changes during the

99    Late Pleistocene to Early Holocene were driven primarily by changing climate (Mottl et al., 2021). In

100   the South American tropics, the species composition and structure of Last Glacial Maximum forests

101   were quite different from those of today, and biomass was also lower than that of contemporary

102   forests (Mayle et al., 2009).

103       Furthermore, the effects of climate change on biodiversity should depend partly on climate

104   displacement rate (climate-change velocity) (Sandel et al., 2011). For example, phylogenetic

105   clustering increased with increasing intensity of Quaternary glacial-interglacial climatic oscillations

106   in South America and Africa (Kissling et al., 2012). There is evidence that vegetation changes in

107   Northern Europe were non-linear and varied greatly among regions in the early-Mid Holocene

108   (Seddon et al., 2014). Paleoclimate simulations since 21,000 years B.P. suggest that there are great

109   similarities between past and future temperature changes in Eurasian temperate grasslands (Fordham

110   et al., 2020). During the last glacial-interglacial transition period, global warming and related climate

change led to changes in ecosystems to a degree comparable to the predicted warming under future high-emission scenarios (Nolan et al., 2018). Therefore, studying the impact of past climate and its effects on contemporary biodiversity patterns will help us understand the potential effects of future climate changes. However, most studies exploring the impact of present climate and paleoclimate drivers on ecosystem functions have focused on forest ecosystems, while grassland ecosystems remain understudied. In addition, it is not yet clear whether taxonomy, function and phylogenetic diversity will vary with climate gradients and climate changes, and the intensity of any such changes remain unclear. Therefore, there is an urgent need to consider the impact of current climate, paleoclimate and its anomalies on contemporary biodiversity and ecosystem functions.

The Mongolian Plateau is located in the arid and semi-arid area of eastern Eurasia. Our previous researches hashave shown that climate is an important direct factor mediating the relationship between species richness and aboveground biomass in the Mongolian plateau steppe (Li et al., 2021; Li et al., 2020). However, in the Late Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climatic fluctuations (Maestre et al., 2021; Tian et al., 2017), which may have a significant impact on current plant diversity and ecosystem function. However, the impacts of climate in different periods and climate legacy effects on aboveground biomass of steppes in the Mongolian Plateau, as well as whether these effects are biodiversity dependent, remain to be evaluated. To address these knowledge gaps, we coupled data from a field survey of 152 sites in the Mongolian Plateau (Fig. S1) to existing databases on present and past climates to explore present climate and the legacy effects of climate during the Last Glacial Maximum and the Mid-Holocene on current biodiversity and biomass.

Here, we aim to evaluate the relative importance of taxonomic, functional, and phylogenetic

diversity on community biomass of steppe in the Mongolian Plateau, and to assess whether and how

climate in different periods and their changes affect the three dimensions of diversity, and their

relationships with community biomass. We specifically ask: (1) Do the three dimensions of diversity

affect community biomass, and if so, to what extent? (2) Whether and how climate at divergent

temporal scales and paleoclimatic changes affect different dimensions of biodiversity? And (3) If

there are effects, how do they affect the biodiversity-biomass relationship?

## 2. Materials and Methods

### 2.1 Study Area

We conducted field surveys in the grasslands of the Mongolian Plateau, including Inner Mongolia

Autonomous Region in China and Mongolia, during June to August of 2014~2018 (Fig. S1). The

Mongolian Plateau is located in the eastern part of Eurasia, with a geographic range of 37.61 °to

53.35 °N, 87.83 °to 125.95 °E, and an elevation range from 85 m to 4203 m a.s.l. (above sea level).

The mean annual temperature (MAT) of the study region ranges from -12 ℃ to 10 ℃ and mean

annual precipitation (MAP) ranges from 26 mm to 641 mm.

### 2.2 Data Collection

#### 2.2.1 Sites Sampled and Vegetation Investigation

We investigated 152 grassland sites set in flat areas with little human interference and a relatively

homogeneous environment. "Little human interference" mainly refers to the selection of areas with

less human activities such as grazing for investigation. Specific indicators include the following

aspects: 1) Avoid choosing areas with manure of cattle and sheep; 2) Dominant species such as

Leymus chinensis, Stipa spp. are eaten less by livestock; 3) There were fewer degradation indicators.

It mainly refers to the decrease in the number of established species or dominant species in the

grassland, while the degeneration indicator plants such as *Convolvulus ammannii*, *Potentilla acaulis*, *Artemisia frigida*, *Stellera chamaejasme* and *Cynanchum hancockianum* appeared in large numbers. These sites were separated by about 50 km. According to the methods and protocols for plant community inventories proposed by Fang et al. (Fang et al., 2009), most of the vegetation surveys in this study were conducted by setting one 10 m x 10 m quadrat at the respective site. However, in a few areas with sparse vegetation and large heterogeneity, we set three 10 m $\times$ 10 m quadrats to ensure the accuracy of the survey data. One or three 10 m $\times$ 10 m quadrats were set in each site (in a few areas with sparse vegetation and large heterogeneity, three 10 m $\times$ 10 m quadrats were set to ensure the accuracy of the survey data). Within each quadrat, five 1 m $\times$ 1 m plots were placed at each corner and at the center of the quadrat to investigate vegetation. A total of 296 vascular plant species were recorded.

