Title: Contemporary biodiversity pattern is affected by climate change at multiple temporal scales in steppe on the Mongolian Plateau

Running Title: Climate change and plant biodiversity

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Abstract

Present and historical climate conditions jointly determine contemporary biodiversity patterns and ecosystem functions. However, it remains unclear how contemporary climate and paleoclimate changes together affect the three dimensions of biodiversity (i.e., taxonomic diversity, functional diversity and phylogenetic diversity) and their relationship with ecosystem functions. Here, we assess the impact of current climate, paleoclimate and its anomalies on contemporary biodiversity and ecosystem functions. We estimated the taxonomic ~~diversity,~~ functional ~~diversity~~ and phylogenetic diversity of grassland on the Mongolian Plateau using vegetation survey data and trait information. We then used Random Forest ~~models~~ and Structural Equation models to assess the relative importance of the present ~~climate~~, the Mid Holocene ~~climate,~~ the Last-Glacial Maximum climate ~~and~~ paleoclimate changes as determinants of diversity and aboveground biomass. Our results showed that paleoclimate changes and modern climate jointly determined contemporary biodiversity patterns, while community biomass was mainly affected by modern climate, namely the aridity index. Modern aridity and temperature were two major influences on all three dimensions of biodiversity. Mid-Holocene climate anomalies had a strong effect on species richness and phylogenetic diversity, while functional diversity was mainly affected by temperature anomalies since the Last Glacial Maximum. These findings suggest that contemporary biodiversity patterns may be affected by processes at divergent temporal scales. Our results show that simultaneously exploring the response of the three dimensions of biodiversity in different periods of climate change

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

Keywords

Aridity index, biodiversity and ecosystem functions, functional diversity, paleoclimate anomaly, phylogenetic diversity, taxonomic diversity

1. Introduction

Global climate changes, such as increasing temperature and changing precipitation, are altering biodiversity patterns at an unprecedented rate, and have serious consequences for ecosystem functions related to biodiversity changes (Mottl et al., 2021; Nolan et al., 2018; Ye et al., 2019). Ecosystem functioning associated with biodiversity, and contemporary diversity patterns and their relationships may be regulated by modern climate, past climate and climate change (Fordham et al., 2020; Eiserhardt et al., 2015; Svenning et al., 2015).

Ecosystem ~~function~~ are strongly influenced by biodiversity (Isbell et al., 2011; Hooper et al., 2005), but understanding the effects of different dimensions of biodiversity (i.e., taxonomic diversity, functional diversity and phylogenetic diversity) on ecosystem functions (BEF) is still a challenge in ecology (Van Der Plas, 2019; Cadotte et al., 2008; Swenson, 2011). Traditionally, most studies of BEF have predominantly focused on the relationship between taxonomic diversity (i.e., species richness) and biomass or productivity. However, only considering taxonomic diversity has the limitation that it may ~~ignores the~~ important ecological processes such as the formation of function traits or the evolutionary history of species (Flynn et al., 2011; Swenson, 2011). The importance of taking into account other aspects of biodiversity, including functional diversity and phylogenetic

diversity, has increasingly been recognized. The effects of plant functional diversity on ecosystem functioning are largely driven by variations in plant functional traits, such as adult plant height and leaf size (Diaz et al., 2016). Phylogenetic diversity (PD) is a key driver of community assembly and ecosystem functions (Srivastava et al., 2012; Cavender-Bares et al., 2009). Previous research had shown that PD may be a better metric than species richness or functional diversity for predicting plant biomass (Cadotte et al., 2008). Communities with higher PD have stronger anti-interference ability because of their evolutionary potential to adapt to changing environmental conditions. However, the role of multi-dimensional biodiversity in driving ecosystem functions in response to climate change still needs further research. Elucidating the impacts of multi-dimensional biodiversity on biomass in ~~the~~ changing world can deepen our understanding of the direct and indirect effects of changes in climate and biodiversity on terrestrial ecosystems, and improve predictions of the ecological consequences of global climate changes.

