

Tree diversity depending on environmental gradients promotes biomass stability via species asynchrony in China's forest ecosystems

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ABSTRACT

There is mounting evidence that biodiversity promotes ecological stability in changing environments. However, understanding diversity–stability relationships and their underlying mechanisms across large-scale tree diversity and natural environmental gradients are still controversial and largely lacking. We used thirty-nine 0.12 ha long-term permanent forest plots spanning China's various forest types to test the effects of multiple abiotic (climate, soil, age and topography) and biotic factors (taxonomic and structural diversity, functional diversity and community-mean traits, and species asynchrony) on biomass stability and its components (mean biomass and biomass variability) over time. We used multiple analytical methods to identify the best explanatory variables and complicated causal relationships for community biomass stability. Our results showed that species richness increased biomass stability by promoting species asynchrony. Structural and functional diversity had a weaker effect on biomass stability. Forest age and structural diversity increased mean biomass and biomass variability significantly and simultaneously. Communities dominated by tree species with high wood density had high biomass stability. Soil nitrogen enhanced biomass stability directly and indirectly through its effects on mean biomass. Soil nitrogen to phosphorus ratio increased biomass stability via increasing species asynchrony. Precipitation indirectly increased biomass stability by affecting tree diversity. Moreover, the direct and indirect effects of soil nutrients on biomass stability were greater than that of climate variables. Our results suggest that species asynchrony is the main mechanism proposed to explain the stabilizing effect of diversity on community biomass, supporting two mechanisms, namely, the biodiversity insurance hypothesis and complementary dynamics. Soil and climate factors also play an important role in shaping diversity–stability relationships. Our results provide a new insight into how tree diversity affects ecosystem stability across diverse community types and large-scale environmental gradients.

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1. Introduction

Environmental changes and biodiversity loss pose significant threats to ecosystem functions and services (Loreau et al., 2001; Worm et al., 2006; Ives and Carpenter, 2007; Cardinale et al., 2012). In particular, the idea that increasing biodiversity can stabilize ecosystem functions has led to long-standing controversies about the relationship between biodiversity and stability (Tilman et al., 2006; Ives and Carpenter, 2007; Kardol et al., 2018; Pennekamp et al., 2018). Accumulating theoretical and empirical evidence suggests that mixed forest communities with higher biodiversity and interaction types are self-sustaining in complex natural environments as well as leading to higher stability (Mougi and Kondoh, 2012; Loreau and de Mazancourt, 2008). Still, the stabilizing effect of biodiversity is of considerable significance, illustrating that biodiversity is crucial to the long-term sustainability of ecosystems facing environmental changes (Loreau and de Mazancourt, 2008; Wang and Loreau, 2016). Identifying whether biodiversity is conducive to stabilizing ecosystem functioning and elucidating causal mechanisms could make improvements to current forest management and conservation strategies (Nabuurs et al., 2013; Jucker et al., 2014; Díaz et al., 2015).

Several classic mechanisms have been proposed to understand and predict the positive relationship between biodiversity and stability (Loreau and de Mazancourt, 2008; Gross et al., 2014; de Mazancourt, 2013; Morin et al., 2014). According to the ‘insurance hypothesis’, the asynchrony of species responses to changes and fluctuations in the environment is considered as the key factor driving the stabilising effect of diversity on ecosystem properties (Ives et al., 1999; Yachi and Loreau, 1999; Loreau and de Mazancourt, 2008). Many studies have suggested that multiple components of biodiversity (taxonomic, functional and/or structural) increase ecosystem stability by enhancing the degree of species asynchrony in grasslands (Loreau and de Mazancourt, 2008; Craven et al., 2018) and forests (Schnabel et al., 2019, 2021; Dolezal et al., 2020; Ouyang et al., 2021). Compensatory dynamics state that interspecies competition generates or amplifies negative covariations in their abundances, such that these variations compensate for each other, yielding less variation in total abundance or biomass at the aggregate ecosystem or community level (Gonzalez and Loreau, 2009). Overyielding effects suggest that biomass production of a diverse community shows higher biomass productivity than expected from monocultures due to facilitation and/or reduction in the strength of competition among interspecific neighbors (Loreau and Hector, 2001; Hector et al., 2010). How these mechanisms govern the relationship between diversity and stability in China’s forest ecosystems remains unknown.

Functional traits affect tree demographic processes such as recruitment, growth and mortality, reflect ecological tradeoffs and capture inherent strategy differentiation in species performance (Lavorel and Garnier, 2002; McGill et al., 2006; Violle et al., 2007). Universally, the resource conservative species with high wood density are related to increased plant survival, shade and drought tolerance, leaf lifespan, nutrient retention, biomechanical stability, defense against herbivores, fungi and pathogens, but exhibit low photosynthetic capacities and growth rates (Van Gelder et al., 2006; Quero et al., 2011; Méndez-Alonzo et al., 2012). Conversely, the resource acquisitive species with low wood density have larger xylem vessels, thin short-lived leaves, high herbivory rates, high hydraulic conductivity, fast photosynthesis rates, as well as carbon gain and growth (Santiago et al., 2004; Markesteijn et al., 2011; Méndez-Alonzo et al., 2012; González-M et al., 2020). Biomass dynamics are driven by associated variation in community-weighted mean traits (Poorter et al., 2017). The mass-ratio hypothesis states that ecosystem functions are strongly determined by the trait of the dominant species in the stands, and measured by community-weighted mean traits (Grime, 1998). Diverse communities that have more dominant stable species could sustain ecosystem functioning and community temporal stability (Yuan et al., 2019; Dolezal et al., 2020). To our knowledge, there is no study to quantify how functional trait

diversity and community-mean traits associated with species’ different strategies affect community temporal stability across large-scale China’s forest ecosystems.

