

Biodiversity contributes to stabilizing ecosystem productivity across spatial scales as much as environmental heterogeneity in a large temperate forest region

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ABSTRACT

Although the destabilizing effects of biodiversity loss on ecosystem functioning at local and larger spatial scales are fairly well understood, the consequences of environmental homogenization have received much less attention. Based on detailed measurements of permanent natural forest plots distributed over a large temperate forest region, we explored the effects of environmental heterogeneity and biodiversity on ecosystem stability at local and larger spatial scales. Our results show that the relationship between environmental heterogeneity and biodiversity, as well as between environmental heterogeneity and stability across scales are mostly nonlinear, and that biodiversity stabilizes ecosystem functioning in these natural forests across scales. The unique contribution of biodiversity to stabilizing ecosystem functioning from local to larger scales is greater than the heterogeneity of climate, soils, topography, vegetation, and land cover. To our knowledge, this study is the first to quantify the effects of environmental heterogeneity on the temporal stability of forest productivity in a large natural forest region. Our results imply that biodiversity contributes to stabilizing forest ecosystems from local to larger spatial scales as much as environmental heterogeneity. Research involving large heterogeneous landscapes is critical to understanding the ecological effects of biodiversity across scales. The results of this study are thus relevant for developing effective conservation and land management strategies.

1. Introduction

The current global biodiversity crisis and large-scale changes in environmental conditions (e.g. global warming and nitrogen deposition) are raising concerns about the consequences of local diversity loss as well as biotic and environmental homogenization (Cardinale et al., 2012; McKinney & Lockwood, 1999; Olden et al., 2004; Vitousek et al., 1997). Numerous studies have presented evidence that biodiversity improves the functioning and stability of local communities (Hautier

et al., 2015; Hautier et al., 2020; Valencia et al., 2020; Wang et al., 2021). Similarly, many studies have shown the influence of other environmental drivers to the functioning and stability of local communities (García-Palacios et al., 2018; Hautier et al., 2015; Ma et al., 2017; Wang et al., 2020). However, little is known on the relative contribution of biodiversity to ecosystem functioning compared to other drivers of ecosystem functioning. To our knowledge, the few studies investigating this question have shown that local plant diversity can impact primary productivity as much as other environmental drivers (Hooper et al.,

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2012; Tilman et al., 2012). Of the many potential factors affecting ecosystem stability, environmental heterogeneity is generally considered to be an important factor that is particularly relevant to conservation since it is amenable to manipulation (Oliver et al., 2010). Many researchers have suggested that the effects of environmental heterogeneity may be widespread, which may buffer against environmental change and affect the stability of local communities (Benton et al., 2003; Luoto & Heikkinen, 2008; Oliver et al., 2010). However, to date, no studies have compared the contribution of plant diversity to the stability of productivity with environmental heterogeneity. Hereafter, by stability we mean the temporal invariability of productivity measured as the ratio of the temporal mean of productivity by its standard deviation (Tilman et al., 2006).

Current biodiversity changes occur at multiple spatial scales in response to climate warming, species invasion, and habitat degradation, prompting us to expand our research on biodiversity-stability relationships and to understand how ecosystem stability changes from local to biogeographic scales (Gonzalez et al., 2020). Wang and Loreau (2014) proposed a theory for scaling up research on the stability of ecosystem functioning from a single local community to a regional meta-community. According to this theory, regional (or gamma) stability of an ecosystem property through time is affected by two key components: alpha stability (the temporal stability of local communities) and spatial asynchrony (asynchronous temporal dynamics among local communities in response to environmental fluctuations; Fig. 1), while all potential ecological drivers should impact gamma stability through these two theoretical components (Wang and Loreau, 2014). This theory further links biodiversity and stability from local to larger spatial scales,

predicting that greater local species diversity (alpha diversity) and higher variation in species composition among communities (beta diversity) may increase gamma stability through local insurance effects of alpha stability and large spatial insurance effects of spatial asynchrony (Wang and Loreau, 2016). Several recent empirical studies on taxa in grasslands (Hautier et al., 2020; Liang et al., 2022; Liang et al., 2021; Wang et al., 2019; Wang et al., 2021; Zhang et al., 2019; Zhang et al., 2018), and on aquatic and terrestrial animals (Catano et al., 2020; Patrick et al., 2021) found positive biodiversity-stability relationships at multiple spatial scales, but studies in forests are still relatively rare (Qiao et al., 2022). Evidence of biodiversity-stability effects in forests refers mainly to limited local scales (Jucker et al., 2014; Morin et al., 2014; Ouyang et al., 2021; Schnabel et al., 2021; Yuan et al., 2019), which restricts our understanding of the scale-dependence of the stabilizing effects of biodiversity at the landscape level.