Changes in community biodiversity and composition caused by climate change have been explored in various ecosystems(Avolio et al., 2021) , including tropical forests in the Amazon , alpine meadows on the Qinghai-Tibet Plateau (Liu et al., 2018) and a heterogeneous California (Esquivel-Muelbert et al., 2019) grassland (Harrison et al., 2015). Dispersal limitation and environmental filtering (i.e., climatic conditions and paleoclimate change) ~~plays~~ an important role in sorting species from the global species pool and in shaping large-scale diversity patterns (Kubota et al., 2018; Liu et al., 2021). Many studies have found that climate changes in the Mid-Holocene and the Quaternary interglacial period are the main driving factors of current species distribution, functional traits and community phylogeny (Svenning and Skov, 2007b). The current patterns of species richness and distribution of European flora are jointly affected by contemporary climatic

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

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

et al., 2020). During the last glacial-interglacial transition period, global warming and related climate change led to changes in ecosystems to a degree comparable to the predicted warming under future high-emission scenarios (Nolan et al., 2018). Therefore, studying the impact of past climate and its ~~changes~~ on contemporary biodiversity patterns will help us understand the potential effects of future climate changes. However, most studies exploring the impact of present climate and paleoclimate drivers on ecosystem functions have focused on forest ecosystems, while grassland ecosystems remain understudied. In addition, it is not yet clear whether taxonomy, function and phylogenetic diversity will vary with climate gradients and climate changes, and the intensity of any such changes remain unclear. Therefore, there is an urgent need to consider the impact of current climate, paleoclimate and its anomalies on contemporary biodiversity and ecosystem functions.

The Mongolian Plateau is located in the arid and semi-arid area of eastern Eurasia. During the Late Quaternary, the Mongolian Plateau experienced severe alternating dry and wet climatic fluctuations (Maestre et al., 2021; Tian et al., 2017), which may have a significant impact on current plant diversity and ecosystem function. However, the impacts of climate in different periods and climate legacy effects on aboveground biomass of steppes in the Mongolian Plateau, as well as whether these effects are biodiversity dependent, remain to be evaluated. To address these knowledge gaps, we coupled data from a field survey of 152 sites in the Mongolian Plateau (Fig. S1) to existing databases on present and past climates to explore present climate and the legacy effects of climate during the Last Glacial Maximum and the Mid-Holocene on current biodiversity and biomass.

Here, we aim to evaluate the relative importance of taxonomic, functional, and phylogenetic diversity on community biomass of steppe in the Mongolian Plateau, and to assess whether and how climate in different periods and their changes affect the three dimensions of diversity, and their

relationships with community biomass. We specifically ask: (1) Do the three dimensions of diversity affect community biomass, and if so, to what extent? (2) Whether and how climate at divergent temporal scales and paleoclimatic changes affect different dimensions of biodiversity? And (3) If there are effects, how do they affect the biodiversity-biomass relationship?

2. Materials and Methods

2.1 Study Area

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

2.2 Data Collection

2.2.1 Sites Sampled and Vegetation Investigation

We investigated 152 grassland sites set in flat areas with limited human interference and a relatively homogeneous environment. These sites were separated by about 50 km. One or three 10 m × 10 m quadrats were set in each site. Within each quadrat, five 1 m × 1 m plots were placed at each corner and at the center of the quadrat (only three 1 m × 1 m plots along the diagonal line of the quadrat in a few sites) to investigate vegetation. A total of 899 plots were investigated and 296 vascular plant species were recorded.

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

156 **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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Table 1 Climate variables included in this study

	Climate variables	Abbreviation
	Mean annual precipitation of the present	MAP
The present climate	Mean annual temperature of the present	MAT
	Aridity index of the present	AI
The Mid-Holocene	Mean annual precipitation of the Mid-Holocene	MAP_{mid}
climate	Mean annual temperature of the Mid-Holocene	MAT_{mid}
The Last Glacial	Mean annual precipitation of the Last Glacial Maximum	MAP_{lgm}
Maximum climate	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

2.2.3 Plant functional traits

The functional traits of each plant species include growth form, life form, phyllotaxy, single or compound leaf, petiole, inflorescence, fruit type, flowering period, fruit ripening period, length of the flowering period, water ecotypes, leaf length, leaf width and plant height (Table S1). These traits were looked up in the Flora of Inner Mongolia (Third Edition) or Flora of China (Online Edition) (http://www.iplant.cn/frps). The trait data for leaf length and leaf width were the median values provided in Flora of China (Fig. S2). For example, if the leaf length of *Leymus chinensis* was described as 7-18 cm in the Flora of China, then leaf length was defined as 12.5 cm.