Beyond diversity and functional traits, ‘multidimensional stability framework (MDSFs)’ has suggested that ecosystem stability responds to different environmental conditions in complex and multidimensional ways, and these responses change the relationships among stability components in different ways (Donohue et al., 2013, 2016). Climatic factors and soil properties are two drivers that influence diversity, asynchronous dynamics and ecosystem stability (Angert et al., 2009; Gilbert et al., 2020). Nutrient eutrophication usually reduces the stabilizing effect of plant diversity on biomass productivity in local communities (Hautier et al., 2015, 2020; Zhang et al., 2016). Affluent soil nutrients have both direct and indirect effects on temporal stability via diversity and asynchrony in natural forests (Yuan et al., 2019; Gilbert et al., 2020). Climate change that influences diversity and the degree of species asynchrony potentially alters the temporal stability of biomass production (Walker et al., 2006; Isbell et al., 2015; García-Palacios et al., 2018; Gilbert et al., 2020). Alternatively, the asynchronous response of species to environmental fluctuations is suggested to be the primary mechanism by which diversity promotes the temporal stability of biomass production (Hector et al., 2010; Hautier et al., 2014). Besides, biodiversity recovery and biomass resilience increase with stand age (Poorter et al., 2016; Villa et al., 2018; Rozendaal et al., 2019). Although forest age is fundamentally related to multiple facets of tree diversity, functional dominance, soil features and biomass production (Becknell et al., 2014; Ali et al., 2016), the effects of forest age on temporal stability are still largely unexplored.

Forest ecosystems play a vital role in biodiversity conservation and carbon cycling (Pan et al., 2011). China’s forest ecosystems are an important part of East Asian forest regions, which have functioned as a strong and persistent carbon sink (Yu et al., 2014; Ge et al., 2019). Here, we focus on temporal stability of community biomass, measured as the ratio of the temporal mean of community biomass to its temporal standard deviation (Lehman and Tilman, 2000). To examine tree diversity–stability relationships in China’s forests and elucidate the underlying mechanisms, we used thirty-nine 0.12 ha permanent sampling plots spanning China’s various forest biomes. These plots had a wide range of diversity gradients (2–124 tree species), as well as latitudinal and environmental gradients linking resource availability for soil properties and climatic conditions. Specifically, we tested the following three hypotheses. (i) Temporal biomass stability increases with increasing tree diversity depending on environmental gradients. (ii) The stabilising effect of tree diversity on temporal biomass stability is predominantly caused by species asynchrony. (iii) Soil properties have greater direct and indirect effects on temporal biomass stability via tree diversity and species asynchrony than climatic factors. By verifying these hypotheses based on the various diversity–stability mechanisms, we expect to gain a more comprehensive and integrated understanding of the processes and underlying mechanisms that drive community biomass stability across diverse community types in China’s forests.

2. Material and methods

2.1. Study sites

We used long-term permanent plot data from different forest ecosystems in China from the Chinese Ecosystem Research Network (CERN; <https://www.cern.org.cn/>), namely Xishuangbanna, Dinghushan, Heshan, Ailaoshan, Huitong, Shengnongjia, Gonggashan, Maoxian, Beijing and Changbaishan (Fig. 1 and Table S1). We used data from the eastern China monsoon region that covered six biomes from tropical to temperate forests, ranging from 21.91° to 42.4°N in latitude and from 101.0° to 128.1°E in longitude. The mean annual temperature and mean annual precipitation in the area varies between 3.8 and 22.5 °C, and 379.4 to 1950.6 mm (1999–2015), respectively. We selected thirty-nine