The effects of environmental heterogeneity on biodiversity and ecosystem stability are well documented for local scales (Collins et al., 2018; Hughes & Roughgarden, 1998; Kallimanis et al., 2010; Oliver et al., 2010; Stein et al., 2014). These effects remain poorly known however across scales (Catano et al., 2020; Qiao et al., 2022), especially considering the multiple facets of environmental heterogeneity. Based on the multiscale framework of stability, environmental heterogeneity may affect the links between biodiversity, asynchrony, and stability from local to larger spatial scales (see Fig. 1 and Table 1 for details on the hypotheses). Higher environmental heterogeneity may increase the available niche space at local scales, allowing more species to coexist, potentially increasing local diversity and the stability of ecosystem functions (Oliver et al., 2010; Stein & Krefl, 2015). Environmental

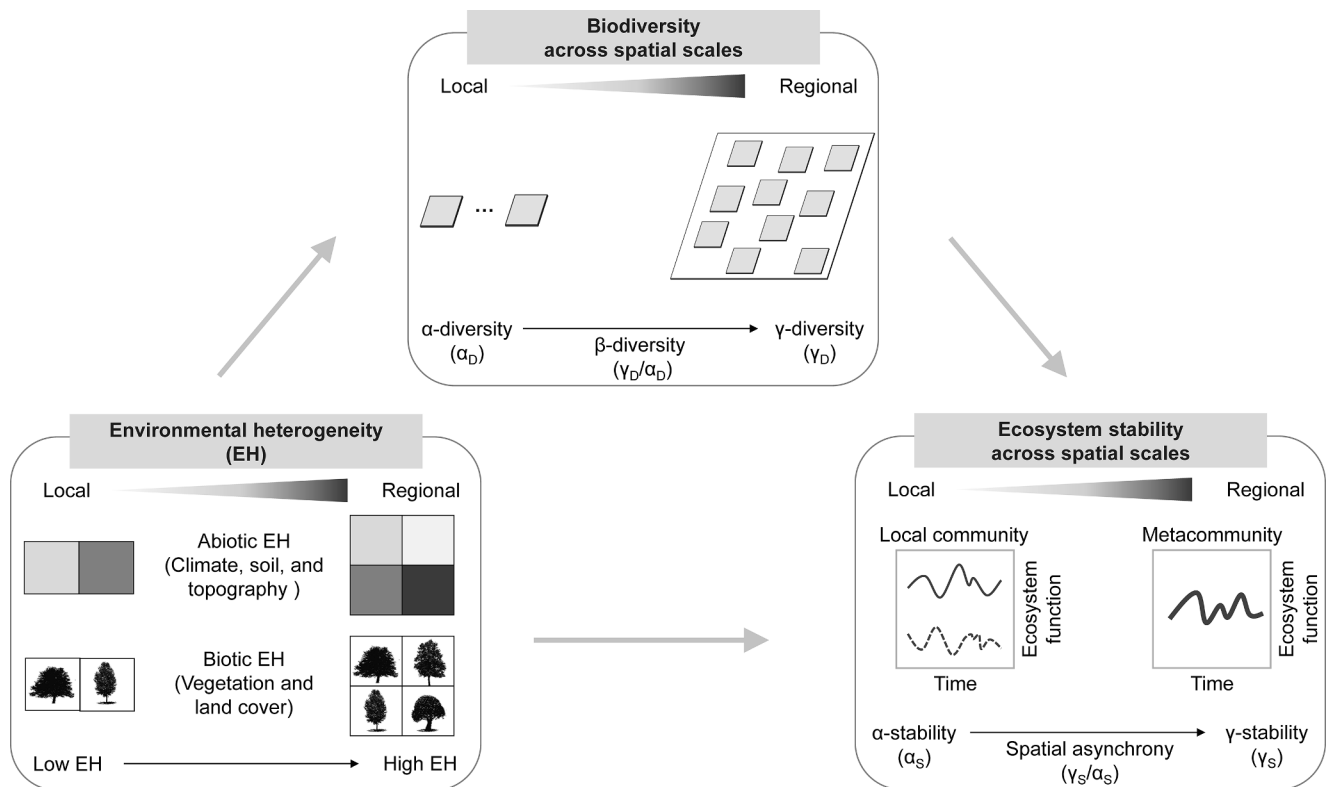


Fig. 1. A theoretical framework of environmental heterogeneity and biodiversity effects on ecosystem stability across spatial scales. Environmental heterogeneity is divided into abiotic environmental heterogeneity and biotic environmental heterogeneity, including climatic heterogeneity, soil heterogeneity, topographic heterogeneity, vegetation heterogeneity and land cover heterogeneity. Biodiversity across scales includes alpha (α) diversity representing the diversity of small-scale local communities, gamma (γ) diversity representing the diversity of regional metacommunities at larger spatial scales, and beta (β) diversity representing species turnover across space. β diversity was defined as the ratio of γ diversity to α diversity. Stability across scales includes alpha (α) stability representing the stability of local communities, gamma (γ) stability representing the stability of regional metacommunities, and spatial asynchrony representing asynchronous temporal dynamics among local communities in response to environmental fluctuations. Spatial asynchrony was defined as the ratio of γ stability to α stability. Stability (local and larger spatial scales) was defined as the temporal invariability of biomass productivity.

Table 1