186 **2.3 Aboveground biomass**

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

190 **2.4 Diversity calculations**

191 **2.4.1 Taxonomic diversity**

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

196 **2.4.2 Functional diversity**

197 The functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional
198 dispersion (FDis) and Rao index (Rao's Q) were calculated based on the Gower distance of
199 functional traits using the 'dbFD' function in the '*FD*' R package (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

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

2.5 Data analysis

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

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

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

model, we identified the climate variables that significantly affected biodiversity and divided them into composite variables. The model contained two composite variables that potentially represent collections of variables in terms of the present climate and paleoclimate change. We calculated Pearson correlations between the climate factors (Fig. S3) and deleted the predictors with high correlation coefficients (>0 .85, $P < 0.05$) to avoid multicollinearity. Before pSEM analysis, all selected predictors were standardized. Second, principal component analyses (PCAs) were used for the composite variables with multiple predictors. For each composite variable, the first principal component (PC1) explained 64~71% of the total variance and was used in the subsequent pSEM analysis (Table S2). Third, pSEM was developed from the full conceptual model. We fitted the component models of the piecewise SEM as linear models and reported the standardized coefficient for each path from each component model. We used Shipley's d-separation test to evaluate the overall fit of the pSEM, as well as Fisher's C statistic and AIC.

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

3. Results

3.1 Effects of biodiversity on aboveground biomass

Among the 11 biodiversity variables, SR, PD and Pielou index identified by the RF model were the three most significant predictors influencing aboveground biomass (Fig. 1a). Taken together,

taxonomic diversity represented by SR, Pielou and Shannon-Wiener index collectively contributed 43.78% to the RF model for aboveground biomass, while phylogenetic diversity represented by PD (including MNTD and MPD) and functional diversity represented by FRic (including FDiv, FEve, FDis and RaoQ) contributed 30.02% and 26.2%, respectively (Fig. 1b).

