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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26 **Abstract**

27 Present and historical climate conditions jointly determine contemporary biodiversity patterns and

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

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

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

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

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

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

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

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

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

37 and modern climate jointly determined contemporary biodiversity patterns, while community

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

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

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

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

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

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

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

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

46 patterns of biodiversity and its relationship with ecosystem functions.

47 **Keywords**

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

49 diversity, taxonomic diversity

50 **1. Introduction**

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

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

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

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

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

56 2020; Eiserhardt et al., 2015; Svenning et al., 2015).

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

58 2005), but understanding the effects of different dimensions of biodiversity (i.e., taxonomic diversity,

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

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

61 and ecosystem functions have predominantly focused on the relationship between taxonomic

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

77   the ecological consequences of global climate changes.

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

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

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

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

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

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

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

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

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

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

88   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 climate (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

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

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

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

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

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

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

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

139 **2. Materials and Methods**

140 **2.1 Study Area**

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

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

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

144 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).

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

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

147 **2.2 Data Collection**

148 **2.2.1 Sites Sampled and Vegetation Investigation**

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

150 homogeneous environment. These sites were separated by about 50 km. One or three 10 m $\times$ 10 m

151 quadrats were set in each site (in a few areas with sparse vegetation and large heterogeneity, three 10

152 m $\times$ 10 m quadrats were set to ensure the accuracy of the survey data). Within each quadrat, five 1 m

153 $\times$ 1 m plots were placed at each corner and at the center of the quadrat to investigate vegetation. A

154 total of 296 vascular plant species were recorded.

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

156   plot. Three 1 m $\times$ 1 m plots along the diagonal line were selected from the five plots to measure the

157   standing biomass of each species. Plant species were cut at ground level and separately bagged, then

158   oven-dried at 65 ℃ to constant weight, and weighed for dry matter.

159   **2.2.2 Climate Data**

160   Mean annual temperature (MAT, ℃) and mean annual precipitation (MAP, mm) were obtained from

161   the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas,

162   http://chelsa-climate.org/) (Karger et al., 2017), a data set consisting of monthly temperature and

163   precipitation climatology from 1979 to 2013. Potential evapotranspiration (PET) was obtained from

164   the CGIAR-CSI (CGIAR Consortium for Spatial Information, http://www.cgiar-csi.org) based on

165   latitude and longitude data for each site (Trabucco and Zomer, 2019). The resolution of both is 30 arc

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

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

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

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

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

171   6000 years ago) and the Last Glacial Maximum (LGM, about 22,000 years ago) were simulated

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

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

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

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

176   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

178 **2.2.3 Plant functional traits**

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

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

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

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

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

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

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

2.3 Aboveground biomass

The aboveground biomass of the community was calculated based on the dry matter accumulation value (g/m^2) of all plant samples in each plot, and the average aboveground biomass of each plot in each quadrat was calculated to represent the aboveground biomass of the plant community (g/m^2).

2.4 Diversity calculations

2.4.1 Taxonomic diversity

We used species richness (SR), Shannon-Wiener index and Pielou index as measures of community taxonomic diversity. The species richness (number of species/m^2) at each site was calculated as the average number of species per plot. The Shannon-Wiener index and Pielou index were calculated using the 'diversity' function in the "*vegan*" R package (Oksanen et al., 2020).

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. 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 to evaluate the