We measured species height, density, coverage and standing biomass of each species in each plot. Three 1 m $\times$ 1 m plots along the diagonal line 10 m $\times$ 10 m quadrat were selected from the five plots to measure the standing biomass of each species. Plant species were cut at ground level and separately bagged, then oven-dried at 65 ℃ to constant weight, and weighed for dry matter.

**2.2.2 Climate Data**

Mean annual temperature (MAT, ℃) and mean annual precipitation (MAP, mm) were obtained from the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas, http://chelsa-climate.org/) (Karger et al., 2017), a data set consisting of monthly temperature and precipitation climatology from 1979 to 2013. Potential evapotranspiration (PET) was obtained from the CGIAR-CSI (CGIAR Consortium for Spatial Information, http://www.cgiar-csi.org) based on latitude and longitude data for each site (Trabucco and Zomer, 2019). The resolution of both is 30 arc

seconds. Aridity was measured using the aridity index (AI, AI =MAP/ PET). Higher AI values

indicate lower aridity and higher humidity. Paleoclimate data were downloaded from Worldclim

(http://worldclim.com/paleo-climate1) with a resolution of 2.5 minutes. The database was made

available by CMIP5 (Coupled Model Intercomparison Project Phase 5) and was calibrated based on

the current climate using WorldClim 1.4. The MAT and MAP of the Mid-Holocene (MID, about

6000 years ago) and the Last Glacial Maximum (LGM, about 22,000 years ago) were simulated

based on CCMS4 (Community Climate System Model version 4). Climate anomaly (i.e., present-day

values minus paleoclimate values) was used to indicate the degree of climate change since the MID

and the LGM (Sandel et al., 2011). Temperature-change velocity from the LGM to the present

(velocity, m/yr) was obtained from DRYAD (https://datadryad.org) (Sandel et al., 2011). The climate

variables used in this study are shown in Table 1.

**Table 1 Climate variables included in this study**

| | Climate variables | Abbreviation |
|---|---|---|
| The present climate (1979-2013) | Mean annual precipitation of the present | MAP |
| | Mean annual temperature of the present | MAT |
| | Aridity index of the present | AI |
| The Mid-Holocene climate | Mean annual precipitation of the Mid-Holocene | $MAP_{mid}$ |
| | Mean annual temperature of the Mid-Holocene | $MAT_{mid}$ |
| The Last Glacial Maximum climate | Mean annual precipitation of the Last Glacial Maximum | $MAP_{lgm}$ |
| | Mean annual temperature of the Last Glacial Maximum | $MAT_{lgm}$ |
| Paleoclimate change | MAP anomaly from the Mid-Holocene to the present | $AMAP_{mid}$ |
| | MAT anomaly from the Mid-Holocene to the present | $AMAT_{mid}$ |

| | |
|---|---|
| MAP anomaly from the Last Glacial Maximum to the present | $AMAP_{lgm}$ |
| MAT anomaly from the Last Glacial Maximum to the present | $AMAT_{lgm}$ |
| Temperature-change velocity from the LGM to the present | Velocity |

189 **2.2.3 Plant functional traits**

190 The functional traits of each plant species include growth form, life form, phyllotaxy, single or

191 compound leaf, petiole, inflorescence, fruit type, flowering period, fruit ripening period, length of the

192 flowering period, water ecotypes, leaf length, leaf width and plant height (Table S1). These traits

193 were looked up in the Flora of Inner Mongolia (Third Edition) or Flora of China (Online Edition)

194 (http://www.iplant.cn/frps). The trait data for leaf length and leaf width were the mean values

195 provided in Flora of China (Fig. S2). For example, if the leaf length of *Leymus chinensis* was

196 described as 7-18 cm in the Flora of China, then leaf length was defined as 12.5 cm.

197 **2.3 Aboveground biomass**

198 The aboveground biomass of the community was calculated based on the dry matter accumulation

199 value ($g/m^2$) of all plant samples in each plot, and the average aboveground biomass of each plot in

200 each quadrat was calculated to represent the aboveground biomass of the plant community ($g/m^2$).

201 **2.4 Diversity calculations**

202 **2.4.1 Taxonomic diversity**

203 We used species richness (SR), Shannon-Wiener index and Pielou index as measures of community

204 taxonomic diversity. The species richness (number of species/$m^2$) at each site was calculated as the

205 average number of species per plot. The Shannon-Wiener index and Pielou index were calculated

206 using the 'diversity' function in the "*vegan*" R package (Oksanen et al., 2020).

207 **2.4.2 Functional diversity**

The functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao index (Rao's Q) were calculated based on the Gower distance of functional traits using the 'dbFD' function in the '*FD*' R package (Laliberté et al., 2015).

