



Biodiversity increased both productivity and its spatial stability in temperate forests in northeastern China



Wen-Qiang Gao^a, Xiang-Dong Lei^{a,*}, Mao-Wei Liang^b, Markku Larjavaara^b, Yu-Tang Li^c, Dong-Li Gao^{a,d}, Hui-Ru Zhang^a

^a Institute of Forest Resource Information Techniques, Chinese Academy of Forestry, Key Laboratory of Forest Management and Growth Modelling, State Forestry and Grassland Administration, Beijing, China

^b Institute of Ecology, College of Urban and Environmental Science, Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

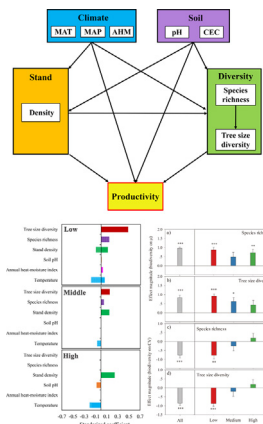
^c Jilin Forestry Inventory and Planning Institute, Changchun, China

^d Planning and Design Institute of the Forest Products Industry of the State Forestry and Grassland Administration, Beijing 100013, China

HIGHLIGHTS

- Biodiversity showed consistent positive effects on productivity and its spatial stability in temperate natural forests
- The intensity of these positive effects decreased with increasing productivity
- Temperature and stand density were also important factors

GRAPHICAL ABSTRACT



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ABSTRACT

Although the relationship between biodiversity and ecosystem functioning has been extensively studied, it remains unclear if the relationships of biodiversity with productivity and its spatial stability vary along productivity gradients in natural ecosystems. Based on a large dataset from 2324 permanent forest inventory plots across northeastern China, we examined the intensity of species richness (SR) and tree size diversity (Hd) effects on aboveground wood productivity (AWP) and its spatial stability among different productivity levels. Structural equation modeling was applied, integrating abiotic (climate and soil) and biotic (stand density) factors. Our results demonstrated that both SR and Hd positively affected AWP and its spatial stability, and the intensity of these positive effects decreased with increasing productivity. At low productivity levels, SR and Hd increased spatial stability by reducing spatial variability and increasing mean AWP. At high productivity levels, stability increased only through mean AWP increase. Moreover, temperature and stand density affected the AWP directly and indirectly via biodiversity, and the strength and direction of these effects varied among different productivity levels. We concluded that biodiversity could simultaneously enhance productivity and its spatial stability in temperate forests, and that the effect intensity was uniform along productivity gradients, which provided a new perspective on relationships within biodiversity—ecosystem functioning.

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* Corresponding author at: Chinese Academy of Forestry, China.
E-mail address: xdlei@ifrit.ac.cn (X.-D. Lei).

1. Introduction

Forests play a crucial role in the terrestrial ecosystem as the most important repositories of biodiversity and components of the global carbon cycle (Houghton et al., 2009; King et al., 2012). However, the role of biodiversity in maintaining forest ecosystem functioning is still debated. Although several studies indicate that declining biodiversity will lead to reduced forest ecosystem functioning (Liang et al., 2016; Chen et al., 2018; Huang et al., 2018; Ouyang et al., 2019), others report negligible (Vilà et al., 2003; Seidel et al., 2013; Fotis et al., 2018) or even negative relationships (Cavard et al., 2010; Laganière et al., 2015; Forrester and Bauhus, 2016). The effect of biodiversity on ecosystem functioning appears to depend on environmental conditions, forest characteristics (e.g., stand density), and management history, all of which affect tree species composition and stand structure (Tilman et al., 2012; reviewed in Ammer, 2019 and van der Plas, 2019; Yuan et al., 2018a; Ali et al., 2020).

At a large scale, environmental variations may drive the modulation of biodiversity effects on forest ecosystem functioning (Jucker et al., 2016a; García-Palacios et al., 2018; Conradi et al., 2020). For example, Jucker et al. (2016a) found that the shape and strength of the relationship between tree diversity and forest productivity (aboveground wood productivity, AWP) critically depend on the environmental context. Thus, studying the environmental regulation of biodiversity–ecosystem functioning relationships (BEFs) may be crucial to understand the mechanisms underlying biodiversity effects on natural communities. In particular, the stress-gradient hypothesis predicts that facilitative interactions among species gradually decrease as environmental conditions improve, while competitive interactions gradually increase (Bertness and Callaway, 1994; Maestre et al., 2009; He et al., 2013). Species interactions are central to explaining positive BEFs in plant communities, as they underpin the role of niche complementarity (Loreau, 1998; Jucker et al., 2016b). Therefore, the biodiversity–productivity relationship varies along stress gradients in response to changes in species interactions. Stress environments encompass most factors affecting the growth of tree species, including light, temperature, water, and nutrient availability (Callaway et al., 2002), with high environmental stress being associated with low productivity (Callaway et al., 2002; Paquette and Messier, 2011). However, research on the intensity of the effect of variations in biodiversity on AWP along productivity gradients is lacking.

