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

4 **List of Authors:**

5 Zijing Li[1,2], Zhiyong Li[3, *], Xuze Tong[4], Lei Dong[1,2], Ying Zheng[1,2], Jinghui Zhang[3], Bailing Miao[5],

6 Lixin Wang[3], Liqing Zhao[3], Lu Wen[3], Guodong Han[6], Frank Yonghong Li[3], Cunzhu Liang[3]

7 **Institutional affiliations:**

8 [1]Yinshanbeilu Grassland Eco-hydrology National Observation and Research Station, China Institute

9 of Water Resources and Hydropower Research, Beijing 100038, China

10 [2]Institute of Water Resources for pastoral Area Ministry of Water Resources, Hohhot 010020, Inner

11 Mongolia

12 [3]Key Laboratory of Ecology and Resource Use of the Mongolian Plateau, Ministry of Education of

13 China; Collaborative Innovation Center for Grassland Ecological Security, Ministry of Education of

14 China; School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, P. R. China

15 [4] Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural

16 Sciences, Beijing 100081, P. R. China

17 [5] Inner Mongolia Meteorological Institute, Hohhot 010051, P. R. China

18 [6]Key Laboratory of Grassland Resources of the Ministry of Education, Key Laboratory of Forage

19 Cultivation, Processing and High Efficient Utilization of the Ministry of Agriculture and Rural

20 Affairs, Inner Mongolia Key Laboratory of Grassland Management and Utilization, College of

21 Grassland, Resources and Environment, Inner Mongolia Agricultural University, Hohhot 010011, P.

22 R. China

23   **Contact Information:** *Corresponding author. E-mail: zylee007@imu.edu.cn; tel: +86 136 7475

24   7329.

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 diversity, functional diversity and

33   phylogenetic diversity of grassland on the Mongolian Plateau using vegetation survey data and trait

34   information. We then used Random Forest models and Structural Equation models to assess the

35   relative importance of the present climate, the Mid Holocene climate, the Last-Glacial Maximum

36   climate and paleoclimate changes as determinants of diversity and aboveground biomass. Our results

37   showed that paleoclimate changes and modern climate jointly determined contemporary biodiversity

38   patterns, while community biomass was mainly affected by modern climate, namely the aridity

39   index. Modern aridity and temperature were two major influences on all three dimensions of

40   biodiversity. Mid-Holocene climate anomalies had a strong effect on species richness and

41   phylogenetic diversity, while functional diversity was mainly affected by temperature anomalies

42   since the Last Glacial Maximum. These findings suggest that contemporary biodiversity patterns

43   may be affected by processes at divergent temporal scales. Our results show that simultaneously

44   exploring the response of the three dimensions of biodiversity in different periods of climate change

45 and the theoretical framework for its impact on community biomass is helpful to provide a more

46 comprehensive understanding of patterns of biodiversity and its relationship with ecosystem

47 functions.

48 **Keywords**

49 Aridity index, biodiversity and ecosystem functions, functional diversity, paleoclimate anomaly,

50 phylogenetic diversity, taxonomic diversity

51 **1. Introduction**

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

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

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

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

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

57 2020; Eiserhardt et al., 2015; Svenning et al., 2015).

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

59 2005), but understanding the effects of different dimensions of biodiversity (i.e., taxonomic diversity,

60 functional diversity and phylogenetic diversity) on ecosystem functions (BEF) is still a challenge in

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

62 BEF have predominantly focused on the relationship between taxonomic diversity (i.e., species

63 richness) and biomass or productivity. However, only considering taxonomic diversity has the

64 limitation that it may ignores the important ecological processes such as the formation of function

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

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

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

68   functioning are largely driven by variations in plant functional traits, such as adult plant height and

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

70   ecosystem functions (Srivastava et al., 2012; Cavender-Bares et al., 2009). Previous research had

71   shown that PD may be a better metric than species richness or functional diversity for predicting

72   plant biomass (Cadotte et al., 2008). Communities with higher PD have stronger anti-interference

73   ability because of their evolutionary potential to adapt to changing environmental conditions.

