

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 ~~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-Mid-Holocene ~~climate~~ and the Last-Glacial
36 Maximum climate and as well as paleoclimate changes as determinants of diversity and aboveground
37 biomass. Our results showed that paleoclimate changes and modern climate jointly determined
38 contemporary biodiversity patterns, while community biomass was mainly affected by modern
39 climate, namely the aridity index. Modern aridity and temperature were two major influences on all
40 three dimensions of biodiversity. Mid-Holocene climate anomalies had a strong effect on species
41 richness and phylogenetic diversity, while functional diversity was mainly affected by temperature
42 anomalies since the Last Glacial Maximum. These findings suggest that contemporary biodiversity
43 patterns may be affected by processes at divergent temporal scales. Our results show that
44 simultaneously exploring the response of the three dimensions of biodiversity in different periods of

45 climate change and the theoretical framework for its impact on community biomass is helpful to
46 provide a more comprehensive understanding of patterns of biodiversity and its relationship with
47 ecosystem functions.

48 **Keywords**

49 Aridity index, ecosystem functions~~biodiversity and ecosystem functions~~, functional diversity,
50 paleoclimate anomaly, 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 functions 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 biodiversity and ecosystem functions have predominantly focused on the relationship between
63 taxonomic diversity (i.e., species richness) and biomass or productivity. However, only considering
64 taxonomic diversity has the limitation that it may ignore ~~the~~ important ecological processes such as
65 the formation of function traits or the evolutionary history of species (Flynn et al., 2011; Swenson,
66 2011). The importance of taking into account other aspects of biodiversity, including functional

67 diversity and phylogenetic diversity, has increasingly been recognized. The effects of plant functional
68 diversity on ecosystem functioning are largely driven by variations in plant functional traits, such as
69 adult plant height and leaf size (Diaz et al., 2016). Phylogenetic diversity (PD) is a key driver of
70 community assembly and ecosystem functions (Srivastava et al., 2012; Cavender-Bares et al., 2009).
71 Previous research had shown that PD may be a better metric than species richness or functional
72 diversity for predicting plant biomass (Cadotte et al., 2008). Communities with higher PD have
73 stronger anti-interference ability because of their evolutionary potential to adapt to changing
74 environmental conditions. However, the role of multi-dimensional biodiversity in driving ecosystem
75 functions in response to climate change still needs further research. Elucidating the impacts of
76 multi-dimensional biodiversity on biomass in ~~the a~~ changing world can deepen our understanding of
77 the direct and indirect effects of changes in climate and biodiversity on terrestrial ecosystems, and
78 improve predictions of the 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 ([Esquivel-Muelbert et al., 2019](#)), alpine meadows on the Qinghai-Tibet Plateau (Liu et al., 2018a)
82 and a heterogeneous California ~~(Esquivel-Muelbert et al., 2019)~~ grassland (Harrison et al., 2015).
83 Dispersal limitation and environmental filtering (i.e., climatic conditions and paleoclimate change)
84 plays an important role in sorting species from the global species pool and in shaping large-scale
85 diversity patterns (Kubota et al., 2018; Liu et al., 2021). Many studies have found that climate
86 changes in the Mid-Holocene and the Quaternary interglacial period are the main driving factors of
87 current species distribution, functional traits and community phylogeny (Svenning and Skov, 2007b).
88 The current patterns of species richness and distribution of European flora are jointly affected by

89 contemporary climatic conditions and climate change during the Late Quaternary glacial-interglacial
90 period (Svenning and Skov, 2007a; Svenning and Skov, 2007b). Contemporary plant functional traits
91 and composition are highly sensitive to climate and influenced by climate from tens of thousands of
92 years ago, with important consequences for ecosystem functions (Blonder et al., 2018; Butler et al.,
93 2017). For example, in Europe patterns of plant functional diversity exhibited prominent
94 glacial-interglacial climate change imprints (Ordonez and Svenning, 2015; Ordonez and Svenning,
95 2017). This is partly due to the non-random removal of functional combinations that may have
96 occurred during the Last-Glacial Maximum (LGM; ~21,000 years ago), increasing functional
97 differences between native and migratory species, leading to smaller and dispersed functional spaces
98 (Ordonez and Svenning, 2017). Evidence derived from the fossil pollen sequence and ecological
99 datasets has shown that the acceleration of biodiversity changes began millennia ago, whereas
100 vegetation changes during the Late Pleistocene to Early Holocene were driven primarily by changing
101 climates (Mottl et al., 2021). In the South American tropics, the species composition and structure of
102 Last Glacial Maximum forests were quite different from those of today, and biomass was also lower
103 than that of 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-effects on contemporary biodiversity patterns will help us understand the potential effects of
115 future climate changes. However, most studies exploring the impact of present climate and
116 paleoclimate drivers on ecosystem functions have focused on forest ecosystems, while grassland
117 ecosystems remain understudied. In addition, it is not yet clear whether taxonomy, function and
118 phylogenetic diversity will vary with climate gradients and climate changes, and the intensity of any
119 such changes remain unclear. Therefore, there is an urgent need to consider the impact of current
120 climate, 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. Our previous
122 researches have shown that climate is an important direct factor mediating the relationship between
123 species richness and aboveground biomass in the Mongolian plateau steppe (Li et al., 2021; Li et al.,
124 2020). However, in the Late Quaternary, the Mongolian Plateau experienced severe alternating dry
125 and wet climatic fluctuations (Maestre et al., 2021; Tian et al., 2017), which may have a significant
126 impact on current plant diversity and ecosystem function. However, the impacts of climate in
127 different periods and climate legacy effects on aboveground biomass of steppes in the Mongolian
128 Plateau, as well as whether these effects are biodiversity dependent, remain to be evaluated. To
129 address these knowledge gaps, we coupled data from a field survey of 152 sites in the Mongolian
130 Plateau (Fig. S1) to existing databases on present and past climates to explore present climate and the
131 legacy effects of climate during the Last Glacial Maximum and the Mid-Holocene on current
132 biodiversity and biomass.

133 Here, we aim to evaluate the relative importance of taxonomic, functional, and phylogenetic
134 diversity on community biomass of steppe in the Mongolian Plateau, and to assess whether and how
135 climate in different periods and their changes affect the three dimensions of diversity, and their
136 relationships with community biomass. We specifically ask: (1) Do the three dimensions of diversity
137 affect community biomass, and if so, to what extent? (2) Whether and how climate at divergent
138 temporal scales and paleoclimatic changes affect different dimensions of biodiversity? And (3) If
139 there are effects, how do they affect the biodiversity-biomass relationship?

140 **2. Materials and Methods**

141 **2.1 Study Area**

142 We conducted field surveys in the grasslands of the Mongolian Plateau, including Inner Mongolia
143 Autonomous Region in China and Mongolia, during June to August of 2014~2018 (Fig. S1). The
144 Mongolian Plateau is located in the eastern part of Eurasia, with a geographic range of 37.61 °to
145 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).
146 The mean annual temperature (MAT) of the study region ranges from -12 °C to 10 °C and mean
147 annual precipitation (MAP) ranges from 26 mm to 641 mm.

148 **2.2 Data Collection**

149 **2.2.1 Sites Sampled and Vegetation Investigation**

150 We investigated 152 grassland sites set in flat areas with ~~little~~limited human interference and a
151 relatively homogeneous environment. These sites were separated by about 50 km. One or three 10 m
152 × 10 m quadrats were set in each site (~~in a few areas with sparse vegetation and large heterogeneity,~~
153 ~~three 10 m × 10 m quadrats were set to ensure the accuracy of the survey data~~). Within each quadrat,
154 five 1 m × 1 m plots were placed at each corner and at the center of the quadrat (~~only three 1 m × 1~~

155 | ~~m plots along the diagonal line of the quadrat in a few sites~~) to investigate vegetation. A total of 899
156 | plots were investigated and 296 vascular plant species were recorded.