**2.4.3 Phylogenetic diversity**

All plant species names recorded in surveys were checked in the plant list (www.theplantlist.org) to obtain acceptable species names. Based on the APG III system (The Angiosperm Phylogeny Group, 2009), we entered the taxonomic information (family/genus/species) of all species into the Phylomatic online plant database (Phylomatic Version 3, http://phylodiversity.net/phylomatic/), selected storedtree = "zanne2014 (Zanne et al., 2014)", and output a phylogenetic tree with branch length and differentiation time (Fig. S2). Faith's phylogenetic diversity (PD, the sum of the phylogenetic branch lengths), the mean pairwise distance (MPD) and the mean nearest taxon distance (MNTD) between species in a community were calculated using the 'mpd' function in the '*picante*' R package (Kembel et al., 2010).

**2.5 Data analysis**

First, we conducted a Random Forest model to estimate the relative importance of the three dimensions of biodiversity to community biomass. The Random Forest model can alleviate multicollinearity and complex interactions between independent variables. We built 5000 regression trees in Random Forest, and each tree was fitted with 2/3 of the data. The other 1/3 of the data was used to estimate the importance of each predictor variable, which was represented by the increase in mean square error (MSE). In the Random Forest model, the variables that ranked first in terms of taxonomic, functional and phylogenetic diversity were selected as proxies for the three dimensions of biodiversity.

To explore the influence of climate in different periods and climate anomalies on biodiversity, we also used the Random Forest model to analyze the relative importance of the present climate, the Mid-Holocene climate, the Last Glacial Maximum climate, and paleoclimate change on the three dimensions of biodiversity. To evaluate the relative importance of climate drivers of biodiversity, we calculated the ratio between the increase in MSE of the predictor and the sum of all the increases in MSE, which is expressed as a percentage.

To study the effects of climate in different periods and climate anomalies on biodiversity and aboveground biomass, we performed piecewise structural equation models (pSEM) to test the direct and indirect causal relationships between the climate in different periods and paleoclimate change, species diversity, functional diversity, phylogenetic diversity and biomass. Model construction procedures involved the following three stages. First, based on the results of the Random Forest model, we identified the climate variables that significantly affected biodiversity and divided them into composite variables. The model contained two composite variables that potentially represent collections of variables in terms of the present climate and paleoclimate change. We calculated Pearson correlations between the climate factors (Fig. S3) and deleted the predictors with high correlation coefficients (>0 .85, $P < 0.05$) to avoid multicollinearity. Before pSEM analysis, all selected predictors were standardized. Second, principal component analyses (PCAs) were used for the composite variables with multiple predictors. For each composite variable, the first principal component (PC1) explained 64~71% of the total variance and was used in the subsequent pSEM analysis (Table S2). Third, pSEM was developed from the full conceptual model (Fig. S4). We fitted the component models of the piecewise SEM as linear models and reported the standardized coefficient for each path from each component model. We used Shipley's d-separation test and

Fisher's C statistic to evaluate the overall fit of the pSEM, ~~as well as Fisher's C statistic~~ and Akaike

information criteria (AIC) to select the best model~~and AIC~~. We used standardized path coefficients to

measure the direct, indirect, and total effect sizes of the present climate and paleoclimate changes on

AGB.

We conducted all analyses in R x64 4.0.5. The Random Forest model was conducted using the

'randomForest' function in the '*randomForest*' package (Cutler et al., 2007; Breiman et al., 2018),

and the significance of the variables was tested using the 'rp.importance' function in the '*rfPermute*'

package (Archer, 2016). PCA was performed using the 'princomp' function in the '*psych*' package in

R (Revelle, 2021). Piecewise structural equation modeling was conducted and tested using the

'*piecewiseSEM*' package (Lefcheck, 2020; Lefcheck and Freckleton, 2015).

**3. Results**

**3.1 Effects of biodiversity on aboveground biomass**

Among the 11 biodiversity variables, SR, PD and Pielou index identified by the RF model were the

three most significant predictors influencing aboveground biomass (Fig. 1a). Taken together,

taxonomic diversity represented by SR, Pielou and Shannon-Wiener index collectively contributed

43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD

(including MNTD and MPD) and functional diversity represented by FRic (including FDiv, FEve,

FDis and RaoQ) contributed 30.02% and 26.2%, respectively (Fig. 1b).

Based on the ranking results from the Random Forest model, SR, PD, and FRic were selected as

agents of taxonomic, phylogenetic, and functional diversity, respectively, and used for subsequent

analysis.