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

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,

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

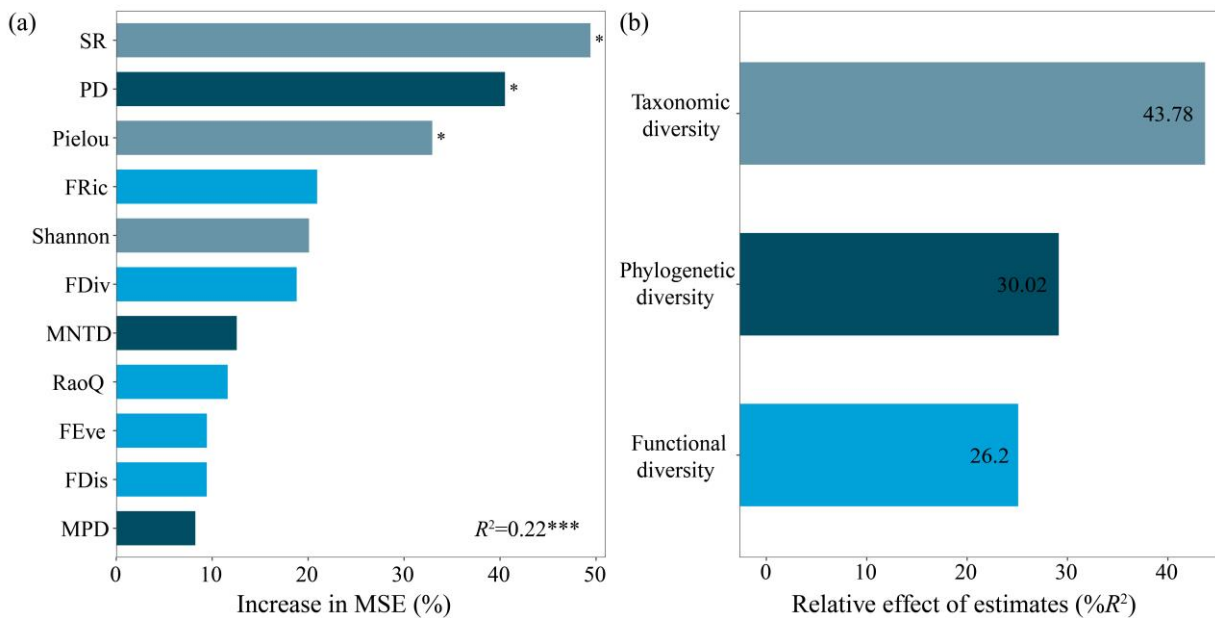
253 43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD

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

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

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

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

258 analysis.

259

260 Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to

261 community biomass. An increase in mean square error (MSE)denotes an increase in the percentage

262 mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

263 **3.2 Paleoclimate and present climate predictors of contemporary diversity**

264 Random Forest models explained 35% (cross-validation $R^2 = 0.35$, $P < 0.001$), 31% (cross-validation

265 $R^2 = 0.31$, $P < 0.001$) and 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) of the variance in SR, PD and

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

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

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

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

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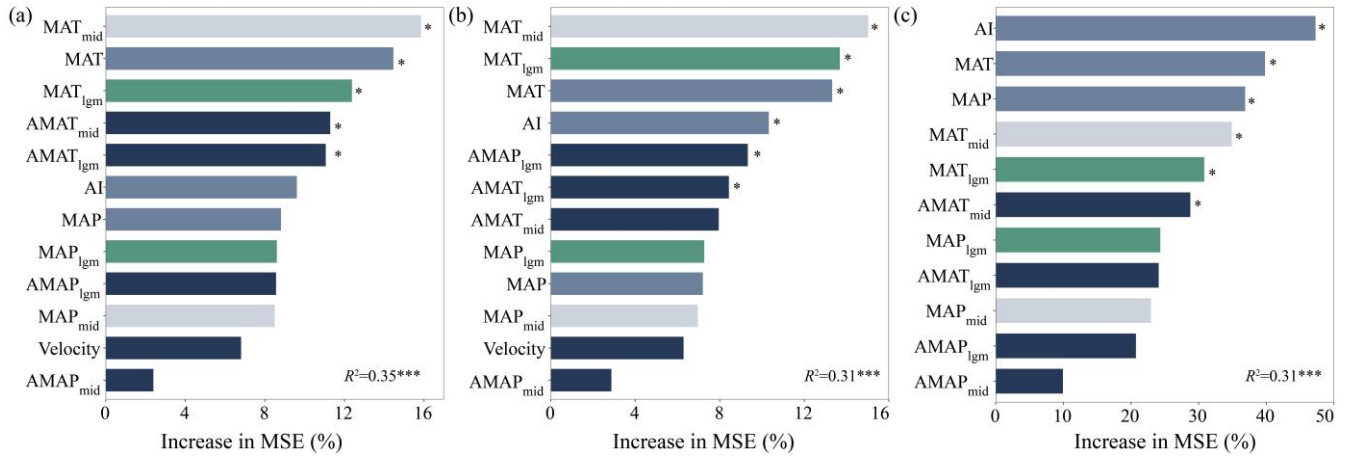
271

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

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

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

275 $P < 0.05$ and ***: $P < 0.001$.

