Negative diversity–productivity relationships in grasslands are constrained by climates and stoichiometry along an elevational gradient

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Abstract

The diversity–productivity relationship in grasslands is predominantly positive but also highly variable because of its complex influencing mechanisms in natural ecosystems. In this study, we investigated plant diversity, biomass, and associated drivers (e.g., climate, soil, and plant traits) along an elevational gradient in grasslands in southwest China. Grassland biomass decreased significantly, but grassland diversity increased with increasing elevation. Consequently, a significant negative relationship between grassland biomass and diversity was detected along the elevational gradient. We also observed that the negative relationship was primarily driven by climatic factors (i.e., temperature and precipitation) and plant stoichiometric traits (i.e., phosphorus limitation) rather than by soil properties at a regional scale. This is inconsistent with previous studies on the positive diversity–productivity relationship, which might weaken the effects of climatic factors at the regional scale. Our results revealed that the negative relationship between diversity and productivity in grasslands was shaped by the combined effects (climate and plants) on productivity and diversity in grasslands.

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Abstract

The diversity–productivity relationship in grasslands is predominantly positive but also highly variable because of its complex influencing mechanisms in natural ecosystems. In this study, we investigated plant diversity, biomass, and associated drivers (e.g., climate, soil, and plant traits) along an elevational gradient in grasslands in southwest China. Grassland biomass decreased significantly, but grassland diversity increased with increasing elevation. Consequently, a significant negative relationship between grassland biomass and diversity was detected along the elevational gradient. We also observed that the negative relationship was primarily driven by climatic factors (i.e., temperature and precipitation) and plant stoichiometric traits (i.e., phosphorus limitation) rather than by soil properties at a regional scale. This is inconsistent with previous studies on the positive diversity–productivity relationship, which might weaken the effects of climatic factors at the regional scale. Our results revealed that the negative relationship between diversity and productivity in grasslands was shaped by the combined effects (climate and plants) on productivity and diversity in grasslands.

Keywords: biomass, climates, diversity, elevational gradient, grasslands, stoichiometry.

Introduction

The diversity–productivity relationship is fundamental for understanding and predicting the impact of biodiversity on ecosystem functions and services (Isbell *et al.* 2011; Fraser *et al.* 2015; Pan *et al.* 2022). Diversity–productivity relationships have been studied globally across various ecosystems, including tropical forests (Poorter *et al.* 2015), temperate forests (Chisholm *et al.* 2013), shrubs (Chen *et al.* 2018), and grasslands (Ladouceur *et al.* 2022). These studies propose a positive diversity–productivity relationship predominant in plant communities worldwide, implying that high diversity could promote productivity. However, the diversity–productivity relationships in grasslands show divergent patterns, including positive linear (Bai*et al.* 2007), positive nonlinear (Craven *et al.* 2016), unimodal (Fraser *et al.* 2015; Wang *et al.* 2022), and neutral patterns (Adler *et al.* 2011). Thus, understanding the realistic relationships and mechanisms underlying these observed divergent patterns is important for accurately predicting how diversity influences productivity in natural ecosystems under environmental changes.

Inconsistent diversity–productivity relationships are mainly determined jointly and/or solely by a wide array of drivers, including climate, plants, and soil properties (Hawkins *et al.* 2003; Hautier*et al.* 2009; Grace *et al.* 2016; Kimmel *et al.*2020). Rising temperatures can alter species interactions leading to biodiversity loss and improper ecosystem functioning (García *et al.* 2018). Precipitation also mediates the strength of the diversity–productivity relationship by changing water availability and soil moisture in steppe grasslands (Hossain & Beierkuhnlein 2018; Li*et al.* 2020). Changes in environmental factors (elevation, temperature, and precipitation) can increase environmental heterogeneity, which modulates the effects of plant diversity on the productivity variability of grasslands (Stein *et al.* 2014; Daleo*et al.* 2023). Productivity and biodiversity in grasslands are also mediated by soil properties, such as soil aridity, pH, and chemical constituency, which can affect the diversity–productivity relationships, likely by changing plant growth parameters and species composition (Ceulemans *et al.* 2013; Palpurina *et al.* 2017; Kimmel *et al.* 2020). Furthermore, several experiments on nitrogen (N) addition to grasslands have indicated that soil nutrient enrichment significantly increases community biomass but decreases community diversity (Hautier *et al.* 2009; Harpole *et al.* 2016; Seabloom *et al.* 2021).