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

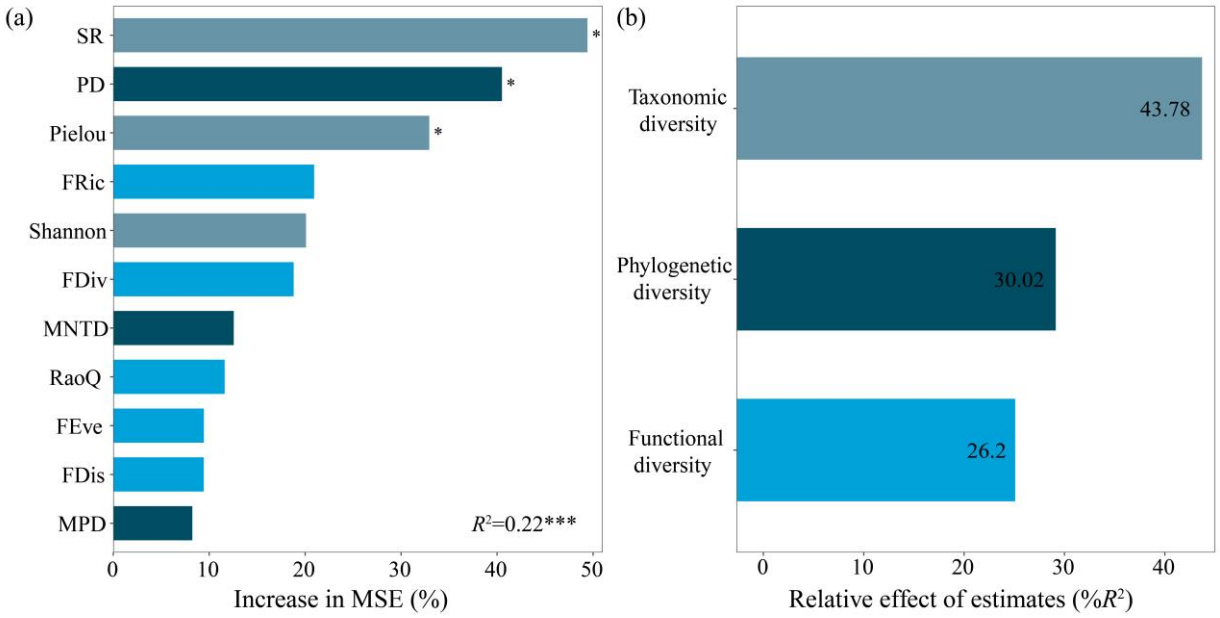

Fig. 1 The importance (a) and relative contributions (b) of the three dimensions of biodiversity to community biomass. An increase in MSE denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

3.2 Paleoclimate and present climate predictors of contemporary diversity

Random Forest models explained 35% (cross-validation $R^2 = 0.35$, $P < 0.001$), 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) and 31% (cross-validation $R^2 = 0.31$, $P < 0.001$) of the variance in SR, PD and FRic, respectively (Fig. 2). Temperatures in different periods, including MAT_{mid}, MAT and MAT_{lgm}, were the main factors driving SR and PD ($P < 0.05$, Fig. 2a and 2b), followed by climate anomalies

in various periods. However, the current climate (i.e., AI, MAT and MAP) had a stronger impact on FRic ($P < 0.05$, Fig. 2c).

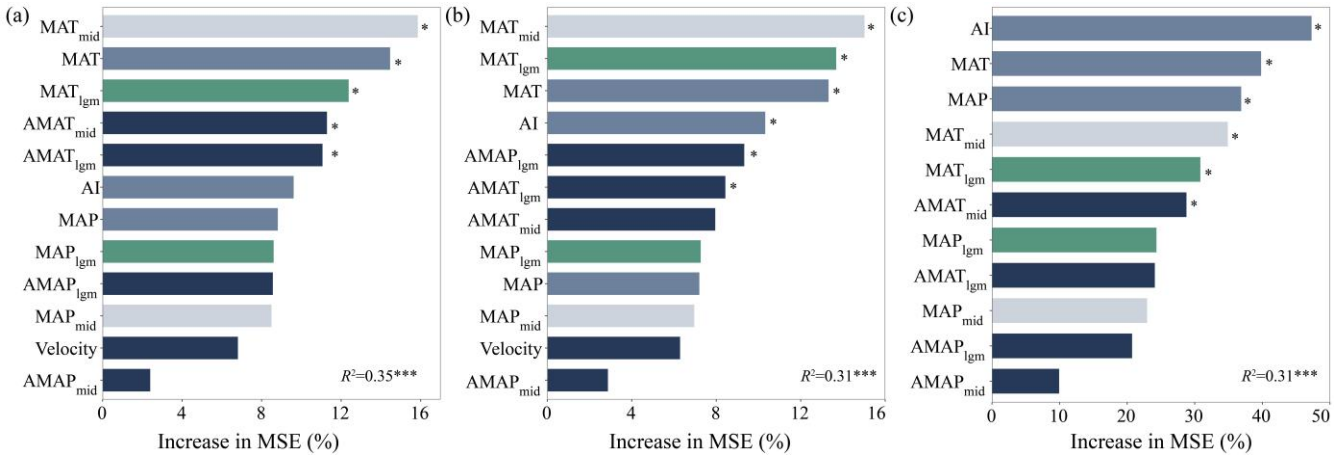

Fig. 2 The importance of climate variables in different periods and paleoclimate change to species richness (a), phylogenetic diversity (b) and functional richness (c). An increase in MSE denotes an increase in the percentage mean square error. Significance levels are as follows: *: $P < 0.05$ and ***: $P < 0.001$.

In terms of relative contributions, the current climate and the paleoclimate changes had greater impacts on the three dimensions of biodiversity. Paleoclimate change was the best predictor of SR (33.90%) and PD (32.10%). Strikingly, the present climate (38.68%) showed a larger contribution to the prediction of FRic than paleoclimate change (26.06%; Fig. 3).