Hypotheses related to key predictions from theories relating environmental heterogeneity, biodiversity and ecosystem stability across spatial scales.

Pathway	Hypotheses and mechanisms	References
Environmental heterogeneity → Biodiversity across scales	Higher environmental heterogeneity may (i) increase the environmental gradient, habitat type, resource, and structural complexity, which increase the available niche space; (ii) provide shelter from adverse environmental conditions and extreme weather; and (iii) increase the probability of speciation events caused by isolation or adaptation to complex environments; those are thought to promote species diversity.	(Stein et al., 2014; Kallimanis et al. 2010; Hughes & Eastwood, 2006)
Biodiversity across scales → Ecosystem stability across scales	Higher species diversity may (i) increase the asynchronous temporal response exhibited by different species to their shared local environment; (ii) promote biomass stability through overyielding. Higher variation and dissimilarity in species composition among communities may respond more effectively (“in asynchrony”) to environmental fluctuations than lower and similar in species composition among communities.	(Loreau & de Mazancourt 2008; Doak et al. 1998; Isbell et al. 2009; Wang & Loreau, 2016; Hautier et al. 2020)
Environmental heterogeneity → Ecosystem stability across scales	Heterogeneous landscapes may provide a wider range of resources and microclimates, which can buffer the impact of population on climate change and produce more stable population dynamics. The increase in the spatial heterogeneity of species composition may lead to the heterogeneity of species abundance through time, in response to environmental variability, and ultimately leads to the stability of ecosystem functions.	(Oliver et al. 2010; Wang & Loreau, 2016; Wilcox et al. 2017; Collins et al. 2018)

heterogeneity and species turnover are expected to be greater at large spatial scales (McGranahan et al., 2016; Wang and Loreau, 2014; Wilcox et al., 2017). Some studies have proposed that environmental heterogeneity should be the main focus for maintaining the stability of ecosystem functioning at larger spatial scales (Wang and Loreau, 2016; Wilcox et al., 2017). Until recently, however, research in this area has been lacking.