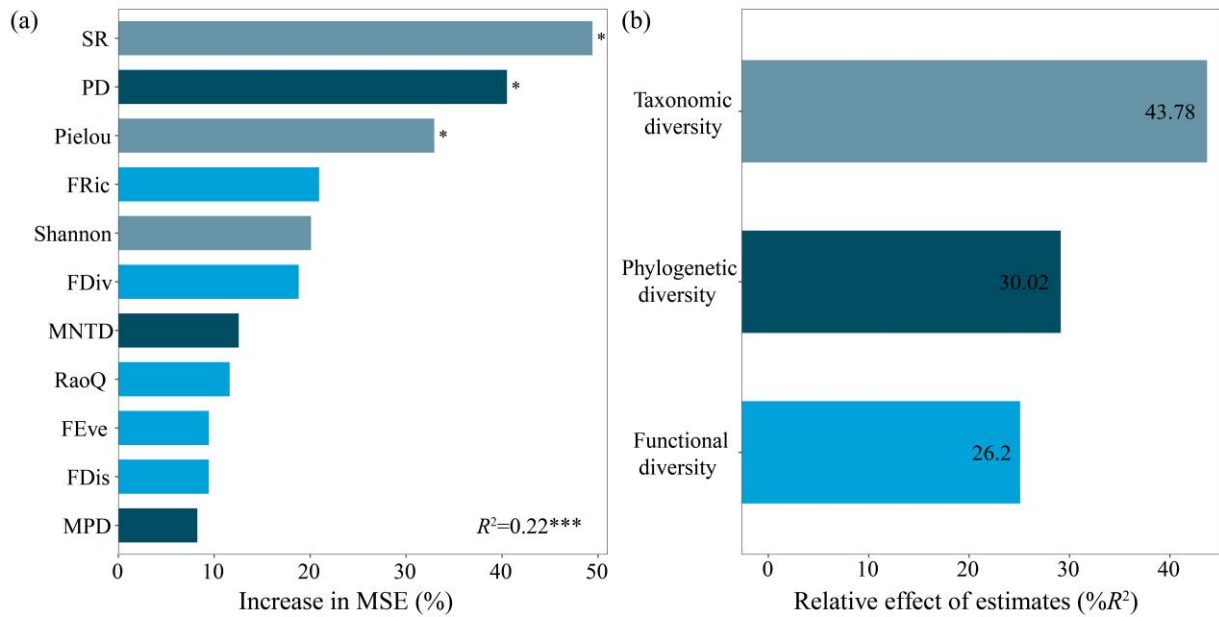



Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to community biomass. An increase in mean square error (MSE)denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

## 3.2 Paleoclimate and present climate predictors of contemporary diversity

Random Forest models explained 35% (cross-validation $R^2 = 0.35$, $P < 0.001$), 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) and 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) of the variance in SR, PD and FRic, respectively (Fig. 2). Temperatures in different periods, including $MAT_{mid}$, MAT and $MAT_{lgm}$, were the main factors driving SR and PD ($P < 0.05$, Fig. 2a and 2b), followed by climate anomalies in various periods. However, the current climate (i.e., AI, MAT and MAP) had a stronger impact on FRic ($P < 0.05$, Fig. 2c).

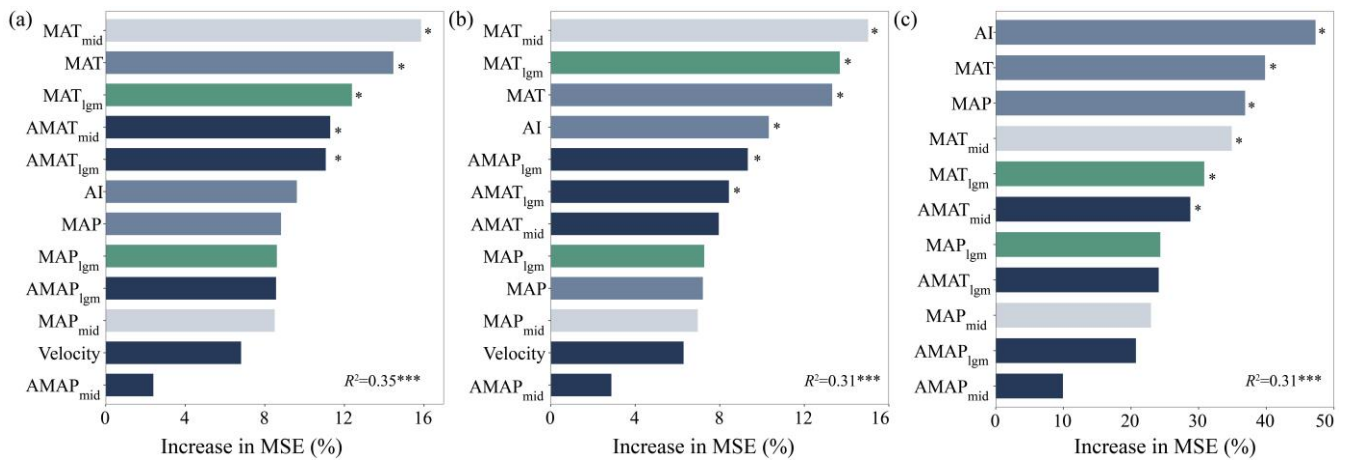



Fig. 2 The importance of climate variables in different periods and paleoclimate change to species richness (a), phylogenetic diversity (b) and functional richness (c). An increase in mean square error (MSE) denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

In terms of relative contributions, the current climate and the paleoclimate changes had greater impacts on the three dimensions of biodiversity. Paleoclimate change was the best predictor of SR (33.90%) and PD (32.10%). Strikingly, the present climate (38.68%) showed a larger contribution to the prediction of FRic than paleoclimate change (26.06%; Fig. 3).