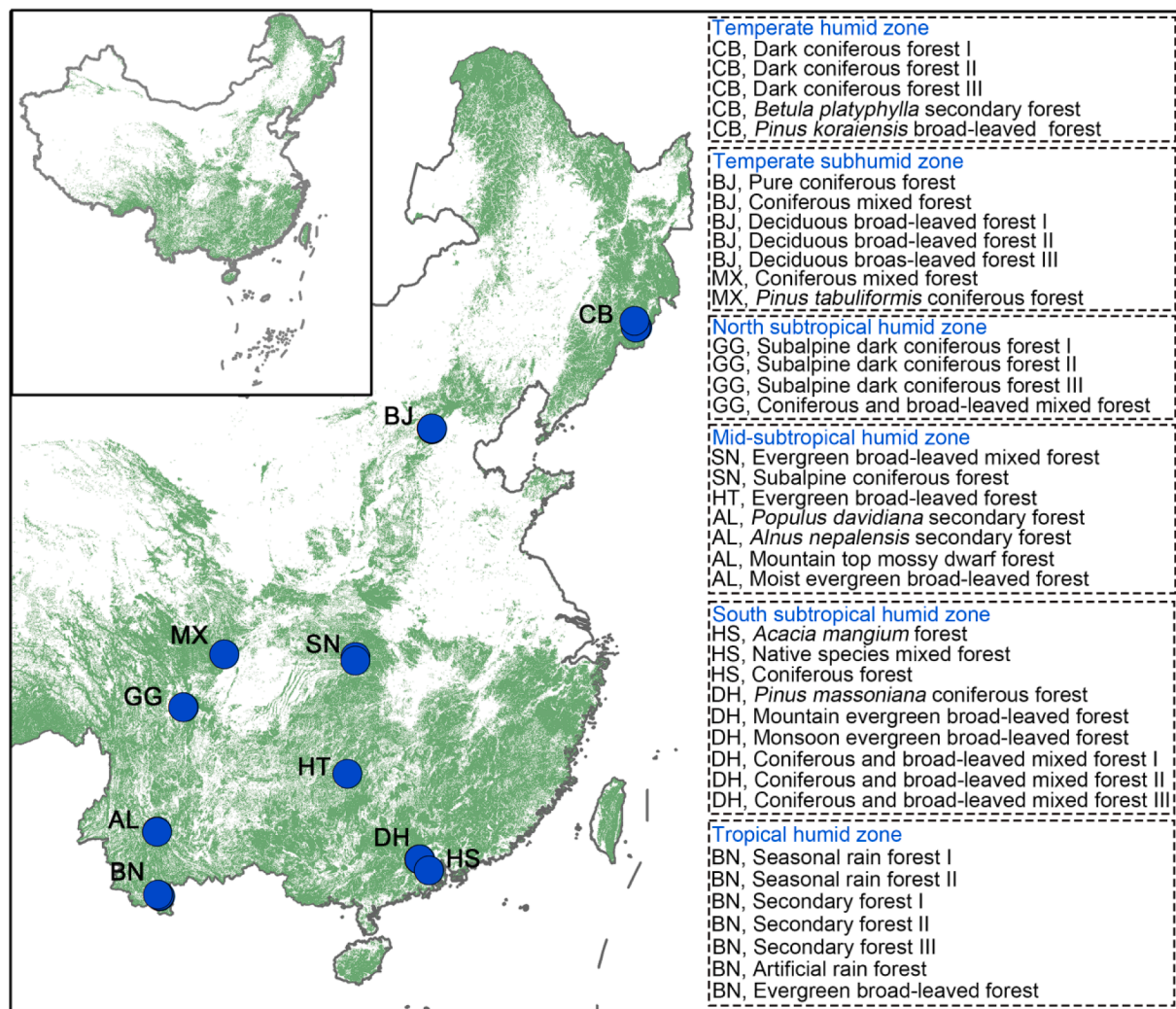


Fig. 1. Map showing the distribution of 39 forest plots in the Chinese Ecosystem Research Network. BN Xishuangbanna; DH Dinghushan; HS Heshan; AL Ailaoshan; HT Huitong; GG Gonggashan; MX Maoxian; BJ Beijing; CB Changbaishan.

0.12 ha (30 m × 40 m) permanent plots within 10 sites. All plots that were not disturbed by human activities or fire were established in mixed forest stands using unified specifications and methods. The plot survey data of this study spanned more than 10 years with 3–11 monitoring times over the 1999–2015 period.

2.2. Forest inventory, functional trait, climate and soil data

For community censuses, each individual tree with a diameter at breast height ≥ 1 cm (DBH, measured at 1.3 m in height) was recorded. Newly recruited individuals that complied with this measurement criterion were also tagged and identified in subsequent surveys. We acquired three key functional traits related to resource acquisition strategies, namely maximum height (MH), wood density (WD) and seed mass (SM). For 794 species in these plots, we extracted WD and SM data from the Global Plant Trait Network Database (available at <http://www.try-db.org>, Kattge et al., 2020) and obtained tree MH data for each species from the Flora of China (<https://iplant.cn>). Missing trait values were filled using values from the nearest-related species of the same genus. We also obtained daily climate data from each site. Soil samples were collected at the same location near each permanent plot during the same period of each community census and were used to measure multiple soil nutrient indices. In this study, we used soil nutrient data from the top layers at 0–20 cm. All the soil and climate data were obtained from CERN.

2.3. Biomass stability and species asynchrony

Plot-level total biomass was calculated by summing the biomass of all living trees in each plot for each census using allometric biomass equations in China. The total biomass included the leaves, branches, stems, and roots of each tree. We quantified the temporal stability of biomass (hereafter ‘biomass stability’) at each plot level as μ/σ (Lehman and Tilman, 2000), where μ is the temporal mean biomass (hereafter ‘mean biomass’) and σ is the temporal standard deviation of biomass (hereafter ‘biomass variability’) of the inventory data with multiple repetitions.

Species asynchrony was calculated for each plot as $1 - \rho = 1 - \sigma_T^2 / (\sum_i \sigma_i^2)^2$, where σ_T is the biomass variance in each plot and σ_i is the standard deviation of biomass for species i in the plot with S species over time (Loreau and de Mazancourt, 2008; Jucker et al., 2014). Here, species asynchrony ranges from 0, where species fluctuations are perfectly asynchronous, to 1, where species fluctuations are perfectly synchronous. Since stability and species asynchrony are correlated, species asynchrony is measured to determine stability changes and its underlying mechanisms.