Stability, a key characteristic of forest ecosystems, refers to the resistance of the ecosystem function to spatial and temporal disturbance (Tilman et al., 2006). Productivity in communities with greater diversity is more stable than that in less diverse communities (Tilman et al., 2006; Isbell et al., 2009; Cardinale et al., 2013; García-Palacios et al., 2018; Craven et al., 2018; Schnabel et al., 2019). Current studies of the biodiversity–stability relationship mainly focus on the temporal stability of productivity and show that greater biodiversity enhances the temporal stability owing to a greater temporal complementarity between species resulting from a higher asynchrony of species responses to environmental fluctuations and high average productivity (Tilman et al., 2006; Isbell et al., 2009; Cardinale et al., 2013; Craven et al., 2018; García-Palacios et al., 2018; Schnabel et al., 2019). Analogous to the temporal stability of productivity, spatial stability is a fundamental ecosystem characteristic that denotes the response of productivity to spatial environmental heterogeneity (Zhong et al., 2017; Wang et al., 2019). It measures productivity similarity across different forest communities, which is defined as the reverse of productivity variability, i.e., the magnitude of spatial changes in forest productivity against environmental heterogeneity (Wang et al., 2019). Compared with the influence of biodiversity on temporal stability (Hector et al., 1999; Wilsey and Polley, 2004; Isbell et al., 2009; Hector et al., 2010; Craven et al., 2018), the potential effect of biodiversity on the spatial stability of forest ecosystem properties (e.g., AWP) has received little attention (however, see Weigelt et al., 2008; Zhong et al., 2017).

A widely held perception is that biodiversity enhances both productivity and stability (Cardinale et al., 2013), which have so far been

evaluated mostly in grasslands (Wilsey and Polley, 2004; Weigelt et al., 2008; Isbell et al., 2009; Craven et al., 2018; Wang et al., 2019), with only a few reports on natural forest ecosystems (however, see Zhong et al., 2017; Mazzochini et al., 2019). If biodiversity simultaneously enhances forest productivity and its stability across different productivity levels, conservation of biodiversity may indeed help maximize and sustain forest productivity (Yachi and Loreau, 1999; Cardinale et al., 2013). In the face of future climatic stress and disturbances, integrating biodiversity effects on AWP and its spatial stability is fundamental to conservation and management goals.

Beyond species diversity, stand structural diversity (e.g., tree size diversity [Hd] measured by the variation in diameter at breast height [DBH]) was found to be a better predictor for ecosystem functioning than species richness (SR; Vilà et al., 2003; Lei et al., 2009; Yuan et al., 2018a, 2018b; Ali et al., 2019). Diverse forest structures result from leaf layering and multilayered canopies, both of which influence forest functions such as photosynthesis and respiration as well as stand productivity (Lei et al., 2009). Species diversity can also promote tree size heterogeneity and indirectly affect forest functioning via structural diversity as previously reviewed (Barry et al., 2019). However, the effects of stand structural diversity on spatial stability of forest productivity are not well understood. Recent studies have revealed that stand density greatly affects forest productivity (Jucker et al., 2016b; Ouyang et al., 2019). Higher stand density increases forest carbon storage and wood productivity through higher canopy packing, which captures more light (Forrester et al., 2018; Morin, 2015). However, their relative importance might depend on environmental conditions (Paquette and Messier, 2011). Therefore, stand density should be considered when evaluating the relationships between biodiversity and AWP.

Here, we integrate abiotic (climate and soil) and biotic (stand density) factors to evaluate the strength and direction of species and structural diversity effects on AWP and its spatial stability among productivity gradients based on 2324 permanent sample plots in temperate natural forests in northeast China. Specifically, our study was designed to address the following questions: 1) Does the positive biodiversity effect on AWP decrease with increasing productivity? On the basis of the stress-gradient hypothesis and the global positive and concave down pattern (Liang et al., 2016), we hypothesized that the positive effect of both SR and structural diversity on AWP decreases along increasing productivity gradients (Fig. S1a). 2) Does the pattern of positive effects of biodiversity on spatial stability remain the same along productivity gradients? The insurance effect hypothesis assumes that biodiversity can increase ecosystem stability (Yachi and Loreau, 1999), and the positive BEF effects may reach saturation in favorable habitats or at high productivity levels with high diversity when additional species are redundant (Tilman et al., 1997; Loreau, 1998). We hypothesized that the effect intensity and direction were consistent (Fig. S1b).

2. Material and methods

2.1. Study area and forest plots

Our study was performed in Jilin Province (40°52'–46°18' N, 121°38'–131°19' E) in northeastern China (Fig. 1). The climate, controlled by the high latitude component of the East Asian monsoon, is temperate continental with warm summers, cold winters, and a short growing season. Mean annual temperature and total annual precipitation from 1981 to 2010 were approximately 3.8 °C and 736 mm, respectively.