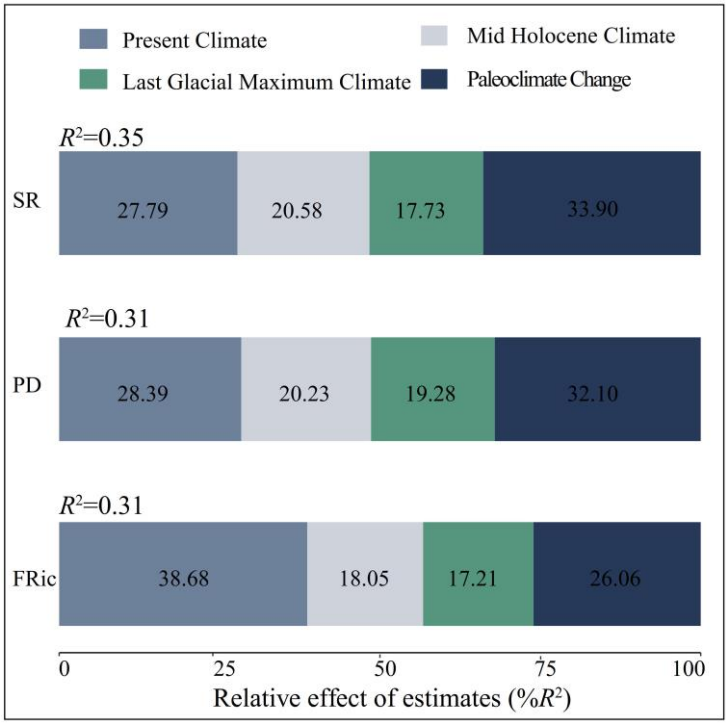

Fig. 3 Relative contributions of present ~~climate, paleo -~~ (mid-Holocene ~~and~~ Last Glacial Maximum~~)~~ and paleoclimate change as drivers of species richness, phylogenetic diversity and functional richness.

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_∂ = 0.46, P < 0.05), PD (r_∂ = 0.35, P < 0.05) and FRic (r_∂ = 0.58, P < 0.05, Fig. 4). However, the paleoclimate change had direct significant negative effects on SR (r_∂ = -0.28, P < 0.05), PD (r_∂ = -0.32, P < 0.05) and FRic (r_∂ = -0.25, P < 0.05, Fig. 4).