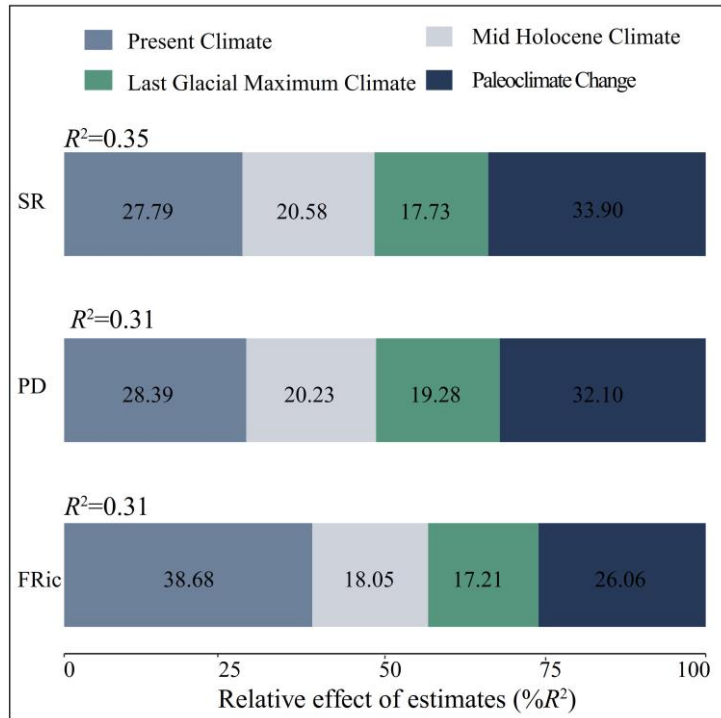



Fig. 3 Relative contributions of present climate, Mid-Holocene, Last Glacial Maximum and paleoclimate change as drivers of species richness, phylogenetic diversity and functional richness.

**3.3 Influence of climate factors on biodiversity and aboveground biomass**

The present climate, MAT of the Mid-Holocene and the Last Glacial Maximum, and paleoclimate change explained 38% ($R^2 = 0.38$), 33% ($R^2 = 0.33$), 36% ($R^2 = 0.36$) and 29% ($R^2 = 0.29$) of the variances in SR, PD, FRic and AGB, respectively (Fig. 4). The present climate had direct and indirect significant associations with AGB via all biodiversity variables (Fig. 4). The present climate was significantly and positively associated with SR ($r_\partial = 0.46$, $P < 0.05$), PD ($r_\partial = 0.35$, $P < 0.05$) and FRic ($r_\partial = 0.58$, $P < 0.05$, Fig. 4). However, the paleoclimate change had direct significant negative effects on SR ($r_\partial = -0.28$, $P < 0.05$), PD ($r_\partial = -0.32$, $P < 0.05$) and FRic ($r_\partial = -0.25$, $P < 0.05$, Fig. 4). MAT$_{mid}$ and MAT$_{lgm}$ had no significant effects on SR, PD, FRic and AGB (Fig. 4).

307

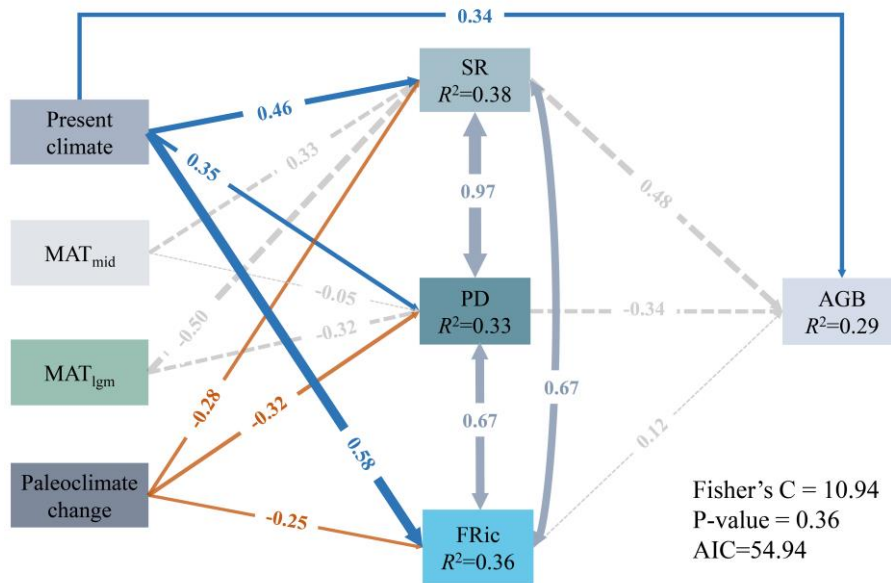



Fig. 4 SEMs fitted to the effects of climate in different periods and paleoclimate change on diversity

and AGB. The present climate is PCA component 1 of the AI and MAT. The paleoclimate change

represents a composite variable including MAT anomaly from the Mid-Holocene to the present,

MAT and MAP anomaly from the Last Glacial Maximum to the present. Numbers adjacent to arrows

represent the standardized path coefficients ($r_\partial$). $R^2$ indicates the proportion of variance explained.

Blue (positive paths) and orange (negative paths) solid arrows indicate significant paths ($P < 0.05$),

and gray dashed arrows indicate non-significant paths ($P > 0.05$).