Plant stoichiometry usually modulates nutrient limitation and utilization for plant growth (Allen & Gillooly 2009; Sperfeld *et al.* 2017). Plant nitrogen, which is a protein component, plays a role in plant biomass production and litter decomposition (Yang *et al.*2018; Yu *et al.* 2020), whereas phosphorus (P) is coupled with C and N and linked to biological processes such as photosynthesis and growth (Delgado-Baquerizo *et al.* 2013; He *et al.* 2020). Plant stoichiometry is associated with soil stoichiometry, which directly regulates plant biomass production by changing soil nutrient availability, and hence indirectly mediates plant community diversity by adjusting plant interspecific interactions (e.g., plant coexistence and competition) (Striebel *et al.* 2009; Ning *et al.* 2021; Gerhard *et al.* 2022). Moreover, climatic factors affect the diversity–productivity relationships by indirectly controlling plant stoichiometry(Dijkstra *et al.* 2012; Yu *et al.* 2015; Qin*et al.* 2022). Some studies have shown that foliar N and P content generally decreases with increasing mean annual temperatures and precipitation (Tang *et al.* 2018). However, the stoichiometric responses to climate differ substantially between plant species. For instance, a global analysis reported that foliar N and P in birch*(Betula)* increased, but foliar N and P in grass*(Calamagrostis)* decreased with increasing temperature (Reich & Oleksyn 2004). In addition, some studies have reported that climate has a weak effect on plant stoichiometry, but there is a significant elevational trend with the C:N and C:P ratios decreasing with elevation (Yang *et al.* 2015). While most studies on the diversity–productivity relationship have focused on one or two specific variables, they ignored the intermixed effects of climate, soil, and plants.

Southwestern China is regarded as a global biodiversity hotspot because of its distinct environmental gradients and complex geomorphological features along its elevational gradients (Rahbek *et al.* 2019). The high diversity and diversity–productivity relationships of grasslands in this region are more sensitive to climate along elevational gradients (Mumbanza *et al.* 2021b). Elevational gradients are considered open-air laboratories where we can investigate natural ecosystem responses to long-term climate change (Malhi *et al.* 2010). Thus, a survey of diversity–productivity relationships in grasslands along elevational gradients could assist in evaluating the underlying mechanisms of plant growth, soil nutrients, and their interactions under changing climatic conditions (Mumbanza *et al.*2021b). Here, we explored the patterns of diversity–productivity relationships and associated drivers (i.e., climatic factors, soil properties, and plant traits) based on intensive field data collected along an elevational gradient in the grasslands of southwest China. Our study was designed to address the following questions: (a) How do plant diversity, biomass, and their relationships in grasslands vary with elevational gradient? (b) How do abiotic factors (i.e., climatic factors and soil properties) and biotic factors (plant nutrients) jointly and/or solely affect the diversity and biomass of grasslands? We hypothesized that plant diversity and grassland biomass would increase with increasing elevation, possibly due to changes in temperature and precipitation, and that a positive relationship between diversity and productivity would be observed along climatic gradients. We hypothesized that plant and soil factors would have a significant positive impact on diversity and productivity, owing to nutrient (N and P) resource limitations, despite the effects of climate change (Striebel *et al.* 2009; Yu *et al.* 2020).

Methods and materials

Study area and field sampling

We set up a grassland transect ([?]1,000 km length) across southwest China along an elevational gradient range from 40–3800 m (Fig 1). The mean annual temperature (MAT) ranged from 7.6–23.6 degC, mean annual precipitation (MAP) ranged from 730–1760 mm. MAT and MAP were closely related to elevational gradients (MAT, $R^2 = 0.74$, $p < 0.001$; MAP, $R^2 = 0.28$, $p < 0.001$; Fig S1). The main vegetation types along the grassland transect were subtropical and temperate montane. Soil types mainly consist of Acrisols, Luvisols, and Cambisols (World Reference Base 2006).

During the 2021 growing season, 98 field sites were surveyed along the transect. For each site, a 30 m x 30 m quadrat was constructed, inside which six sub-plots (1 m x 1 m) were selected and investigated in the center and four corners (only three 1 m x 1 m plots in the quadrat for some sites). In total, 546 plots were investigated. The geographical coordinates and elevation of each site were recorded using a global positioning system (GPS).