Sample plots were identified using the 9th National Forest Inventory in Jilin Province in 2014 (State Forestry Administration, 2013). Systematic sampling was used in a 4 × 8 km grid across Jilin Province. Each plot was rectangular with an area of 600 m² (24.5 × 24.5 m). In all, 2324 plots of natural origin and without major human disturbances (the cutting intensity less than 1% by basal area) were selected for the study (Fig. 1). According to the protocols of the National Forest Inventory standards issued by the State Forestry Administration of China,

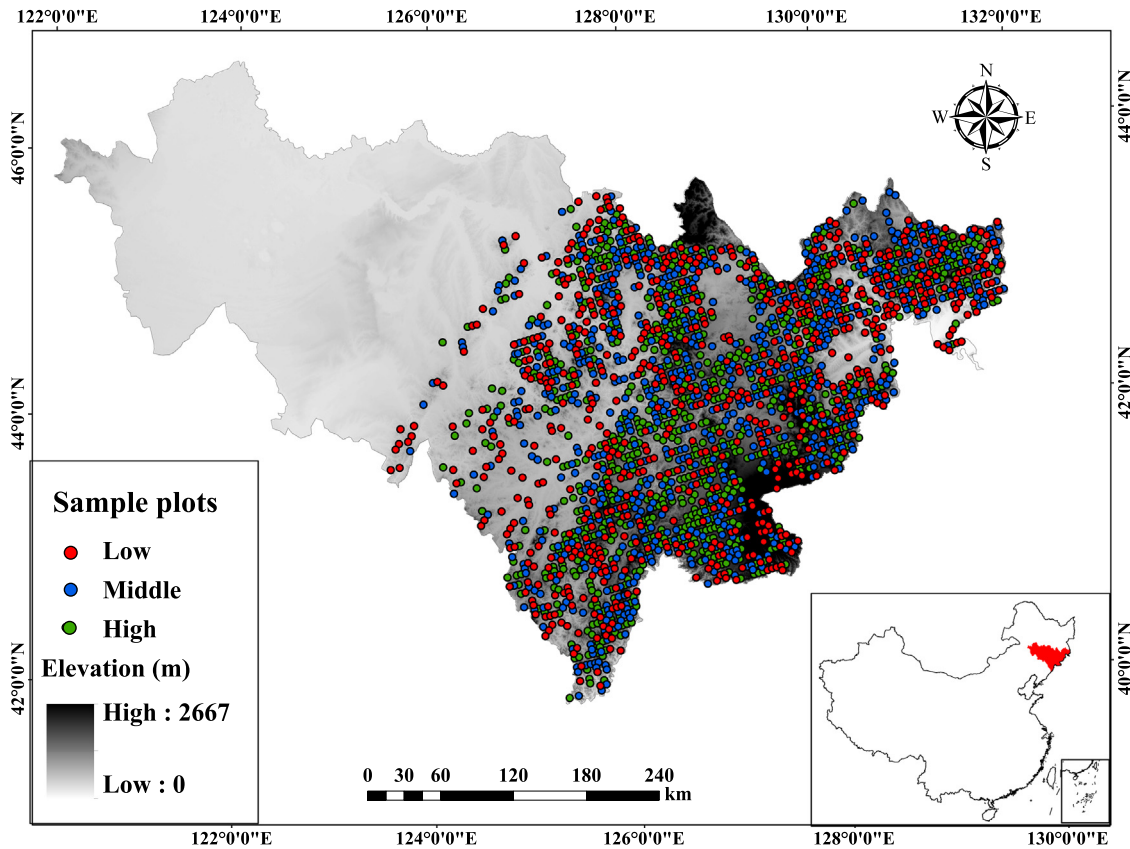


Fig. 1. Geospatial distribution of forest plots among different productivity levels in Jilin Province, northeast China.

geographic location (latitude and longitude) and altitude, tree species name, DBH (1.3 m) of individual trees with DBH ≥ 5 cm, and stand age were recorded. The stand age represents the average age of dominant tree species in the stand. The biome types included broad-leaved mixed forest, coniferous broad-leaved mixed forest, coniferous mixed forest, broad-leaved forest, and coniferous forest (1374, 242, 42, 483, and 183 plots, respectively).

2.2. Environmental data

MAT and mean annual precipitation (MAP) and annual heat-moisture index (AHM) were used as climate variables in the analysis. AHM is a biologically relevant indicator of aridity, which was calculated as the ratio of temperature to precipitation: $(MAT + 10)/(MAP/1000)$ (Wang et al., 2012). We extracted climate variables from ClimateAP v2.20 (Wang et al., 2017) for the geographical locations of the plots and calculated their average values from 1981 to 2010.

Edaphic variables included soil pH and cation exchange capacity (CEC, me/100 g), which represents the available soil nutrients for plant growth (Conradi et al., 2020). We derived these soil variables from the China Dataset of Soil Properties for Land Surface Modelling at 1 km resolution (Wei et al., 2013). Soil pH and CEC were averaged for a 0–0.5 m soil profile.

2.3. Aboveground wood productivity and its spatial stability

At plot level, AWP represents annual aboveground biomass increment of all tree species. We estimated productivity based on stand age and aboveground biomass (Eq. (1)),

$$AWP = \frac{AGB}{Age}, \quad (1)$$

where AWP is aboveground wood productivity ($t \text{ ha}^{-1} \text{ year}^{-1}$); AGB and Age are stand aboveground biomass per hectare ($t \text{ ha}^{-1}$) and stand age, respectively. AGB was calculated from the sum of individual tree biomass in the plot using species-specific DBH-based allometric equations (Li and Lei, 2010). The 2324 plots were classified into three levels of similar sample size according to their productivity: low (763 plots with the average $1.34 \pm 0.46 t \text{ ha}^{-1} \text{ year}^{-1}$), medium (775 plots with the average $2.3 \pm 0.23 t \text{ ha}^{-1} \text{ year}^{-1}$), and high (786 plots with the average $3.53 \pm 0.79 t \text{ ha}^{-1} \text{ year}^{-1}$).