157 | We measured species height, density, coverage and standing biomass of each species in each
158 | plot. Three 1 m × 1 m plots along the diagonal line were selected from the five plots to measure the
159 | standing biomass of each species. ~~All p~~Plant species were cut at ground level and ~~were~~ separately
160 | bagged, then oven-dried at 65 °C to constant weight, and weighed for dry matter.

161 | 2.2.2 Climate Data

162 | Mean annual temperature (MAT, °C) and ~~the~~ mean annual precipitation (MAP, mm) were obtained
163 | from the CHELSA database (Climatologies at High Resolution for the Earth's Land Surface Areas,
164 | <http://chelsa-climate.org/>) (Karger et al., 2017), a data set consisting of monthly temperature and
165 | precipitation climatology from 1979 to 2013. Potential ~~evapo-transpiration~~ evapotranspiration (PET)
166 | was obtained from the CGIAR-CSI (CGIAR Consortium for Spatial Information,
167 | <http://www.cgiar-csi.org>) based on latitude and longitude data for each site (Trabucco and Zomer,
168 | 2019). The resolution of both is 30 arc seconds. Aridity was measured using the aridity index (AI, AI
169 | =MAP/ PET). Higher AI values indicate lower aridity and higher humidity. Paleoclimate data were
170 | downloaded from Worldclim (<http://worldclim.com/paleo-climate1>) with a resolution of 2.5 minutes.
171 | The database was made available by CMIP5 (Coupled Model Intercomparison Project Phase 5) and
172 | was calibrated based on the current climate using WorldClim 1.4. The MAT and MAP of the
173 | Mid-Holocene (MID, about 6000 years ago) and the Last Glacial Maximum (LGM, about 22,000
174 | years ago) were simulated based on CCMS4 (Community Climate System Model version 4). Climate
175 | anomaly (i.e., present-day values minus paleoclimate values) was used to indicate the degree of
176 | climate change variability since the MID and the LGM (Sandel et al., 2011). Temperature-change

177 velocity from the LGM to the present (velocity, m/yr) was obtained from DRYAD
 178 (<https://datadryad.org>) (Sandel et al., 2011). The climate variables used in this study are shown in
 179 Table 1.

180

Table 1 Climate variables included in this study

	Climate variables	Abbreviation
The present climate <u>(1979-2013)</u>	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

181

2.2.3 Plant functional traits

182 The functional traits of each plant species include growth form, life form, phyllotaxy, single or
 183 compound leaf, petiole, inflorescence, fruit type, flowering period, fruit ripening period, length of the
 184 flowering period, water ecotypes, leaf length, leaf width and plant height (Table S1). These traits
 185 were looked up in the Flora of Inner Mongolia (Third Edition) or Flora of China (Online Edition)

186 | (<http://www.iplant.cn/frps>). The trait data for leaf length and leaf width were the **median-mean** values
187 provided in Flora of China (Fig. S2). For example, if the leaf length of *Leymus chinensis* was
188 described as 7-18 cm in the Flora of China, then leaf length was defined as 12.5 cm.

189 **2.3 Aboveground biomass**

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

193 **2.4 Diversity calculations**

194 **2.4.1 Taxonomic diversity**

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

199 **2.4.2 Functional diversity**

200 The functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional
201 dispersion (FDis) and Rao index (Rao's Q) were calculated based on the Gower distance of
202 functional traits using the 'dbFD' function in the 'FD' R package (Laliberté et al., 2015).

203 **2.4.3 Phylogenetic diversity**

204 All plant species names recorded in surveys were checked in the plant list (www.theplantlist.org) to
205 obtain acceptable species names. Based on the APG III system (The Angiosperm Phylogeny Group,
206 2009), we entered the taxonomic information (family/genus/species) of all species into the
207 Phylomatic online plant database (Phylomatic Version 3, <http://phylodiversity.net/phyloomatic/>),

208 selected storedtree = “zanne2014 (Zanne et al., 2014)”, and output a phylogenetic tree with branch
209 length and differentiation time (Fig. S2). Faith’s phylogenetic diversity (PD, the sum of the
210 phylogenetic branch lengths), the mean pairwise distance (MPD) and the mean nearest taxon
211 distance (MNTD) between species in a community were calculated using the ‘mpd’ function in the
212 ‘*picante*’ R package (Kembel et al., 2010).

213 **2.5 Data analysis**

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

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

228 To study the effects of climate in different periods and climate anomalies on biodiversity and
229 aboveground biomass, we performed piecewise structural equation models (pSEM) to test the direct

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

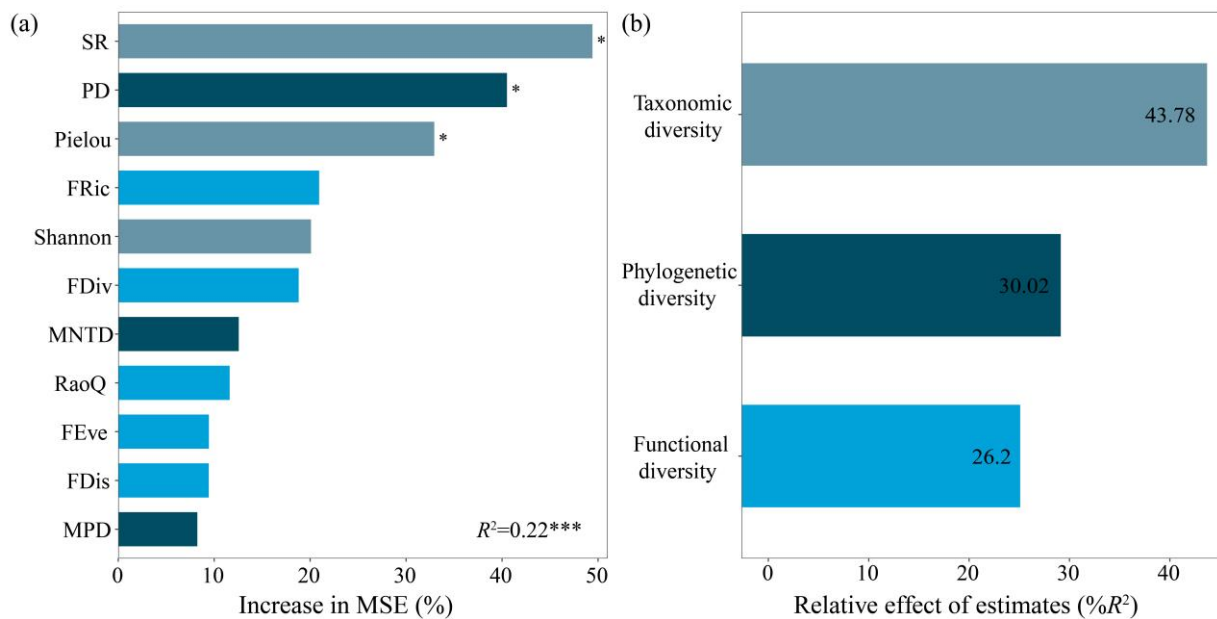
245 We conducted all analyses in R x64 4.0.5. The Random Forest model was conducted using the
246 'randomForest' function in the 'randomForest' package (Cutler et al., 2007; Breiman et al., 2018),
247 and the significance of the variables was tested using the 'rp.importance' function in the 'rfPermute'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

251 **3. Results**

252 **3.1 Effects of biodiversity on aboveground biomass**

253 Among the 11 biodiversity variables, SR, PD and Pielou index identified by the RF model were the
 254 three most significant predictors influencing aboveground biomass (Fig. 1a). Taken together,
 255 taxonomic diversity represented by SR, Pielou and Shannon-Wiener index collectively contributed
 256 43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD
 257 (including MNTD and MPD) and functional diversity represented by FRic (including FDiv, FEve,
 258 FDis and RaoQ) contributed 30.02% and 26.2%, respectively (Fig. 1b).

259 Based on the ranking results from the Random Forest model, SR, PD, and FRic were selected as
 260 agents of taxonomic, ~~phylogenetic~~functional, and ~~functional~~phylogenetic diversity, respectively, and
 261 used for subsequent analysis.