Plant biomass, diversity, and plant traits

All species in the plots were recorded, and all ground-level plants were grouped by species and were harvested and stored in the envelopes. Aboveground vegetation was weighed using live biomass and then oven-dried to a constant weight at 65 degC to weigh the dry biomass for further analyses. Two or three dominant plant species were selected from each site and sealed in a paper envelope to measure the foliar element content. The Shannon-Wiener index, Simpson index, and species richness (SR) were calculated as measures of community biodiversity at the plot and site scales. Species richness (number of species/m^2) at each site was calculated as the average number of species in each plot. The community biodiversity index was calculated by the "vegan" package in R (Dixon 2003). Three topsoil samples (0–10 cm depth) were collected with a 7 cm auger in each site, then sealed in plastic bags and stored at -20 for further analysis.

Leaf C content, N content, and $\delta\ ^{13}C$ were measured using an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher Scientific, Waltham, MA, USA) connected to an elemental analyzer (Flash 2000 EA-HT, Thermo Fisher Scientific). Leaf P content was determined using the molybdate/stannous chloride method after H_2SO_4–H_2O_2digestion (Kuo 1996), and the extraction solution was analyzed using an automated discrete analyzer (DeChem-Tech GmnH Inc. Hamburg, Germany).

Soil properties

Soil samples were air-dried and homogenized using a 2 mm sieve, and the visible roots and small stones were removed for further measurements. Soil organic carbon (SOC) and soil total nitrogen (STN) were determined using an elemental analyzer (Vario EL, Elementar Analysensysteme GmbH, Langenselbold, Germany) after the removal of soil carbonates using 1N HCl for 24 h. Bulk density was determined using 5-cm-diameter soil cores. Soil pH and clay content were extracted from a global compilation of the soil profile database (*https://soilgrids.org/*). The dominant herbaceous leaves were oven-dried at 60 ºC for 48 h to achieve constant weight, after which they were weighed and ground using an ultra-centrifugal mill (JXFSTPRP-32, JingXin, China).

Climatic data collection

Mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) data at a resolution of 30 arcseconds were obtained from the WorldClim database (*http://www.worldclim.org*). Elevation data were extracted from the shuttle radar topography mission database (SRTM) (*https://srtm.csi.cgiar.org*) with a 30-arcsecond resolution based on the geographical coordinates of the sites. The extracted analysis was performed using the "geodata" R package.

Statistical analysis

Linear regression models generally explore the relationships between climatic factors, community diversity, and biomass. Linear and quadratic functions were fitted to the diversity–productivity relationships across plots and site levels. Model comparisons were performed based on the explained variance and the significance of the corresponding coefficients (slope and quadratic terms). Variation partitioning analysis (VPA) was conducted to test the contribution of climates, plants, and soils to diversity and biomass using the "vegan" package in R. The Random Forest (RF) algorithm using the "randomForest" package, was used to detect the relative importance of predictors selected to explain variations in the diversity and biomass. One-way analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) multiple comparison test ($p<0.05$) were used to evaluate the statistical significance of diversity, biomass, and leaf stoichiometric properties at different elevations. Structural equation modeling (SEM) using the "piecewiseSEM" package was used to clarify the direct and indirect effects of climates, soils, and plants on the community biomass and diversity by. All statistical analyses were performed using R software v.4.2.1 (R Core Team, Vienna, Austria; URL: https://www.Rproject.org/).

Results

Variations in biomass and diversity along climatic gradients

Grassland biomass decreased significantly ($p<0.001$) with increasing elevation (Fig. 2 a), whereas it increased with increasing MAT and MAP (Fig. 2 b, c). For plant diversity, the Shannon diversity index significantly increased with elevation and decreased with MAT ($p<0.001$) (Fig. 2 d, e); however, there was no significant change with MAP ($p>0.05$) (Fig. 2f). We detected a negative relationship between grassland biomass and plant diversity, including the Shannon diversity index (slope = -210.67, $p<0.01$), Simpson diversity index (slope=-493.00, $p<0.01$), and species richness (slope = -48.33, $p<0.01$) (Fig. 2 g-i). However, we observed that both delta biomass and delta elevation were significantly and positively correlated with Bray–Curtis dissimilarity values (β diversity, $p < 0.001$) (Fig. 3 a, b)

