Title: Contemporary biodiversity pattern is affected by climate change at multiple temporal scales in steppe on the Mongolian Plateau

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 ~~diversity~~, functional ~~diversity~~ and phylogenetic diversity of grassland on the Mongolian Plateau using vegetation survey data and trait information. We then used Random Forest ~~models~~ and Structural Equation models to assess the relative importance of the present ~~climate~~, the ~~Mid~~ Mid-Holocene ~~climate~~ and ~~–~~the Last-Glacial Maximum climate ~~and~~ 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~~biodiversity and 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 ~~(BEF)~~ 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 ignores ~~the~~ 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 the 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 (Esquivel-Muelbert et al., 2019) grassland (Harrison et al., 2015).

Dispersal limitation and environmental filtering (i.e., climatic conditions and paleoclimate change)

plays 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 Skov, 2007a; Svenning and Skov, 2007b). Contemporary plant functional traits

and composition are highly sensitive to climate and influenced by climate from tens of thousands of

years ago, with important consequences for ecosystem functions (Blonder et al., 2018; Butler et al.,

2017). For example, in Europe patterns of plant functional diversity exhibited prominent

glacial-interglacial climate change imprints (Ordonez and Svenning, 2015; Ordonez and Svenning,

2017). This is partly due to the non-random removal of functional combinations that may have

occurred during the Last-Glacial Maximum (LGM; ~21,000 years ago), increasing functional

differences between native and migratory species, leading to smaller and dispersed functional spaces

(Ordonez and Svenning, 2017). Evidence derived from the fossil pollen sequence and ecological

datasets has shown that the acceleration of biodiversity changes began millennia ago, whereas

vegetation changes during the Late Pleistocene to Early Holocene were driven primarily by changing

climates (Mottl et al., 2021). In the South American tropics, the species composition and structure of

Last Glacial Maximum forests were quite different from those of today, and biomass was also lower

than that of contemporary forests (Mayle et al., 2009).

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

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

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

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

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

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

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

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 ~~changes~~ 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 have 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~~limited~~ human interference and a relatively homogeneous environment. These sites were separated by about 50 km. One or three 10 m × 10 m quadrats were set in each site (in a few areas with sparse vegetation and large heterogeneity, three 10 m × 10 m quadrats were set to ensure the accuracy of the survey data). Within each quadrat, five 1 m × 1 m plots were placed at each corner and at the center of the quadrat ~~(only three 1 m × 1~~

m plots along the diagonal line of the quadrat in a few sites) to investigate vegetation. A total of 899

plots were investigated and 296 vascular plant species were recorded.

We measured species height, density, coverage and standing biomass of each species in each

plot. Three 1 m × 1 m plots along the diagonal line were selected from the five plots to measure the

standing biomass of each species. All pPlant species were cut at ground level and were 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 the 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 evapo-transpiration 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 variability 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

2.2.3 Plant functional traits

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

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

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

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

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

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

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

189 **2.3 Aboveground biomass**

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

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

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

193 **2.4 Diversity calculations**

194 **2.4.1 Taxonomic diversity**

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

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

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

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

199 **2.4.2 Functional diversity**

200 The functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional

201 dispersion (FDis) and Rao index (Rao's Q) were calculated based on the Gower distance of

202 functional traits using the 'dbFD' function in the '*FD*' R package (Laliberté et al., 2015).

203 **2.4.3 Phylogenetic diversity**

204 All plant species names recorded in surveys were checked in the plant list (www.theplantlist.org) to

205 obtain acceptable species names. Based on the APG III system (The Angiosperm Phylogeny Group,

206 2009), we entered the taxonomic information (family/genus/species) of all species into the

207 Phylomatic online plant database (Phylomatic Version 3, http://phylodiversity.net/phylomatic/),

208 selected storedtree = "zanne2014 (Zanne et al., 2014)", and output a phylogenetic tree with branch

209 length and differentiation time (Fig. S2). Faith's phylogenetic diversity (PD, the sum of the

210 phylogenetic branch lengths), the mean pairwise distance (MPD) and the mean nearest taxon

211 distance (MNTD) between species in a community were calculated using the 'mpd' function in the

212 '*picante*' R package (Kembel et al., 2010).