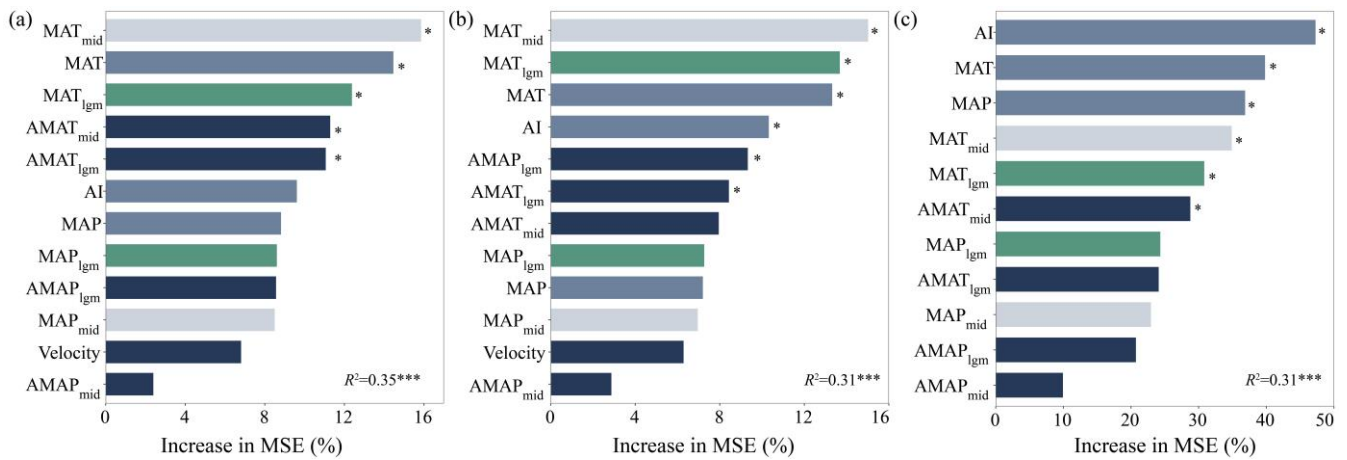
262 Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to
 263 community biomass. An increase in mean square error (MSE) denotes an increase in the percentage
 264 mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.
 265

266 **3.2 Paleoclimate and present climate predictors of contemporary diversity**

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

268 $R^2 = 0.31, P < 0.001$) and 31% (cross-validation $R^2 = 0.31, P < 0.001$) of the variance in SR, PD and
 269 FRic, respectively (Fig. 2). Temperatures in different periods, including MAT_{mid} , MAT and MAT_{lgm} ,
 270 were the main factors driving SR and PD ($P < 0.05$, Fig. 2a and 2b), followed by climate anomalies
 271 in various periods. However, the current climate (i.e., AI, MAT and MAP) had a stronger impact on
 272 FRic ($P < 0.05$, Fig. 2c).

273



274

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

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

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

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

279

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

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

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

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

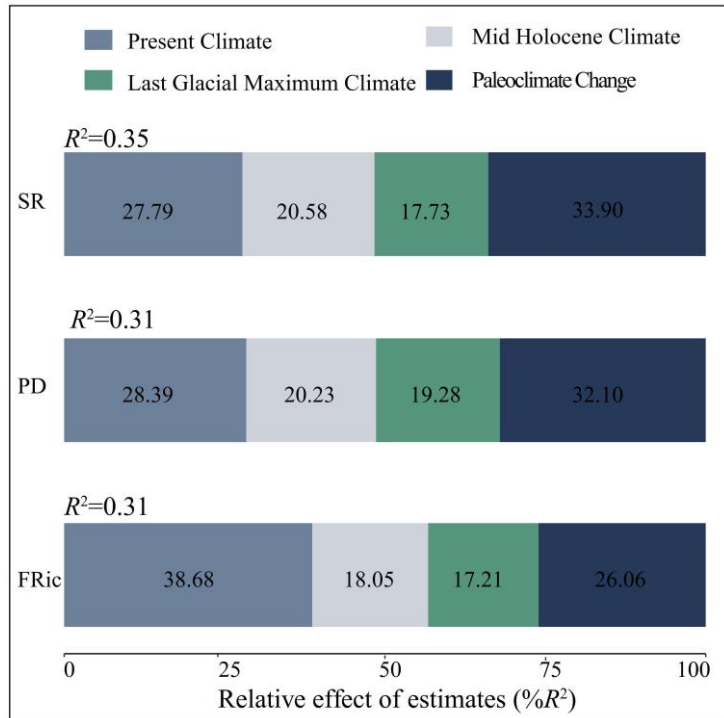
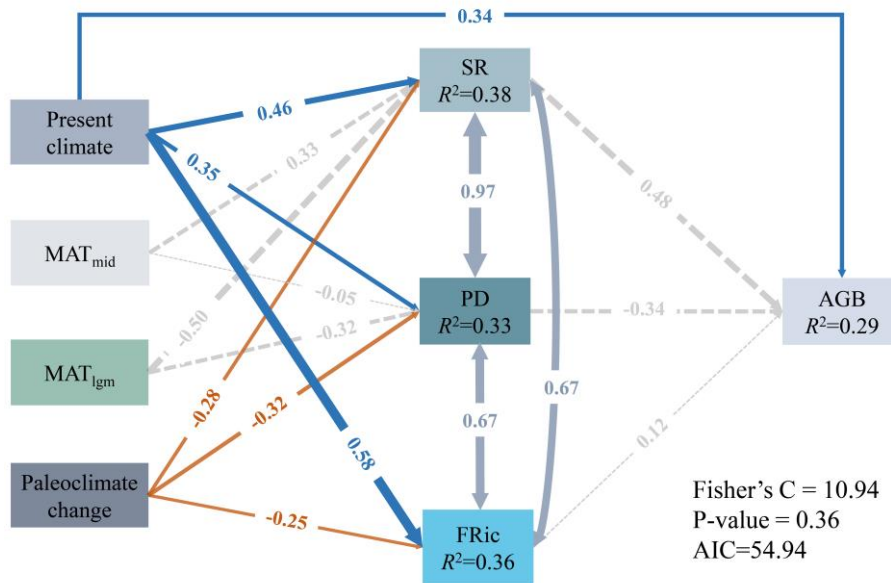


Fig. 3 Relative contributions of present, ~~climate, paleo~~ (Mid-Holocene and Last Glacial Maximum) ~~climate~~ and paleoclimate change as drivers of species richness, phylogenetic diversity and functional richness.

3.3 Influence of climate factors on biodiversity and aboveground biomass

The present climate, MAT of the Mid-Holocene and the Last Glacial Maximum, and paleoclimate change explained 38% ($R^2 = 0.38$), 33% ($R^2 = 0.33$), 36% ($R^2 = 0.36$) and 29% ($R^2 = 0.29$) of the variances in SR, PD, FRic and AGB, respectively (Fig. 4). The present climate had direct and indirect significant associations with AGB via all biodiversity variables (Fig. 4). The present climate was significantly and positively associated with SR ($r_{\partial} = 0.46$, $P < 0.05$), PD ($r_{\partial} = 0.35$, $P < 0.05$) and FRic ($r_{\partial} = 0.58$, $P < 0.05$, Fig. 4). However, the paleoclimate change had direct significant negative effects on SR ($r_{\partial} = -0.28$, $P < 0.05$), PD ($r_{\partial} = -0.32$, $P < 0.05$) and FRic ($r_{\partial} = -0.25$, $P < 0.05$, Fig. 4).



297

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

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

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

301 MAT and MAP anomaly from the Last Glacial Maximum from the Mid-Holocene to the present

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

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

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

305 0.05).