315

For the present climate, the direct effects of AI on SR ($r_\partial = 0.33$, $P < 0.05$), PD ($r_\partial = 0.27$, $P <$

0.05), FRic ($r_\partial = 0.49$, $P < 0.05$), and AGB ($r_\partial = 0.37$, $P < 0.05$) were all significantly positive, while

the direct effects of MAT on the three dimensions of biodiversity (SR, $r_\partial = -0.34$; PD, $r_\partial = -0.36$;

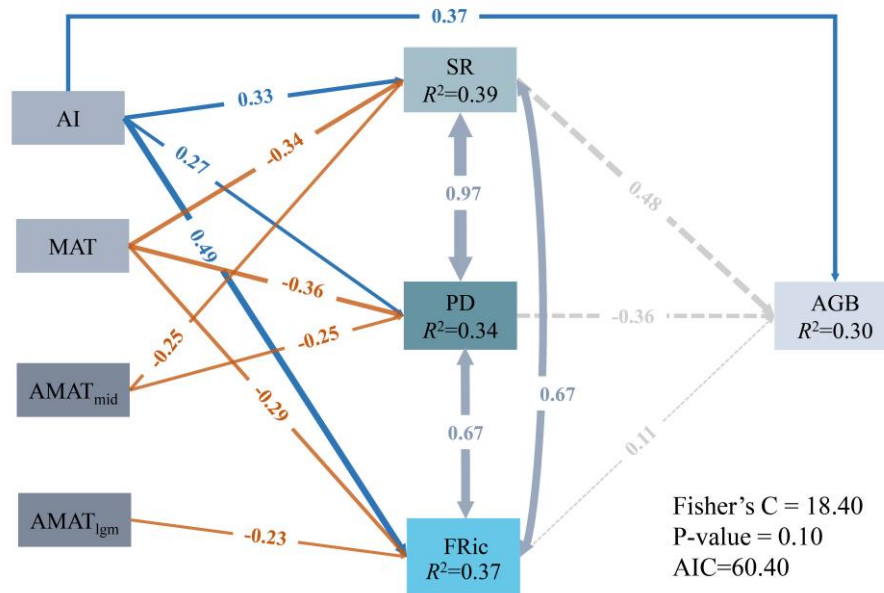
FRic, $r_\partial = -0.29$; $P < 0.05$ in all cases) were all significantly negative (Fig. 5). In addition, SR ($r_\partial =$

$-0.25$, $P < 0.05$) and PD ($r_\partial = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the

Mid-Holocene to the present (AMAT$_{mid}$), but FRic ($r_\partial = -0.23$, $P < 0.05$) was mainly driven by MAT

anomaly from the Last Glacial Maximum to the present (AMAT$_{lgm}$; Fig. 5). AI accounted for the

323 largest proportion of variation in AGB (80.06%), followed by MAT at 10.81% (Table 2). The direct

324 effect (($r_{\partial} = 0.37$) of AI on AGB was greater than the indirect effect ($r_{\partial} = 0.12$, Table 2).

325

326    Fig. 5 The effects of present climate (AI and MAT) and paleoclimate change (AMAT$_{mid}$ and

327   AMAT$_{lgm}$) on diversity and AGB. Numbers adjacent to arrows represent the standardized path

328   coefficients. $R^2$ indicates the proportion of variance explained. Blue (positive paths) and orange

329 (negative paths) solid arrows indicate significant paths ($P < 0.05$), and gray dashed arrows indicate

330            non-significant paths ($P > 0.05$).

331  Table 2 The direct, indirect, total effects and the relative contribution of the present climate and

332       paleoclimate change on AGB in the structural equation model

| Variables | Direct effect | Indirect effect | Total effect | Relative contribution (%) |
|---|---|---|---|---|
| AI | 0.37 | 0.12 | 0.49 | 80.06 |
| MAT | 0 | -0.07 | -0.07 | 10.81 |
| AMAT$_{lgm}$ | 0 | -0.03 | -0.03 | 4.95 |
| AMAT$_{mid}$ | 0 | -0.03 | -0.03 | 4.18 |

## 4. Discussion

### 4.1 The effects of different dimensions of biodiversity on aboveground biomass

Our research showed that, without considering the influence of climatic conditions, taxonomic

diversity was the most important factor influencing the aboveground biomass of Mongolian Plateau

grasslands, followed by phylogenetic diversity and functional diversity. However, a large number of

studies have emphasized the importance of phylogenetic diversity and functional diversity for

ecosystem functions (Srivastava et al., 2012; Cadotte et al., 2008; Swenson et al., 2012). For example,

research on subtropical forests in northern China showed that functional diversity is more important

than taxonomic diversity in controlling aboveground biomass, which is related to the acquisitive

resource use strategy of functional traits (Hanif et al., 2019). However, in Mongolian Plateau

grasslands taxonomic diversity may be more critical. Selection effects and compensatory effects are

the main mechanisms through which biodiversity impacts on biomass. The grassland community

structure of the Mongolian Plateau is relatively simple, and biomass mainly depends on the number

or dominance of dominant species. However, functional traits considered in this study, such as leaf

size and plant height, do not have a strong impact on biomass. The Mongolian Plateau is located in

an arid and semi-arid area, and drought-tolerant species invest a lot in seed resources, leaf structure

and root biomass (Wolf et al., 2021). Studies have shown that these traits are negatively correlated

with aboveground biomass, while functional traits consistent with growth strategies, such as leaf

nitrogen concentration and photosynthetic utilization efficiency, can promote aboveground biomass

(Wolf et al., 2021).