213 **2.5 Data analysis**

214 First, we conducted a Random Forest model to estimate the relative importance of the three

215 dimensions of biodiversity to community biomass. The Random Forest model can alleviate

216 multicollinearity and complex interactions between independent variables. We built 5000 regression

217 trees in Random Forest, and each tree was fitted with 2/3 of the data. The other 1/3 of the data was

218 used to estimate the importance of each predictor variable, which was represented by the increase in

219 mean square error (MSE). In the Random Forest model, the variables that ranked first in terms of

220 taxonomic, functional and phylogenetic diversity were selected as proxies for the three dimensions of

221 biodiversity.

222 To explore the influence of climate in different periods and climate anomalies on biodiversity,

223 we also used the Random Forest model to analyze the relative importance of the present climate, the

224 Mid-Holocene climate, the Last Glacial Maximum climate, and paleoclimate change on the three

225 dimensions of biodiversity. To evaluate the relative importance of climate drivers of biodiversity, we

226 calculated the ratio between the increase in MSE of the predictor and the sum of all the increases in

227 MSE, which is expressed as a percentage.

228 To study the effects of climate in different periods and climate anomalies on biodiversity and

229 aboveground biomass, we performed piecewise structural equation models (pSEM) to test the direct

230   and indirect causal relationships between the climate in different periods and paleoclimate change,

231   species diversity, functional diversity, phylogenetic diversity and biomass. Model construction

232   procedures involved the following three stages. First, based on the results of the Random Forest

233   model, we identified the climate variables that significantly affected biodiversity and divided them

234   into composite variables. The model contained two composite variables that potentially represent

235   collections of variables in terms of the present climate and paleoclimate change. We calculated

236   Pearson correlations between the climate factors (Fig. S3) and deleted the predictors with high

237   correlation coefficients (>0 .85, $P < 0.05$) to avoid multicollinearity. Before pSEM analysis, all

238   selected predictors were standardized. Second, principal component analyses (PCAs) were used for

239   the composite variables with multiple predictors. For each composite variable, the first principal

240   component (PC1) explained 64~71% of the total variance and was used in the subsequent pSEM

241   analysis (Table S2). Third, pSEM was developed from the full conceptual model. We fitted the

242   component models of the piecewise SEM as linear models and reported the standardized coefficient

243   for each path from each component model. We used Shipley's d-separation test to evaluate the

244   overall fit of the pSEM, as well as Fisher's C statistic and AIC.

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

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

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

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

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

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

251   **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~~functional~~, and functional ~~phylogenetic~~ diversity, respectively, and used for subsequent analysis.