276

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

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

279 (33.90%) and PD (32.10%). Strikingly, the present climate (38.68%) showed a larger contribution to

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

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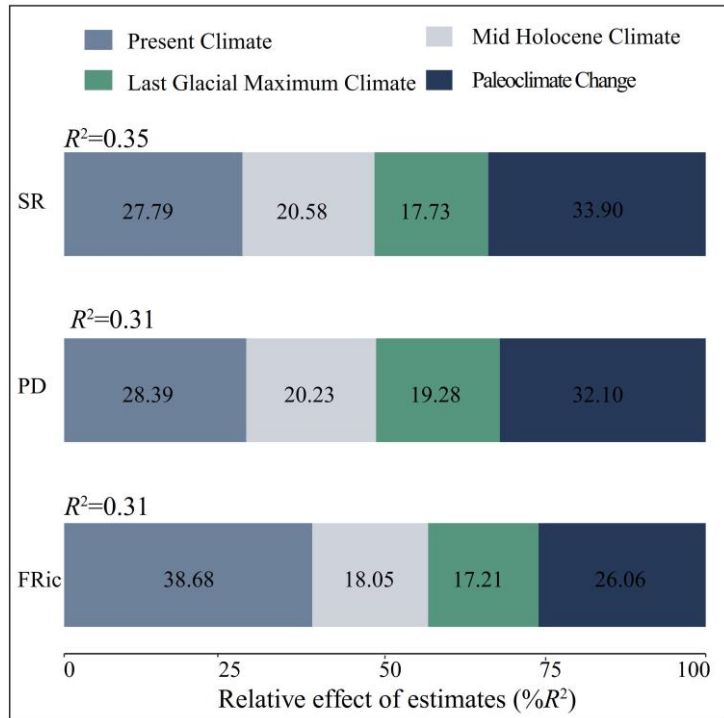
Fig. 3 Relative contributions of present climate, Mid-Holocene, Last Glacial Maximum and

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 ($r_\partial = -0.25$, $P < 0.05$,
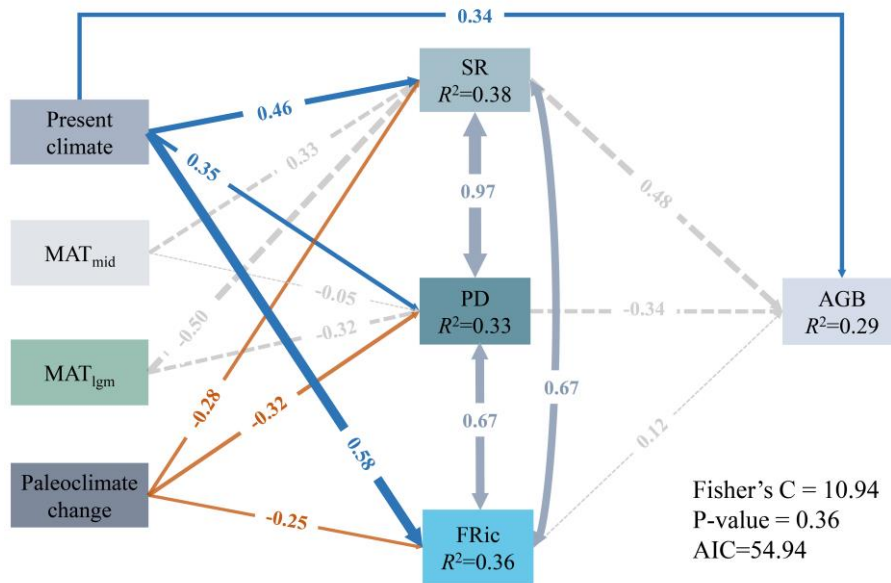
Fig. 4).

