No generality in biodiversity-productivity relationships along elevation in temperate and subtropical forest landscapes

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ABSTRACT

An improved understanding of biodiversity-productivity relationships (BPRs) along environmental gradients is crucial for effective ecosystem management and biodiversity conservation. The *stress-gradient hypothesis* suggests that BPRs are stronger in stressful environments compared to more favorable conditions. However, there is limited knowledge regarding the variation of BPRs along elevational gradients and their generality across different landscapes. To study how BPRs change with elevation, we harnessed inventory data on 6,431 trees from 152 plots surveyed twice in eight to ten year intervals in mountain forests of temperate Europe and subtropical Asia. We quantified the relationship between aboveground productivity and different biodiversity measures, including taxonomic, functional, and phylogenetic diversity. To elucidate the processes underlying BPRs, we studied the variation of different functional traits along elevation across landscapes. We found no general pattern of BPRs across landscapes and elevations. Relationships were neutral for all biodiversity measures in temperate forests, and negative for taxonomic and functional diversity in subtropical forests. BPRs were largely congruent between taxonomic, functional and phylogenetic diversity. We found only weak support for the *stress-gradient hypothesis*, with BPRs turning from negative to positive (effect not significant) close to the tree line in subtropical forests. In temperate forests, however, elevation patterns were strongly modulated by species identity effects as influenced by specific traits. The effect of traits such as community-weighted mean of maximum plant height and wood density on productivity was congruent across landscapes. Our study highlights the context-dependence of BPRs across elevation gradients and landscapes. Species traits are key modulating factors of BPRs and should be considered more explicitly in studies of the functional role of biodiversity. Furthermore, our findings highlight that potential trade-offs between conserving biodiversity and fostering ecosystem productivity exist, which require more attention in policy and management.

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1. Introduction

Forests are a critical component of the Earth's biosphere. They harbor a large proportion of terrestrial species and provide essential ecosystem functions and services to society—such as timber production and climate change mitigation (Pan et al., 2013; van der Plas, 2019)—which are inherently linked to tree productivity. Within regions, productivity can be affected by plant diversity, usually referred to as biodiversity-productivity relationships (hereafter BPRs; Liang et al., 2016; Fei et al., 2018; Qiao et al., 2021). Two mutually non-exclusive mechanisms have been proposed to explain the effect of biodiversity on productivity, niche-complementarity and selection effects (Tilman et al., 1997; Loreau and Hector, 2001). Under niche complementarity, facilitation between species, complementary resource use, and reduction of diseases and pests lead to higher productivity in species-rich stands, linked to functional differences between species such as variations in specific traits (e.g., the difference in shade tolerance) (Finegan et al., 2015; Cadotte, 2017; Bongers et al., 2021). The selection effect arises from the notion that certain functionally important species are more productive than others; as the occurrence probability of these species increases with increasing species richness, higher productivity arises in more diverse stands (Tilman et al., 1997). The selection effect is usually associated with specific traits such as maximum plant height or specific leaf area (Finegan et al., 2015; Cadotte, 2017).

Global studies have suggested an overall positive BPR (Liang et al., 2016). Manipulation experiments have been used to quantify the effects of tree species diversity on productivity under similar environmental conditions (Huang et al., 2018). In mature and managed temperate forests of Europe, positive BPRs have been found and attributed to complementarity effects (Pretzsch and Schütze, 2009; Lu et al., 2016). Similarly, for subtropical forests in China, positive BPRs were reported and likewise attributed to complementary effects (Castro-Izaguirre et al., 2016; Ouyang et al., 2019). However, in addition to positive BPRs also hump-shaped (Fei et al., 2018; Brun et al., 2019), neutral (Staples et al., 2019; Bordin et al., 2023) and even negative BPRs have been observed (Cheng et al., 2018; Fei et al., 2018). How generalizable BPRs actually are across the globe (cf. Liang et al., 2016) thus remains unclear. Site conditions, such as the prevailing climate and soil conditions, have been suggested to contribute to the variation in BPRs (Jucker et al., 2016; Fei et al., 2018). As climate change is accelerating, particularly the effects of climate on BPRs require further attention for effective ecosystem management fostering productivity and biodiversity conservation (Fei et al., 2018; Jactel et al., 2018; Mori et al., 2021).

The *stress-gradient hypothesis* predicts that under increasingly stressful environmental conditions, positive interactions such as facilitation and mutualism will become more common relative to competitive interactions (see Maestre et al., 2009). This suggests that BPRs are more positive in harsh environments, while BPRs are weak or even negative under favorable environmental conditions. Patterns partly consistent with this hypothesis have been reported for climatic gradients at the continental scale, with BPRs intensifying under harsh climatic conditions (Jucker et al., 2016; Fei et al., 2018). However, studying climate effects at the continental scale is challenging, as a number of environmental factors as well as biogeographic history covary with climate. Elevational gradients are thus regularly used to study the effects of climate as they provide steep climatic gradients within a small region (Körner, 2007; Mayor et al., 2017; Peters et al., 2019; Albrecht et al., 2021). Various studies addressed how species or productivity change with elevation (Peters et al., 2019; Luo et al., 2023), but to our knowledge no study has explicitly addressed how BPRs vary across elevational gradients to date. Furthermore, it remains unclear whether BPRs change universally with elevation across different biomes, or whether these changes are contingent on local factors.

Variation in BPRs across studies may also result from different diversity measures being investigated. BPRs have been found to vary depending on whether taxonomic, functional, or phylogenetic diversity is being considered (Brun et al., 2019; Qiao et al., 2021). Taxonomic diversity is most frequently used in BPRs (Jucker et al., 2016; Liang et al., 2016; Fei et al., 2018). However, taxonomic diversity does not account for functional differences between species which can be crucial for ecosystem processes such as productivity (Brun et al., 2019; Qiao et al., 2021). Functional diversity is more directly linked to ecosystem functioning than taxonomic diversity, because it quantifies functional differences or ecological niche preferences among species (Cadotte et al., 2009; Finegan et al., 2015). Likewise, phylogenetic diversity quantifies the evolutionary history of species communities and may encompass cryptic traits that are relevant to ecosystem functioning (Cadotte et al., 2009). Therefore, functional and phylogenetic diversity may be better able to capture important processes underlying BPRs such as niche complementary. To better understand selection effects in the context of BPRs specific plant functional traits are of critical importance (Roscher et al., 2012; Finegan et al., 2015; He et al., 2023), especially those related to competitive ability, growth rate and recruitment of trees. For example, community-weighted mean (CWM) of leaf traits (e.g., specific leaf area) have been found to be important predictors of aboveground biomass increment and carbon sequestration (Finegan et al., 2015).