We calculated the spatial stability of AWP among productivity gradients using a widely implemented index, coefficient of variation (CV) (Weigelt et al., 2008; Cardinale et al., 2013; Wang et al., 2019), i.e., the reverse of productivity variability, calculated as the ratio of mean productivity (μ) to standard deviation (SD) of AWP with the same tree SR within plots (Eq. (2)). Biodiversity also increases ecosystem stability via increasing μ (Jucker et al., 2014; Weigelt et al., 2008).

$$CV = \frac{SD}{\mu}, \quad (2)$$

2.4. Biodiversity indices

In this study, we used tree SR for measuring species diversity, i.e., number of tree species in a plot. We also considered stand structural diversity, i.e., Hd (Eq. (3)), which was quantified by DBH class abundance based on Shannon index for each plot (Lei et al., 2009).

$$Hd = - \sum_{i=1}^d p_i \cdot \log p_i, \quad (3)$$

where p_i is the relative basal area of the i_{th} diameter class in a given plot, and d is the number of diameter classes. Diameter width class was set to 2 cm.

2.5. Statistical analyses

Forest productivity data were natural log-transformed prior to all analyses for normal distribution. A linear regression model was used for plots from each productivity level to fit AWP and its spatial stability with each biodiversity metric as an independent variable, and standardized slopes were used to quantify the direction and magnitude of biodiversity effect on AWP/spatial stability at different productivity levels.

We also conducted structural equation modeling (SEM) to test the causal linkages between environmental (climate and soil) and stand density factors, biodiversity (SR and Hd), and AWP, and to examine how the biodiversity–AWP relationship changed among productivity groups when controlling for environmental and stand factors (Fig. S2). All environmental variables, biodiversity indices, and AWP were standardized to a mean of zero and a standard deviation of one. To avoid the bias induced by multicollinear variables, we excluded MAP from a pair of candidate variables with a correlation coefficient larger than 0.75. As soil CEC had weak or non-significant effects on AWP and biodiversity, we excluded it from analyses (Tables S2–S5). Consequently, the full model included two climate factors (MAT and AHM), soil pH, stand density, and two biodiversity indices (SR and Hd). We conducted SEM based on the hypothesized mechanisms (Fig. S2), and the best-fit model was evaluated based on a non-significant Chi-square (χ^2) test statistic ($p > 0.05$), comparative fit index (CFI) > 0.95 , and lowest AIC value. We only reported the results derived from the selected best-fit model. SEM was performed using SPSS Amos v24 (IBM SPSS, Chicago, IL, USA). One-way analysis of variance was used to test differences of SR, Hd, and stand density among three productivity levels (i.e., low, medium, and high productivity). Summary statistics of stand variables are listed in Table S1.

3. Results

3.1. Bivariate biodiversity–AWP relationships

AWP was positively related to both SR ($R^2 = 0.07$, $p < 0.001$; Fig. 2a) and Hd ($R^2 = 0.21$, $p < 0.001$; Fig. 2b). However, the strengths (standardized slope) of these biodiversity–AWP relationships varied with biodiversity metrics and productivity gradients, showing a decrease with increasing productivity (Fig. 2). AWP increased with SR at low ($R^2 = 0.06$, $p < 0.001$), medium ($R^2 = 0.01$, $p = 0.006$), and high ($R^2 = 0.01$, $p = 0.007$) productivity levels (Fig. 2a); but increased with Hd at low ($R^2 = 0.40$, $p < 0.001$) and medium ($R^2 = 0.02$, $p < 0.001$) productivity levels, showing a decreasing trend with Hd at the high productivity level ($R^2 = 0.004$, $p = 0.046$) (Fig. 2b).

3.2. Structural equation modeling results

The final model from the SEM revealed that abiotic factors (MAT and AHM) combined with biotic factors (SR, Hd, and stand density) explained 43%, 4%, and 11% of the variation in AWP at low, medium, and high productivity levels, respectively (Fig. 3). However, the pathways of these effects varied along the productivity gradient. There was a clear pattern in the strength of biodiversity effect on AWP after controlling for climate, soil, and stand density within productivity levels (Fig. 3). SR had a positive indirect effect on AWP via Hd, and its strength decreased with increasing productivity levels ($\beta = 0.21$, $\beta = 0.05$, and $\beta = 0$ at low, medium, and high productivity levels, respectively; Figs. 3 and 4). However, the direct effect of SR on AWP was not found for all productivity levels (Figs. 3 and 4). Additionally, the positive effect of Hd on AWP decreased with increasing productivity levels ($\beta = 0.69$, $\beta = 0.16$, and $\beta = 0$ at low, medium, and high productivity levels, respectively; Figs. 3 and 4).

