

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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25

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

89 Skov, 2007a; Svenning and Skov, 2007b). Contemporary plant functional traits and composition are
90 highly sensitive to climate and influenced by climate from tens of thousands of years ago, with
91 important consequences for ecosystem functions (Blonder et al., 2018; Butler et al., 2017). For
92 example, in Europe patterns of plant functional diversity exhibited prominent glacial-interglacial
93 climate change imprints (Ordonez and Svenning, 2015; Ordonez and Svenning, 2017). This is partly
94 due to the non-random removal of functional combinations that may have occurred during the
95 Last-Glacial Maximum (LGM; ~21,000 years ago), increasing functional differences between native
96 and migratory species, leading to smaller and dispersed functional spaces (Ordonez and Svenning,
97 2017). Evidence derived from the fossil pollen sequence and ecological datasets has shown that the
98 acceleration of biodiversity changes began millennia ago, whereas vegetation changes during the
99 Late Pleistocene to Early Holocene were driven primarily by changing climate (Mottl et al., 2021). In
100 the South American tropics, the species composition and structure of Last Glacial Maximum forests
101 were quite different from those of today, and biomass was also lower than that of contemporary
102 forests (Mayle et al., 2009).

103 Furthermore, the effects of climate change on biodiversity should depend partly on climate
104 displacement rate (climate-change velocity) (Sandel et al., 2011). For example, phylogenetic
105 clustering increased with increasing intensity of Quaternary glacial-interglacial climatic oscillations
106 in South America and Africa (Kissling et al., 2012). There is evidence that vegetation changes in
107 Northern Europe were non-linear and varied greatly among regions in the early-Mid Holocene
108 (Seddon et al., 2014). Paleoclimate simulations since 21,000 years B.P. suggest that there are great
109 similarities between past and future temperature changes in Eurasian temperate grasslands (Fordham
110 et al., 2020). During the last glacial-interglacial transition period, global warming and related climate

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

120 The Mongolian Plateau is located in the arid and semi-arid area of eastern Eurasia. Our previous
121 researches have shown that climate is an important direct factor mediating the relationship between
122 species richness and aboveground biomass in the Mongolian plateau steppe (Li et al., 2021; Li et al.,
123 2020). However, in the Late Quaternary, the Mongolian Plateau experienced severe alternating dry
124 and wet climatic fluctuations (Maestre et al., 2021; Tian et al., 2017), which may have a significant
125 impact on current plant diversity and ecosystem function. However, the impacts of climate in
126 different periods and climate legacy effects on aboveground biomass of steppes in the Mongolian
127 Plateau, as well as whether these effects are biodiversity dependent, remain to be evaluated. To
128 address these knowledge gaps, we coupled data from a field survey of 152 sites in the Mongolian
129 Plateau (Fig. S1) to existing databases on present and past climates to explore present climate and the
130 legacy effects of climate during the Last Glacial Maximum and the Mid-Holocene on current
131 biodiversity and biomass.

132 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 °C to 10 °C 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 × 10 m
151 quadrats were set in each site (in a few areas with sparse vegetation and large heterogeneity, three 10
152 m × 10 m quadrats were set to ensure the accuracy of the survey data). Within each quadrat, five 1 m
153 × 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 × 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 °C to constant weight, and weighed for dry matter.

159 **2.2.2 Climate Data**

160 Mean annual temperature (MAT, °C) 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.

186 **2.3 Aboveground biomass**

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

190 **2.4 Diversity calculations**

191 **2.4.1 Taxonomic diversity**

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

196 **2.4.2 Functional diversity**

197 The functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional
198 dispersion (FDis) and Rao index (Rao’s Q) were calculated based on the Gower distance of
199 functional traits using the ‘dbFD’ function in the ‘*FD*’ R package (Lalibert e et al., 2015).

200 **2.4.3 Phylogenetic diversity**

201 All plant species names recorded in surveys were checked in the plant list (www.theplantlist.org) to
202 obtain acceptable species names. Based on the APG III system (The Angiosperm Phylogeny Group,
203 2009), we entered the taxonomic information (family/genus/species) of all species into the
204 Phylomatic online plant database (Phylomatic Version 3, <http://phylodiversity.net/phyloomatic/>),
205 selected storedtree = “zanne2014 (Zanne et al., 2014)”, and output a phylogenetic tree with branch
206 length and differentiation time (Fig. S2). Faith’s phylogenetic diversity (PD, the sum of the
207 phylogenetic branch lengths), the mean pairwise distance (MPD) and the mean nearest taxon

208 distance (MNTD) between species in a community were calculated using the ‘mpd’ function in the
209 ‘*picante*’ R package (Kembel et al., 2010).