Here, our objective was to investigate how BPRs in unmanaged forest landscapes change along elevation gradients extending all the way to the upper tree line (i.e., the cold-induced range limit of forest ecosystems), and whether patterns differ between regions with contrasting climates, i.e., temperate Europe and subtropical Asia (Fig. 1). We use forest inventory data, surveyed twice in eight to ten year intervals, to quantify annual aboveground productivity and taxonomic, functional and phylogenetic diversity, addressing the following questions:

(i) Are there significant BPRs within each landscape, and are BPRs consistent across landscapes? We predict a positive relationship between biodiversity and forest productivity across diversity measures (i.e., taxonomic, functional and phylogenetic diversity) within landscapes, but expect weaker BPRs in subtropical compared to temperate mountain forests due to more favorable environmental conditions.

(ii) Do BPRs change with elevation and are the changes consistent across landscapes? We predict that BPRs will be stronger in high-elevation areas close to the tree line compared to low-elevation zones, due to a dominance of facilitation processes among species in harsh environments and a more pronounced niche complementarity effect (i.e., *the stress-gradient hypothesis*). We expect similar changes in BPRs with elevation in the two studied landscapes due to similar gradients of environmental harshness (from relatively few environmental limitations in low-elevation zones to harsh environments at the tree line).

(iii) Do functional traits influence BPRs across elevations and are the same traits affecting BPRs across landscapes? We hypothesized that growth-related traits directly influence productivity and ultimately modulate the elevational change of the BPRs in both landscapes.

2. Materials and methods

2.1. Study landscape and forest plots

Our study contrasts two topographically complex mountain forest landscapes, Berchtesgaden National Park (BNP), located in the northern limestone Alps, Germany (47°32′10″ N, 12°58′33″ E; Fig. 1a), and Yulong Mountain (YMT), part of the Hengduan Mountains in southwest China (27°00′12″ N, 100°10′50″ E; Fig. 1b). These landscapes are located in different climatic zones, i.e., temperate and subtropical, but have otherwise similar characteristics, in particular comparable elevation gradients (ca. 1,150 m of relative distance to the tree line) of continuous and unmanaged mature forests. This setting provides a unique opportunity to investigate the importance of biodiversity on forest productivity
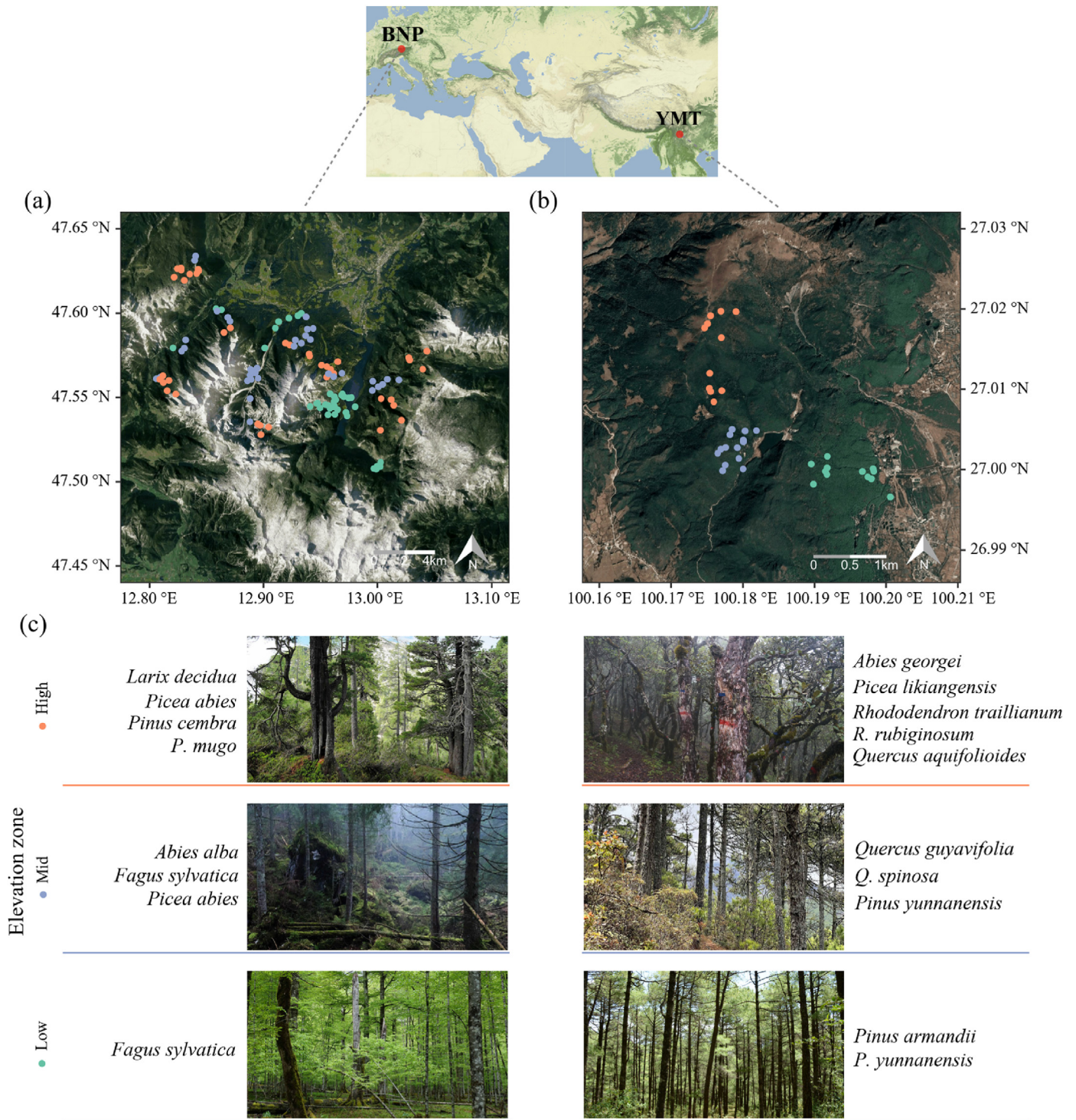
Fig. 1. Location of the two study landscapes and the inventory plots and forest types investigated. (a–b) The distribution of forest plots along the elevation gradients in Berchtesgaden National Park (BNP) in southeastern Germany and in Yulong Mountain (YMT) in southwest China. (c) Typical images of mature forest stands in three elevation zones and their dominant tree species (images of BNP by Rupert Seidl and YMT by Yahuang Luo). Points indicate the location of the inventory plots and colors represent elevation zones: green represents low-, blue mid-, and orange high-elevation forests (relative to the respective landscape-specific tree line). The point positions are slightly shifted when overlapping for improved visibility. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in different climatic conditions and to assess the effect of elevation on BPRs.