2.4. Taxonomic, functional and structural diversity

We measured multiple aspects of biodiversity (taxonomic, functional

and structural) to examine the diversity–stability relationships. We calculated the three taxonomic diversity indicators for each census in each plot including species richness (S), Shannon–Wiener diversity index (H'), and Simpson diversity index (D). We used the R package ‘FD’ (Laliberté and Legendre, 2010) to calculate three functional trait diversity indices (functional richness, functional divergence and functional evenness) and three community-weighted mean (CWM) traits (CWM_{MH}, CWM_{WD} and CWM_{SM}) based on MH, WD and SM using relative species abundances for each census in each plot. We calculated three structural diversity indices that reflect multiple aspects of tree diversity such as variation, diversity and inequality (Schnabel et al., 2019; Ouyang et al., 2021) based on the DBH in each plot, namely standard deviation (Stdv), coefficient of variation (CV) and Gini coefficient (GC).

2.5. Environment and other drivers

We used multiple abiotic factors about each plot to explain the direct effects of multiple abiotic factors on stability as well as indirect effects through biotic factors. We calculated two climate variables including mean annual temperature (°C) and mean annual precipitation (mm). We selected nitrogen (N, kg g⁻¹), phosphorus (P, kg g⁻¹) and nitrogen to phosphorus ratio (N:P) as soil nutrients that might potentially influence biomass stability. According to the plot information, forest age and topography (i.e., elevation and slope), latitude and longitude, census times and intervals were obtained as predictors that might affect biomass stability. We initially used 24 biotic and abiotic variables to describe potential predictors affecting biomass stability (Table S2).

2.6. Statistical analyses

We performed ln-transformed biomass stability and its components (mean biomass and biomass variability) prior to all analyses. Simple linear regressions and pairwise Pearson’s correlation coefficients were used to test the relationship between predictor variables and biomass stability and its components. To remove the multicollinear variables, after standardizing all variables, a variance inflation factor (VIF) of less than 3 was used to identify any multicollinear variables. These variables were then excluded from subsequent analyses. We calculated the VIF using the R package ‘CAR’ (Fox and Monette, 1992). Multiple regression modeling (MRM) was used to examine the effects of multiple predictors on biomass stability and its components. We selected the best model results via the Akaike information criterion (AIC). This analysis was conducted using the R package ‘MuMIn’ (Bartoń, 2016).

Linear mixed-effect modeling (LMM) was used to assess the effects of multiple abiotic and biotic factors on biomass stability and its components. Both forest type and site were treated as random factors to account for the autocorrelation effects, using the restricted maximum likelihood to generate unbiased estimates of the model parameters. The R syntax was as follows: model = lme (response variable ~ effect variable, random = ~1|forest type/site). The significance threshold was set to $\alpha = 0.05$. We performed the LMM using the lme() function in the R package ‘nlme’ (Zuur et al., 2009).

Structural equation modeling (SEM) was used to disentangle direct and indirect drivers of temporal stability based on a prior hypothesis about causal relationships that were informed by preexisting knowledge of the mechanisms driving diversity–biomass stability relationships. We considered a full model that included all possible pathways and then sequentially removed pathways that had little impact (<0.1) and did not reach a significant level of $P < 0.05$ to obtain the final model. Maximum likelihood estimation was used to estimate path coefficients, and the fit statistics of the final model were evaluated using the ratio of Chi-square and df (χ^2/df), AIC value and root mean squared error (RMSE). SEM analyses were performed using AMOS 21.0 (AMOS Development Corporation).

3. Results

3.1. Associations of predictor variables with biomass stability

Linear regression revealed that, among all predictor variables, species asynchrony was strongly and positively related to biomass stability across all forests ($P < 0.001$, Fig. 2a). CWM_{WD} was positively associated with biomass stability ($P < 0.01$, Fig. 2b). Soil N was positively correlated with biomass stability ($P < 0.05$, Fig. 2c) and mean biomass ($P < 0.05$, Fig. 2f). In addition, forest age was positively correlated with mean biomass ($P < 0.001$, Fig. 2d) and biomass variability ($P < 0.05$, Fig. 2g). Stdv DBH was strongly and positively related to mean biomass ($P < 0.001$, Fig. 2e) and biomass variability ($P < 0.001$, Fig. 2h). Species asynchrony was negatively correlated with biomass variability ($P < 0.01$, Fig. 2i). Other variables did not significantly affect biomass stability and its two components (all $P > 0.05$). Species asynchrony significantly increased with increasing species richness ($P < 0.05$), Shannon–Wiener diversity index ($P < 0.001$) and Simpson diversity index ($P < 0.001$) (Table S2).

3.2. Dominant determinants for biomass stability

The best MRM results respectively explained 59.41% of biomass stability, 56.47% of mean biomass, and 52.80% of biomass variability. Specifically, species asynchrony had the strongest positive effect on biomass stability, followed by soil N and CWM_{WD}. Soil N:P had a negative effect on biomass stability (Fig. 3a). Stdv DBH showed the strongest positive effect on mean biomass, followed closely by soil N and forest age, whereas soil N:P had a negative effect on mean biomass (Fig. 3b). Stdv DBH and forest age had a positive effect on biomass variability, while species asynchrony and precipitation had a negative effect on biomass variability (Fig. 3c).