74   However, the role of multi-dimensional biodiversity in driving ecosystem functions in response to

75   climate change still needs further research. Elucidating the impacts of multi-dimensional biodiversity

76   on biomass in the changing world can deepen our understanding of the direct and indirect effects of

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

78   ecological consequences of global climate changes.

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

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

81   alpine meadows on the Qinghai-Tibet Plateau (Liu et al., 2018) and a heterogeneous California

82   (Esquivel-Muelbert et al., 2019) grassland (Harrison et al., 2015). Dispersal limitation and

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

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

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

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

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

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

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

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

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

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

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

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

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

96   Glacial Maximum (LGM; ~21,000 years ago), increasing functional differences between native and

97   migratory species, leading to smaller and dispersed functional spaces (Ordonez and Svenning, 2017).

98   Evidence derived from the fossil pollen sequence and ecological datasets has shown that the

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

100   Late Pleistocene to Early Holocene were driven primarily by changing climates (Mottl et al., 2021).

101   In the South American tropics, the species composition and structure of Last Glacial Maximum

102   forests were quite different from those of today, and biomass was also lower than that of

103   contemporary forests (Mayle et al., 2009).

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

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

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

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

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

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

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

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

112 change led to changes in ecosystems to a degree comparable to the predicted warming under future

113 high-emission scenarios (Nolan et al., 2018). Therefore, studying the impact of past climate and its

114 changes on contemporary biodiversity patterns will help us understand the potential effects of future

115 climate changes. However, most studies exploring the impact of present climate and paleoclimate

116 drivers on ecosystem functions have focused on forest ecosystems, while grassland ecosystems

117 remain understudied. In addition, it is not yet clear whether taxonomy, function and phylogenetic

118 diversity will vary with climate gradients and climate changes, and the intensity of any such changes

119 remain unclear. Therefore, there is an urgent need to consider the impact of current climate,

120 paleoclimate and its anomalies on contemporary biodiversity and ecosystem functions.

121   The Mongolian Plateau is located in the arid and semi-arid area of eastern Eurasia. During the

122 Late Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climatic

123 fluctuations (Maestre et al., 2021; Tian et al., 2017), which may have a significant impact on current

124 plant diversity and ecosystem function. However, the impacts of climate in different periods and

125 climate legacy effects on aboveground biomass of steppes in the Mongolian Plateau, as well as

126 whether these effects are biodiversity dependent, remain to be evaluated. To address these knowledge

127 gaps, we coupled data from a field survey of 152 sites in the Mongolian Plateau (Fig. S1) to existing

128 databases on present and past climates to explore present climate and the legacy effects of climate

129 during the Last Glacial Maximum and the Mid-Holocene on current biodiversity and biomass.

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

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

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

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

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

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

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

137 **2. Materials and Methods**

138 **2.1 Study Area**

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

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

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

142 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).

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

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

145 **2.2 Data Collection**

146 **2.2.1 Sites Sampled and Vegetation Investigation**

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

148 homogeneous environment. These sites were separated by about 50 km. One or three 10 m × 10 m

149 quadrats were set in each site. Within each quadrat, five 1 m × 1 m plots were placed at each corner

150 and at the center of the quadrat (only three 1 m × 1 m plots along the diagonal line of the quadrat in a

151 few sites) to investigate vegetation. A total of 899 plots were investigated and 296 vascular plant

152 species were recorded.

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

154 plot. All plant species were cut at ground level and were separately bagged, then oven-dried at 65 °C

155 to constant weight, and weighed for dry matter.