Berchtesgaden National Park is characterized by a temperate climate with mean annual temperatures ranging from 4.9 °C to 7.3 °C and mean annual precipitation sums ranging from 1,380 to 2,020 mm (Thom and Seidl, 2022). The low-elevation zone (submontane) is naturally

dominated by European beech (*Fagus sylvatica* L.), while in the mid-elevation zone (montane), mixed forests dominated by beech, Norway spruce (*Picea abies* (L.) H. Karst.) and silver fir (*Abies alba* Mill.) are the main forest type. The high-elevation zone (subalpine) below the tree line (at approximately 1,750 m a.s.l.) is dominated by spruce, European larch (*Larix decidua* L.), Swiss stone pine (*Pinus cembra* L.) and dwarf

3

mountain pine (*Pinus mugo* Turra) (Fig. 1c). Regular forest management ceased in the national park in 1978, but due to former management, the share of spruce is still elevated. A total of 150 forest plots (0.05 ha in size) were selected from a larger systematic forest inventory (Thom and Seidl, 2022), covering an elevation gradient from 605 to 1,726 m a.s.l. (Appendix S1: Table S1). From these, we included 114 plots with forests in mid to late development stage (i.e., establishment, optimum, plenter and terminal stage, sensu Zenner et al., 2016) in our analyses to grant comparability to our second study landscape.

Yulong Mountain is characterized by mean annual temperatures ranging from 4.9 °C to 11.8 °C and mean annual precipitation sums ranging from 1058 to 1621 mm (Luo et al., 2016). The climate is subtropical at low elevations, gradually transitioning into a temperate climate at high elevations. The area is covered by pine forests (*Pinus armandii* Franch. and *P. yunnanensis* Franch.) at low-elevations and mixed forests of pine and oak (*Quercus guyavifolia* H. Lév. and *Q. spinosa* David ex Franch.) at mid-elevations. The high-elevation zone up to the tree line (at approximately 3850 m a.s.l.) consists of mixed forests dominated by oak (*Q. aquifolioides* Rehder & E.H. Wilson*)*, Smith fir (*Abies georgei* Orr), Lijiang spruce (*Picea likiangensis* (Franch.) E. Pritz.) and rhododendrons (*Rhododendron traillianum* Forrest & W. W. Sm. and *R. rubiginosum* Franch., Fig. 1c). A total of 19 study plots (0.1 ha in size) were established in 2013 (Luo et al., 2019), covering an elevation gradient from 2690 to 3835 m a.s.l. (Appendix S1: Table S1). Each plot was divided into two subplots (0.05 ha in size) here, to achieve a consistent sample plot area across both landscapes.

To compare elevation effects between the two study landscapes, we used relative distance to tree line as an indicator. Absolute elevations differed substantially between both landscapes, while the elevational gradient was comparable (ca. 1,150 m), and sampling in both landscapes extended all the way to the tree line. We thus calculated the absolute difference between the elevation of a given plot and the elevation of the tree line in each landscape (hereafter referred to as distance to tree line). To account for potential non-linear changes in BPRs along the elevation gradients resulting from differences in forest types, we grouped plots of each landscape into high-, mid-, and low-elevation zones according to their forest types i.e., 0 to 330 m from tree line, 330 to 800 m from tree line, and 800 to 1,200 m from tree line, respectively.

2.2. Forest inventory data

Two inventories of all sample plots were conducted in both landscapes. At BNP, the first census was conducted between 2010 and 2012 and the second in 2021 (average time interval between censuses 10 years; Thom and Seidl, 2022). At YMT, the first census was conducted in 2013 and 2014 and the second one in 2021 (average time interval of 8 years; Luo et al., 2022). For each census, we identified all individual trees at a plot with a diameter at breast height (DBH) $\geq$ 6 cm to species level. Smaller trees were excluded because they contribute little to forest productivity in mid to late forest development stages. We measured DBH using diameter tape at a tree height of 1.3 m.

2.3. Forest productivity

To quantify aboveground biomass (AGB), we mainly used allometric equations from published sources for YMT (Luo et al., 2020) and BNP (Zianis et al., 2005), while allometric equations for a few rare species were derived from the TRY database (Kattge et al., 2020). We estimated the AGB of each tree individual (including the stem, branch, and foliage compartments) by using species-specific allometric equations (Appendix S1: Table S2) and DBH data from the two censuses. We then applied a conversion factor of 0.5 (Martin et al., 2018) to convert the estimated AGB of each tree to units of aboveground carbon (AGC). We calculated

three plot-level metrics for the analyses: (1) the initial AGC stock from the first census (AGC1; Mg C·ha^{-1}); (2) AGC increment (Mg C·ha^{-1}·y^{-1}) by summing the gain in AGC between censuses of all surviving individuals with DBH $\geq$6 cm in the first census and dividing by the time between measurements; (3) AGC recruitment (Mg C·ha^{-1}·y^{-1}) by summing the AGC of all individuals that recruited into DBH $\geq$6 cm between censuses (i.e., DBH was below 6 cm in the first, but above 6 cm in the second census) and dividing by the time between measurements. Trees present in the first census but not in the second census (i.e., dying trees) were assumed to not contribute to stand productivity and were removed from the dataset. We then calculated total AGC productivity (Mg C·ha^{-1}·y^{-1}) as the sum of AGC increment and AGC recruitment (Yuan et al., 2018).

2.4. Biodiversity measures

We used the data from the initial census in each plot to estimate taxonomic, functional, and phylogenetic diversity. To quantify taxonomic diversity, we used the exponential Shannon entropy index (Jost, 2006), which is a diversity measure that considers both abundance and evenness of species. First, we calculated the Shannon entropy as:

$$H = -\sum_{i=1}^{S} p_i \ln p_i \tag{1}$$

where S is the number of species in the community, p_i is the proportional basal area of species i relative to the total basal area of the community, and ln refers to the natural logarithmic function. We then used the exponent of H (i.e., scaling the maximum to the number of assessed taxonomic groups) as a measure of taxonomic diversity.