306

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

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

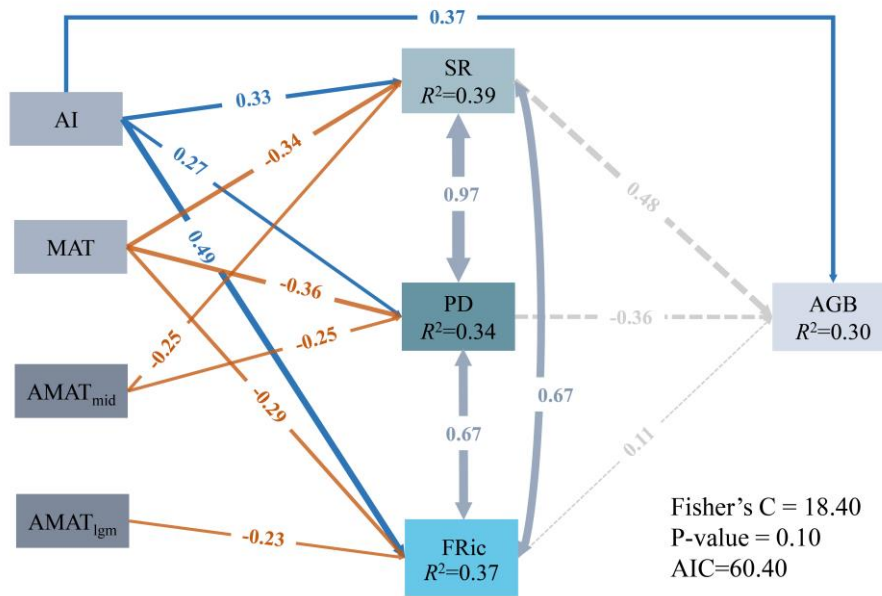
309 the direct effects of MAT on the three dimensions of biodiversity (SR, $r_{\delta} = -0.34$; PD, $r_{\delta} = -0.36$;

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

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

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

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



314

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

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

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

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

319 paths ($P > 0.05$).

320 4. Discussion

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

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

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

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

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

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

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

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

329 resource use strategy of functional traits (Hanif et al., 2019). However, in Mongolian Plateau
330 grasslands taxonomic diversity may be more critical. Selection effects and compensatory effects are
331 the main mechanisms through which biodiversity impacts on biomass. The grassland community
332 structure of the Mongolian Plateau is relatively simple, and biomass mainly depends on the number
333 or dominance of dominant species. However, functional traits considered in this study, such as leaf
334 size and plant height, do not have a strong impact on biomass. The Mongolian Plateau is located in
335 an arid and semi-arid area, and drought-tolerant species invest a lot in seed resources, leaf structure
336 and root biomass (Wolf et al., 2021). Studies have shown that these traits are negatively correlated
337 with aboveground biomass, while functional traits consistent with growth strategies, such as leaf
338 nitrogen concentration and photosynthetic utilization efficiency, can promote aboveground biomass
339 (Wolf et al., 2021).

340 Secondly, phylogenetic diversity also had a significant impact on aboveground biomass.
341 Phylogenetic diversity contains the evolutionary information of species ecology. It is influenced by
342 the average degree of correlation between species and the number of existing species, and can reflect
343 the evolutionary sequence of characteristics related to habitat and resource utilization (Srivastava et
344 al., 2012). If species make better use of all available resources, productivity may increase. Therefore,
345 our research suggests that protecting taxonomic diversity and conserving evolutionarily different
346 species are equally important in effectively maintaining high-yielding communities.

347 **4.2 Relationship between paleoclimate anomalies and current biodiversity patterns**

348 Although a rich body of research has explored the factors affecting biodiversity patterns and their
349 relationships with biomass (Van Der Plas, 2019; Tilman et al., 2012), it is not clear how current
350 climate and paleoclimate together affect the relationship, especially in grassland communities. further

351 ~~studies are still needed.~~ Here, our results showed that paleoclimate changes and present climate
352 factors were critical variables influencing contemporary biodiversity patterns. This illustrates the
353 importance of historical factors, such as evolution, as well as contemporary factors, such as climate,
354 in determining the geographic ranges of species and the accumulation of species in the region (Fine,
355 2015). Previous studies aiming to explain patterns of biodiversity have focused on the current
356 climate (Harrison et al., 2015), energy (Kreft and Jetz, 2007), soil attributions (Ulrich et al., 2014),
357 human activities (Hautier et al., 2015; Newbold et al., 2015) or water availability (Jiao et al., 2021;
358 Liu et al., 2021). Modern climate research on biodiversity and ecosystem functions has been widely
359 confirmed (Yang et al., 2011; Liu et al., 2021; Walther et al., 2002), but our research shows that the
360 pattern of biodiversity is also affected by past climates, and especially climate ~~change~~ anomalies.
361 Based on climate-related traits, climate anomalies ~~Paleoclimate changes~~ filtered the filtered the
362 regional species pool ~~based on climate-related traits~~, which in turn affected contemporary
363 biodiversity patterns.

364 Species richness is affected by the significant positive effects of AI, and the significant negative
365 effects of MAT and AMAT_{mid}. Jansson's research showed that the total number of vascular plant
366 species decreased with increasing temperature change since the LGM in mainland areas (Jansson,
367 2003), which is inconsistent with our results. We found that the species richness of Mongolian
368 Plateau grassland is more affected by temperature changes since the Mid-Holocene. In Europe, the
369 richness of widespread species was largely controlled by the modern climate, while the LGM climate
370 and climatic heterogeneity were codominant with modern climate as controls of richness for
371 restricted and intermediate species, which appear to still be associated with their glacial refugia
372 (Svenning and Skov, 2007b).

373 Phylogenetic diversity (PD) is usually used to quantify the uniqueness of a region's evolution. On longer timescales, the effects of climate on speciation and extinction may cumulatively affect
374 current PD patterns (Svenning et al., 2015). Our research showed that PD was negatively correlated
375 with MAT and AMAT_{mid} temperature anomalies in the Mid-Holocene, but not significantly related to
376 temperature anomalies during the Last Glacial Maximum. However, the PD of global forest
377 ecosystems is positively associated with temperature and precipitation and is negatively associated
378 with Quaternary precipitation change (Kubota et al., 2018). This indicates the importance of
379 paleoprecipitation variation in shaping the pattern of contemporary phylogenetic diversity in forest
380 ecosystems, possibly by survival and recolonization from refugia along hydrological gradients
381 (Blonder et al., 2018). Additionally, Quaternary glacial-interglacial climate oscillations led to the
382 extinction of trees in many parts of the globe, for example in Australia (Macphail et al., 1995) and
383 Europe (Svenning, 2003), affecting the PD of global forest ecosystems. Liu et al. showed that
384 herbaceous plants were mainly affected by climate change since Mid-Holocene, while woody plants
385 were mainly affected by climate change since the LGM, which may be due to the differences in
386 morphology of herbaceous and woody plants (Liu et al., 2018b; Wang et al., 2021). Woody plants
387 with large conduits are vulnerable to drought or freezing and cause clogging of conduits (Zanne et al.,
388 2014), and thus, are more susceptible to cold Quaternary climate oscillations. Herbs can mitigate the
389 effects of extreme weather by producing underground buds and stems, or wilting aboveground parts
390 (Qian et al., 2017). ~~Phylogenetic studies reveal that major ecological niches are more conserved~~
391 ~~through evolutionary history than expected, implying that adaptations to major climate changes have~~
392 ~~not readily been accomplished in all lineages (Donoghue, 2008).~~
393

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

395 climate anomaly. This may be due to the intolerance of plant traits to past climatic conditions
396 (Bhagwat and Willis, 2008) and the postglacial migration lag (Svenning et al., 2008). In the Late
397 Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climate fluctuations
398 (Tian et al., 2017), and likely experienced a non-random removal of functional combinations and
399 change in functional diversity (Ordonez and Svenning, 2017). Previous research has indicated that
400 the magnitude of past glacial-to-interglacial warming was sufficient at most locations across the
401 globe (including the Mongolian Plateau) to drive moderate to large changes in vegetation
402 composition and structure (Nolan et al., 2018). When climate changes, inappropriate species may be
403 quickly ruled out, and appropriate species may migrate more slowly, resulting in a negative
404 correlation between the paleoclimate anomaly and contemporary FD in the Mongolian Plateau. This
405 is also limited by the spreading ability or migration potential of plants after the glaciers retreated,
406 when species with inappropriate characteristics disappeared from the community and were not
407 replaced by other species (Blonder et al., 2018). Studies in Europe indicate that the lagging effect of
408 glacial-interglacial climate instability ~~and accessibility~~ on functional diversity is >10,000 years
409 (Ordonez and Svenning, 2015).