Similarly, the results of LMM indicated that species asynchrony was the dominant driver affecting biomass stability ($F = 17.01$, $P < 0.001$), followed closely by CWM_{WD} ($F = 13.94$, $P < 0.01$), soil N ($F = 13.87$, $P < 0.01$) and species richness ($F = 4.62$, $P < 0.05$). Of them, forest age was the most important factor affecting mean biomass ($F = 13.45$, $P < 0.01$), followed closely by Stdv DBH ($F = 9.39$, $p < 0.01$), soil N ($F = 7.84$, $P < 0.05$) and soil N:P ($F = 5.34$, $p < 0.05$). Forest age was the most important factor affecting biomass variability ($F = 9.23$, $P < 0.01$), followed closely by CWM_{WD} ($F = 7.48$, $P < 0.05$), Stdv DBH ($F = 6.52$, $P < 0.05$), precipitation ($F = 6.62$, $P < 0.05$), and species asynchrony ($F = 4.25$, $P < 0.05$) (Table 1).

3.3. Structural equation models: direct and indirect effects on biomass stability

The SEM results showed that multiple biotic and abiotic factors directly and indirectly explained 44% of biomass stability across China’s forest ecosystems. Of them, species asynchrony had the strongest positive direct effect on biomass stability (0.45) [hereafter values in parentheses are the standardized path coefficients of direct or indirect effects], followed by direct positive effects on soil N (0.30) and CWM_{WD} (0.28). Yet, species richness did not directly affect biomass stability, but indirectly increased biomass stability by promoting species asynchrony (0.16). Interestingly, soil N:P increased biomass stability by increasing species asynchrony (0.15). Forest age (0.28), precipitation (0.49) and elevation (−0.28) significantly and directly affected species richness but did not directly influence biomass stability (Fig. 4a).

For two components of biomass stability, that is the mean biomass and biomass variability, the SEM results explained 44% of mean biomass and 47% of biomass variability, respectively. Stdv DBH (0.63) and soil N (0.22) directly increased mean biomass. Forest age indirectly increased mean biomass via increasing Stdv DBH (0.18). Moreover, Stdv DBH strongly and directly increased biomass variability (0.50), whereas species asynchrony (−0.39) and precipitation (−0.23) directly

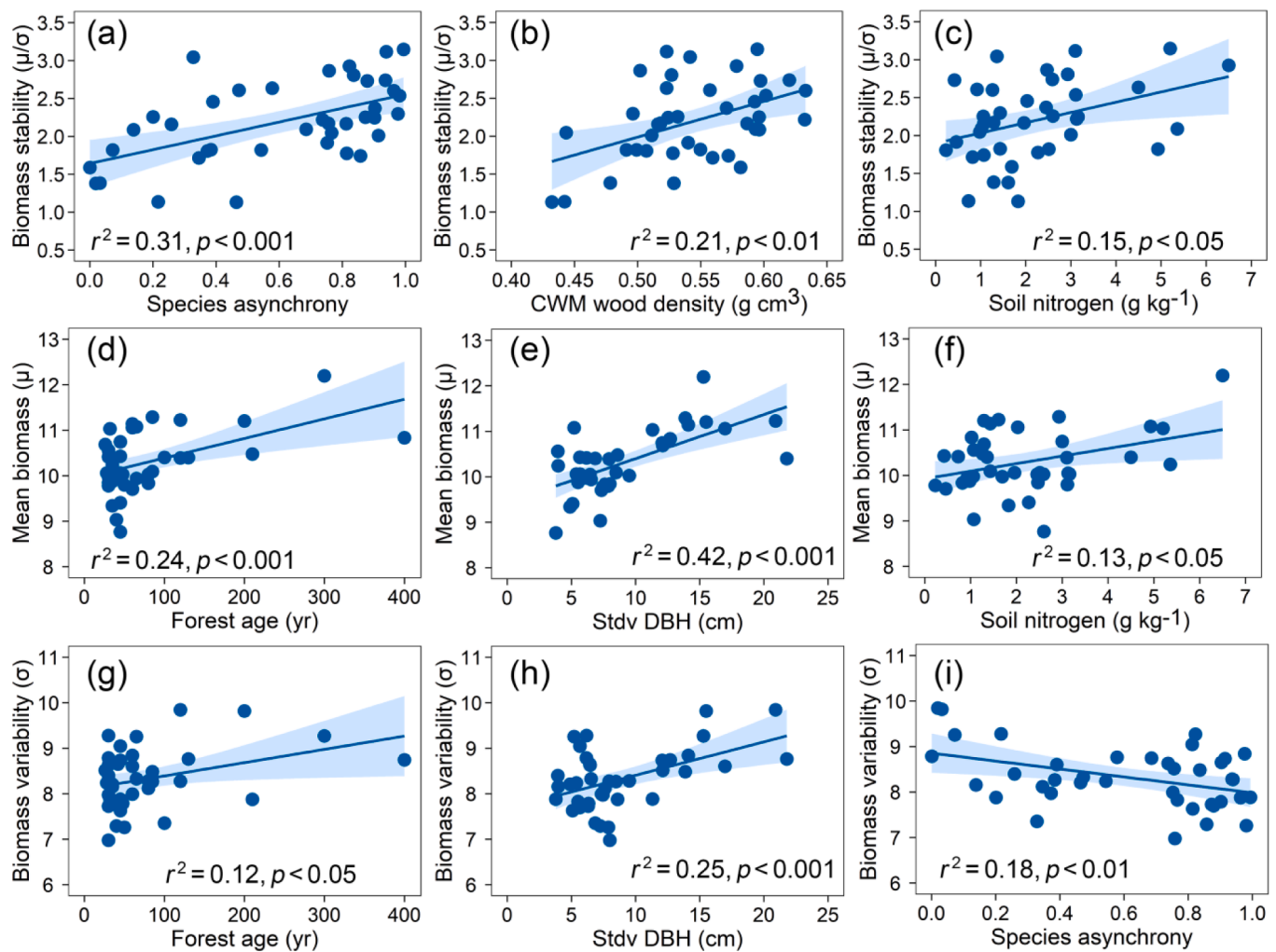


Fig. 2. Relationships of biomass stability and its two components (natural log transformed) to predictor variables across 39 forest plots. Filled areas indicate 95% confidence intervals. Note that only a significance level of $P < 0.05$ is shown.