To quantify functional diversity, we selected four functional traits (Appendix S1: Table S2): maximum plant height (H_{max}), specific leaf area (SLA), wood density (WD), and seed mass (SM). These traits were selected as they are considered to be important parts of the plant economic spectrum related to competitive ability, growth rate, and recruitment, and thus important for aboveground productivity (Staples et al., 2019). The trait data of BNP species were compiled from the TRY plant trait database (Kattge et al., 2020). For YMT, functional traits were measured according to a standardized protocol (Cornelissen et al., 2003), with full details of trait measurements provided in Luo et al. (2019). We used the trait-based mean pairwise functional distance (MFD) as a measure of functional diversity. We also estimated the community-weighted mean (CWM) of individual trait values (Finegan et al., 2015) using the 'dbFD' function in the 'FD' package (Laliberté and Legendre, 2010) in R. CWM values for each trait were calculated as:

$$CWM = \sum_{j=1}^{S} p_j t_j \tag{2}$$

where S is the number of species in the community, p_j is the proportional basal area of species j in the community, and t_j is the trait value of species j.

To quantify phylogenetic diversity, we first constructed a complete phylogenetic tree for all species recorded across both landscapes, following the method described by Jin and Qian (2022). We applied the 'S.PhyloMaker' function in the 'V.PhyloMaker2' package to generate the required phylogenetic tree for both landscapes (Jin and Qian, 2022). We then pruned the phylogenetic tree for each landscape from the complete phylogenetic tree. Based on the phylogenetic relationships, we estimated the mean pairwise phylogenetic distance (MPD) as a measure of phylogenetic diversity (Tucker et al., 2017). The values of MFD and MPD were calculated using the 'mpd' function in the 'picante' package (Kembel et al., 2010), and both were weighted by the proportional basal area of

tree species. The correlation between functional and taxonomic diversity was 0.71 in BNP and 0.69 in YMT, and the correlation between phylogenetic and taxonomic diversity was 0.57 in BNP and 0.60 in YMT (Appendix S1: Fig. S2).

2.5. Statistical analysis

All analyses were conducted in R 4.1.2 (R Core Team, 2021). To interpret the comparable direction and magnitude of parameter estimates across elevations and landscapes, the predictor variables were z-transformed and response variables were transformed using the natural logarithm. To address the first research question, we used separate linear models for each landscape to examine the overall effects of taxonomic, functional, and phylogenetic diversity on AGC productivity. Specifically, we ran separate models for each diversity measure and landscape, and calculated the corresponding AIC values (Akaike information criterion) and coefficient of determination (R-squared) for each model. We included initial aboveground carbon stocks (i.e., AGC1, see Appendix: Fig. S3 for the detailed information) as a covariate in these models to account for the effects of forest development stage and disturbance history on productivity (Finegan et al., 2015). The model formula used was: 'AGC_productivity ~ AGC1 + diversity_measure'. We then compared BPRs, i.e., the slopes of the three diversity measures, between landscapes.

To address the second question, we first assessed the elevational patterns of productivity and diversity measures in each landscape. We used separate linear models for each landscape with either productivity or one of the three diversity measures as response variable and distance to tree line (continuous variable) as predictor. A quadratic term for distance to tree line was used when the relationships were nonlinear. Then, we assessed whether BPRs change with elevation by testing effects of the different diversity measures on productivity separately for the three elevation zones. Specifically, we modeled productivity as a function of initial aboveground carbon stocks (AGC1), elevation zone (i.e., accounting for variation in productivity among elevation zones), and an interaction between diversity measure and elevation zone (testing whether diversity effects on productivity varied among elevation zones). The model formula was: 'AGC_productivity ~ AGC1 + elevation_zone + elevation_zone: diversity_measure'. We ran separate models for each diversity measure and landscape. The strength of BPRs (slopes and coefficient of determination) was compared for each diversity measure and elevation zone between the studied landscapes. To address the third question, we analyzed elevational patterns of different CWM traits in each landscape. We then used linear models to examine the overall effect

of each CWM trait on productivity across all elevations in each landscape (model formula: AGC_productivity ~ AGC1 + CWM_trait).

3. Results

3.1. Biodiversity-productivity relationships across mountain landscapes

Overall, we found no significant relationship between productivity and taxonomic diversity, functional diversity, and phylogenetic diversity at BNP (Table 1). In YMT, taxonomic and functional diversity had a significant negative relationship with productivity, while phylogenetic diversity had no significant effect on productivity (Table 1). Initial aboveground carbon (AGC1) had significant positive effects on productivity in YMT and marginally significant effects in BNP (Table 1).

3.2. The effects of elevation on biodiversity, productivity and BPRs

With increasing distance to the tree line (i.e., decreasing absolute elevation), productivity showed a unimodal pattern in both landscapes, with lowest values at high elevations close to the tree line, and highest values at intermediate elevations (Fig. 2a and b). While we found a stronger increase in productivity from high to intermediate elevations at BNP, patterns were less clear at YMT, where productivity was similar across high and low elevations (Fig. 2a and b). All diversity measures followed a unimodal pattern over elevation in BNP, with the highest values at low elevations and lowest values at intermediate elevations (Fig. 2c–e, and g). In YMT, all three diversity measures were highest at high elevations and either decreased with increasing distance from tree line in a unimodal way as for taxonomic diversity (Fig. 2d) or linearly as for functional and phylogenetic diversity (Fig. 2f–h).

Testing effects of diversity on productivity separately for each elevation zone in BNP, we only found a marginally significant negative effect of functional diversity ($t = -1.861$, $P = 0.066$) on productivity in the high-elevation zone and a positive effect of phylogenetic diversity ($t = 1.870$, $P = 0.064$) in the mid-elevation zone, but no significant effects of all diversity measures on productivity in any elevation zone (Fig. 3a–c and e; Appendix S1: Table S4). All diversity measures indicated negative, but non-significant BPRs in low- and high-elevation zones, respectively, with positive but non-significant BPRs in the mid-elevation zone of BNP (Fig. 3a–c and e; Appendix S1: Table S4). In YMT, we found a significant negative effect of taxonomic diversity ($t = -2.405$, $P = 0.022$) on productivity in the mid-elevation zone, but not in any of the other zones and no significant effects for functional and phylogenetic diversity in any

Table 1
Results of the linear models for the effects of taxonomic, functional and phylogenetic diversity on productivity, individually for each landscape.