210 **2.5 Data analysis**

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

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

225 To study the effects of climate in different periods and climate anomalies on biodiversity and
226 aboveground biomass, we performed piecewise structural equation models (pSEM) to test the direct
227 and indirect causal relationships between the climate in different periods and paleoclimate change,
228 species diversity, functional diversity, phylogenetic diversity and biomass. Model construction
229 procedures involved the following three stages. First, based on the results of the Random Forest

230 model, we identified the climate variables that significantly affected biodiversity and divided them
231 into composite variables. The model contained two composite variables that potentially represent
232 collections of variables in terms of the present climate and paleoclimate change. We calculated
233 Pearson correlations between the climate factors (Fig. S3) and deleted the predictors with high
234 correlation coefficients (>0.85 , $P < 0.05$) to avoid multicollinearity. Before pSEM analysis, all
235 selected predictors were standardized. Second, principal component analyses (PCAs) were used for
236 the composite variables with multiple predictors. For each composite variable, the first principal
237 component (PC1) explained 64~71% of the total variance and was used in the subsequent pSEM
238 analysis (Table S2). Third, pSEM was developed from the full conceptual model. We fitted the
239 component models of the piecewise SEM as linear models and reported the standardized coefficient
240 for each path from each component model. We used Shipley's d-separation test to evaluate the
241 overall fit of the pSEM, as well as Fisher's C statistic and AIC.

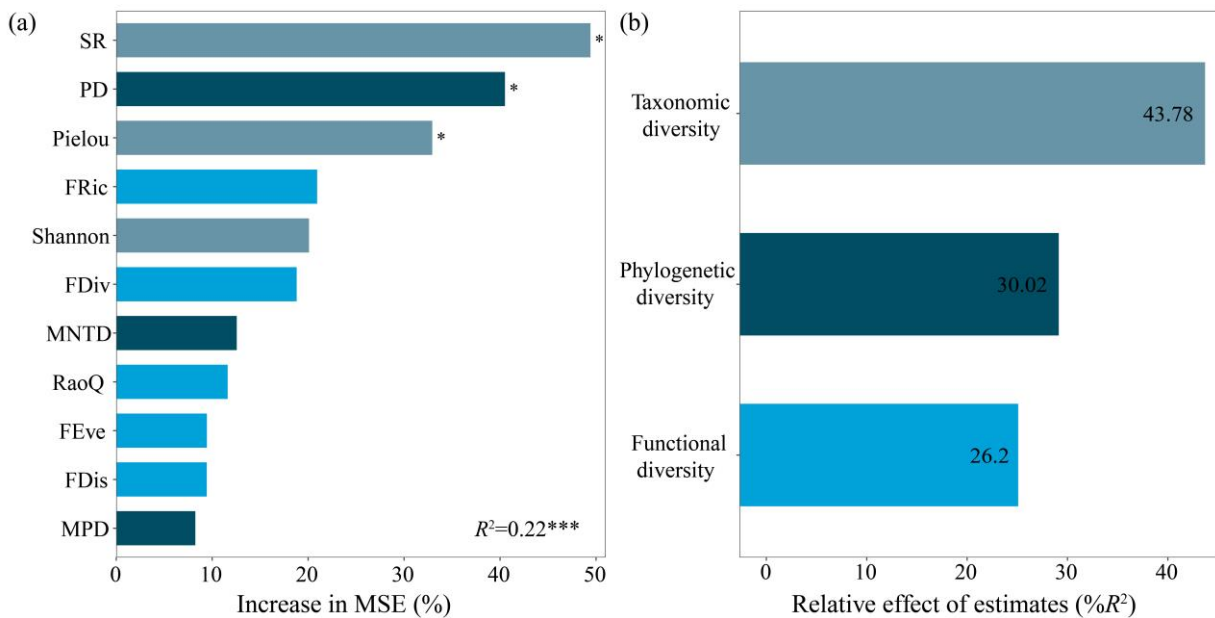
242 We conducted all analyses in R x64 4.0.5. The Random Forest model was conducted using the
243 'randomForest' function in the 'randomForest' package (Cutler et al., 2007; Breiman et al., 2018),
244 and the significance of the variables was tested using the 'rp.importance' function in the 'rfPermute'
245 package (Archer, 2016). PCA was performed using the 'princomp' function in the 'psych' package in
246 R (Revelle, 2021). Piecewise structural equation modeling was conducted and tested using the
247 'piecewiseSEM' package (Lefcheck, 2020; Lefcheck and Freckleton, 2015).

248 **3. Results**

249 **3.1 Effects of biodiversity on aboveground biomass**

250 Among the 11 biodiversity variables, SR, PD and Pielou index identified by the RF model were the
251 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.