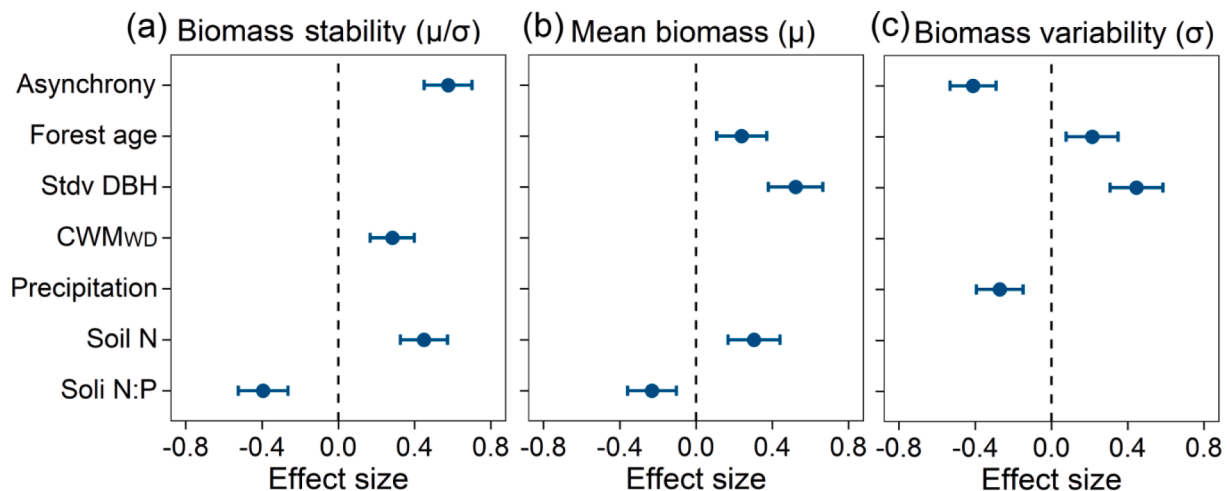


Fig. 3. Multiple regression modeling results of biomass stability and its components using individual predictor variables ($P < 0.05$). Their effect sizes (circles) were compared to determine differences in the strength of predictor variables on biomass stability and its two components, and lines represent standard errors.

decreased biomass variability. Soil N:P (−0.13) and species richness (−0.14) indirectly decreased biomass variability by reducing species asynchrony. Forest age indirectly increased biomass variability by increasing Stdv DBH (0.24). Soil N (0.16) and Stdv DBH (0.46) indirectly

increased biomass stability via enhancing mean biomass. Species asynchrony (0.32) and precipitation (0.19) indirectly increased biomass stability via reducing biomass variability. Stdv DBH indirectly decreased biomass stability via reducing biomass variability (0.41). Moreover,

Table 1

Summary of the linear mixed-effect modeling for multiple biotic and abiotic factors on biomass stability and its components across 39 forest plots.

Variables	Biomass stability		Mean biomass		Biomass variability	
	F-value	P-value	F-value	P-value	F-value	P-value
Species richness	4.62	0.0397				
Species asynchrony	17.01	0.0004			4.25	0.0488
Forest age			13.45	0.0013	9.23	0.0059
Stdv DBH			9.39	0.0055	6.52	0.0178
CWM _{WD}	13.94	0.0011			7.48	0.0118
Precipitation					6.62	0.0170
Soil N	13.87	0.0011	7.84	0.0102		
Soil N:P			5.34	0.0302		

biomass variability (−0.81) had a greater influence on biomass stability than mean biomass (0.73) (Fig. 4b).

4. Discussion

4.1. Taxonomic and structural diversity more strongly associated with biomass stability than functional diversity or community-mean traits

Previous studies including field observations of grassland ecosystems (Hautier et al., 2014, 2015, 2020; Zhang et al., 2016; Gilbert et al., 2020), forest experiments (Morin et al., 2014; Schnabel et al., 2019, 2021), and theoretical models (Mougi and Kondoh, 2012; Loreau and de Mazancourt, 2008) indicate that plant diversity increases ecological stability. We found a consistent positive, albeit weaker, relationship between three taxonomic diversity indices and biomass stability under various diversity gradients (Table S2), supporting our first hypothesis. Our findings reinforce the important stabilizing effect of taxonomic diversity for biomass stability in mixed-species forest stands, congruent with studies on existing experimental and natural forest systems (Morin et al., 2014; Yuan et al., 2019; Schnabel et al., 2019, 2021). Furthermore, any process that affects either mean biomass or biomass alters biomass stability. The positive effect of diversity on mean total biomass partly accounts for the overyielding effect in small plots or populations (Hector et al., 2010; de Mazancourt et al., 2013; Loreau and de Mazancourt, 2008). Our results showed that three taxonomic diversity indices were insignificantly and inconsistently related to mean biomass and were insignificantly and negatively correlated with biomass variability (Table S2), and did not significantly increased biomass stability via mean biomass directly and indirectly (Fig. 4). Together, our findings

highlight, to a lesser extent, overyielding effects in stabilizing community biomass across large-scale environmental gradients or a wide range of diversity gradients.