Landscape	Models	Est.	SE	t	P	AIC	R^2
BNP($N = 114$)	(1) AGC1 + Taxonomic diversity					284.01	0.029
	AGC1	0.123	0.069	1.780	0.078		
	Taxonomic diversity	−0.041	0.087	−0.465	0.643		
	(2) AGC1 + Functional diversity					284.11	0.028
	AGC1	0.123	0.069	1.788	0.077		
	Functional diversity	−0.033	0.081	−0.415	0.679		
	(3) AGC1 + Phylogenetic diversity					283.48	0.035
	AGC1	0.118	0.069	1.715	0.089		
	Phylogenetic diversity	0.078	0.078	0.990	0.324		
YMT($N = 38$)	(4) AGC1 + Taxonomic diversity					32.30	0.416
	AGC1	**0.684**	**0.200**	**3.418**	**0.002**		
	Taxonomic diversity	**−0.203**	**0.046**	**−4.410**	**<0.001**		
	(5) AGC1 + Functional diversity					43.85	0.225
	AGC1	**0.583**	**0.229**	**2.545**	**0.015**		
	Functional diversity	**−0.153**	**0.065**	**−2.369**	**0.023**		
	(6) AGC1 + Phylogenetic diversity					48.50	0.130
	AGC1	**0.540**	**0.243**	**2.226**	**0.033**		
	Phylogenetic diversity	−0.070	0.070	−0.994	0.327		

Notes: Table shows the estimates (Est.) and their standard error (SE), the t values (t), associated P-values (P), the corresponding AIC values (Akaike information criterion) and coefficient of determination (R^2) for each model. Estimates with significance with $P < 0.05$ are shown in bold. 'BNP', Berchtesgaden National Park; 'YMT', Yulong Mountain; 'AGC1', initial aboveground carbon stocks.
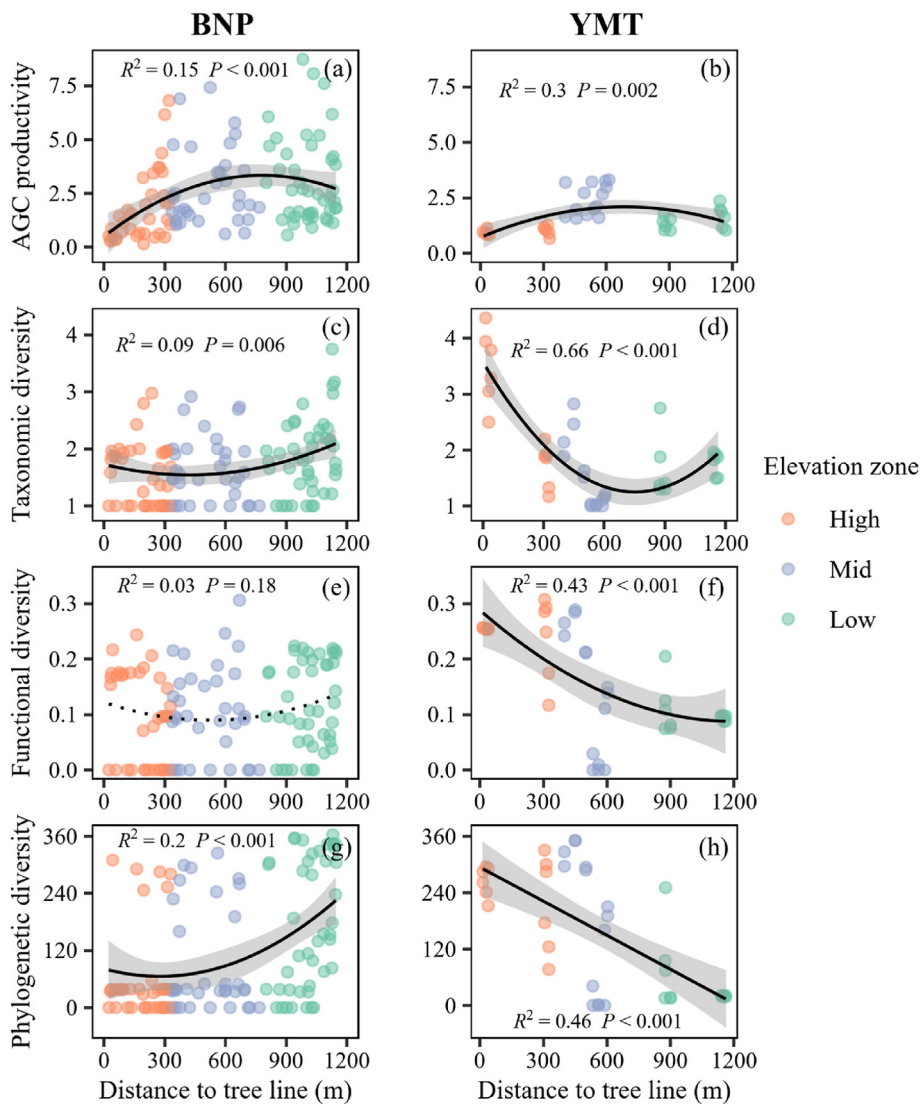
Fig. 2. Change of productivity and biodiversity measures along elevation gradients measured as distance to the tree line. (a–b) Aboveground carbon (AGC) productivity (Mg C·ha^{-1}·y^{-1}), (c–d) taxonomic diversity (exponent of Shannon entropy), (e–f) functional diversity (mean pairwise functional distance), (g–h) phylogenetic diversity (mean pairwise phylogenetic distance). Colored points showed different elevation zones: green represents the low-elevation zone (Low); blue represents the mid-elevation zone (Mid); orange represents the high-elevation zone (High). Solid lines represent significant relationships ($P < 0.05$) and the shaded area indicates the 95% confidence interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

zone (Fig. 3b–d and f; Appendix S1: Table S4). Thus, we found no overall support for stronger and positive diversity effects on productivity at high elevations, but the slopes of BPRs for functional and phylogenetic diversity in YMT were positive in the high-elevation zone, but negative in the mid- and low-elevation zone, yet these effects were not significant (Appendix S1: Table S4).

3.3. Elevational pattern of tree traits and their effects on productivity

With increasing distance to tree line, the CWM of maximum plant height increased in both landscapes (Appendix S1: Fig. S1a and b). At BNP, the CWM of specific leaf area increased with distance to tree line, while in YMT, CWM of specific leaf area showed a decreasing trend (Appendix S1: Fig. S1c and f). CWM of wood density and seed mass showed a concave pattern in BNP (i.e., lowest values at intermediate elevations), while in YMT, CWM of wood density decreased and CWM of seed mass showed a slight upward trend with increasing distance to tree line (Appendix S1: Fig. S1g and j).