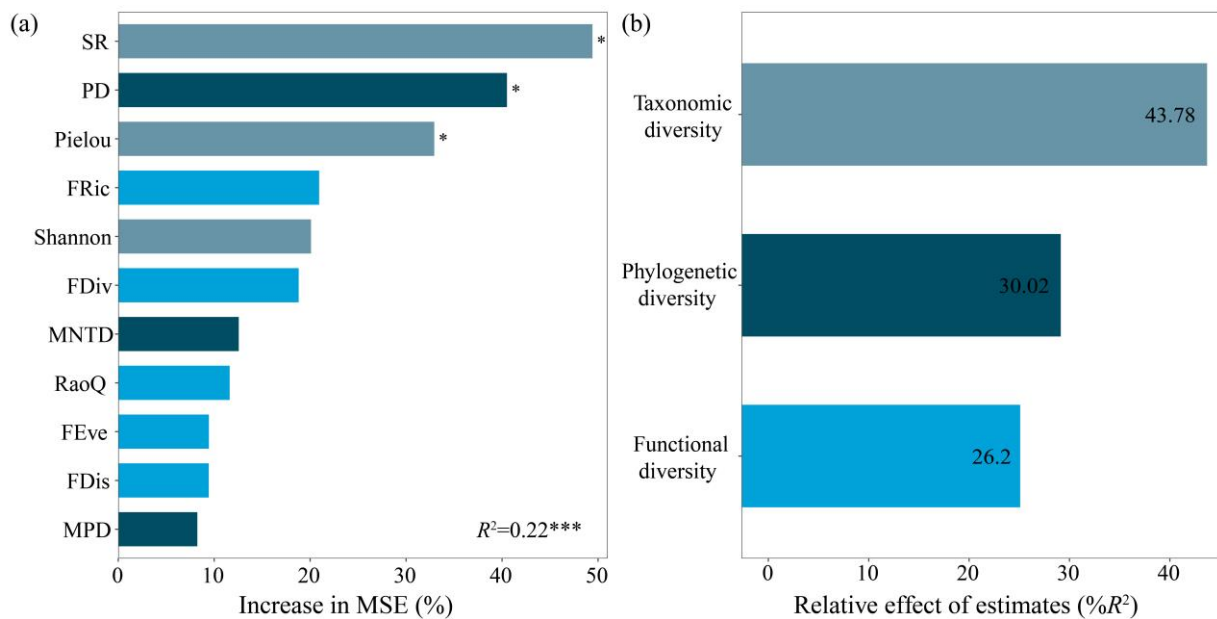



Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to community biomass. An increase in mean square error (MSE) denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

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

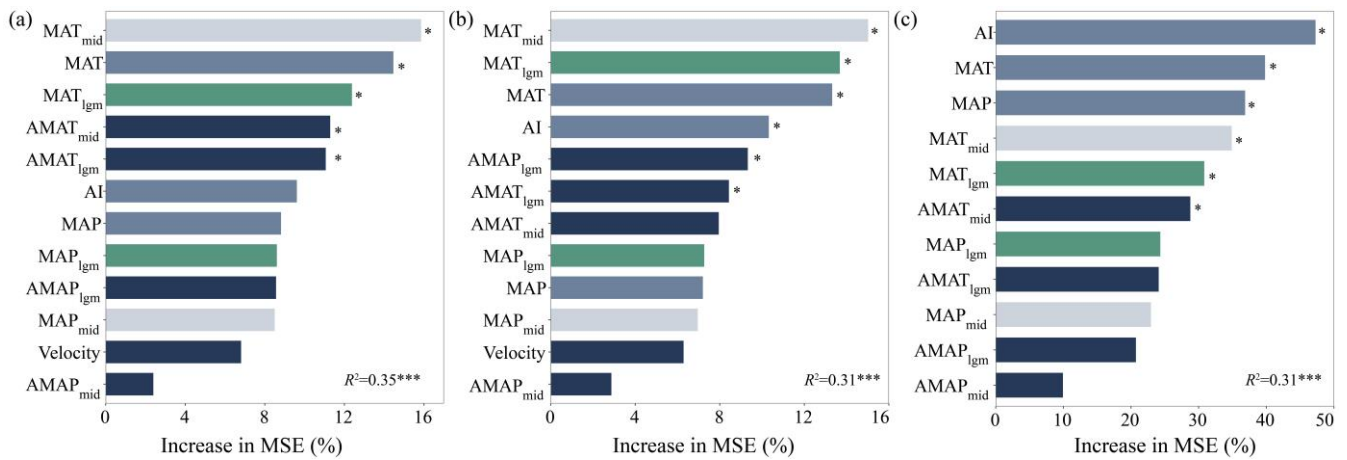
268 $R^2 = 0.31$, $P < 0.001$) and 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) of the variance in SR, PD and

269 FRic, respectively (Fig. 2). Temperatures in different periods, including MAT_{mid}, MAT and MAT_{lgm},

270 were the main factors driving SR and PD ($P < 0.05$, Fig. 2a and 2b), followed by climate anomalies

271 in various periods. However, the current climate (i.e., AI, MAT and MAP) had a stronger impact on

272 FRic ($P < 0.05$, Fig. 2c).

273

275 Fig. 2 The importance of climate variables in different periods and paleoclimate change to species

276 richness (a), phylogenetic diversity (b) and functional richness (c). An increase in mean square error

277 (MSE) denotes an increase in the percentage mean square error. Significance levels are as follows: *:

278 $P < 0.05$ and ***: $P < 0.001$.