410 **4.3 Effects of climate on the relationship between biodiversity and biomass**

411 The influence of climate on relationship between contemporary diversity and biomass may be
412 caused by climate change and human activities in the Mongolian Plateau grasslands.~~The influence of~~
413 ~~paleoclimate anomalies on contemporary species and phylogeny diversity may be caused by climate~~
414 ~~change and human activities in the Mongolian Plateau grasslands.~~ In the eastern part of the
415 Mongolian Plateau, the interval of 35230 to 25150 yr B.P. was a forest-steppe landscape under humid
416 conditions, represented by Pinaceae, Compositae and Chenopodiaceae (Tian et al., 2017).

417 Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe landscape,
418 and drought began to intensify. During the Last Glacial Maximum period, the vegetation types on the
419 Mongolian Plateau were mainly polar ~~and~~, alpine ~~deserts~~ and temperate deserts (Ray and Adams,
420 2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene, xerophytes had
421 declined sharply, and plants of humid climates had increased. The humidity increased during the
422 early Holocene, and generally humid conditions lasted from 10,400 until 7000 yr BP and the region
423 experienced the Lavliakan humid phase (Yin et al., 2011; Lioubimtseva, 2004), with more
424 hygrophilous species, such as Cyperaceae (Tian et al., 2017). This climate condition was also
425 conducive to the development and spread of Compositae and Gramineae families in the steppes of
426 Central Asia (Lioubimtseva, 2004). Since approximately 5200 yr BP to present, the climate has
427 become more arid, with corresponding vegetation change and strong aeolian activity (Yin et al.,
428 2011). ~~Furthermore, palaeoecological and archaeological evidence shows that people have shaped~~
429 ~~most of terrestrial nature for at least 12,000 years, including burning, hunting, cultivation and~~
430 ~~domestication. In the Mongolian Plateau, especially in the Inner Mongolia region of northern China,~~
431 ~~grazing appeared at ~5.7–5.5 ka and further intensified again after ~4.2–4.0 ka (Huang et al., 2021).~~
432 ~~The intensification of grazing activities also causes changes in biodiversity.~~

433 As far as aboveground biomass is concerned, after taking into account climatic factors, it is
434 mainly directly affected by aridity index, while the three dimensions of biodiversity have no
435 significant impact on it, which is consistent with our previous research (Li et al., 2020). [A](#)
436 [meta-analysis of 40 global grasslands plant communities showed that the response of plant diversity](#)
437 [to climate warming was an important factor in determining grassland aboveground biomass](#) (Shao et
438 al., 2021). ~~Similarly, Paleoclimate-paleoclimate~~ changes also have no direct effects on aboveground

439 biomass, which indirectly affects aboveground biomass through regulating biodiversity. This is
440 mainly because paleoclimatic filtering can alter the historical legacies of species and functional
441 diversity (removal or accumulation over time of species and functional states) through evolutionary,
442 extinction, or recolonization (Svenning et al., 2015). Legacies in the species and functional traits
443 pool further 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 (Ma) to the emergence
447 of species domestication in agricultural societies 10,000 years ago (Strömberg and Staver, 2022).
448 Paleoecological 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 and further intensified again after ~4.2–4.0 ka (Huang et al., 2021). A large
452 number of studies have shown that the intensification of grazing activities also causes changes in
453 biodiversity and biomass (Liang et al., 2021; Herrero-Járegui and Oesterheld, 2018; D'Áz et al.,
454 2007). Therefore, there is an urgent need for future research to develop systematic analytical
455 frameworks to assess the importance of paleoclimate and climate change in shaping contemporary
456 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

467 **Authors' Contributions**

468 Z. Li analyzed the data and wrote the first draft of the manuscript. Zh. Li, J. Zhang, G. Han, F.Y. Li
469 and C. Liang contributed to later versions of the manuscript and all authors provided constructive
470 comments to improve the manuscript. F.Y. Li and C. Liang designed and led the field survey. Z. Li,
471 Zh. Li, X. Tong, J. Zhang, L. Dong, Y. Zheng, B. Miao, W. Ma, L. Zhao, L. Wang, L. Wen, C. Liang
472 and F.Y. Li conducted the experiment and collected the data.

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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490 **References**

- 491 Archer, E.: rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics, 2016.
- 492 Avolio, M. L., Komatsu, K. J., Collins, S. L., Grman, E., Koerner, S. E., Tredennick, A. T., Wilcox, K. R.,
493 Baer, S., Boughton, E. H., Britton, A. J., Foster, B., Gough, L., Hovenden, M., Isbell, F., Jentsch, A., Johnson,
494 D. S., Knapp, A. K., Kreyling, J., Langley, J. A., Lortie, C., McCulley, R. L., McLaren, J. R., Reich, P. B.,
495 Seabloom, E. W., Smith, M. D., Suding, K. N., Suttle, K. B., and Tognetti, P. M.: Determinants of community
496 compositional change are equally affected by global change, *Ecol Lett*, 24, 1892-1904, 10.1111/ele.13824,
497 2021.
- 498 Bhagwat, S. A. and Willis, K. J.: Species persistence in northerly glacial refugia of Europe: a matter of chance
499 or biogeographical traits?, *Biogeogr*, 35, 464-482, 10.1111/j.1365-2699.2007.01861.x, 2008.
- 500 Blonder, B., Enquist, B. J., Graae, B. J., Kattge, J., Maitner, B. S., Morueta-Holme, N., Ordonez, A., Simova,
501 I., Singarayer, J., Svenning, J. C., Valdes, P. J., and Violle, C.: Late Quaternary climate legacies in
502 contemporary plant functional composition, *Glob Change Biol*, 24, 4827-4840, 10.1111/gcb.14375, 2018.
- 503 Breiman, L., Cutler, A., Liaw, A., and MatthewWiener: Package ‘randomForest’: Breiman and Cutler’s
504 Random Forests for Classification and Regression, 2018.
- 505 Buisson, E., Archibald, S., Fidelis, A., and Suding, K. N.: Ancient grasslands guide ambitious goals in
506 grassland restoration, *Science*, 377, 594-598, 10.1126/science.abo4605, 2022.
- 507 Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A., Atkin, O. K.,
508 Kattge, J., Amiaud, B., Blonder, B., Boenisch, G., Bond-Lamberty, B., Brown, K. A., Byun, C., Campetella,
509 G., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., Craven, D., de Vries, F. T., D áz, S., Domingues,
510 T. F., Forey, E., Gonz ález-Melo, A., Gross, N., Han, W., Hattings, W. N., Hickler, T., Jansen, S., Kramer, K.,
511 Kraft, N. J. B., Kurokawa, H., Laughlin, D. C., Meir, P., Minden, V., Niinemets, Ü., Onoda, Y., Peñuelas, J.,
512 Read, Q., Sack, L., Schamp, B., Soudzilovskaia, N. A., Spasojevic, M. J., Sosinski, E., Thornton, P. E.,
513 Valladares, F., van Bodegom, P. M., Williams, M., Wirth, C., and Reich, P. B.: Mapping local and global
514 variability in plant trait distributions, *P Natl Acad Sci USA*, 114, E10937-E10946, 10.1073/pnas.1708984114,

515 2017.

516 Cadotte, M. W., Cardinale, B. J., and Oakley, T. H.: Evolutionary history and the effect of biodiversity on
517 plant productivity, *P Natl Acad Sci USA*, 105, 17012-17017, 10.1073/pnas.0805962105, 2008.