Shifts in plant and soil stoichiometric traits along elevational gradients

Along the transects, grass biomass responded differently to increasing elevations in terms of foliar and soil stoichiometric traits. In particular, no significant correlations of leaf C and P content with elevational gradients were found (Fig. 4 a, c), whereas leaf N content exhibited a notable positive trend with increasing elevation ($p < 0.001$; Fig. 4 b). The leaf C:N ratio decreased with increasing elevation (slope=-0.003, $p<0.001$; Fig. S2a). In addition, relatively weak upward and downward trends were observed in the leaf N:P and leaf C:P ratios, respectively. (Fig. S2 b, c). The leaf C:N ratio showed a significantly positive relationship with biomass, and leaf C:P and N:P ratios were strongly negatively correlated with biomass (Fig. 4 d, e, f), and in contrast to the weak effect of elevation on plants, both soil C and N exhibited extensive upward trends with increasing elevation ($p<0.001$; Fig. S3 a, b), whereas there was no significant effect of elevation on the soil C:N ratio (Fig. S3 c).

Drivers of diversity–productivity relationships in grasslands

Variation partitioning analysis (VPA) evaluated the contributions of climate, plants, and soil to grassland biomass and diversity (Fig. 5). Climatic variables explained the greatest variation in biomass (16%), followed by plants (10%), soils/climates (5%), and climates/plants (4%) (Fig. 5a). Similarly, climatic variables were the most important factors, explaining 11% of the grassland diversity (Fig. 5b). It was observed that the plant biomass positively correlated with the MAT, MAP, and leaf P contents, but negatively correlated to the elevation, leaf N:P ratio (Fig. S5). In contrast, plant diversity was negatively correlated with MAT and leaf N:P and positively correlated with elevation, MAP, and leaf P content (Fig. S5).

The RF algorithm further revealed that climatic factors such as elevation, MAT, and MAP and plant variables such as leaf P and diversity were important drivers of biomass with a relative importance of 16.01%, 13.31%, 11.14%, 9.83%, and 8.77%, respectively (Fig. 6 a). With respect to plant diversity, elevation, MAT, BD, MAP, and STN were the most important drivers accounting for 10.64%, 10.51%, 9.81%, 7.76%, and 6.63% of relative importance, respectively (Fig. 6 b). SEM analysis also indicated that climatic gradients were key factors constraining both grassland biomass and diversity, with direct/indirect effects on the grass community and relevant soil and/or plant properties (Fig. 7).

Discussion

In this study, we investigated the relationships between grass diversity, aboveground biomass, and associated drivers based on intensive field plot datasets along an elevational gradient in the grasslands of southwestern China. Our results showed a negative relationship between grassland biomass and plant diversity along the elevational gradient, which was in contrast to our hypothesis, and the prevailing view showed that plant diversity tends to exert a positive effect on plant biomass (Grace*et al.* 2016; Chen *et al.* 2018). We found that the negative diversity–productivity relationship in grasslands was largely constrained by the climate and stoichiometry in the study region.

Notable climatic gradients (MAT and MAP) were observed in the field plot dataset (Fig S1). We found a significant negative relationship between elevation and biomass and a positive correlation between MAT, MAP, and biomass (Fig 2). We detected opposite patterns for plant diversity, showing that diversity was positively related to elevation and negatively related to MAT and MAP (Fig 2). These results suggest that the impact of diversity on community biomass is a response to environmental stress and that plant diversity and biomass are simultaneously regulated by environmental factors (Loreau*et al.* 2001; Steudel *et al.* 2012; Wang *et al.*2022). Furthermore, we found that delta biomass and delta elevation were significantly positively correlated with Bray–Curtis dissimilarity values (β diversity, Fig 3), implying that the environmental heterogeneity caused by climatic gradients might be the key factor in explaining the variability in biomass and diversity (Stein *et al.*2014; Qiao *et al.* 2022; Daleo *et al.* 2023). For instance, we found higher diversity but lower biomass in the highlands owing to environmental heterogeneity caused by notable changes in elevation and environmental stress limited by lower temperature and precipitation (Fig 8). This evidence further underpins that the relationship between diversity and grassland biomass is strongly controlled by environmental gradients (Lundholm 2009; Daleo *et al.* 2023).