In addition, stand density directly and indirectly affected AWP via biodiversity, and the total effect increased with productivity levels. MAT similarly affected AWP directly and indirectly via SR, Hd, and

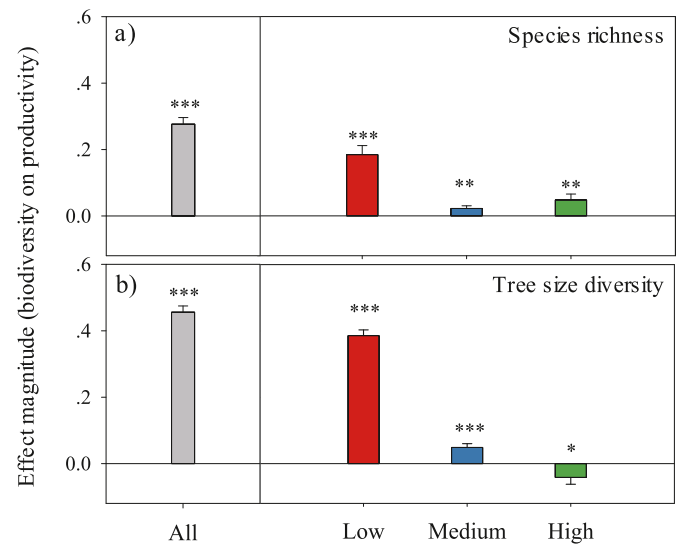


Fig. 2. Effects of species richness (SR) and tree size diversity (Hd) on aboveground wood productivity along the productivity gradients ($n = 763$, $n = 775$, and $n = 786$ for low, medium, and high productivity levels, respectively). The intensity of effects is described by standardized coefficients from multiple linear models. Vertical bar denotes standard deviation. * $p < .05$, ** $p < .01$, *** $p < .001$.

stand density, but the intensity and direction varied among productivity levels (Figs. 3 and 4). AHM had only weak negative indirect effects on AWP at low productivity levels (Figs. 3 and 4). Soil pH displayed weak/non-significant direct and indirect effects on AWP and biodiversity for all productivity levels (Fig. 3 and Tables S3–S5).

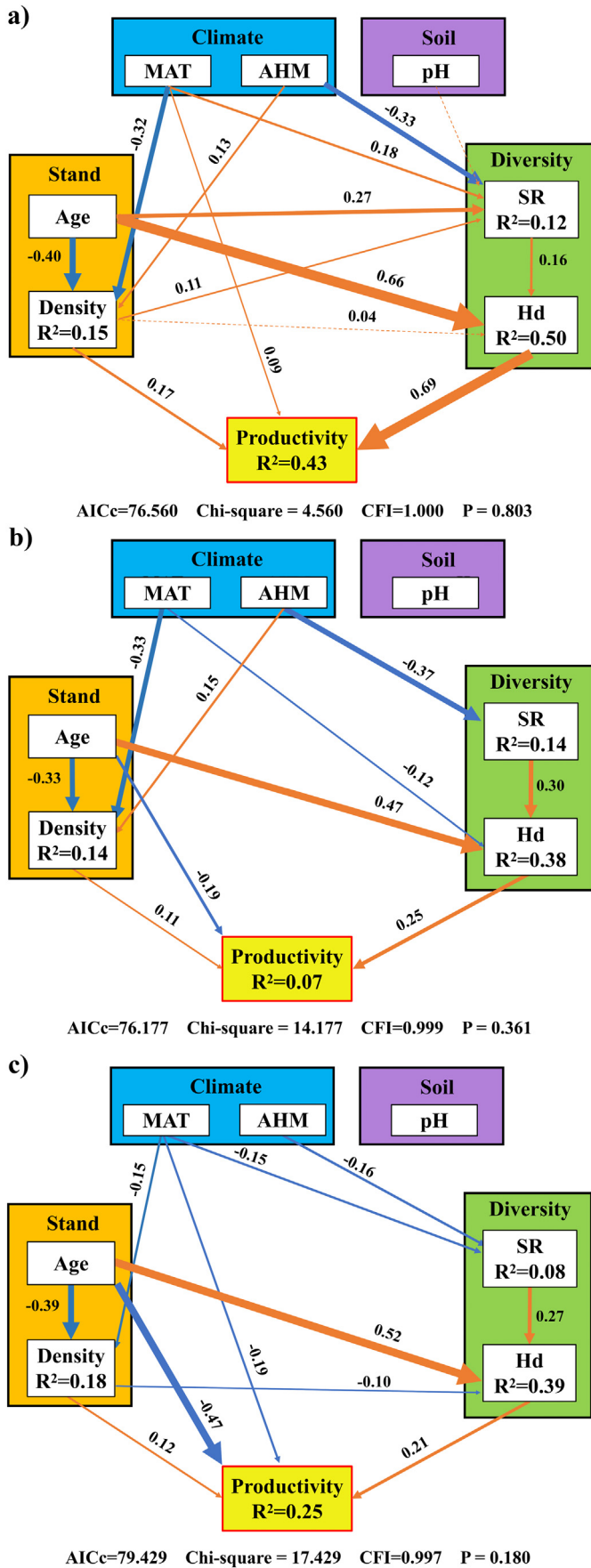
3.3. Biodiversity–spatial stability of AWP relationships

The spatial stability of AWP was positively correlated with both SR and Hd, which were both positively correlated with average AWP ($R^2 = 0.93$, $p < 0.001$; $R^2 = 0.69$, $p < 0.001$; Fig. 5) and negatively correlated with CV ($R^2 = 0.57$, $p < 0.001$; $R^2 = 0.73$, $p < 0.001$). Furthermore, the strengths (standardized slope) of these biodiversity–stability relationships varied with biodiversity metrics and productivity gradients, showing a decrease with increasing productivity (Fig. 5). CV was negatively correlated with SR ($R^2 = 0.59$, $p = 0.002$) and Hd ($R^2 = 0.77$, $p < 0.001$) at low productivity levels, but had no significant relationship at medium and high productivity levels (Fig. 5).