In both landscapes, we found a significant positive overall effect of maximum plant height and a significant negative effect of wood density on forest productivity (Fig. 4a, b, e and f; Appendix S1: Table S5). Specific leaf area had a significant negative effect on productivity in YMT, but no significant effect in BNP (Fig. 4c and d; Appendix S1: Table S5). Seed mass had no significant effect on productivity in any of the two

landscapes (Fig. 4g and h; Appendix S1: Table S5).

4. Discussion

We examined biodiversity-productivity relationships (BPRs) for multiple diversity dimensions along elevational gradients in unmanaged, mature temperate and subtropical forests. In contrast to positive BPRs reported by previous studies (Lu et al., 2016; Fichtner et al., 2018; Huang et al., 2018; Qiao et al., 2021), we found either no significant BPRs for our temperate forest landscape, or significant negative BPRs for taxonomic and functional diversity in subtropical forests. Furthermore, when testing whether BPRs change with elevation, we found no support for stronger and positive effects of diversity at high elevations. Across landscapes, we found consistent effects of CWM maximum plant height (positive) and CWM wood density (negative) on forest productivity.

4.1. No evidence for a universal positive biodiversity-productivity relationship

A number of studies have reported positive BPRs in both subtropical forests of China (Castro-Izaguirre et al., 2016; Ouyang et al., 2019) and temperate forests of Europe (Pretzsch and Schütze, 2009; Morin et al., 2011; Lu et al., 2016; Ammer, 2019). The neutral BPRs across diversity dimensions in the temperate mountain forests of BNP as well as the
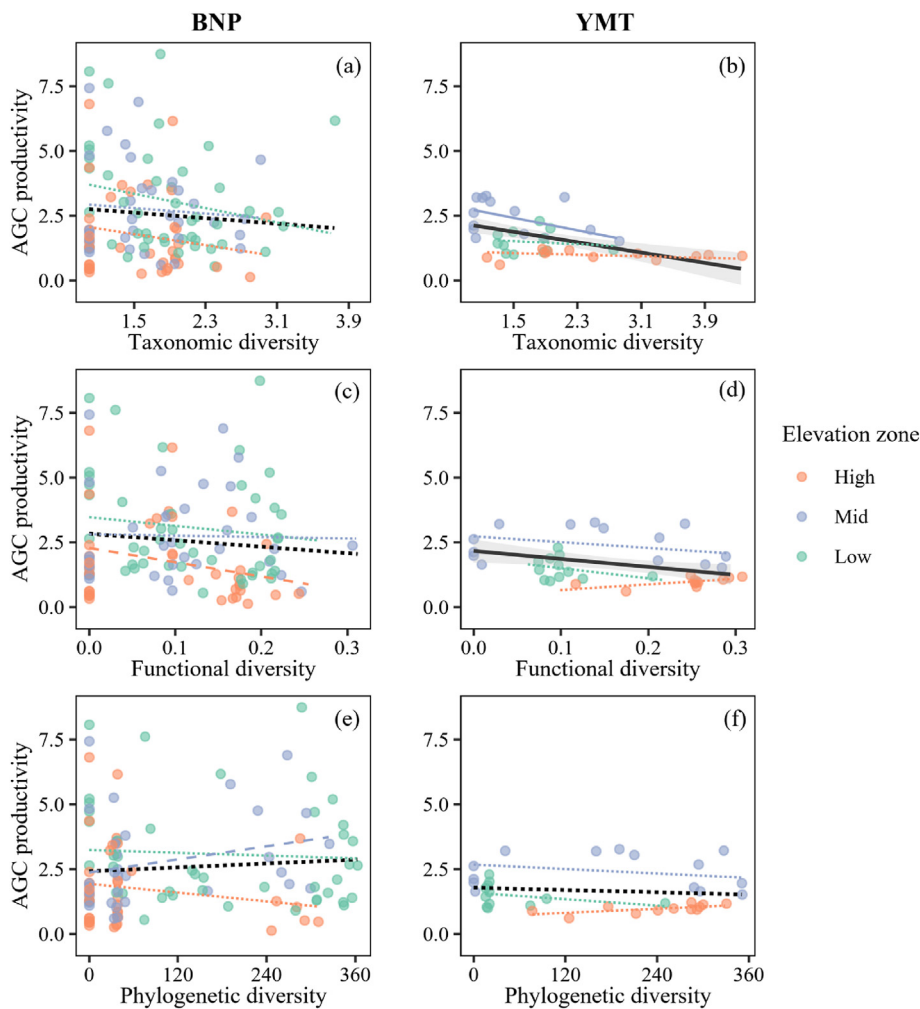
Fig. 3. Biodiversity-productivity relationships across elevation within each landscape. Partial effects curves show relationships between AGC productivity (Mg C·ha^{-1}·y^{-1}) and (a–b) taxonomic (exponent of Shannon entropy), (c–d) functional (mean pairwise functional distance), and (e–f) phylogenetic diversity (mean pairwise phylogenetic distance). Colored points show different elevation zones: green represents the low-, blue the mid-, and orange the high-elevation zone. Black lines represent the overall biodiversity-productivity relationships across all elevation zones from models of Table 1 and are shown for illustrative purposes; shaded area indicates the 95% confidence interval. Solid lines represent significant relationships ($P < 0.05$), dashed lines represent marginally significant relationships ($0.05 < P < 0.1$), and dotted lines represent nonsignificant relationships ($P > 0.1$; see Appendix S1: Table S4 for more details of model results). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

negative overall BPRs for taxonomic and functional diversity in subtropical forest of YMT are thus rather surprising. In contrast to other studies that compared BPRs across sites with similar environmental conditions (Pretzsch and Schütze, 2009; Lu et al., 2016; Fichtner et al., 2018; Huang et al., 2018), our overall BPRs as well as the effects of traits on productivity result partly from simultaneous changes in productivity, tree diversity and trait characteristics along elevation. This was more pronounced in YMT, where low and mid elevations are dominated by pine and oak forests which are characterized by high productivity but low to moderate taxonomic and functional diversity compared to the diverse but less productive forests at high elevations. These simultaneous changes along elevation resulted in the observed negative BPRs at YMT. Moreover, diversity can not only affect productivity, but productivity can also affect diversity, with low productivity leading to less competition between species and thus allowing more species to coexist (Adler et al., 2011). High diversity at high elevation could thus result from a feedback of productivity on biodiversity (Grace et al., 2016; Dee et al., 2023). Future studies should address explicitly how effects of productivity on tree diversity change along elevation gradients.