Our findings reported structural diversity, that is tree size variability, resulted in a simultaneous increase in mean biomass and biomass variability, ultimately achieving a weak positive effect on biomass stability over time (Figs. 2–4). This result further supports our first hypothesis. In mixed stands with canopy complexity, structural diversity has been increasingly recognized as an important determinant of increasing forest biomass and productivity, representing complementarity effects (Zhang and Chen, 2015; Dănescu et al., 2016; Fotis et al., 2017). Our results indicated that structural diversity promoted mean biomass and biomass stability over time, emphasizing that species interactions contribute to stabilizing forest biomass production across forest sites. This result supports compensatory dynamics in China's forest ecosystems. In particular, our analysis demonstrated that forest age directly increased taxonomic diversity and structural diversity, and indirectly enhanced mean biomass and biomass variability by promoting structural diversity, ultimately increasing biomass stability (Fig. 4). Our analysis highlights that forest age is a key aspect for maintaining tree diversity and biomass stability, with possible important implications for conservation of old-growth forests.

For functional trait diversity and community-mean traits, we found a significant positive relationship between CWM_{WD} and temporal biomass stability. Species with low wood density tend to be fast-growing resource-acquisitive species and maintain high biomass gain, while species with high wood density tend to be slow-growing resource-conservative species with low growth rates and biomass (Van Gelder et al., 2006; Chave et al., 2009). Our large-scale study suggested that communities dominated by slow-growing species with high wood density had high biomass stability in these forests, possibly because species with high wood density were related to high plant survival and mechanical stability. Furthermore, tree maximum height and seed mass as important factors in plant ecological strategies are closely related to species dominance and competitive ability (Baraloto et al., 2005; Kraft et al., 2008; Westoby et al., 2002). Our results exhibited a weak effect of CWM_{MH} and CWM_{SM} on biomass stability, and all CWM traits were weakly and insignificantly correlated with mean biomass and biomass variability (Table S2). Three functional trait diversity indices were weakly and inconsistently associated with biomass stability and its two components (Table S1). As such, more studies are needed to test the effects of functional trait diversity and CWM traits on community biomass stability in forests.

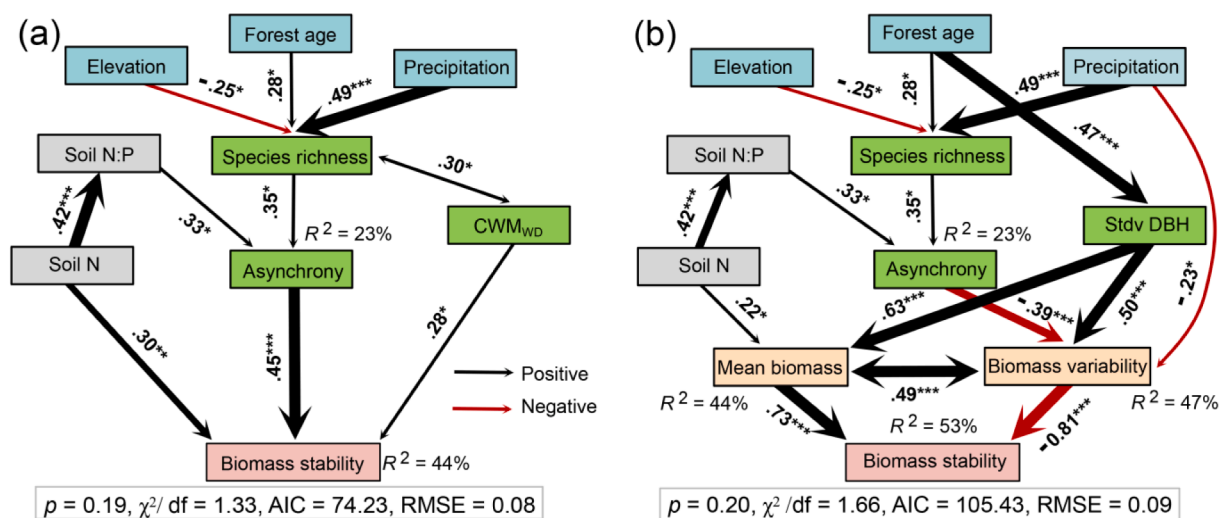


Fig. 4. Direct and indirect effects of multiple biotic and abiotic factors on biomass stability across 39 forest plots. The numbers on the arrows indicate standardized path coefficients. R^2 indicates the proportion of variance explained. * $P < 0.05$; ** $P < 0.05$; *** $P < 0.05$.