The standardized slope of SR effect on μ shifted from 0.871 [0.555–1.198] ($R^2 = 0.76$, $p < 0.001$) to 0.491 [−0.032–1.013] ($R^2 = 0.24$, $p = 0.062$) to 0.723 [0.326–1.119] ($R^2 = 0.52$, $p = 0.002$) under low, medium, and high productivity conditions, respectively (Fig. 5). The effect strength of Hd on μ decreased from low to high productivity ($R^2 = 0.84$, $p < 0.001$; $R^2 = 0.39$, $p = 0.013$; $R^2 = 0.19$, $p > 0.05$, respectively) (Fig. 5).

4. Discussion

To our knowledge, our study is the first to discern the correlation of species richness and structural diversity with aboveground wood productivity (AWP) and its spatial stability along productivity gradients in temperate forests. We identified that high SR and Hd would significantly enhance AWP when controlling for climate, soil, and stand density across different productivity levels. Moreover, the strength of this positive effect on AWP decreased with increasing productivity levels; consistent effects were found for the spatially averaged AWP. Meanwhile, the negative effect of both biodiversity metrics on the spatial variability of AWP was only found in low productivity plots. Our results suggested that biodiversity (SR and Hd) simultaneously enhanced AWP



and its spatial stability (e.g., decreasing CV of AWP, increasing average AWP), and the effect intensity decreased from low to high forest productivity. This also highlighted the importance of diverse structures to improve AWP and its spatial stability, which may facilitate forest sustainability, especially in those with low productivity.

4.1. Biodiversity effect on AWP

We observed consistent positive effects of both SR and Hd on AWP at low and middle productivity levels in temperate forest when controlling for climate, soil, and stand density. Furthermore, we found that the magnitude and direction of biodiversity–AWP relationships strongly depended on the productivity level. The positive effect of biodiversity (SR and Hd) on AWP decreased along a large productivity gradient from low to high, suggesting that the niche complementarity effects decreased with increasing productivity and thus supporting our first hypothesis (Fig. S1a). This was consistent with the predictions of the stress-gradient hypothesis, as well as with the findings in global forests, i.e., a positive and concave down pattern of BEFs (Liang et al., 2016), grasslands (Wang et al., 2019), and forest ecosystems among different climate gradients and site conditions (Paquette and Messier, 2011; Pretzsch et al., 2013; Toigo et al., 2015; Wu et al., 2015; Jucker et al., 2016a; Ratcliffe et al., 2017). For example, Paquette and Messier (2011) showed that the complementarity outcome of species interactions in a high-stress environment may be more important than that under favorable habitats for forests from boreal to temperate regions in eastern Canada.

Competitive interactions could also help to elucidate the shifts of biodiversity–AWP relationships, as competition gradually increases with environmental improvement (Bertness and Callaway, 1994; Maestre et al., 2009; Paquette and Messier, 2011; He et al., 2013; Rees, 2013). Stand density characterizes this competition; a strong biodiversity effect on AWP is present at low productivity levels and low stand density, whereas the effect of biodiversity on AWP is weak at high productivity levels and high stand density (Condés et al., 2013; Jucker et al., 2016b), which is consistent with our results, i.e., stand density in high-productivity plots was higher than that in low-productivity plots (Fig. S4). Another possible mechanism for the weak biodiversity effect in high-productivity plots is the saturation effect, i.e., high SR in highly productive groups (Fig. S4) reached a plateau following an asymptotic curve, which was also found in European temperate forests (Morin et al., 2011). This was also in line with niche theory, which assumes that resource use among species is complementary, but niche overlap increases with increasing SR and Hd (Wu et al., 2015).

4.2. Biodiversity effect on the spatial stability of AWP

Our work showed that high biodiversity (SR and Hd), not only enhanced AWP, but also decreased its spatial variation and increased average AWP in the temperate forests of northeast China. This is consistent with the insurance hypothesis, which assumes that biodiversity can increase ecosystem stability (Yachi and Loreau, 1999), as well as with the results of tropical tree diversity experiments considering temporal stability (Schnabel et al., 2019), and a study of global natural grasslands (Wang et al., 2019). These results support our second hypothesis, which had not been tested in forest ecosystems, and reinforce the results of the longest running biodiversity manipulation experiment across

Fig. 3. Final structural equation models of the direct and indirect effects of abiotic and biotic factors on aboveground wood productivity at (a) low (n = 763), (b) medium (n = 775), and (c) high (n = 786) productivity levels. Solid lines represent significant paths (p < 0.05; orange, positive; blue, negative). Values indicate standardized correlation coefficients; R², proportion of variance explained; MAT, mean annual temperature; AHM, annual heat-moisture index; pH, soil pH; Density, stand density; SR, species richness; Hd, tree size diversity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