279

280   In terms of relative contributions, the current climate and the paleoclimate changes had greater

281 impacts on the three dimensions of biodiversity. Paleoclimate change was the best predictor of SR

282 (33.90%) and PD (32.10%). Strikingly, the present climate (38.68%) showed a larger contribution to

283 the prediction of FRic than paleoclimate change (26.06%; Fig. 3).

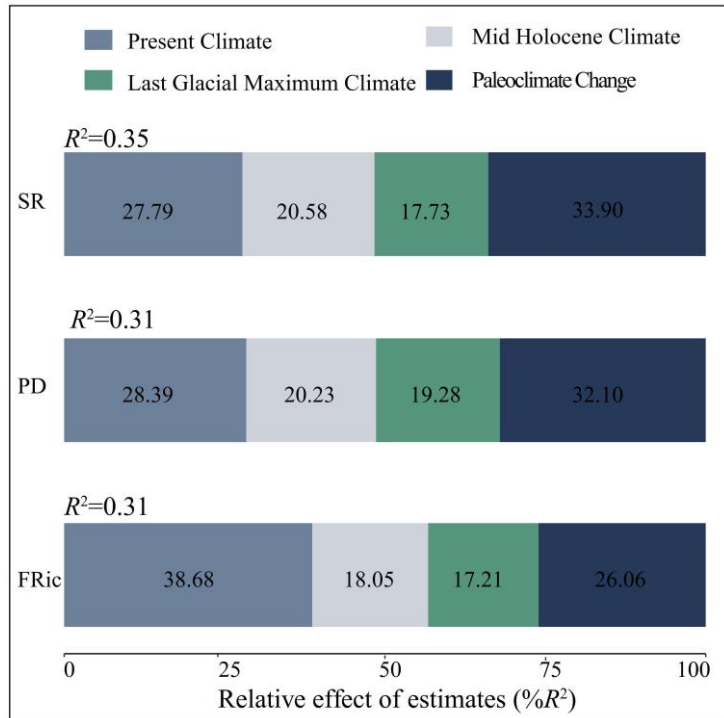



Fig. 3 Relative contributions of present, ~~climate, paleo - (mid~~Mid-Holocene and Last Glacial

Maximum~~)~~ climate 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

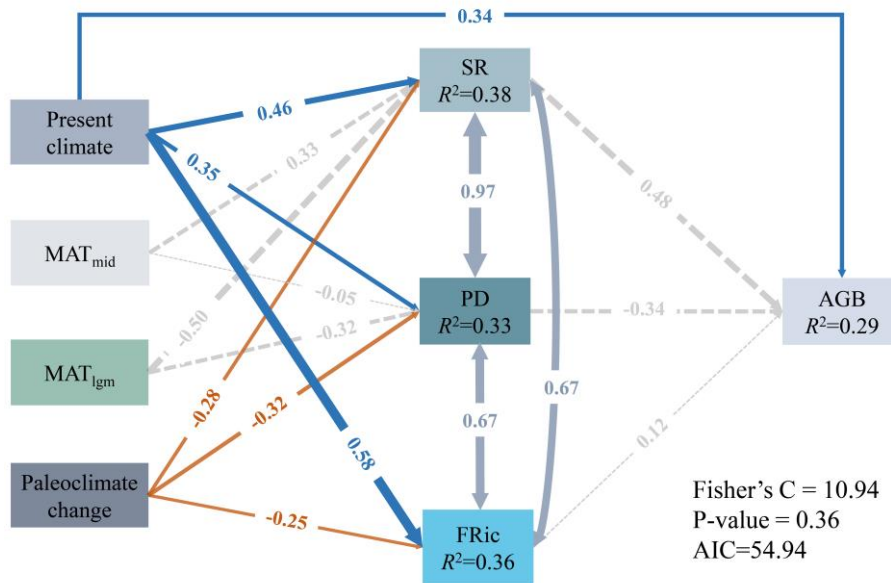
variances in SR, PD, FRic and AGB, respectively (Fig. 4). The present climate had direct and

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).