4.2. Tree diversity increases biomass stability by promoting species asynchrony

Consistent with previous studies in many forest (Yuan et al., 2019; Dolezal et al., 2020) and grassland ecosystems (Xu et al., 2021; Craven et al., 2018), results demonstrated that species asynchrony was the strongest determinant of biomass stability in China's forests (Figs. 2–4). These results confirm the idea that asynchronous dynamics among species are an important mechanism for stabilizing biomass of diverse communities. Loreau and de Mazancourt (2013) found that species asynchrony responses to changing environmental conditions stabilizes ecosystem functioning and is expected to be a major factor causing compensatory dynamics between species. Coexisting communities with high species asynchrony are expected to optimize tree canopy occupancy faster when forced by the external abiotic environment (Gonzalez and Loreau, 2009; Morin et al., 2014). This mechanism has been shown to explain the stabilizing effects of species diversity in many studies (Hector et al., 2010; de Mazancourt et al., 2013).

More importantly, studies of both forests and grasslands show that plant species richness strongly increases species asynchrony (Hautier et al., 2014; Jucker et al., 2014; Craven et al., 2018; Schnabel et al., 2021). Bivariate analysis indicated that three taxonomic diversity indices were significantly and positively related to species asynchrony (Table S2). In addition, the final SEM analysis demonstrated that the stabilizing effect of taxonomic diversity (specifically species richness) on community biomass stability was mediated by promoting species asynchrony, and species asynchrony increased biomass stability via reducing biomass variability in China's forests (Fig. 4). Our study supports the predictions that tree diversity has a stabilizing effect on community biomass. Together, these findings are consistent with the idea of the biodiversity insurance hypothesis, supporting the second hypothesis. This results supports the finding of previous grassland and forest studies, which found that plant species richness increases community temporal stability of biomass productivity by enhancing species asynchrony (Craven et al., 2018; Hautier et al., 2020; Schnabel et al., 2021). Overall, our results provided strong evidence that tree diversity promotes ecosystem stability because the degree of asynchrony is strengthened in more diverse communities. Similar results were found through a global meta-analysis (Xu et al., 2021).

4.3. Soil properties have a stronger influence on biomass stability than climatic factors

For abiotic variables, we found that soil nutrients, especially soil nitrogen, significantly and directly increased biomass stability. Soil nitrogen directly increased mean biomass and biomass stability, and indirectly enhanced biomass stability by promoting mean biomass (Figs. 2–4). Gilbert et al. (2020) reported similar results that soil organic matter directly increases temporal stability of primary production in grasslands. Furthermore, studies reported that variations in species asynchronous responses to environmental fluctuations have been found to influence temporal stability (Loreau and de Mazancourt, 2008; Hautier et al., 2015, 2020; Zhang et al., 2016; Gilbert et al., 2020). Our results showed that soil nitrogen:phosphorus ratio increases biomass stability via enhancing species asynchrony, highlighting the role of asynchrony of species responses to environmental conditions. Our analysis suggests that soil properties have a direct and indirect influence on biomass stability.

Plant species richness declines with latitudinal and altitudinal gradients, which is the most common phenomenon in nature (Gaston, 2000; Kraft et al., 2011). Both latitudinal and altitudinal gradients that include many composite factors such as climate, soil properties, biogeography and history shape the geographic distribution patterns of tree diversity. Changes in biodiversity caused by environmental changes may be a major factor determining ecosystem stability (Ives and Carpenter, 2007; Hooper et al., 2012; Hautier et al., 2015). Our results showed that

precipitation had a direct effect on species richness but not on biomass stability. Note that precipitation indirectly affected species asynchrony by altering species richness, ultimately affecting biomass stability. Gilbert et al. (2020) found that soil properties have a greater impact on the stability of primary production than climate variability in 29 grasslands. Consistently, our analysis consistently supported our third hypothesis that soil properties had greater direct and indirect influences on community biomass stability through tree diversity and asynchrony than climate variables across China's forest ecosystems.

5. Conclusions

Combining theoretical and empirical work, this study utilizes multiple abiotic and biotic variables to explain the diversity–biomass stability relationships across China's forest ecosystems and determines several important pathways and underlying mechanisms through multiple analyses. In this study, this strong positive effect of asynchrony on stability supports asynchronous dynamics among species. Plant species richness promotes community biomass stability via enhancing species asynchrony, which is a key causal process underlying forest temporal stability. This finding supports the biodiversity insurance hypothesis. Species asynchrony decreased biomass stability via reducing biomass variability, and structural diversity significantly increased mean biomass and biomass variability especially in old-growth forests, emphasizing the complementary dynamics. Functional trait diversity and CWM trait values, besides variation in CWM wood density, weakly affected community biomass stability and its two components. Soil nutrients directly and indirectly influence biomass stability via enhancing species asynchrony and mean biomass. Climatic variables affected species asynchrony primarily by affecting tree diversity, further affecting biomass stability. Our work highlights the stabilizing effect of biodiversity on forest functioning across China's forest ecosystems. This study provides insights into the complex interrelationships between tree diversity and community temporal stability as well as how various environmental conditions affect these processes and their underlying mechanisms. This insight can be used to inform the conservation and management of various forests.

CRedit authorship contribution statement

Anchi Wu: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Guoyi Zhou:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Honglin He:** Conceptualization, Data curation, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Yann Hautier:** Validation, Visualization, Methodology, Software, Writing – original draft, Writing – review & editing. **Xuli Tang:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Juxiu Liu:** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Qianmei Zhang:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Silong Wang:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Anzhi Wang:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Luxiang Lin:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Yiping Zhang:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Zongqiang Xie:** Investigation, Data curation, Writing – original draft, Writing – review & editing. **Ruiying Chang:** Investigation, Data curation, Writing – original draft, Writing – review & editing.

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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