Secondly, phylogenetic diversity also had a significant impact on aboveground biomass.

Phylogenetic diversity contains the evolutionary information of species ecology. It is influenced by

the average degree of correlation between species and the number of existing species, and can reflect

the evolutionary sequence of characteristics related to habitat and resource utilization (Srivastava et

al., 2012). If species make better use of all available resources, productivity may increase. Therefore,

our research suggests that protecting taxonomic diversity and conserving evolutionarily different

species are equally important in effectively maintaining high-yielding communities.

**4.2 Relationship between paleoclimate anomalies and current biodiversity patterns**

Although a rich body of research has explored the factors affecting biodiversity patterns and the~~ir~~

relationship~~s~~ between biodiversity and~~with~~ biomass (Van Der Plas, 2019; Tilman et al., 2012) , it is

not clear how current climate and paleoclimate together affect the relationship, especially in

grassland communities. Here, our results showed that paleoclimate changes and present climate

factors were critical variables influencing contemporary biodiversity patterns. This illustrates the

importance of historical factors, such as evolution, as well as contemporary factors, such as climate,

in determining the geographic ranges of species and the accumulation of species in the region (Fine,

2015). Previous studies aiming to explain patterns of biodiversity have focused on the current

climate (Harrison et al., 2015), energy (Kreft and Jetz, 2007), soil attributions (Ulrich et al., 2014),

human activities (Hautier et al., 2015; Newbold et al., 2015) or water availability (Jiao et al., 2021;

Liu et al., 2021). Modern climate research on biodiversity and ecosystem functions has been widely

confirmed (Walther et al., 2002; Liu et al., 2021; Yang et al., 2011), but our research shows that the

pattern of biodiversity is also affected by past climates, and especially climate anomalies. Based on

climate-related traits, climate anomalies filtered the regional species pool, which in turn affected

contemporary biodiversity patterns.

Species richness is affected by the significant positive effects of AI, and the significant negative

377     effects of MAT and $AMAT_{mid}$. Jansson's research showed that the total number of vascular plant

378     species decreased with increasing temperature change since the LGM in mainland areas (Jansson,

379     2003), which is inconsistent with our results. We found that the species richness of Mongolian

380     Plateau grassland is more affected by temperature changes since the Mid-Holocene. In Europe, the

381     richness of widespread species was largely controlled by the modern climate, while the LGM climate

382     and climatic heterogeneity were codominant with modern climate as controls of richness for

383     restricted and intermediate species, which appear to still be associated with their glacial refugia

384     (Svenning and Skov, 2007b).

385     Phylogenetic diversity (PD) is usually used to quantify the uniqueness of a region's evolution.

386     On longer timescales, the effects of climate on speciation and extinction may cumulatively affect

387     current PD patterns (Svenning et al., 2015). Our research showed that PD was negatively correlated

388     with MAT and $AMAT_{mid}$, but not significantly related to temperature anomalies during the Last

389     Glacial Maximum. However, the PD of global forest ecosystems is positively associated with

390     temperature and precipitation and is negatively associated with Quaternary precipitation change

391     (Kubota et al., 2018). This indicates the importance of paleoprecipitation variation in shaping the

392     pattern of contemporary phylogenetic diversity in forest ecosystems, possibly by survival and

393     recolonization from refugia along hydrological gradients (Blonder et al., 2018). Additionally,

394     Quaternary glacial-interglacial climate oscillations led to the extinction of trees in many parts of the

395     globe, for example in Australia (Macphail et al., 1995) and Europe (Svenning, 2003), affecting the

396     PD of global forest ecosystems. ~~Liu et al.~~It was ~~showed~~ shown that herbaceous plants were mainly

397     affected by climate change since Mid-Holocene, while woody plants were mainly affected by climate

398     change since the LGM, which may be due to the differences in morphology of herbaceous and

woody plants (Liu et al., 2018b; Wang et al., 2021). Woody plants with large conduits are vulnerable to drought or freezing and cause clogging of conduits (Zanne et al., 2014), and thus, were more~~are more~~ susceptible to cold Quaternary climatic conditions~~climate oscillations~~. In contrast, herbs~~Herbs~~ can mitigate the effects of extreme weather by producing underground buds and stems, or by wilting of aboveground parts (Qian et al., 2017).

Our results suggested that functional richness was negatively related to Last Glacial Maximum climate anomaly. This may be due to the intolerance of plant traits to past climatic conditions (Bhagwat and Willis, 2008) and the postglacial migration lag (Svenning et al., 2008). In the Late Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climate fluctuations (Tian et al., 2017), and likely experienced a non-random removal of functional combinations and change in functional diversity (Ordonez and Svenning, 2017). Previous research has indicated that the magnitude of past glacial-to-interglacial warming was sufficient at most locations across the globe (including the Mongolian Plateau) to drive moderate to large changes in vegetation composition and structure (Nolan et al., 2018). When climate changes, inappropriate species may be quickly ruled out, and appropriate species may migrate more slowly, resulting in a negative correlation between the paleoclimate anomaly and contemporary FD in the Mongolian Plateau. This is also limited by the spreading ability or migration potential of plants after the glaciers retreated, when species with inappropriate characteristics disappeared from the community and were not replaced by other species (Blonder et al., 2018). Studies in Europe indicate that the lagging effect of glacial-interglacial climate instability on functional diversity is >10,000 years (Ordonez and Svenning, 2015).

