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

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**

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

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

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

research has 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. "Little human interference" mainly refers to the selection of areas with

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

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

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

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

155   grassland, while the degeneration indicator plants such as *Convolvulus ammannii*, *Potentilla acaulis,*

156   *Artemisia frigida*, *Stellera chamaejasme* and *Cynanchum hancockianum* appeared in large numbers.

157   These sites were separated by about 50 km. According to the methods and protocols for plant

158   community inventories proposed by Fang et al. (Fang et al., 2009), most of the vegetation surveys in

159   this study were conducted by setting one 10 m x 10 m quadrat at the respective site. However, in a

160   few areas with sparse vegetation and large heterogeneity, we set three 10 m $\times$ 10 m quadrats to

161   ensure the accuracy of the survey data.. Within each quadrat, five 1 m $\times$ 1 m plots were placed at

162   each corner and at the center of the quadrat to investigate vegetation. A total of 296 vascular plant

163   species were recorded.

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

165   plot. Three 1 m $\times$ 1 m plots along the diagonal line of the 10 m $\times$ 10 m quadrat were selected from

166   the five plots to measure the standing biomass of each species. Plant species were cut at ground level

167   and separately bagged, then oven-dried at 65 ℃ to constant weight, and weighed for dry matter.

168   **2.2.2 Climate Data**

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

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

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

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

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

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

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

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

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

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

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

180 6000 years ago) and the Last Glacial Maximum (LGM, about 22,000 years ago) were simulated

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

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

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

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

185 variables used in this study are shown in Table 1.

186 **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 | $AMAT_{lgm}$ |

**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)

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

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

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

208     functional traits using the 'dbFD' function in the '*FD*' R package (Lalibertéet al., 2015).

209     **2.4.3 Phylogenetic diversity**

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

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

212     2009), we entered the taxonomic information (family/genus/species) of all species into the

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

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

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

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

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

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

219     **2.5 Data analysis**

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

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

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

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

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

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

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

227     biodiversity.

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

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

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

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

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

233      MSE, which is expressed as a percentage.

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

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

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

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

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

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

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

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

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

243      correlation coefficients ($>0.85$, $P < 0.05$) to avoid multicollinearity. Before pSEM analysis, all

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

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

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

247      analysis (Table S2). Third, pSEM was developed from the full conceptual model (Fig. S4). We fitted

248      the component models of the piecewise SEM as linear models and reported the standardized

249      coefficient for each path from each component model. We used Shipley's d-separation test and

250      Fisher's C statistic to evaluate the overall fit of the pSEM, and Akaike information criteria (AIC) to

251      select the best model. We used standardized path coefficients to measure the direct, indirect, and total

252  effect sizes of the present climate and paleoclimate changes on AGB.