518 Cavender-Bares, J., Kozak, K. H., Fine, P. V., and Kembel, S. W.: The merging of community ecology and
519 phylogenetic biology, *Ecology Lett*, 12, 693-715, 10.1111/j.1461-0248.2009.01314.x, 2009.

520 Cutler, D. R., Edwards, J. T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., and Lawler, J. J.: Random
521 forest for classification ecology, *Ecology*, 88, 2783-2792, 10.1890/07-0539.1 2007.

522 Diaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C.,
523 Prentice, I. C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J.,
524 Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Sheremet'ev, S. N., Jactel, H., Baraloto, C., Cerabolini,
525 B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J. S., Gunther, A., Falczuk, V., Ruger, N.,
526 Mahecha, M. D., and Gorne, L. D.: The global spectrum of plant form and function, *Nature*, 529, 167-171,
527 10.1038/nature16489, 2016.

528 D'Áz, S., Lavorel, S., McIntyre, S. U. E., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G.,
529 Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W. E. I., Clark, H., and Campbell, B. D.: Plant trait
530 responses to grazing - a global synthesis, *Glob Change Biol*, 13, 313-341, 10.1111/j.1365-2486.2006.01288.x,
531 2007.

532 Eiserhardt, W. L., Borchsenius, F., Plum, C. M., Ordonez, A., and Svenning, J. C.: Climate-driven extinctions
533 shape the phylogenetic structure of temperate tree floras, *Ecol Lett*, 18, 263-272, 10.1111/ele.12409, 2015.

534 Ellis, E. C., Gauthier, N., Klein Goldewijk, K., Bliege Bird, R., Boivin, N., Diaz, S., Fuller, D. Q., Gill, J. L.,
535 Kaplan, J. O., Kingston, N., Locke, H., McMichael, C. N. H., Ranco, D., Rick, T. C., Shaw, M. R., Stephens,
536 L., Svenning, J. C., and Watson, J. E. M.: People have shaped most of terrestrial nature for at least 12,000
537 years, *P Natl Acad Sci USA*, 118, 10.1073/pnas.2023483118, 2021.

538 Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T. R., Lloyd, J.,
539 Monteagudo-Mendoza, A., Arroyo, L., Alvarez-Davila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B.
540 H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., Bonal, D., Davila Cardozo, N.,
541 Erwin, T., Fauset, S., Herault, B., Laurance, S., Poorter, L., Qie, L., Stahl, C., Sullivan, M. J. P., Ter Steege, H.,
542 Vos, V. A., Zuidema, P. A., Almeida, E., Almeida de Oliveira, E., Andrade, A., Vieira, S. A., Aragao, L.,
543 Araujo-Murakami, A., Arets, E., Aymard, C. G., Baraloto, C., Camargo, P. B., Barroso, J. G., Bongers, F.,
544 Boot, R., Camargo, J. L., Castro, W., Chama Moscoso, V., Comiskey, J., Cornejo Valverde, F., Lola da Costa,
545 A. C., Del Aguila Pasquel, J., Di Fiore, A., Fernanda Duque, L., Elias, F., Engel, J., Flores Llampazo, G.,
546 Galbraith, D., Herrera Fernandez, R., Honorio Coronado, E., Hubau, W., Jimenez-Rojas, E., Lima, A. J. N.,
547 Umetsu, R. K., Laurance, W., Lopez-Gonzalez, G., Lovejoy, T., Aurelio Melo Cruz, O., Morandi, P. S., Neill,
548 D., Nunez Vargas, P., Pallqui Camacho, N. C., Parada Gutierrez, A., Pardo, G., Peacock, J., Pena-Claros, M.,
549 Penuela-Mora, M. C., Petronelli, P., Pickavance, G. C., Pitman, N., Prieto, A., Quesada, C., Ramirez-Angulo,
550 H., Rejou-Mechain, M., Restrepo Correa, Z., Roopsind, A., Rudas, A., Salomao, R., Silva, N., Silva Espejo, J.,
551 Singh, J., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres-Lezama, A., Valenzuela Gamarra, L., van de
552 Meer, P. J., van der Heijden, G., van der Hout, P., Vasquez Martinez, R., Vela, C., Vieira, I. C. G., and Phillips,

553 O. L.: Compositional response of Amazon forests to climate change, *Glob Change Biol*, 25, 39-56,
554 10.1111/gcb.14413, 2019.

555 Fine, P. V. A.: Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity, *Annu Rev*
556 *Ecol Evol S*, 46, 369-392, 10.1146/annurev-ecolsys-112414-054102, 2015.

557 Flynn, D. F. B., Mirotnick, N., Jain, M., Palmer, M. I., and Naeem, S.: Functional and phylogenetic
558 diversity as predictors of biodiversity-ecosystem-function relationships, *Ecology*, 92, 1573-1581,
559 10.1890/10-1245.1, 2011.

560 Fordham, D. A., Jackson, S. T., Brown, S. C., Huntley, B., Brook, B. W., Dahl-Jensen, D., Gilbert, M. T. P.,
561 Otto-Bliesner, B. L., Svensson, A., Theodoridis, S., Wilmshurst, J. M., Buettel, J. C., Canteri, E., McDowell,
562 M., Orlando, L., Pilowsky, J., Rahbek, C., and Nogues-Bravo, D.: Using paleo-archives to safeguard
563 biodiversity under climate change, *Science*, 369, 10.1126/science.abc5654, 2020.

564 Hanif, M. A., Yu, Q., Rao, X., and Shen, W.: Disentangling the Contributions of Plant Taxonomic and
565 Functional Diversities in Shaping Aboveground Biomass of a Restored Forest Landscape in Southern China,
566 *Plants (Basel)*, 8, 612, 10.3390/plants8120612, 2019.

567 Harrison, S. P., Gornish, E. S., and Copeland, S.: Climate-driven diversity loss in a grassland community, *P*
568 *Natl Acad Sci USA*, 112, 8672-8677, 10.1073/pnas.1502074112, 2015.

569 Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., and Reich, P. B.: Anthropogenic
570 environmental changes affect ecosystem stability via biodiversity, *Science*, 348, 336-340,
571 10.1126/science.aaa1788, 2015.

572 Herrero-Jáuregui, C. and Oesterheld, M.: Effects of grazing intensity on plant richness and diversity: a
573 meta-analysis, *Oikos*, 127, 757-766, 10.1111/oik.04893, 2018.

574 Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M.,
575 Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., J., V., and Wardle, D. A.: Effects of
576 biodiversity on ecosystem functioning: a consensus of current knowledge, *Ecol Monogr*, 75, 3-35,
577 10.1890/04-0922 2005.

578 Huang, X., Zhang, J., Ren, L., Zhang, S., and Chen, F.: Intensification and Driving Forces of Pastoralism in
579 Northern China 5.7 ka Ago, *Geophys Res Lett*, 48, e2020GL092288, 10.1029/2020GL092288, 2021.

580 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid,
581 B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S., and Loreau, M.: High plant diversity
582 is needed to maintain ecosystem services, *Nature*, 477, 199-202, 10.1038/nature10282, 2011.

583 Jansson, R.: Global patterns in endemism explained by past climatic change, *P Roy Soc B-Biol Sci*, 270,
584 583-590, 10.1098/rspb.2002.2283, 2003.

585 Jiao, W., Wang, L., Smith, W. K., Chang, Q., Wang, H., and D'Odorico, P.: Observed increasing water
586 constraint on vegetation growth over the last three decades, *Nat Commun*, 12, 3777,
587 10.1038/s41467-021-24016-9, 2021.

588 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder,
589 H. P., and Kessler, M.: Climatologies at high resolution for the earth's land surface areas, *Scientific Data*, 4,
590 170122, 10.1038/sdata.2017.122, 2017.

591 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P.,
592 and Webb, C. O.: Picante: R tools for integrating phylogenies and ecology, *Bioinformatics*, 26, 1463-1464,
593 10.1093/bioinformatics/btq166, 2010.