297

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

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

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

301   MAT and MAP anomaly from the Last Glacial Maximum<s>from the Mid-Holocene</s> to the present to

302 the present. Numbers adjacent to arrows represent the standardized path coefficients (r_∂). R^2 indicates

303 the proportion of variance explained. Blue (positive paths) and orange (negative paths) solid arrows

304 indicate significant paths ($P < 0.05$), and gray dashed arrows indicate non-significant paths ($P >$

305   0.05).

306

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

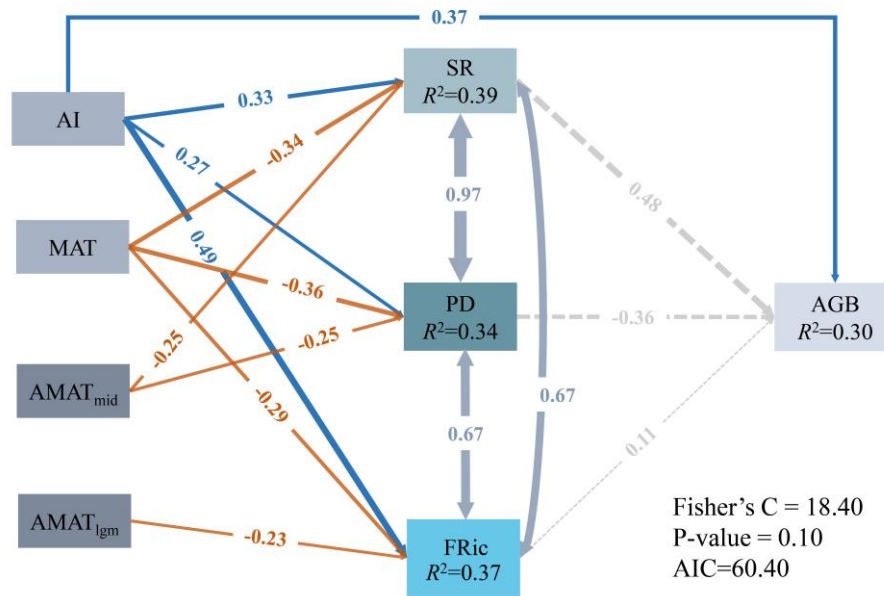
308 0.05), FRic ($r_\partial = 0.49$, $P < 0.05$), and AGB ($r_\partial = 0.37$, $P < 0.05$) were all significantly positive, while

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

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

311 -0.25, $P < 0.05$) and PD ($r_\partial = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the

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

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

314

315   Fig. 5 The effects of present climate (AI and MAT) and Climate anomalies (AMAT$_{mid}$ and AMAT$_{lgm}$)

316   on diversity and AGB. Numbers adjacent to arrows represent the standardized path coefficients. R^2

317   indicates the proportion of variance explained. Blue (positive paths) and orange (negative paths)

318   solid arrows indicate significant paths ($P < 0.05$), and gray dashed arrows indicate non-significant

319   paths ($P > 0.05$).

320   **4. Discussion**

321   **4.1 The effects of different dimensions of biodiversity on aboveground biomass**

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

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

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

325   studies have emphasized the importance of phylogenetic diversity and functional diversity for~~to~~

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

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

328   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 their

relationships 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. further

~~studies are still needed.~~ 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 (Yang et al., 2011; Liu et al., 2021; Walther et al., 2002), but our research shows that the pattern of biodiversity is also affected by past climates, and especially climate ~~change~~ anomalies. Based on climate-related traits, climate anomalies~~Paleoclimate changes~~ filtered the filtered the regional species pool ~~based on climate-related traits~~, which in turn affected contemporary biodiversity patterns.