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

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

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

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

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

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

259  **3. Results**

260  **3.1 Effects of biodiversity on aboveground biomass**

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

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

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

264  43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD

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

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

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

268  agents of taxonomic, phylogenetic, and functional diversity, respectively, and used for subsequent
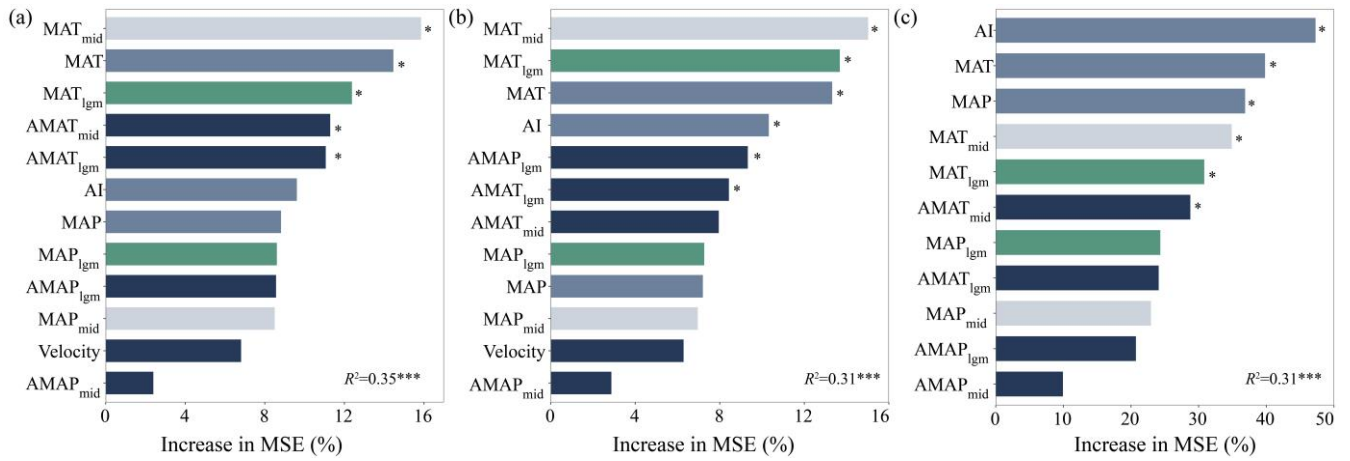
269  analysis.
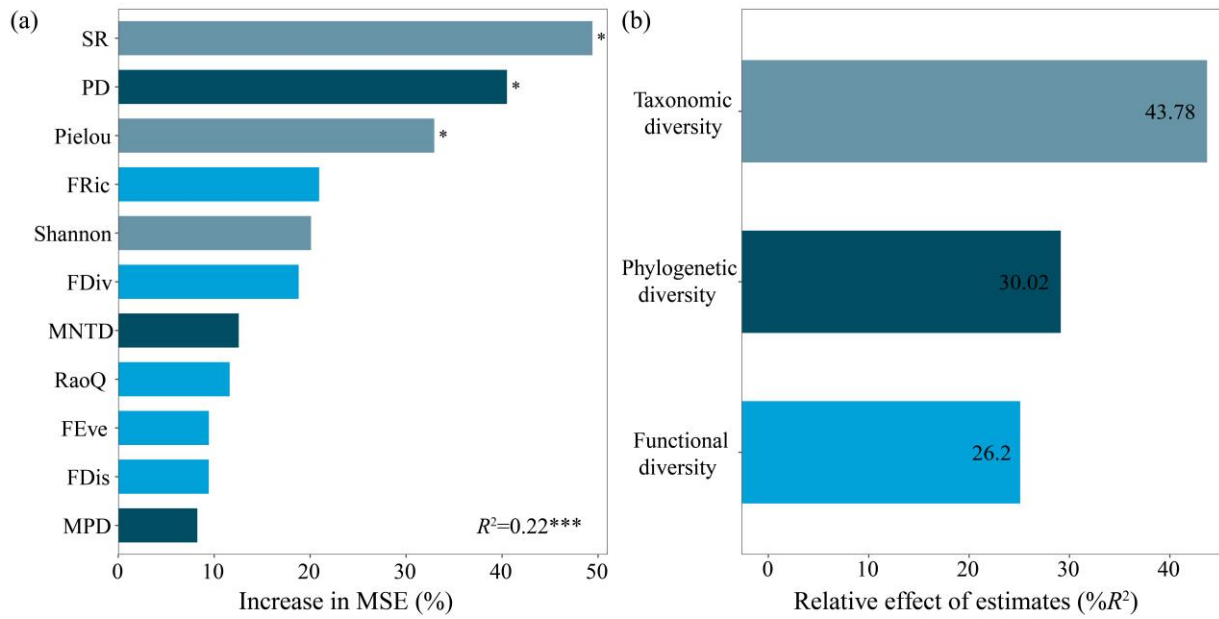
Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to community biomass. An increase in mean square error (MSE)denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