293

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

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

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

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

298   represent the standardized path coefficients (r_{∂}). R^2 indicates the proportion of variance explained.

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

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

301

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

303   0.05), FRic ($r_{\partial} = 0.49$, $P < 0.05$), and AGB ($r_{\partial} = 0.37$, $P < 0.05$) were all significantly positive, while

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

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

306   -0.25, $P < 0.05$) and PD ($r_{\partial} = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the

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

308   anomaly from the Last Glacial Maximum to the present (AMAT_{lgm}; Fig. 5).
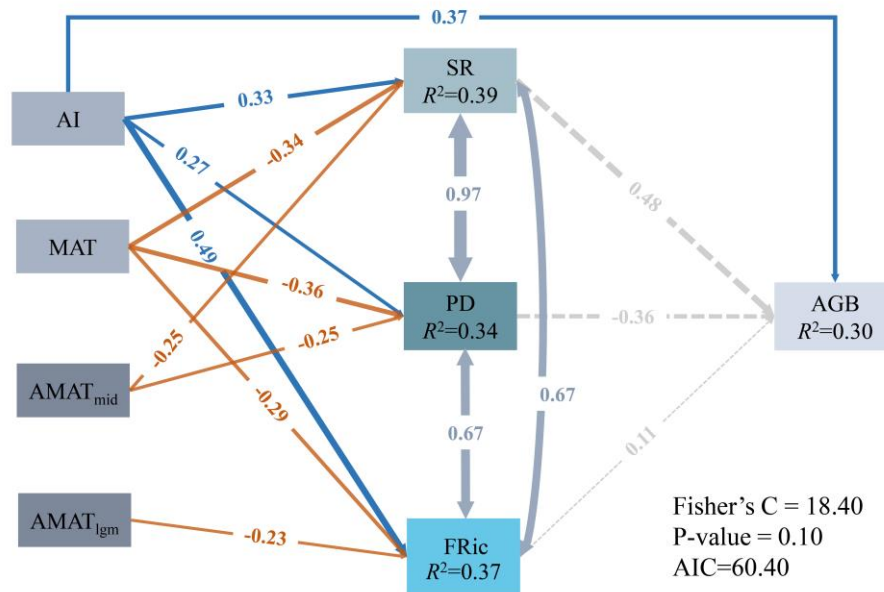
Fig. 5 The effects of present climate (AI and MAT) and Climate anomalies (AMAT$_{mid}$ and AMAT$_{lgm}$)

on diversity and AGB. Numbers adjacent to arrows represent the standardized path coefficients. 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 ($P > 0.05$).

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

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

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

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

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

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

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

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

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

333 nitrogen concentration and photosynthetic utilization efficiency, can promote aboveground biomass

334 (Wolf et al., 2021).

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

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

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

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

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

340 our research suggests that protecting taxonomic diversity and conserving evolutionarily different

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

342 **4.2 Relationship between paleoclimate anomalies and current biodiversity patterns**

343 Although a rich body of research has explored the factors affecting biodiversity patterns and their

344 relationships with biomass (Van Der Plas, 2019; Tilman et al., 2012) , it is not clear how current

345 climate and paleoclimate together affect the relationship, especially in grassland communities. Here,

346 our results showed that paleoclimate changes and present climate factors were critical variables

347   influencing contemporary biodiversity patterns. This illustrates the importance of historical factors,

348   such as evolution, as well as contemporary factors, such as climate, in determining the geographic

349   ranges of species and the accumulation of species in the region (Fine, 2015). Previous studies aiming

350   to explain patterns of biodiversity have focused on the current climate (Harrison et al., 2015), energy

351   (Kreft and Jetz, 2007), soil attributions (Ulrich et al., 2014), human activities (Hautier et al., 2015;

352   Newbold et al., 2015) or water availability (Jiao et al., 2021; Liu et al., 2021). Modern climate

353   research on biodiversity and ecosystem functions has been widely confirmed (Walther et al., 2002;

354   Liu et al., 2021; Yang et al., 2011), but our research shows that the pattern of biodiversity is also

355   affected by past climates, and especially climate anomalies. Based on climate-related traits, climate

356   anomalies filtered the regional species pool, which in turn affected contemporary biodiversity

357   patterns.