2.2.2 Climate Data

157 Mean annual temperature (MAT, °C) and the mean annual precipitation (MAP, mm) were obtained

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

159 http://chelsa-climate.org/) (Karger et al., 2017). Potential evapo-transpiration (PET) was obtained

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

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

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

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

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

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

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

167 6000 years ago) and the Last Glacial Maximum (LGM, about 22,000 years ago) were simulated

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

169 values minus paleoclimate values) was used to indicate the degree of climate variability since the

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

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

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

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

	Climate variables	Abbreviation
The present climate	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}
	MAP anomaly from the Mid-Holocene to the present	$AMAP_{mid}$
	MAT anomaly from the Mid-Holocene to the present	$AMAT_{mid}$
Paleoclimate change	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 median 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

186

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 (Laliberté 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/phylomatic/),

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 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

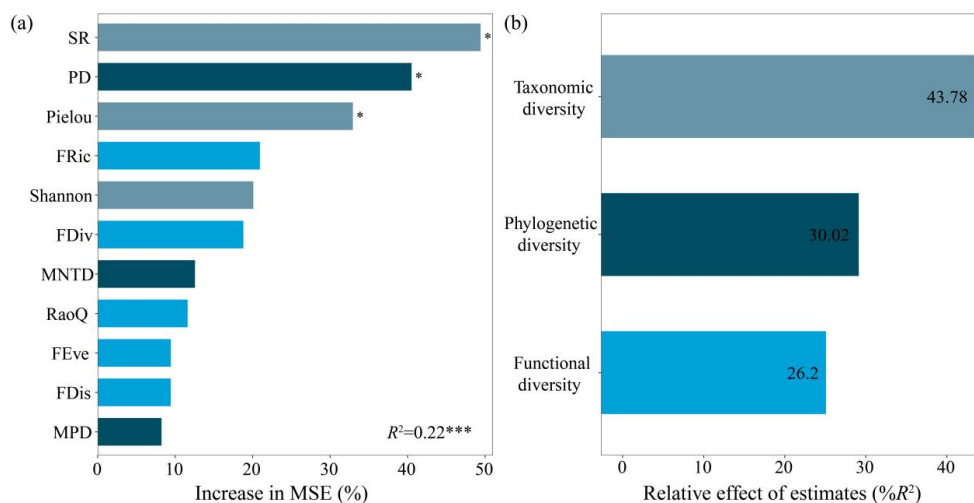
253   43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD

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, functional, and phylogenetic 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 MSE denotes an increase in the percentage mean square error.

262   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

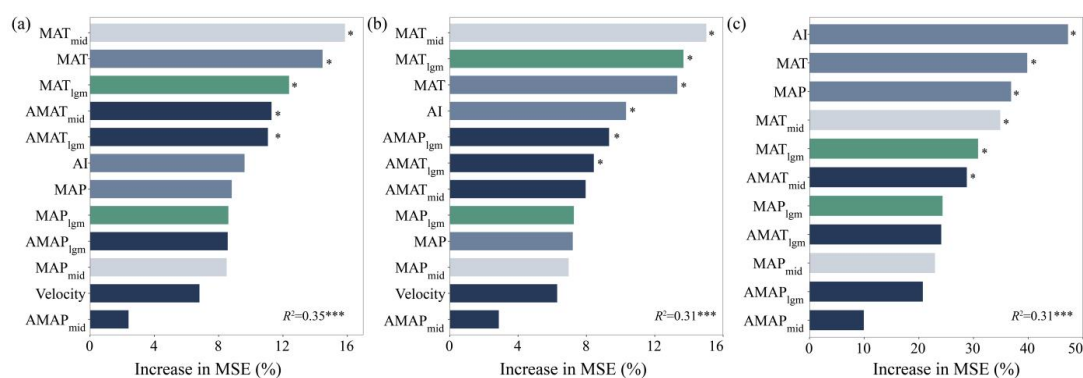
265    $R^2 = 0.31$, $P < 0.001$) and 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) of the variance in SR, PD and

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).

270

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 MSE denotes an

274   increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***:

275                                    $P < 0.001$.