594 Kissling, W. D., Eiserhardt, W. L., Baker, W. J., Borchsenius, F., Couvreur, T. L., Balslev, H., and Svenning, J.
595 C.: Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide, *P Natl Acad Sci*
596 *USA*, 109, 7379-7384, 10.1073/pnas.1120467109, 2012.

597 Kreft, H. and Jetz, W.: Global patterns and determinants of vascular plant diversity, *P Natl Acad Sci USA*, 104,
598 5925-5930, 10.1073/pnas.0608361104, 2007.

599 Kubota, Y., Kusumoto, B., Shiono, T., Ulrich, W., and Duarte, L.: Environmental filters shaping angiosperm
600 tree assembly along climatic and geographic gradients, *J Veg Sci*, 29, 607-618, 10.1111/jvs.12648, 2018.

601 Laliberté, E., Legendre, P., and Shipley, B.: Package 'FD': Measuring functional diversity (FD) from multiple
602 traits, and other tools for functional ecology, 2015.

603 Lefcheck, J.: Package 'piecewiseSEM': Piecewise Structural Equation Modeling, 2020.

604 Lefcheck, J. S. and Freckleton, R.: piecewiseSEM: Piecewise structural equation modelling in r for ecology,
605 evolution, and systematics, *Methods Ecol Evol*, 7, 573-579, 10.1111/2041-210x.12512, 2015.

606 Li, Z., Li, Z., Tong, X., Zhang, J., Dong, L., Zheng, Y., Ma, W., Zhao, L., Wang, L., Wen, L., Dang, Z.,
607 Tuvshintogtokh, I., Liang, C., and Li, F. Y.: Climatic humidity mediates the strength of the species richness–
608 biomass relationship on the Mongolian Plateau steppe, *Sci Total Environ*, 718, 137252,
609 10.1016/j.scitotenv.2020.137252, 2020.

610 Li, Z., Liang, M., Li, Z., Mariotte, P., Tong, X., Zhang, J., Dong, L., Zheng, Y., Ma, W., Zhao, L., Wang, L.,
611 Wen, L., Tuvshintogtokh, I., Gornish, E. S., Dang, Z., Liang, C., Li, F. Y., and Schöb, C.: Plant functional
612 groups mediate effects of climate and soil factors on species richness and community biomass in grasslands of
613 Mongolian Plateau, *J Plant Ecol*, 14, 679-691, 10.1093/jpe/rtab021, 2021.

614 Liang, M., Liang, C., Hautier, Y., Wilcox, K. R., and Wang, S.: Grazing-induced biodiversity loss impairs
615 grassland ecosystem stability at multiple scales, *Ecol Lett*, 24, 2054-2064, 10.1111/ele.13826, 2021.

616 Lioubimtseva, E.: Climate change in arid environments: revisiting the past to understand the future, *Prog Phys*
617 *Geog*, 28, 502-530, 10.1191/0309133304pp422oa, 2004.

618 Liu, D., Zhang, C., Ogaya, R., Fernandez-Martinez, M., Pugh, T. A. M., and Penuelas, J.: Increasing climatic
619 sensitivity of global grassland vegetation biomass and species diversity correlates with water availability, *New*
620 *Phytol*, 230, 1761-1771, 10.1111/nph.17269, 2021.

621 Liu, H., Mi, Z., Lin, L., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., Zhao, X., Sanders,

622 N. J., Classen, A. T., Reich, P. B., and He, J. S.: Shifting plant species composition in response to climate
623 change stabilizes grassland primary production, *P Natl Acad Sci USA*, 115, 4051-4056,
624 10.1073/pnas.1700299114, 2018a.

625 Liu, Y., Su, X., Shrestha, N., Xu, X., Wang, S., Li, Y., Wang, Q., Sandanov, D., and Wang, Z.: Effects of
626 contemporary environment and Quaternary climate change on drylands plant diversity differ between growth
627 forms, *Ecography*, 42, 334-345, 10.1111/ecog.03698, 2018b.

628 MacPhail, M. K., Colhoun, E. A., and Fitzsimons, S. J.: Key Periods in the Evolution of the Cenozoic
629 Vegetation and Flora in Western Tasmania: the Late Pliocene, *Australian Journal of Botany*, 43,
630 10.1071/bt9950505, 1995.

631 Maestre, F. T., Benito, B. M., Berdugo, M., Concostrina-Zubiri, L., Delgado-Baquerizo, M., Eldridge, D. J.,
632 Guirado, E., Gross, N., Křī, S., Bagousse-Pinguet, Y. L., Ochoa-Hueso, R., and Soliveres, S.: Biogeography
633 of global drylands, *The New phytologist*, 231, 540-558, 10.1111/nph.17395, 2021.

634 Mayle, F. E., Burn, M. J., Power, M., and Urrego, D. H.: Past Climate Variability in South America and
635 Surrounding Regions, Springer2009.

636 Mottl, O., Flantua, S. G. A., Bhatta, K. P., Felde, V. A., Giesecke, T., Goring, S., Grimm6, E. C., Haberle, S.,
637 Hooghiemstra, H., Ivory, S., Kuneš, P., Wolters, S., Seddon, A. W. R., and Williams, J. W.: Global acceleration
638 in rates of vegetation change over the past 18,000 years, *Science*, 372, 860-864, 10.1126/science.abg1685,
639 2021.

640 Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., Borger, L., Bennett, D. J.,
641 Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M. J., Feldman, A.,
642 Garon, M., Harrison, M. L., Alhousseini, T., Ingram, D. J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L.,
643 Kleyer, M., Correia, D. L., Martin, C. D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H. R., Purves, D. W.,
644 Robinson, A., Simpson, J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J.
645 P., and Purvis, A.: Global effects of land use on local terrestrial biodiversity, *Nature*, 520, 45-50,
646 10.1038/nature14324, 2015.

647 Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush,
648 M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S.,
649 Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., Kim, S.-H., Latorre, C., Leydet, M., Lézine, A.-M.,
650 Liu, K.-B., Liu, Y., Lozhkin, A. V., McGlone, M. S., Marchant, R. A., Momohara, A., Moreno, P. I., Müller, S.,
651 Otto-Bliesner, B. L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P. E., Tipton, J., Vincens, A., Weng, C.,
652 Xu, Q., Zheng, Z., and Jackson, S. T.: Past and future global transformation of terrestrial ecosystems under
653 climate change, *Science*, 361, 920-923, 10.1126/science.aan5360, 2018.

654 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B.,
655 Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., and Wagner, H.: Package 'vegan': Community
656 Ecology Package, 2020.

657 Ordonez, A. and Svenning, J.-C.: Geographic patterns in functional diversity deficits are linked to
658 glacial-interglacial climate stability and accessibility, *Global Ecol Biogeogr*, 24, 826-837, 10.1111/geb.12324,

659 2015.

660 Ordonez, A. and Svenning, J. C.: Consistent role of Quaternary climate change in shaping current plant
661 functional diversity patterns across European plant orders, *Sci Rep-UK*, 7, 42988, 10.1038/srep42988, 2017.

662 Qian, H., Jin, Y., and Ricklefs, R. E.: Phylogenetic diversity anomaly in angiosperms between eastern Asia
663 and eastern North America, *P Natl Acad Sci USA*, 114, 11452-11457, 10.1073/pnas.1703985114, 2017.

664 Ray, N. and Adams, J. M.: A GIS-based Vegetation Map of the World at the Last Glacial Maximum
665 (25,000-15,000 BP). *Internet Archaeology*, 11, 1-44, 10.11141/ia.11.2, 2001.

666 Revelle, W.: Package ‘psych’: Procedures for Psychological, Psychometric, and Personality Research, 2021.

667 Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J., and Svenning, J. C.: The
668 influence of Late Quaternary climate-change velocity on species endemism, *Science*, 334, 660-664,
669 10.1126/science.1210173, 2011.

670 Seddon, A. W. R., Macias-Fauria, M., and Willis, K. J.: Climate and abrupt vegetation change in Northern
671 Europe since the last deglaciation, *Holocene*, 25, 25-36, 10.1177/0959683614556383, 2014.