## 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 ***: $P < 0.001$.
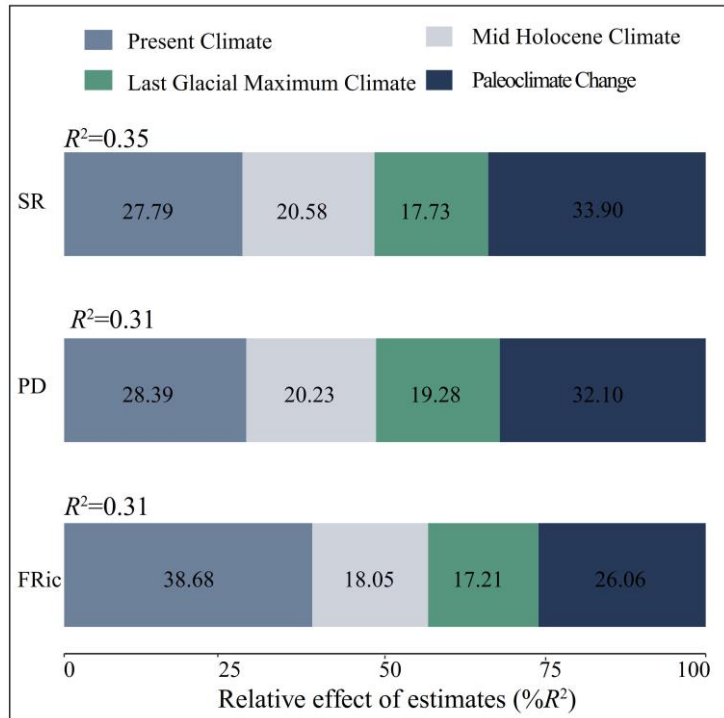
In terms of relative contributions, the current climate and the paleoclimate changes had greater impacts on the three dimensions of biodiversity. Paleoclimate change was the best predictor of SR (33.90%) and PD (32.10%). Strikingly, the present climate (38.68%) showed a larger contribution to the prediction 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 ($r_\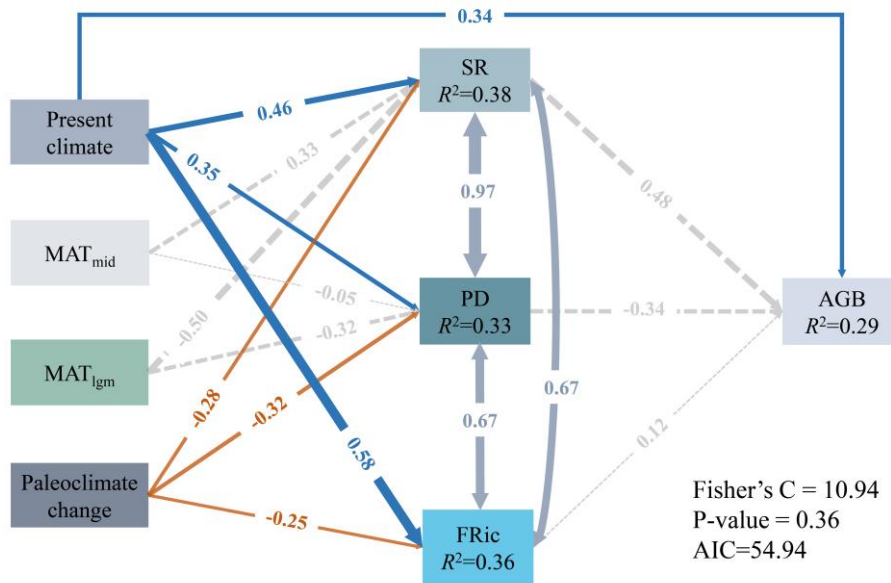partial = 0.46$, $P < 0.05$), PD ($r_\partial = 0.35$, $P < 0.05$) and FRic ($r_\partial = 0.58$, $P < 0.05$, Fig. 4). However, the paleoclimate change had direct significant negative effects on SR ($r_\partial = -0.28$, $P < 0.05$), PD ($r_\partial = -0.32$, $P < 0.05$) and FRic ($r_\partial = -0.25$, $P < 0.05$, Fig. 4). $MAT_{mid}$ and $MAT_{lgm}$ had no significant effects on SR, PD, FRic and AGB (Fig. 4).

Fisher's C = 10.94
P-value = 0.36
AIC=54.94

304

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

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

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

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

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

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

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

312

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

314　0.05), FRic ($r_\partial = 0.49$, $P < 0.05$), and AGB ($r_\partial = 0.37$, $P < 0.05$) were all significantly positive, while

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

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

317　$-0.25$, $P < 0.05$) and PD ($r_\partial = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the