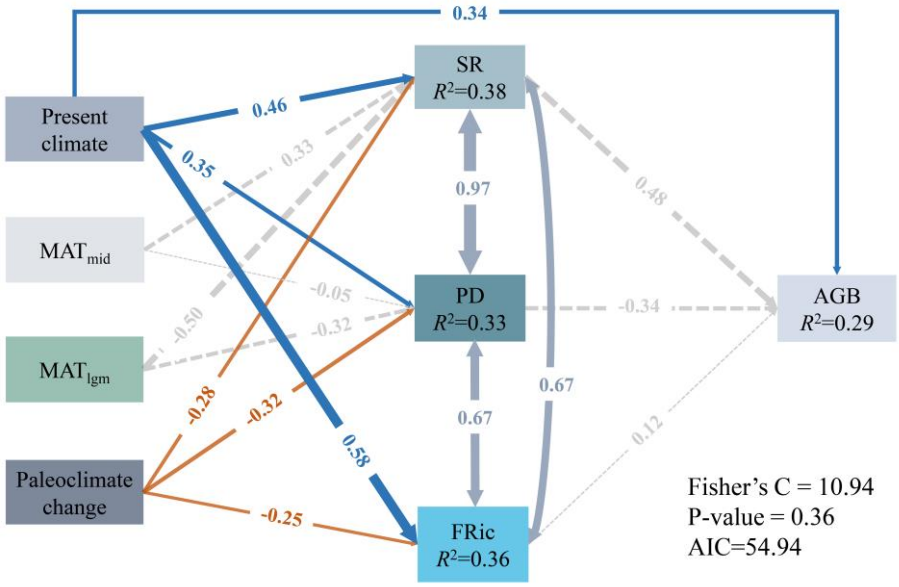

Fig. 4 SEMs fitted to the effects of climate in different periods and paleoclimate change on diversity and AGB. The present climate is PCA component 1 of the AI and MAT. The paleoclimate change represents a composite variable including MAT anomaly from the Mid-Holocene to the present, MAT and MAP anomaly from the Mid-Holocene to the present. Numbers adjacent to arrows represent the standardized path coefficients (r_∂). R^2 indicates the proportion of variance explained. Blue (positive paths) and orange (negative paths) solid arrows indicate significant paths ($P < 0.05$), and gray dashed arrows indicate non-significant paths ($P > 0.05$).

For the present climate, the direct effects of AI on SR ($r_\partial = 0.33$, $P < 0.05$), PD ($r_\partial = 0.27$, $P < 0.05$), FRic ($r_\partial = 0.49$, $P < 0.05$), and AGB ($r_\partial = 0.37$, $P < 0.05$) were all significantly positive, while the direct effects of MAT on the three dimensions of biodiversity (SR, $r_\partial = -0.34$; PD, $r_\partial = -0.36$; FRic, $r_\partial = -0.29$; $P < 0.05$ in all cases) were all significantly negative (Fig. 5). In addition, SR ($r_\partial = -0.25$, $P < 0.05$) and PD ($r_\partial = -0.25$, $P < 0.05$) were negatively affected by MAT anomaly from the Mid-Holocene to the present ($AMAT_{mid}$), but FRic ($r_\partial = -0.23$, $P < 0.05$) was mainly driven by MAT anomaly from the Last Glacial Maximum to the present ($AMAT_{lgm}$; Fig. 5).

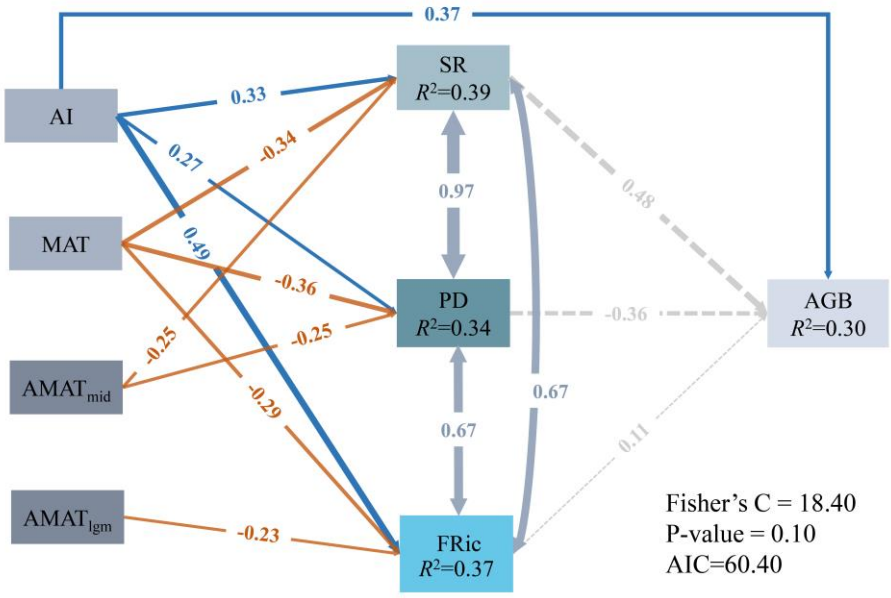

Fig. 5 The effects of present climate (AI and MAT) and paleoclimate change ($AMAT_{mid}$ and $AMAT_{lgm}$) on diversity and AGB. Numbers adjacent to arrows represent the standardized path coefficients. R^2 indicates the proportion of variance explained. Blue (positive paths) and orange (negative paths) solid arrows indicate significant paths ($P < 0.05$), and gray dashed arrows indicate non-significant paths ($P > 0.05$).