In BNP, elevational patterns in diversity were weaker, often nonlinear and characterized by high variation within elevation zones. These patterns and the resulting neutral BPRs may be partially explained by legacy effects of former forest management, resulting in higher proportions of Norway spruce also at lower elevations. Norway spruce is one of the most productive species in the area. Consequently, a past human selection effect, i.e., reducing diversity but favoring a productive species, might counteract the complementarity effect found in other studies

(Pretzsch and Schütze, 2009; Lu et al., 2016). This is in line with Shovon et al. (2022), indicating that dominant and more productive tree species influence the direction of BPRs.

One important conclusion of our work is that BPRs vary between landscapes, calling into question that there is a universal global relationship between tree biodiversity and productivity (Liang et al., 2016). A possible explanation for the differences between BNP and YMT could be that the competition for resources may be more intense under more favorable environmental conditions in subtropical compared to temperate mountain forests (Jucker et al., 2016; Fei et al., 2018). However, since our elevation gradients reached the tree line in both landscapes, climatic conditions may only be more favorable in YMT at low elevations. The more likely explanation for the different BPRs in the two landscapes is the contrasting elevational patterns in diversity and traits between both landscapes. Previous analyses of the first inventory from YMT revealed that taxonomic diversity is positively correlated to aboveground tree biomass (Luo et al., 2019). These earlier results and our new findings of negative BPRs together indicate that tree diversity can affect aboveground biomass and productivity differently.

4.2. Weak evidence for the stress-gradient hypothesis

To assess whether the relationship between biodiversity and productivity changes across elevation zones, we tested the effects of different diversity measures on productivity separately for different elevation zones. According to *the stress-gradient hypothesis* (Maestre et al., 2009), BPRs should differ along elevation due to a shift in species interactions
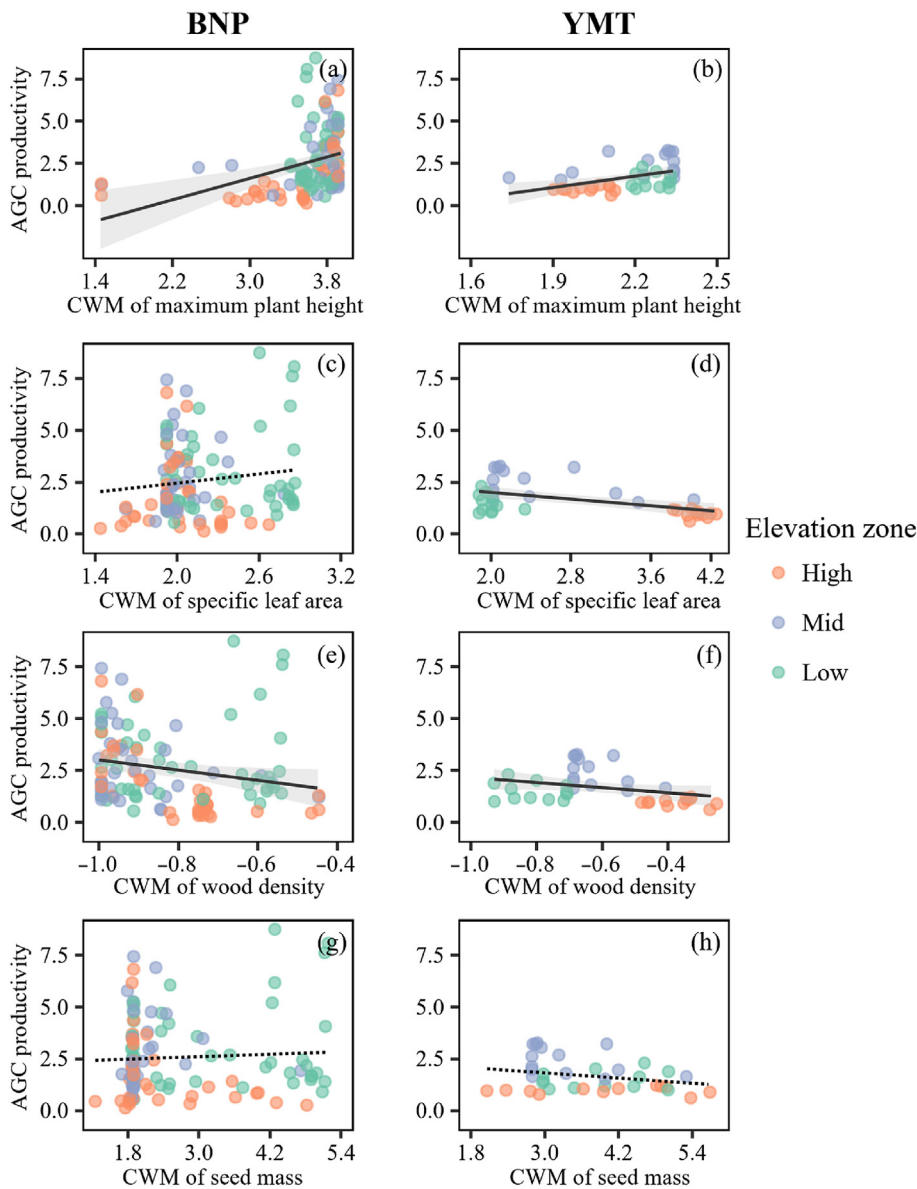
Fig. 4. Effects of community-weighted mean (CWM) of traits on productivity across elevation within each landscape. Effects of (a–b) CWM of maximum plant height (H_{max}), (c–d) CWM of specific leaf area (SLA), (e–f) CWM of wood density (WD), (g–h) CWM of seed mass (SM) on AGC productivity (Mg C·ha^{-1}·y^{-1}). Note that functional traits were transformed by the natural logarithm. Colored points indicate different elevation zones: green represents the low-elevation zone (Low); blue represents the mid-elevation zone (Mid); orange represents the high-elevation zone (High). Solid lines represent significant relationships ($P < 0.05$), and dotted lines represent non-significant relationships ($P > 0.1$; see Appendix S1: Table S5 for more details of model results). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

from competitive exclusion to facilitation (Paquette and Messier, 2011; Jucker et al., 2016), with stronger positive BPRs expected in harsh high elevation areas. Specifically, a few highly productive and competitive species can dominate the community at low elevation due to competitive exclusion. Conversely, under harsh conditions (e.g., high elevation), facilitation favors niche complementarity and promotes positive BPRs. However, we did not find significant support for complementarity effects on productivity neither along the entire investigated elevation gradient nor specifically for high elevations.