The known environmental heterogeneity studies face two major challenges: 1) the challenge to capture a comprehensive set of variables representing environmental heterogeneity (Catano et al., 2020; Collins et al., 2018; Stein & Krefl, 2015). Environmental heterogeneity is a multi-faceted issue, including land cover, vegetation, climate, soils, and topography (Stein & Krefl, 2015). Plant communities may respond differently to these different facets of environmental heterogeneity (Heidrich et al., 2020). Some studies may thus have a one-sided understanding of the role of environmental heterogeneity, depending on

which facet of environmental heterogeneity is used. 2) Studies using simple linear effects may not be able to assess the actual shape of the relationship between environmental heterogeneity and biodiversity (or stability; (Heidrich et al., 2020). The “area-heterogeneity trade-off” hypothesis claims that because all species have a finite ecological niche width, increased heterogeneity leads to a decrease in the average effective area available per species, which increases the probability of stochastic extinctions and leads to a decline in species richness (Allouche et al., 2012; Ben-Hur and Kadmon, 2020). This mechanism is usually accompanied by a fragmentation effect of heterogeneity, which may lead to unimodal patterns in the heterogeneity-diversity relationships (Heidrich et al., 2020). Many studies have suggested that empirical data are more consistent with the unimodal pattern predicted by the area-heterogeneity trade-off than the pattern predicted by classical ecological niche theory. Stein et al. (2014) and Ben-Hur and Kadmon (2020) called for more empirical studies that focus on the non-linear effects to understand the actual shape of the environmental heterogeneity and species diversity relationship (HDR).

Based on a large data set of forest plots distributed over a large temperate forest area of Northeast China, we aim to answer the following question: How and to what extent is ecosystem stability in natural forests driven by multiple facets of environmental heterogeneity and biodiversity across scales. Accordingly, we will test 3 hypotheses (Heidrich et al., 2020; Oliver et al., 2010; Stein & Krefl, 2015; Wang and Loreau, 2016): Hypothesis I: the relationship between environmental heterogeneity and biodiversity across scales is linear. Hypothesis II: the relationship between environmental heterogeneity and stability across scales is also linear. Hypothesis III: both environmental heterogeneity and biodiversity are important drivers determining the stability of natural forests at multiple spatial scales. Fig. 1 and Table 1 provide more details on these hypotheses.

2. Methods

2.1. Study area

Altogether 300 circular field plots of 0.1 ha are distributed in the temperate forests of four provinces in Northeast China (39°42'48" to 53°19'21"N; 119°48'12" to 134°01'01"E). The region includes eight mountain landscapes with a relatively steep terrain and elevations ranging between 97 and 1,255 m. The region is characterized by a temperate continental climate, with long, cold winters and warm summers. The long-term average annual temperature and precipitation are 2.8°C and 700 mm, respectively. The dominant vegetation type in the region is a mixed forest of broad-leaved tree species and *Pinus koraiensis*. The entire study area covers approximately 700,000 km² (Fig. 2). All individual tree species with diameters at breast height (DBH) ≥ 5 cm were identified and mapped, and measured for DBH and tree height (Cornelissen et al., 2003).

Some areas were densely sampled, while others were sparsely sampled. In order to minimise the problem of uneven sampling, a subset of plots (300 out of 455) that were relatively evenly distributed across the study area was used (Fig. 2). Each of the forest plots and its nearest n neighbouring plots were used to define a particular regional metacommunity (Qiao et al., 2022; Xing and He, 2019; Zhang et al., 2020). Each metacommunity was thus composed of $N = n + 1$ local communities (the n nearest local communities + the central local community), where N defines the spatial extent of each metacommunity (Supporting Information Appendix S1: Fig. S1). By expanding the spatial extent of the study area from a single local community to a regional metacommunity, it is possible to study the relationship between environmental heterogeneity, biodiversity, and stability from local to greater biogeographic scales. A Mantel correlogram was used to assess the spatial correlation of the community composition among the studied plots (Legendre & Legendre, 2012). We found that neighboring communities tend to exhibit a similar community composition when the