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

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

17

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

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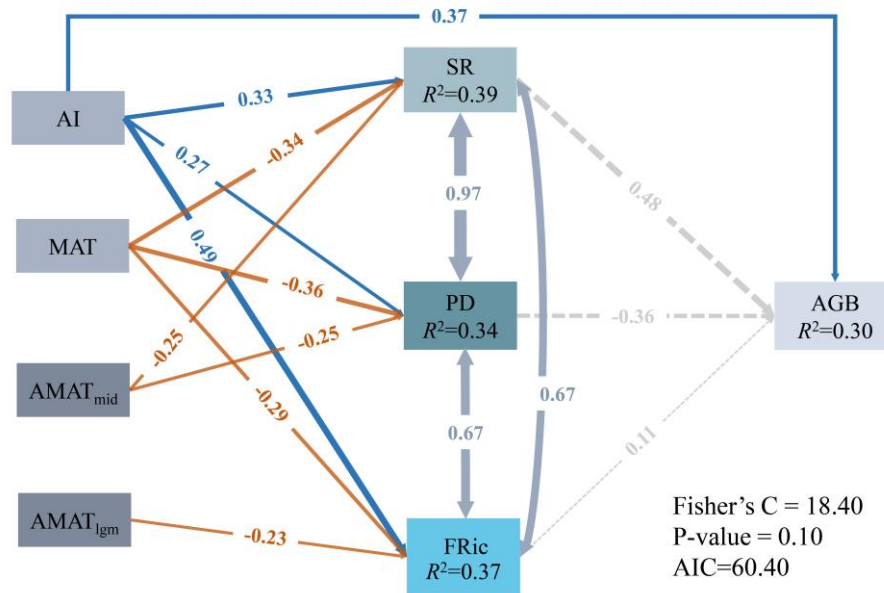


322

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

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

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

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

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

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

329                   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 relationship between biodiversity and 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

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

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

376　2003), which is inconsistent with our results. We found that the species richness of Mongolian

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

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

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

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

381　(Svenning and Skov, 2007b).

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

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

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

385　with MAT and AMAT$_{mid}$, but not significantly related to temperature anomalies during the Last

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

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

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

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

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

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

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

393　PD of global forest ecosystems. It was shown that herbaceous plants were mainly affected by climate

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

395　LGM, which may be due to the differences in morphology of herbaceous and woody plants (Liu et

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

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

398 Quaternary climatic conditions. In contrast, herbs can mitigate the effects of extreme weather by

399 producing underground buds and stems, or by wilting of aboveground parts (Qian et al., 2017).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

415 Svenning, 2015).

416 **4.3 Effects of climate on the relationship between biodiversity and biomass**

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

418    caused by a combination of climate change and human activities in the Mongolian Plateau grasslands.

419    In the eastern part of the Mongolian Plateau, the interval of 35230 to 25150 yr B.P. was a

420    forest-steppe landscape under humid conditions, represented by Pinaceae, Compositae and

421    Chenopodiaceae (Tian et al., 2017). Subsequently, the forest patches gradually shrank, the vegetation

422    transitioned to the steppe landscape, and drought began to intensify. During the Last Glacial

423    Maximum period, the vegetation types on the Mongolian Plateau were mainly polar, alpine and

424    temperate deserts (Ray and Adams, 2001), and the main plants were Compositae and

425    Chenopodiaceae. By the Holocene, xerophytes had declined sharply, and plants of humid climates

426    had increased. The humidity increased during the early Holocene, and generally humid conditions

427    lasted from 10,400 until 7000 yr BP and the region experienced the Lavliakan humid phase

428    (Lioubimtseva, 2004; Yin et al., 2011), with more hygrophilous species, such as Cyperaceae (Tian et

429    al., 2017). This climate condition was also conducive to the development and spread of Compositae

430    and Gramineae families in the steppes of Central Asia (Lioubimtseva, 2004). Since approximately

431    5200 yr BP to present, the climate has become more arid, with corresponding vegetation change and

432    strong aeolian activity (Yin et al., 2011).

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 changes also have no direct effects on aboveground biomass,

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

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

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

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

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

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

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

446  communities, from the evolution of the *Homo* in savannas 2 million years ago to the emergence of

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

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

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

450  2021). In the Mongolian Plateau, especially in the Inner Mongolia region of northern China, grazing

451  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).

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

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

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

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

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

457  **5. Conclusion**

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

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

460  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**

467

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.

473    **Data available**

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

475    author.

476    **Conflict of interest statement**

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

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