672 Shao, J., Zhou, X., Groenigen, K. J., Zhou, G., Zhou, H., Zhou, L., Lu, M., Xia, J., Jiang, L., Hungate, B. A.,
673 Luo, Y., He, F., Thakur, M. P., and Mayfield, M.: Warming effects on grassland productivity depend on plant
674 diversity, *Global Ecol Biogeogr*, 31, 588-598, 10.1111/geb.13441, 2021.

675 Srivastava, D. S., Cadotte, M. W., MacDonald, A. A., Marushia, R. G., and Mirotnick, N.: Phylogenetic
676 diversity and the functioning of ecosystems, *Ecol Lett*, 15, 637-648, 10.1111/j.1461-0248.2012.01795.x, 2012.

677 Strömberg, C. A. E. and Staver, A. C.: The history and challenge of grassy biomes-Grassy biomes are >20
678 million years old but are undervalued and under threat today, *Science*, 377, 592-593, 10.1126/science.add1347,
679 2022.

680 Svenning, J.-C.: Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora, *Ecol*
681 *Lett*, 6, 646-653, 10.1046/j.1461-0248.2003.00477.x, 2003.

682 Svenning, J.-C. and Skov, F.: Could the tree diversity pattern in Europe be generated by postglacial dispersal
683 limitation?, *Ecol Lett*, 10, 453-460, 10.1111/j.1461-0248.2007.01038.x, 2007a.

684 Svenning, J.-C. and Skov, F.: Ice age legacies in the geographical distribution of tree species richness in
685 Europe, *Global Ecol Biogeogr*, 16, 234-245, 10.1111/j.1466-822x.2006.00280.x, 2007b.

686 Svenning, J.-C., Normand, S., and Skov, F.: Postglacial dispersal limitation of widespread forest plant species
687 in northern Europe, *Ecography*, 31, 316-326, 10.1111/j.2008.0906-7590.05206.x, 2008.

688 Svenning, J.-C., Eiserhardt, W. L., Normand, S., Ordonez, A., and Sandel, B.: The Influence of Paleoclimate
689 on Present-Day Patterns in Biodiversity and Ecosystems, *Annu Rev Ecol Evol S*, 46, 551-572,
690 10.1146/annurev-ecolsys-112414-054314, 2015.

691 Swenson, N. G.: The role of evolutionary processes in producing biodiversity patterns, and the

692 interrelationships between taxonomic, functional and phylogenetic biodiversity, *Am J Bot*, 98, 472-480,
693 10.3732/ajb.1000289, 2011.

694 Swenson, N. G., Erickson, D. L., Mi, X., Bourg, N. A., Forero-Montaña, J., Ge, X., Howe, R., Lake, J. K., Liu,
695 X., Ma, K., Pei, N., Thompson, J., Uriarte, M., Wolf, A., Wright, S. J., Ye, W., Zhang, J., Zimmerman, J. K.,
696 and Kress, W. J.: Phylogenetic and functional alpha and beta diversity in temperate and tropical tree
697 communities, *Ecology*, 93, S112-S125, 2012.

698 The Angiosperm Phylogeny Group: An update of the Angiosperm Phylogeny Group classification for the
699 orders and families of flowering plants APG II, *Bot J Linn Soc*, 161, 105-121, 10.1111/boj.12385, 2009.

700 Tian, F., Wang, Y., Chi, Z., Liu, J., Yang, H., Jiang, N., and Tang, W.: Late Quaternary vegetation and climate
701 reconstruction based on pollen data from southeastern Inner Mongolia, China, *Rev Palaeobot Palyno*, 242,
702 33-42, 10.1016/j.revpalbo.2017.03.003, 2017.

703 Tilman, D., Reich, P. B., and Isbell, F.: Biodiversity impacts ecosystem productivity as much as resources,
704 disturbance, or herbivory, *P Natl Acad Sci USA*, 109, 10394-10397, 10.1073/pnas.1208240109 2012.

705 Trabucco, A. and Zomer, R. J.: Global Aridity Index and Potential Evapo-Transpiration (ET₀) Climate
706 Database v2, 10.6084/m9.figshare.7504448.v3, 2019.

707 Ulrich, W., Soliveres, S., Maestre, F. T., Gotelli, N. J., Quero, J. L., Delgado-Baquerizo, M., Bowker, M. A.,
708 Eldridge, D. J., Ochoa, V., Gozalo, B., Valencia, E., Berdugo, M., Escobar, C., Garcia-Gomez, M., Escudero,
709 A., Prina, A., Alfonso, G., Arredondo, T., Bran, D., Cabrera, O., Cea, A., Chaieb, M., Contreras, J., Derak, M.,
710 Espinosa, C. I., Florentino, A., Gaitan, J., Muro, V. G., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J. R.,
711 Hernandez, R. M., Huber-Sannwald, E., Jankju, M., Mau, R. L., Hughes, F. M., Miriti, M., Moneris, J.,
712 Muchane, M., Naseri, K., Pucheta, E., Ramirez-Collantes, D. A., Raveh, E., Romao, R. L., Torres-Diaz, C.,
713 Val, J., Veiga, J. P., Wang, D., Yuan, X., and Zaady, E.: Climate and soil attributes determine plant species
714 turnover in global drylands, *J Biogeogr*, 41, 2307-2319, 10.1111/jbi.12377, 2014.

715 Van der Plas, F.: Biodiversity and ecosystem functioning in naturally assembled communities, *Biol Rev*, 94,
716 1220-1245, 10.1111/brv.12499, 2019.

717 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M.,
718 Hoegh-Guldberg, O., and Bairlein, F.: Ecological responses to recent climate change, *Nature*, 416, 389-395,
719 10.1038/416389a, 2002.

720 Wang, Q., Li, Y., Zou, D., Su, X., Cai, H., Luo, A., Jiang, K., Zhang, X., Xu, X., Shrestha, N., and Wang, Z.:
721 Phylogenetic niche conservatism and variations in species diversity–climate relationships, *Ecography*, 44,
722 1856-1868, 10.1111/ecog.05759, 2021.

723 Wolf, A. A., Funk, J. L., Selmants, P. C., Morozumi, C. N., Hernandez, D. L., Pasari, J. R., and Zavaleta, E. S.:
724 Trait-based filtering mediates the effects of realistic biodiversity losses on ecosystem functioning, *P Natl Acad
725 Sci USA*, 118, 10.1073/pnas.2022757118, 2021.

726 Yang, H., Wu, M., Liu, W., Zhang, Z. H. E., Zhang, N., and Wan, S.: Community structure and composition in
727 response to climate change in a temperate steppe, *Glob Change Biol*, 17, 452-465,

- 728 10.1111/j.1365-2486.2010.02253.x, 2011.
- 729 Ye, J. S., Delgado-Baquerizo, M., Soliveres, S., and Maestre, F. T.: Multifunctionality debt in global drylands
730 linked to past biome and climate, *Glob Change Biol*, 25, 2152-2161, 10.1111/gcb.14631, 2019.
- 731 Yin, Y., Liu, H., He, S., Zhao, F., Zhu, J., Wang, H., Liu, G., and Wu, X.: Patterns of local and regional grain
732 size distribution and their application to Holocene climate reconstruction in semi-arid Inner Mongolia, China,
733 *Palaeogeogr Palaeocl*, 307, 168-176, 10.1016/j.palaeo.2011.05.011, 2011.
- 734 Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., McGlenn, D. J.,
735 O'Meara, B. C., Moles, A. T., Reich, P. B., Royer, D. L., Soltis, D. E., Stevens, P. F., Westoby, M., Wright, I. J.,
736 Aarssen, L., Bertin, R. I., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M. R., Oleksyn, J., Soltis, P.
737 S., Swenson, N. G., Warman, L., and Beaulieu, J. M.: Three keys to the radiation of angiosperms into freezing
738 environments, *Nature*, 506, 89-92, 10.1038/nature12872, 2014.
- 739