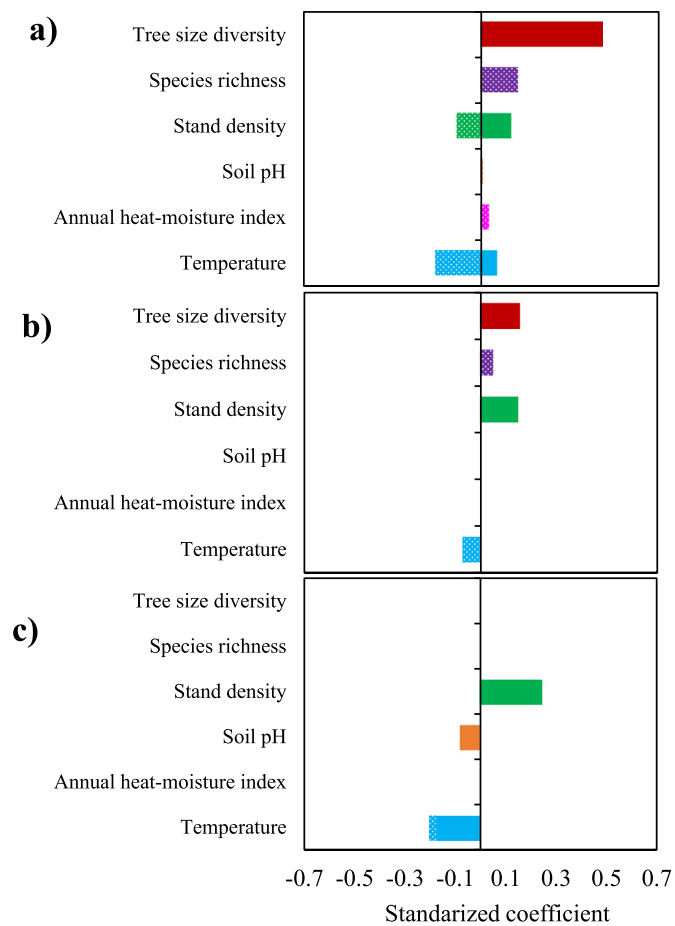


Fig. 4. Beta coefficients of climate, soil, stand, and diversity factors on aboveground wood productivity for (a) low ($n = 763$), (b) medium ($n = 775$), and (c) high ($n = 786$) productivity groups. Filled and dotted bars indicate the direct and indirect effect of abiotic and biotic factors on aboveground wood productivity.

ecosystems worldwide, which considered the effect of biodiversity both on community biomass and on its temporal variability (Kardol et al., 2018).

Specifically, our results showed that the consistent positive effects of both SR and Hd on spatial average AWP decrease from low to high productivity levels in temperate forest ecosystems. At low productivity levels, the spatial stability of AWP increased not only by reducing spatial variability of AWP but also by increasing average AWP, suggesting that biodiversity simultaneously enhanced AWP and its spatial stability in low productivity/stressful environments. However, with high productivity/favorable conditions, stability increased just by increasing average AWP, and not by decreasing its spatial variability. This is consistent with results of Schnabel et al. (2019) in a tropical tree diversity experiment with favorable climatic conditions (annual mean temperature and precipitation of 26 °C and 2661 mm, respectively). These authors suggested that high SR and structural diversity will be more beneficial for stabilizing forest productivity against spatial environmental heterogeneity in low- than in high-productivity areas. Zhong et al. (2017) found that the strength of the species diversity effect on the spatial stability of productivity increased along elevation gradients in subtropical mountain forests. Moreover, based on a global network of dryland ecosystems, García-Palacios et al. (2018) showed that SR may have a greater stabilizing role across time under the most arid conditions.

There may be various underlying mechanisms for explaining the different relationships between biodiversity and spatial stability of AWP among productivity levels. The strong positive effect of biodiversity on the spatial stability of AWP (i.e., negative biodiversity effect on spatial

variation) in low-productivity forests might be caused by facilitative interactions (e.g., reduced competition) among neighboring trees, and niche partitioning (e.g., diverse tree size structures and species composition), which generally increases tree resistance to perturbations and environmental fluctuations (Pretzsch et al., 2013; Jucker et al., 2014). However, the weak or non-significant biodiversity effect on the spatial stability of AWP in high-productivity forests might be caused by species saturation, similar to that of the biodiversity–AWP relationship, i.e., high SR and Hd in highly productive groups reaches a plateau, following an asymptotic curve (see Figs. S3 and S4).

Additionally, the different responses of biodiversity and AWP to climate might lead to different biodiversity effects on spatial stability along productivity gradients. Our work revealed that environmental effects on biodiversity (SR and Hd) and AWP varied among productivity levels. We found that the temperature effect on AWP shifted from positive to non-significant to negative under low-, moderate-, and high-productivity conditions, respectively, which is similar to results from neotropical forests (Malhi et al., 2004). The effects of temperature on stand density and Hd were stronger at low than at high productivity levels. However, Kardol et al. (2018) and Wang et al. (2019) found a discordant trend in both types of biodiversity–AWP/stability relationships along the productivity/stress gradients. They showed that the effect of biodiversity on AWP and stability decreased (Kardol et al., 2018) and increased (Wang et al., 2019) along the productivity/stress gradients. This contradiction was probably due to differences in experimental settings: Kardol et al. (2018) included a low number of tree species, whereas the study by Wang et al. (2019) was focused on grassland ecosystems. Further studies are needed to test whether biodiversity metrics (including functional diversity/composition and phylogenetic diversity) drive the biodiversity–productivity and biodiversity–spatial stability relationships, and to better understand the mechanisms underlying these relationships in different forest ecosystems. Moreover, we observed only weak or non-significant effects of soil on AWP, which may be due to the coarse soil data at 1 km resolution. Additionally, these effects can be easily overwhelmed by the covariant biodiversity and stand density factors on AWP (Wu et al., 2015).