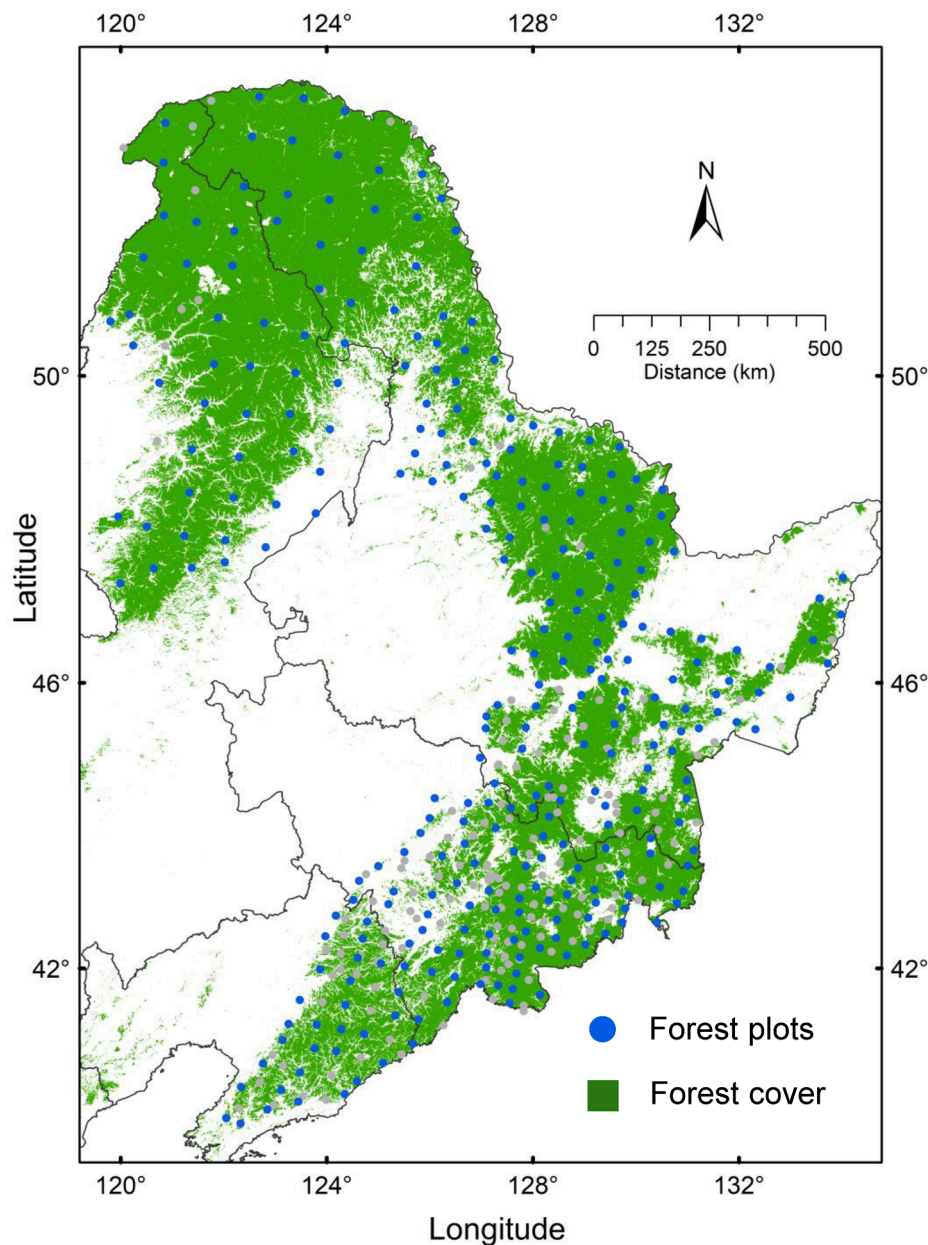


Fig. 2. Location of plots. Location of permanent inventory forest plots of this study shown on a forest cover map produced from global land cover data. A total of 300 (blue points) out of 445 forest plots (grey points) were included in the analysis, to ensure an even sampling coverage across the region of temperate forests. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

spatial extent of regional communities is less than about 180 km (Supporting Information Appendix S1: Fig. S2). Environmental heterogeneity, diversity, stability, and other variables were assessed at 6 different spatial extent of metacommunities ($N = 5$ to 10). The maximum spatial extent of each metacommunity does not exceed 180 km (Supporting Information Appendix S1: Fig. S3).