Species richness is affected by the significant positive effects of AI, and the significant negative effects of MAT and $AMAT_{mid}$. Jansson's research showed that the total number of vascular plant species decreased with increasing temperature change since the LGM in mainland areas (Jansson, 2003), which is inconsistent with our results. We found that the species richness of Mongolian Plateau grassland is more affected by temperature changes since the Mid-Holocene. In Europe, the richness of widespread species was largely controlled by the modern climate, while the LGM climate and climatic heterogeneity were codominant with modern climate as controls of richness for restricted and intermediate species, which appear to still be associated with their glacial refugia (Svenning and Skov, 2007b).

Phylogenetic diversity (PD) is usually used to quantify the uniqueness of a region's evolution. On longer timescales, the effects of climate on speciation and extinction may cumulatively affect current PD patterns (Svenning et al., 2015). Our research showed that PD was negatively correlated with MAT and $AMAT_{mid}$ ~~temperature anomalies~~ in the Mid-Holocene, but not significantly related to temperature anomalies during the Last Glacial Maximum. However, the PD of global forest ecosystems is positively associated with temperature and precipitation and is negatively associated with Quaternary precipitation change (Kubota et al., 2018). This indicates the importance of paleoprecipitation variation in shaping the pattern of contemporary phylogenetic diversity in forest ecosystems, possibly by survival and recolonization from refugia along hydrological gradients (Blonder et al., 2018). Additionally, Quaternary glacial-interglacial climate oscillations led to the extinction of trees in many parts of the globe, for example in Australia (Macphail et al., 1995) and Europe (Svenning, 2003), affecting the PD of global forest ecosystems. Liu et al. showed that herbaceous plants were mainly affected by climate change since Mid-Holocene, while woody plants were mainly affected by climate 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, are more susceptible to cold Quaternary climate oscillations. Herbs can mitigate the effects of extreme weather by producing underground buds and stems, or wilting aboveground parts (Qian et al., 2017). ~~Phylogenetic studies reveal that major ecological niches are more conserved through evolutionary history than expected, implying that adaptations to major climate changes have not readily been accomplished in all lineages (Donoghue, 2008).~~

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 and accessibility 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 climate change and human activities in the Mongolian Plateau grasslands. The influence of

paleoclimate anomalies on contemporary species and phylogeny diversity may be caused by 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).

417 Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe landscape,

418 and drought began to intensify. During the Last Glacial Maximum period, the vegetation types on the

419 Mongolian Plateau were mainly polar ~~and~~, alpine ~~deserts~~ and temperate deserts (Ray and Adams,

420 2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene, xerophytes had

421 declined sharply, and plants of humid climates had increased. The humidity increased during the

422 early Holocene, and generally humid conditions lasted from 10,400 until 7000 yr BP and the region

423 experienced the Lavliakan humid phase (Yin et al., 2011; Lioubimtseva, 2004), with more

424 hygrophilous species, such as Cyperaceae (Tian et al., 2017). This climate condition was also

425 conducive to the development and spread of Compositae and Gramineae families in the steppes of

426 Central Asia (Lioubimtseva, 2004). Since approximately 5200 yr BP to present, the climate has

427 become more arid, with corresponding vegetation change and strong aeolian activity (Yin et al.,

428 2011). ~~Furthermore, palaeoecological and archaeological evidence shows that people have shaped~~

429 ~~most of terrestrial nature for at least 12,000 years, including burning, hunting, cultivation and~~

430 ~~domestication. In the Mongolian Plateau, especially in the Inner Mongolia region of northern China,~~

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

432 ~~The intensification of grazing activities also causes changes in biodiversity.~~

433   As far as aboveground biomass is concerned, after taking into account climatic factors, it is

434 mainly directly affected by aridity index, while the three dimensions of biodiversity have no

435 significant impact on it, which is consistent with our previous research (Li et al., 2020). A

436 meta-analysis of 40 global grasslands plant communities showed that the response of plant diversity

437 to climate warming was an important factor in determining grassland aboveground biomass (Shao et

438 al., 2021). Similarly, ~~Paleoclimate~~ 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 evolutionary, 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 and further intensified again after ~4.2–4.0 ka (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

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

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

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

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

465 key role in shaping contemporary biodiversity patterns.

466

Authors' Contributions

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

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

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

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

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

Data available

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

475 author.

Conflict of interest statement

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

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