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

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

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

361   2003), which is inconsistent with our results. We found that the species richness of Mongolian

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

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

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

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

366   (Svenning and Skov, 2007b).

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

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

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

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

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

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

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

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

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

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

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

378   PD of global forest ecosystems. Liu et al. showed that herbaceous plants were mainly affected by

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

380   since the LGM, which may be due to the differences in morphology of herbaceous and woody plants

381   (Liu et al., 2018b; Wang et al., 2021). Woody plants with large conduits are vulnerable to drought or

382   freezing and cause clogging of conduits (Zanne et al., 2014), and thus, are more susceptible to cold

383   Quaternary climate oscillations. Herbs can mitigate the effects of extreme weather by producing

384   underground buds and stems, or wilting aboveground parts (Qian et al., 2017).

385   Our results suggested that functional richness was negatively related to Last Glacial Maximum

386   climate anomaly. This may be due to the intolerance of plant traits to past climatic conditions

387   (Bhagwat and Willis, 2008) and the postglacial migration lag (Svenning et al., 2008). In the Late

388   Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climate fluctuations

389   (Tian et al., 2017), and likely experienced a non-random removal of functional combinations and

390   change in functional diversity (Ordonez and Svenning, 2017). Previous research has indicated that

391   the magnitude of past glacial-to-interglacial warming was sufficient at most locations across the

392   globe (including the Mongolian Plateau) to drive moderate to large changes in vegetation

393   composition and structure (Nolan et al., 2018). When climate changes, inappropriate species may be

394   quickly ruled out, and appropriate species may migrate more slowly, resulting in a negative

395   correlation between the paleoclimate anomaly and contemporary FD in the Mongolian Plateau. This

396   is also limited by the spreading ability or migration potential of plants after the glaciers retreated,

397   when species with inappropriate characteristics disappeared from the community and were not

398   replaced by other species (Blonder et al., 2018). Studies in Europe indicate that the lagging effect of

399   glacial-interglacial climate instability on functional diversity is >10,000 years (Ordonez and

400   Svenning, 2015).

401   **4.3 Effects of climate on the relationship between biodiversity and biomass**

402   The influence of climate on relationship between contemporary diversity and biomass may be

403   caused by climate change and human activities in the Mongolian Plateau grasslands. In the eastern

404   part of the Mongolian Plateau, the interval of 35230 to 25150 yr B.P. was a forest-steppe landscape

405   under humid conditions, represented by Pinaceae, Compositae and Chenopodiaceae (Tian et al.,

406   2017). Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe

407   landscape, and drought began to intensify. During the Last Glacial Maximum period, the vegetation

408   types on the Mongolian Plateau were mainly polar, alpine and temperate deserts (Ray and Adams,

409   2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene, xerophytes had

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

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

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

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

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

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

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

417 2011).

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

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

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

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

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

423 al., 2021). Similarly, paleoclimate changes also have no direct effects on aboveground biomass,

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

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

426 (removal or accumulation over time of species and functional states) through evolutionary, extinction,

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

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

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

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

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

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

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

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

435 2021). In the Mongolian Plateau, especially in the Inner Mongolia region of northern China, grazing

436 appeared at ∼5.7–5.5 ka and further intensified again after ∼4.2–4.0 ka (Huang et al., 2021). A large

437 number of studies have shown that the intensification of grazing activities also causes changes in

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

439 2007). Therefore, there is an urgent need for future research to develop systematic analytical

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

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

442 **5. Conclusion**

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

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

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

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

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

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

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

450 key role in shaping contemporary biodiversity patterns.

451

452 **Authors' Contributions**

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

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

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

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

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

Data available

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

460 author.

Conflict of interest statement

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

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