The only hint that biodiversity may be more important for productivity at higher elevation in line with the *stress-gradient hypothesis* was found at YMT, where BPRs tended to be negative at low and mid-elevation zones, but positive close to the tree line (albeit not significant). The rather negative BPRs in low elevation forest may be explained by the high competitive ability of pine species (Luo et al., 2022). In contrast, in BNP the strongest positive BPRs (albeit not significant) were found for mid elevation areas. At BNP, high elevation areas are dominated by conifers and low-elevation areas are naturally stocked with broadleaved species, whereas mixed forests of conifer and broadleaved species occur at mid elevations. It is thus in mid elevation areas where complementarity effects may be expected to be most pronounced in BNP

(Pretzsch and Schütze, 2009; Lu et al., 2016), overriding a potential facilitation effect in higher elevation forests.

Another plausible reason why BPRs did not change significantly with elevation is that factors such as soil conditions, topography and soil biota, which influence plant diversity and productivity (Jucker et al., 2016; Fei et al., 2018; Liang et al., 2019; Fahey et al., 2023), may lead to variation between plots independent of elevation, masking elevational patterns in BPRs. Future studies interested in BPRs along environmental gradients should thus explore effects of edaphic factors and soil microbial communities to better understand their generality across different climatic zones.

4.3. Species traits modulate biodiversity-productivity relationships

Previous studies have shown that productivity is modulated by many plant functional traits (see He et al., 2023) in line with a selection effect, such as maximum plant height (Fotis et al., 2018; Luo et al., 2019), wood density (Yuan et al., 2018) and leaf traits (e.g., specific leaf area and leaf nitrogen concentrations etc., Finegan et al., 2015). Productivity is frequently driven by a few tall species in both temperate (Fotis et al., 2018) and subtropical (Luo et al., 2019) forests due to the

disproportional competitive advantage of taller trees in harvesting light (Poorter et al., 2008). In contrast, wood density was generally found to be negatively correlated with productivity, suggesting that trees with low wood density typically grow faster (Yuan et al., 2018; Luo et al., 2019). These trait-based relationships thus modulate BPRs.

Here, we found – consistently across both studied landscapes – a significant positive effect of maximum plant height and a negative effect of wood density on productivity. The effects of community traits may thus mask diversity effects on productivity across elevations. In BNP, for example, the mid-elevation zone was dominated by tree species with the potential to grow taller with lower wood density, which indicates a fast-growing acquisitive strategy typical for species with high productivity. Diversity was, however, lowest in mid elevation areas, which underlines that specific traits may alter general BPRs. Similarly, the low- and mid-elevation zones in YMT are dominated by highly competitive tree species with high growth rates (i.e., relatively lower wood density and higher maximum plant height), leading to reduced species diversity but potentially higher productivity. The species identity and selection effects are thus the likely cause for the neutral to negative BPRs found across our two studied landscapes.

4.4. Implications

An improved understanding of biodiversity-productivity relationships (BPRs) along environmental gradients can help to identify where co-benefits between fostering biodiversity and increasing productivity exist. This has important implications for forest management and conservation practices, and can influence climate change mitigation efforts via nature-based solutions (Jucker et al., 2016; Fei et al., 2018; Mori et al., 2021). Our findings have at least four important implications: First, we did not find strong differences between BPRs using taxonomic, functional, and phylogenetic diversity as biodiversity indicator. This suggests that while functional and phylogenetic diversity are more closely related to the processes underlying BPRs, also taxonomic diversity has indicative value for understanding the effects of biodiversity on ecosystem functioning (Brun et al., 2019; Huang et al., 2020). Second, we did not find robust support for stronger positive BPRs with harsher environmental conditions. Our analysis along a steep elevation gradient thus does not support the notion that the positive role of biodiversity will be amplified under harsher climatic conditions (cf. Morin et al., 2011). Third, we found high variability in BPRs, both between landscapes as well as within landscapes. Our results thus do not support the notion of a universal relationship of biodiversity and productivity in forest ecosystems (cf. Liang et al., 2016). Rather, our analyses point towards species traits as key modulating factors of BPRs. In fact, the effects of key traits, such as maximum tree height and wood density, on productivity were consistent across landscapes and elevation zones, suggesting that trait-based approaches have the potential to yield broadly applicable insights into ecosystem functioning (Roscher et al., 2012; Finegan et al., 2015; Cadotte, 2017). Finally, we did not find support for generally positive BPRs, and rather identified neutral or negative relationships between biodiversity and productivity in temperate and subtropical forest landscapes spanning wide environmental gradients. This suggests that when considering the linkages between conserving biodiversity and fostering the ability of ecosystems to contribute to climate change mitigation (Mori et al., 2021), a more nuanced perspective on the interactions within the biosphere is needed for forest management strategies that, among others, aim to produce woody biomass. Such strategies may not adequately preserve the multifaceted dimensions of biodiversity, including taxonomic, functional, and phylogenetic diversity. Consequently, management practices need to consider local differences in BPRs and incorporate a broader understanding of biodiversity, moving beyond general assumptions of BPRs to address the specific needs and characteristics of each landscape. This is crucial for aligning conservation efforts with the goals of climate change mitigation, emphasizing the need for policies and management practices that recognize the complex trade-offs between conserving biodiversity and fostering ecosystem productivity.

Data availability

The data supporting the findings of this study are available in Figshare at https://doi.org/10.6084/m9.figshare.25470016.

CRediT authorship contribution statement

Jiayun Zou: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Yahuang Luo:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Data curation, Conceptualization. **Rupert Seidl:** Writing – review & editing, Writing – original draft, Resources, Conceptualization. **Dominik Thom:** Writing – review & editing, Methodology. **Jie Liu:** Writing – review & editing, Investigation. **Lisa Geres:** Writing – review & editing, Investigation, Data curation. **Tobias Richter:** Writing – review & editing, Investigation, Data curation. **Linjiang Ye:** Investigation. **Wei Zheng:** Investigation. **Liangliang Ma:** Investigation. **Jie Song:** Investigation. **Kun Xu:** Resources, Investigation. **Dezhu Li:** Resources, Funding acquisition, Conceptualization. **Lianming Gao:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Sebastian Seibold:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100187.

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