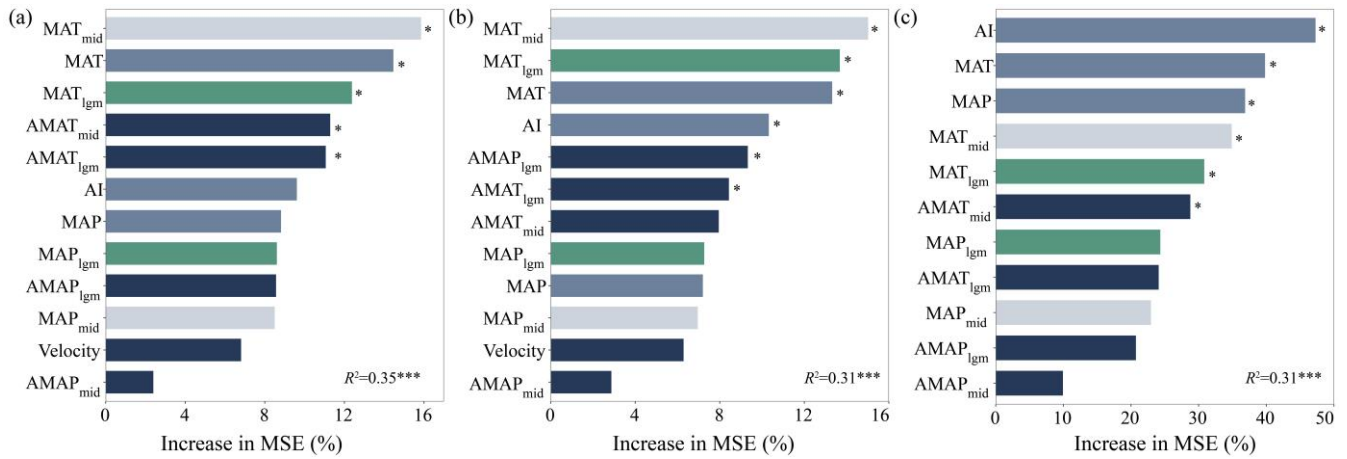
259
 260 Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to
 261 community biomass. An increase in mean square error (MSE) denotes an increase in the percentage
 262 mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

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_{lgn} ,
 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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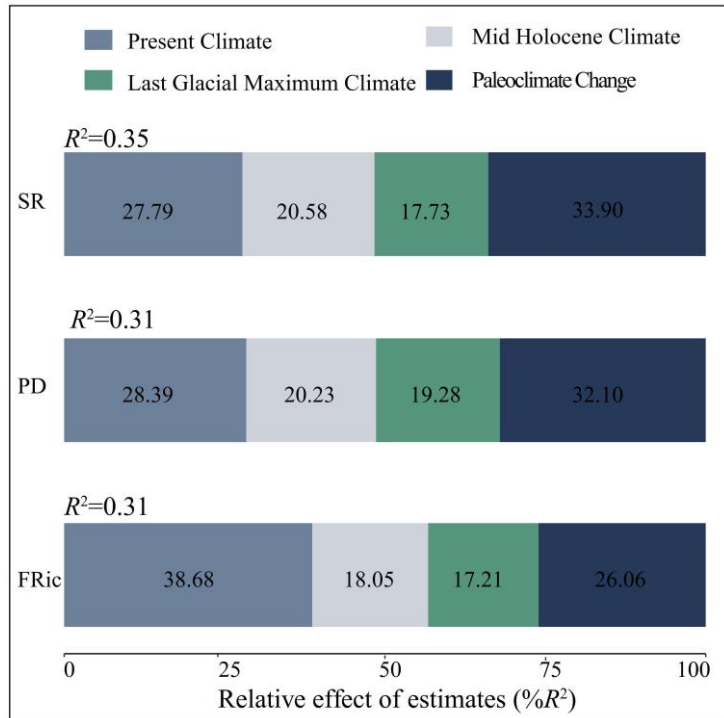
272 Fig. 2 The importance of climate variables in different periods and paleoclimate change to species
 273 richness (a), phylogenetic diversity (b) and functional richness (c). An increase in mean square error
 274 (MSE) denotes an increase in the percentage mean square error. Significance levels are as follows: *:
 275

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).



281

282

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

283

paleoclimate change as drivers of species richness, phylogenetic diversity and functional richness.