4. Discussion

4.1 The effects of different dimensions of biodiversity on aboveground biomass

Our research showed that, without considering the influence of climatic conditions, taxonomic diversity was the most important factor influencing the aboveground biomass of Mongolian Plateau grasslands, followed by phylogenetic diversity and functional diversity. However, a large number of studies have emphasized the importance of phylogenetic diversity and functional diversity 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

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

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

4.2 Relationship between paleoclimate anomalies and current biodiversity patterns

Although a rich body of research has explored the factors affecting biodiversity patterns and their relationships with biomass, further studies are still needed. Here, our results showed that paleoclimate changes and present climate factors were critical variables influencing contemporary biodiversity patterns. This illustrates the importance of historical factors, such as evolution, as well

as contemporary factors, such as climate, in determining the geographic ranges of species and the accumulation of species in the region (Fine, 2015). Previous studies aiming to explain patterns of biodiversity have focused on the current climate (Harrison et al., 2015), energy (Kreft and Jetz, 2007), soil attributions (Ulrich et al., 2014), human activities (Hautier et al., 2015; Newbold et al., 2015) or water availability (Jiao et al., 2021; Liu et al., 2021). Modern climate research on biodiversity and ecosystem functions has been widely confirmed (Yang et al., 2011; Liu et al., 2021; Walther et al., 2002), but our research shows that the pattern of biodiversity is also affected by past climates, and especially climate change in a region. Paleoclimate changes filtered the regional species pool based on climate-related traits, which in turn affected contemporary biodiversity patterns.

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

Phylogenetic diversity (PD) is usually used to quantify the uniqueness of a region's evolution. Our research showed that PD was negatively correlated with MAT and temperature anomalies in the 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

part of the Mongolian Plateau, the interval of 35230 to 25150 yr B.P. was a forest-steppe landscape under humid conditions, represented by Pinaceae, Compositae and Chenopodiaceae (Tian et al., 2017). Subsequently, the forest patches gradually shrank, the vegetation transitioned to the steppe landscape, and drought began to intensify. During the Last Glacial Maximum period, the vegetation types on the Mongolian Plateau were mainly ~~polar and alpine deserts and temperate deserts~~ (Ray and Adams, 2001), and the main plants were Compositae and Chenopodiaceae. By the Holocene, xerophytes had declined sharply, and plants of humid climates had increased. The humidity increased during the early Holocene, and generally humid conditions lasted from 10,400 until 7000 yr BP and the region experienced the Lavliakan humid phase (Lioubimtseva, 2004; Yin et al., 2011), with more hygrophilous species, such as Cyperaceae (Tian et al., 2017). This climate condition was also conducive to the development and spread of Compositae and Gramineae families in the steppes of Central Asia (Lioubimtseva, 2004). Since approximately 5200 yr BP to present, the climate has become more arid, with corresponding vegetation change and strong aeolian activity (Yin et al., 2011). Furthermore, palaeoecological and archaeological evidence shows that people have shaped most of terrestrial nature for at least 12,000 years, including burning, hunting, cultivation and domestication (Ellis et al., 2021). In the Mongolian Plateau, especially in the Inner Mongolia region of northern China, grazing appeared at ~5.7–5.5 ka and further intensified again after ~4.2–4.0 ka (Huang et al., 2021). The intensification of grazing activities also causes changes in biodiversity.

As far as aboveground biomass is concerned, after taking into account climatic factors, it is mainly directly affected by aridity index, while the three dimensions of biodiversity have no significant impact on it, which is consistent with our previous research (Li et al., 2020). Paleoclimate changes also have no direct effects on aboveground biomass, which indirectly affects aboveground

biomass through regulating biodiversity.

5. Conclusion

We conclude that unique evolutionary and ecological histories played key roles in explaining biodiversity patterns in the Mongolian Plateau. When climatic conditions are not considered, taxonomic diversity, phylogenetic diversity and functional diversity all have effects on community biomass, and taxonomic diversity has a more obvious impact on biomass. However, the climate after the Last Glacial Maximum has left a strong legacy affecting contemporary biodiversity patterns. These findings extend our understanding of the spatial and temporal scale of climate effects on biodiversity and aboveground biomass, providing additional confidence that the paleoclimate had a key role in shaping contemporary biodiversity patterns.

Authors' Contributions

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

Data available

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

Conflict of interest statement

The authors declare that they have no conflict of interest.

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