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

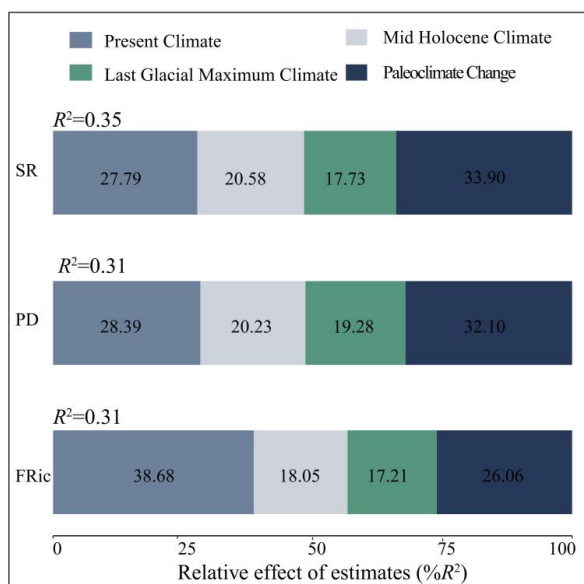



Fig. 3 Relative contributions of present climate, paleo - (mid-Holocene and Last Glacial Maximum)

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

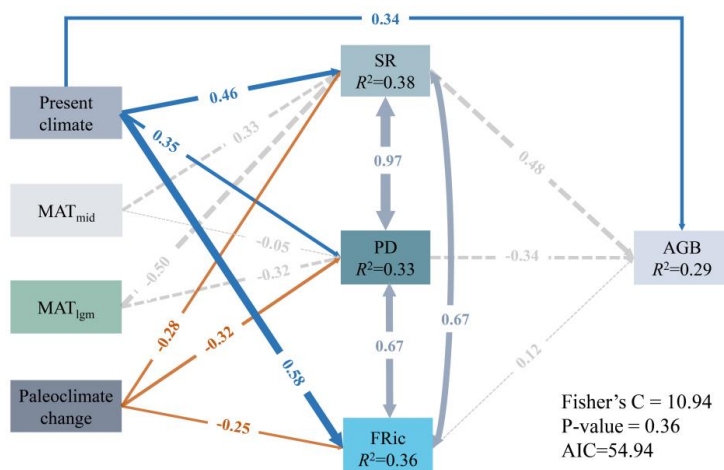
variances in SR, PD, FRic and AGB, respectively (Fig. 4). The present climate had direct and

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).

294

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

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

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

298   MAT and MAP anomaly from the Mid-Holocene to the present. Numbers adjacent to arrows

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

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

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

302

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

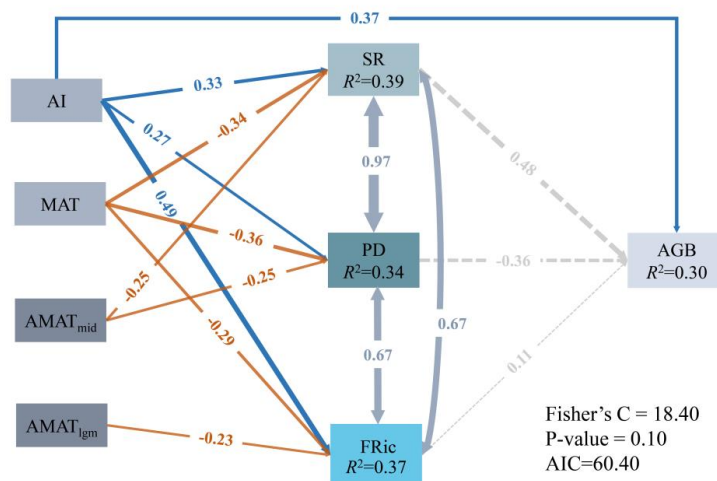
304   0.05), FRic ($r_\partial = 0.49$, $P < 0.05$), and AGB ($r_\partial = 0.37$, $P < 0.05$) were all significantly positive, while

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

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

307   0.25, $P < 0.05$) and PD ($r_\partial = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the

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

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

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

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

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

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

315   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 to

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

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

327   effects are the main mechanisms through which biodiversity impacts on biomass. The grassland

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

329   the number or dominance of dominant species. However, functional traits considered in this study,

330   such as leaf size and plant height, do not have a strong impact on biomass. The Mongolian Plateau is

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

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

333   correlated with aboveground biomass, while functional traits consistent with growth strategies, such

334   as leaf nitrogen concentration and photosynthetic utilization efficiency, can promote aboveground

335   biomass (Wolf et al., 2021).