Another possible explanation for our results is that shifts in ecological stoichiometric characteristics along elevational gradients may also affect the relationship between diversity and community biomass. We found that plant stoichiometric factors were the second most important variable explaining the variation in biomass production (Fig 5,6), supported by the significantly positive relationships of leaf C:N with biomass and the negative correlations of leaf C:P and leaf N:P with biomass (Fig 4). The stoichiometry variation could result from nutrient limitation and nutrient-use strategies along elevational gradients (Harpole *et al.* 2011; Palpurina *et al.* 2019). For example, lowlands are usually regarded as high-resource habitats because of their higher temperature, precipitation, and nutrient supply (N and P), which can facilitate the rapid growth of one or two species and contribute to major community productivity. A reverse pattern (high diversity but low biomass) was detected in the highlands, which could result from low resource limitations (e.g., P limitation). In the present study, leaf N content exhibited a notable upward trend with increasing elevation, but there was no remarkable variation in leaf P content, leading to an increase in leaf N:P with increasing elevation (Fig 8). This finding agrees well with previous studies showing that leaf N content increased with elevation, and lower leaf N:P was present in high-elevation areas (Mumbanza *et al.* 2021a; Qin *et al.* 2022). Typically, a higher leaf N:P ratio would reduce plant growth rate and biomass production because a higher growth rate requires more ribosomes and proteins; thus, plants need to produce more ribosomal ribonucleic acid (rRNA) by maintaining a higher P content and lower N:P (Elser *et al.* 1996; Sardans & Peñuelas 2013). Therefore, P limitation is one of the key drivers determining the diversity-biomass relationship in the highlands.

We also found that the effect of diversity on productivity in grasslands was influenced mainly by climatic factors and plant stoichiometry rather than by soil properties (Fig 5,7). This finding suggests that the effect of diversity on productivity changes in response to environmental gradients and that the diversity–productivity relationships are non-uniform because they are easily offset by co-varying environmental factors (Adler *et al.* 2011; Li *et al.* 2020). Many previous studies have reported that patterns of diversity and productivity are dominated by spatial climatic variations (Seddon *et al.* 2016; Jiao *et al.* 2017). For instance, some studies have verified that MAP is a crucial factor regulating aboveground biomass (Guo *et al.* 2012; Hossain & Beierkuhnlein 2018), whereas others have shown that the combined effects of MAT, MAP, and resource availability, predominate the patterns of diversity and productivity (Grace *et al.* 2016; Li *et al.* 2020; Wang *et al.* 2022). However, some studies also pose challenges, showing that diversity continues to have a stronger impact on biomass, outperforming other factors such as climate and nutrient availability (Wu *et al.* 2016; Duffy *et al.* 2017). The inconsistent diversity–productivity relationships could be attributed to research scales and methods. At a community scale or in a control experiment, species interaction may be the principal force for the diversity–productivity relationships and a certain positive diversity–productivity relationship is often observed due to species interaction (e.g., complementarity effect and insurance effect) (Cardinale *et al.* 2007; Isbell *et al.* 2009). At a regional scale or a natural observation, environmental variables would be the key drivers for the patterns of diversity and productivity (Chisholm*et al.* 2013; Li *et al.* 2020). Community-scale manipulative experiments can easily reflect the diversity effect in a plant community owing to certain experimental conditions, whereas the factors that control the diversity–productivity relationships are more complicated at a regional scale (e.g., spatial heterogeneity, human disturbances, and nutrient availability). Therefore, research scales must be considered when explaining inconsistent diversity–productivity relationships, and both experimental and observational investigations must be conducted.

Conclusion

In this study, we explored the relationship between grass diversity and aboveground biomass and the effects of environmental factors on these interactions using data from intensive field plots along an elevational gradient. Our results showed a significant negative relationship between diversity and biomass along an elevational gradient. These negative relationships were mainly driven by climatic factors and plant stoichiometric traits, implying that climatic factors and nutrient limitations caused by environmental gradients determine patterns of diversity and productivity. These results suggest that previous controversies regarding the relationship between diversity and productivity may weaken the impact of climatic factors at regional scales, thus providing new insights into the long-standing debate over the relationship between diversity and productivity. These results would also provide a better understanding of the joint effects of climatic factors, soil properties, and plant nutrient limitations on productivity and diversity in grasslands under climate change.

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