284

3.3 Influence of climate factors on biodiversity and aboveground biomass

285

The present climate, MAT of the Mid-Holocene and the Last Glacial Maximum, and paleoclimate

286

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

287

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

288

indirect significant associations with AGB via all biodiversity variables (Fig. 4). The present climate

289

was significantly and positively associated with SR ($r_{\partial} = 0.46$, $P < 0.05$), PD ($r_{\partial} = 0.35$, $P < 0.05$)

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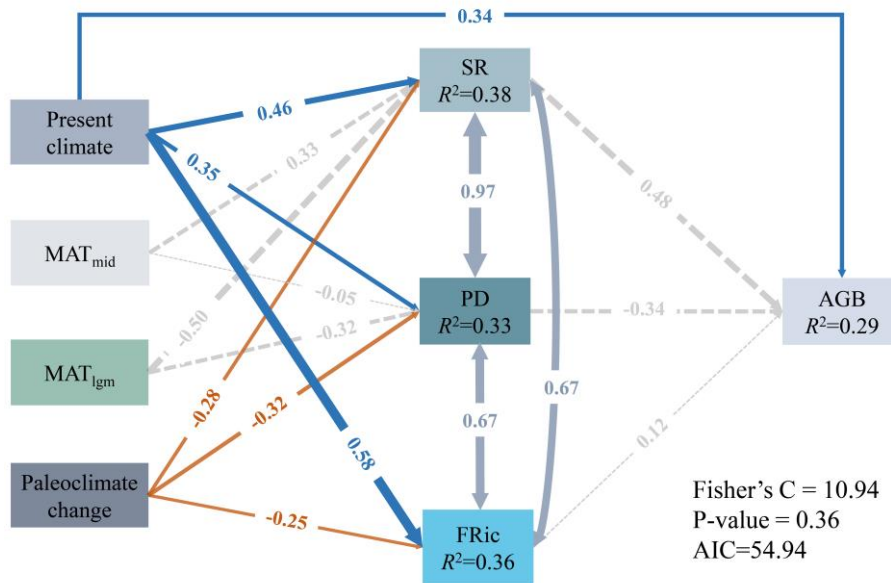
and FRic ($r_{\partial} = 0.58$, $P < 0.05$, Fig. 4). However, the paleoclimate change had direct significant

291

negative effects on SR ($r_{\partial} = -0.28$, $P < 0.05$), PD ($r_{\partial} = -0.32$, $P < 0.05$) and FRic ($r_{\partial} = -0.25$, $P < 0.05$,

292

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_{δ}). 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 ($r_{\delta} = 0.33$, $P < 0.05$), PD ($r_{\delta} = 0.27$, $P <$

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

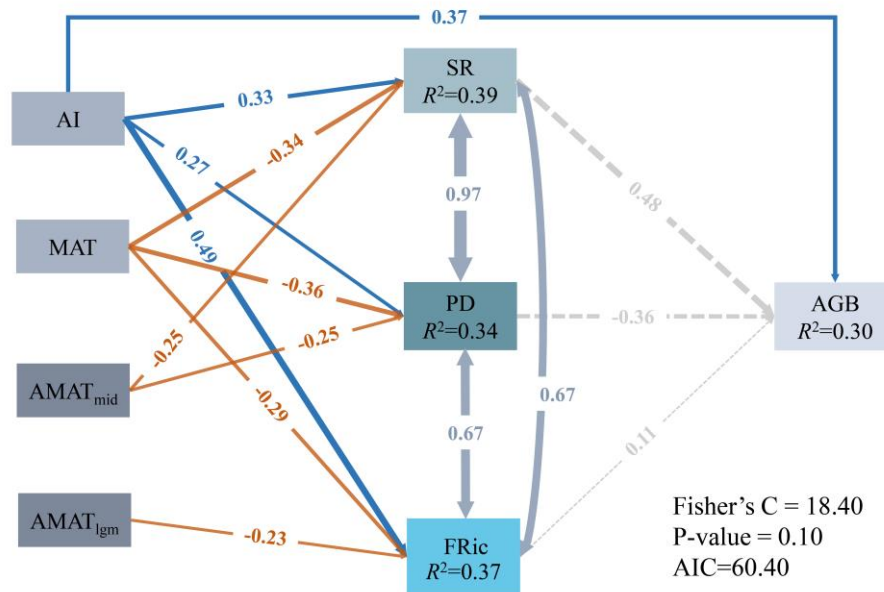
304 the direct effects of MAT on the three dimensions of biodiversity (SR, $r_{\delta} = -0.34$; PD, $r_{\delta} = -0.36$;

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

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

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

308 anomaly from the Last Glacial Maximum to the present ($AMAT_{lgm}$; Fig. 5).



309

310 Fig. 5 The effects of present climate (AI and MAT) and Climate anomalies (AMAT_{mid} and AMAT_{lgm})

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

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

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

314 paths ($P > 0.05$).

315 4. Discussion

316 4.1 The effects of different dimensions of biodiversity on aboveground biomass

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

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

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

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

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

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

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

324 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-J áregui and Oesterheld, 2018; D íaz 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.

458 **Data available**

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

461 **Conflict of interest statement**

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

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