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

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

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

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

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

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

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

343   **4.2 Relationship between paleoclimate anomalies and current biodiversity patterns**

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

345   relationships with biomass, further studies are still needed. Here, our results showed that

346   paleoclimate changes and present climate factors were critical variables influencing contemporary

347   biodiversity patterns. This illustrates the importance of historical factors, such as evolution, as well

348   as contemporary factors, such as climate, in determining the geographic ranges of species and the

349   accumulation of species in the region (Fine, 2015). Previous studies aiming to explain patterns of

350   biodiversity have focused on the current climate (Harrison et al., 2015), energy (Kreft and Jetz,

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

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

353   biodiversity and ecosystem functions has been widely confirmed (Yang et al., 2011; Liu et al., 2021;

354   Walther et al., 2002), but our research shows that the pattern of biodiversity is also affected by past

355   climates, and especially climate change in a region. Paleoclimate changes filtered the regional

356   species pool based on climate-related traits, 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   Our research showed that PD was negatively correlated with MAT and temperature anomalies in the

369   Mid-Holocene, but not significantly related to temperature anomalies during the Last Glacial

370   Maximum. However, the PD of global forest ecosystems is positively associated with temperature

371   and precipitation and is negatively associated with Quaternary precipitation change (Kubota et al.,

372   2018). Phylogenetic studies reveal that major ecological niches are more conserved through

373   evolutionary history than expected, implying that adaptations to major climate changes have not

374   readily been accomplished in all lineages (Donoghue, 2008).

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

376   climate anomaly. This may be due to the tolerance of plant traits to past climatic conditions (Bhagwat

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

378   the Mongolian Plateau experienced severe alternating dry and wet climate fluctuations (Tian et al.,

379   2017), and likely experienced a non-random removal of functional combinations and change in

380   functional diversity (Ordonez and Svenning, 2017). Previous research has indicated that the

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

382   (including the Mongolian Plateau) to drive moderate to large changes in vegetation composition and

383   structure (Nolan et al., 2018). When climate changes, inappropriate species may be quickly ruled out,

384   and appropriate species may migrate more slowly, resulting in a negative correlation between the

385   paleoclimate anomaly and contemporary FD in the Mongolian Plateau. This is also limited by the

386   spreading ability or migration potential of plants after the glaciers, when species with inappropriate

387   characteristics disappeared from the community and were not replaced by other species (Blonder et

388   al., 2018). Studies in Europe indicate that the lagging effect of glacial-interglacial climate instability

389   and accessibility on functional diversity is >10,000 years (Ordonez and Svenning, 2015).

390   The influence of paleoclimate anomalies on contemporary species and phylogeny diversity may

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

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

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

394   2017). Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe

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

396   types on the Mongolian Plateau were mainly polar and alpine deserts and temperate deserts (Ray and

397   Adams, 2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene,

398   xerophytes had declined sharply, and plants of humid climates had increased. The humidity increased

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

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

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

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

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

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

405   2011). Furthermore, palaeoecological and archaeological evidence shows that people have shaped

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

407   domestication (Ellis et al., 2021). In the Mongolian Plateau, especially in the Inner Mongolia region

408   of northern China, grazing appeared at ∼5.7–5.5 ka and further intensified again after ∼4.2–4.0 ka

409   (Huang et al., 2021). The intensification of grazing activities also causes changes in biodiversity.

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

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

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

413   changes also have no direct effects on aboveground biomass, which indirectly affects aboveground

414   biomass through regulating biodiversity.

415   **5. Conclusion**

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

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

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

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

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

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

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

423   key role in shaping contemporary biodiversity patterns.

424

425   **Authors' Contributions**

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

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

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

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

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

431   **Data available**

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

433   author.

434   **Conflict of interest statement**

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

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