In addition to environment, biodiversity, and stand factors, human intervention can also modify the tree species composition and growth, and thus affect the relationships between biodiversity and AWP and its spatial stability (Newbold et al., 2015; van der Plas et al., 2016; Gonzalez et al., 2020). For example, Ouyang et al. (2021) showed that human activities had significant effects on tree species and structural diversity, and forest stability. Therefore, all plots for this study were selected from natural forests without major human disturbances according to a cutting intensity of less than 1% by basal area; however, there may be enrichments in some plots due to silvicultural practice. Although information on enrichments is not available, enrichment planting in natural forests was widely applied only in recent years and the tree species was predominantly Korean pine, which grows very slowly in its early stages and therefore has not reached the 5 cm threshold of DBH measurement in a plot. Thus, we believe this will not affect the results of this study. In addition, recent studies have reported that functional traits can capture the degree of functional redundancy and niche overlap well, which have a greater explanatory power for biomass and productivity than SR alone (Lasky et al., 2014; Luo et al., 2019). Therefore, further studies should consider the effects of functional diversity and functional trait composition on AWP and its stability. The relationships between ecosystem multifunctionality and biodiversity also need to be examined in the future (Yuan et al., 2020).

5. Conclusions

Our results demonstrate that both SR and Hd positively affect AWP and its spatial stability, and the strength of these effects decreases

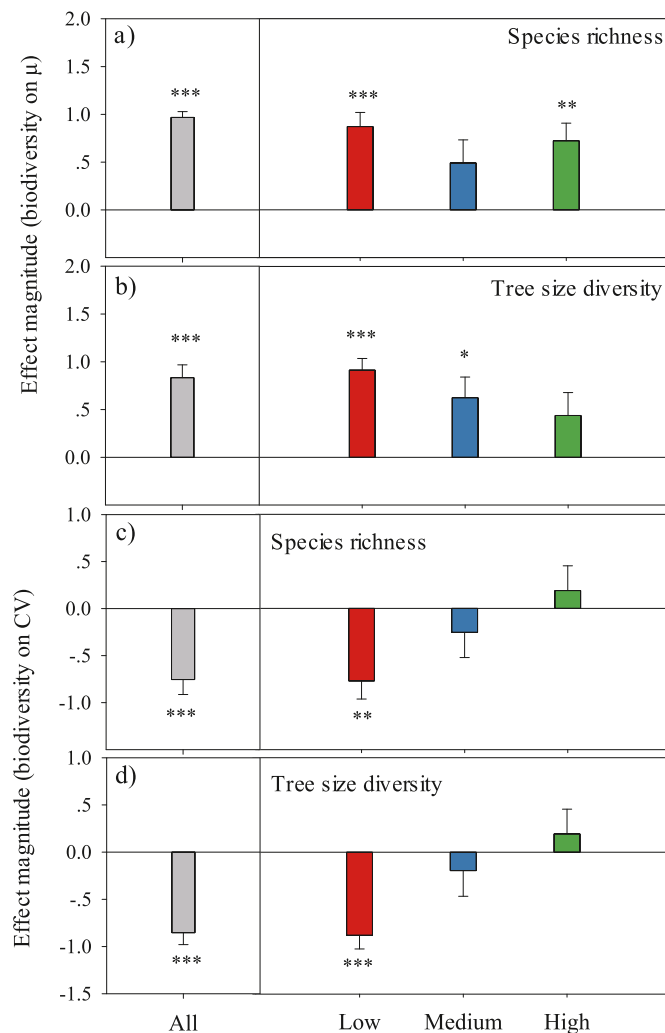


Fig. 5. Effect of species richness (SR) and tree size diversity (Hd) on spatial stability of aboveground wood productivity (mean(μ)/standard deviation) along the productivity gradients. The intensity of effects is described by standardized coefficients from multiple linear models. Vertical bar denotes standard deviation. * $p < .05$, ** $p < .01$, *** $p < .001$.

with increasing productivity. The mechanism underlying both effects might be the same as that responsible for variations in strength of niche complementarity (e.g., facilitative interactions) and saturation effects along low–high stress/productivity gradients (Jucker et al., 2016a; García-Palacios et al., 2018; Schnabel et al., 2019). The results provide a new perspective on biodiversity–ecosystem function relationships and have important implications for ecological restoration and improving the productivity and stability of forest ecosystems with different productivity levels.

Data availability

The dataset used for this paper is available as supplementary files (Tables S1–S5). More information about the dataset is available upon request to the corresponding author.

CRediT authorship contribution statement

WQG and XDL designed the experiment and performed data analyses. YTL and DLG collected the data. WQG and XDL wrote the paper. MWL, ML, and HRZ helped frame the study and contributed to the writing. All authors contributed to the final preparation of the manuscript.

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.scitotenv.2021.146674>.

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