**4.3 Effects of climate on the relationship between biodiversity and biomass**

The influence of climate on relationship between contemporary diversity and biomass may be caused by a combination of climate change and human activities in the Mongolian Plateau grasslands. In the eastern part of the Mongolian Plateau, the interval of 35230 to 25150 yr B.P. was a forest-steppe landscape under humid conditions, represented by Pinaceae, Compositae and Chenopodiaceae (Tian et al., 2017). Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe landscape, and drought began to intensify. During the Last Glacial Maximum period, the vegetation types on the Mongolian Plateau were mainly polar, alpine and temperate deserts (Ray and Adams, 2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene, xerophytes had declined sharply, and plants of humid climates had increased. The humidity increased during the early Holocene, and generally humid conditions lasted from 10,400 until 7000 yr BP and the region experienced the Lavliakan humid phase (Lioubimtseva, 2004; Yin et al., 2011), with more hygrophilous species, such as Cyperaceae (Tian et al., 2017). This climate condition was also conducive to the development and spread of Compositae and Gramineae families in the steppes of Central Asia (Lioubimtseva, 2004). Since approximately 5200 yr BP to present, the climate has become more arid, with corresponding vegetation change and strong aeolian activity (Yin et al., 2011).

As far as aboveground biomass is concerned, after taking into account climatic factors, it is mainly directly affected by aridity index, while the three dimensions of biodiversity have no significant impact on it, which is consistent with our previous research (Li et al., 2020). A meta-analysis of 40 global grasslands plant communities showed that the response of plant diversity to climate warming was an important factor in determining grassland aboveground biomass (Shao et al., 2021). Similarly, paleoclimate changes also have no direct effects on aboveground biomass,

which indirectly affects aboveground biomass through regulating biodiversity. This is mainly

because paleoclimatic filtering can alter the historical legacies of species and functional diversity

(removal or accumulation over time of species and functional states) through evolution~~ary~~, extinction,

or recolonization (Svenning et al., 2015). Legacies in the species and functional traits pool further

affect ecosystem function, leading to changes in biomass (Svenning et al., 2015).

In addition, the relationship between biodiversity and biomass is also affected by human

activities (Buisson et al., 2022). Human history has become profoundly intertwined with grassland

communities, from the evolution of the *Homo* in savannas 2 million years ago ~~(Ma)~~ to the emergence

of species domestication in agricultural societies 10,000 years ago (Strömberg and Staver, 2022).

Palaeoecological and archaeological evidence shows that people have shaped most of terrestrial

nature for at least 12,000 years, including burning, hunting, cultivation and domestication (Ellis et al.,

2021). In the Mongolian Plateau, especially in the Inner Mongolia region of northern China, grazing

appeared at ~5.7–5.5 ka B.P. and further intensified again after ~4.2–4.0 ka B.P. (Huang et al., 2021).

A large number of studies have shown that the intensification of grazing activities also causes

changes in biodiversity and biomass (Liang et al., 2021; Herrero-Jáuregui and Oesterheld, 2018;

Díaz et al., 2007). Therefore, there is an urgent need for future research to develop systematic

analytical frameworks to assess the importance of paleoclimate and climate change in shaping

contemporary biodiversity and ecosystems, particularly under the influence of human activities.

**5. Conclusion**

We conclude that unique evolutionary and ecological histories played key roles in explaining

biodiversity patterns in the Mongolian Plateau. When climatic conditions are not considered,

taxonomic diversity, phylogenetic diversity and functional diversity all have effects on community

465 biomass, and taxonomic diversity has a more obvious impact on biomass. However, the climate after

466 the Last Glacial Maximum has left a strong legacy affecting contemporary biodiversity patterns.

467 These findings extend our understanding of the spatial and temporal scale of climate effects on

468 biodiversity and aboveground biomass, providing additional confidence that the paleoclimate had a

469 key role in shaping contemporary biodiversity patterns.

470

471 **Authors' Contributions**

472 Z. Li analyzed the data and wrote the first draft of the manuscript. Zh. Li, J. Zhang, G. Han, F.Y. Li

473 and C. Liang contributed to later versions of the manuscript and all authors provided constructive

474 comments to improve the manuscript. F.Y. Li and C. Liang designed and led the field survey. Z. Li,

475 Zh. Li, X. Tong, J. Zhang, L. Dong, Y. Zheng, B. Miao, W. Ma, L. Zhao, L. Wang, L. Wen, C. Liang

476 and F.Y. Li conducted the experiment and collected the data.

477 **Data available**

478 The data that support the findings of this study are available on request from the corresponding

479 author.

480 **Conflict of interest statement**

481 The authors declare that they have no conflict of interest.

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