2.2. Quantifying environmental heterogeneity

Following the classification of environmental heterogeneity by Stein and Krefl (2015), we subdivided the total heterogeneity into five components, climatic heterogeneity, soil heterogeneity, topographic heterogeneity, vegetation heterogeneity, and land cover heterogeneity. Measured variables were selected for each of the five facets of environmental heterogeneity (Bar-Massada & Wood, 2014; Stein & Krefl, 2015; Udy et al., 2021). Environmental heterogeneity of each regional

community was quantified as the difference between constituent plots (Udy et al., 2021). Specifically, to quantify environmental heterogeneity, we used the following measures: range (RA; max. – min.), standard deviation (s.d.), coefficient of variation (CV; the ratio of the standard deviation to the mean). Then we examined the statistical behaviour and collinearity of all variables for the final selection (Heidrich et al., 2020; Qiao et al., 2021). Precipitation CV, soil pH s.d., elevation CV, tree height s.d., land cover type were selected to represent five facet of environmental heterogeneity in this study.

Abiotic environmental heterogeneity involves micro- to macro-climatic conditions or micro-topographic structural elements for large-scale topographic relief (Stein et al., 2015). Following Duraes and Loisel (2004), the coefficient of variation of the annual mean precipitation was used to quantify climatic heterogeneity in the metacommunities. The climatic data in this study, such as the annual average precipitation, are extracted from WorldClim 2.1 (Fick &

Hijmans, 2017). To quantify soil heterogeneity, the coefficient of variation of the soil pH was used. The soil data in this study were extracted from the Harmonized World Soil Database (FAO et al., 2012). Topographic heterogeneity is a frequently used measure of heterogeneity, and is most often quantified as the elevation range and coefficient of variation (Finch et al., 2008; Oliver et al., 2010). The coefficient of variation of the elevation was used to quantify topographic heterogeneity in the metacommunities. The elevation of each local plot was measured in the field.

Forest structural heterogeneity was used to denote the vegetation heterogeneity of the forest community (Heidrich et al., 2020). The vertical forest structure is an essential attribute of forest structure (Enquist et al., 2009). To quantify structural heterogeneity, the standard deviations of the individual tree heights of the entire metacommunity were used (Stein & Krefl, 2015). The Global Land Cover Classifications of the University of Maryland, Department of Geography (UMD) were used for our data analysis, with a spatial resolution of 1 km for the entire globe (Hansen et al., 2000). The UMD classification describes the geographic distribution of 13 classes of land cover (see more detail in Appendix S2). The number of land cover types in each metacommunity was used to quantify the land cover heterogeneity (Kohn et al., 1994; Stein & Krefl, 2015).

2.3. Biodiversity and stability across spatial scales

We measured species diversity at both the local (α) and the larger (γ) spatial scale. Simpson-based diversity metrics, which take into account both the number of species and the evenness of species abundance, are predicted by theory to best explain the stability of ecosystems at different spatial scales (de Mazancourt et al., 2013; Wang and Loreau, 2016; Wang et al., 2021). Among these metrics, the inverse of the Simpson concentration index is actually a true diversity index, that is the diversity of order 2 (Jost, 2006). As such it provides an effective number of species and greater sensitivity to species relative frequencies. Therefore, we quantify species diversity in different years using the inverse of the Simpson concentration index, $1/\sum_i p_i^2$, where p_i is the observed relative abundance of species i . Specifically, alpha diversity (α_D) was measured as the inverse of a weighted average of local community Simpson indices, weighted by the ratio of total biomass of the local community to that of the metacommunity. Gamma diversity (γ_D) was measured as the inverse of Simpson index of the metacommunity. Following theoretical models, beta diversity (β_D) was defined multiplicatively, that is the ratio of gamma diversity to alpha diversity (Wang and Loreau, 2014, 2016).

Corresponding to the diversity measures across scales, we also measured ecosystem stability at local and larger spatial scales (Liang et al., 2021; Wang and Loreau, 2016). Stability is defined as the temporal invariability of biomass productivity (Hector et al., 2010; Jucker et al., 2014; Morin et al., 2014). During the summer of 2017, an increment borer with an auger diameter of 5.15 mm was used to extract incremental cores from the north side of each tree (21,407 in total) at the height of 1.3 m. The incremental core of each tree must pass through the center of the tree and must be more than 2 cm in length. The biomass accumulation of all individuals with DBH \geq 5 cm was calculated for total productivity using a set of regional- and species-specific allometric models with DBH and wood density as independent variables (Qiao et al., 2022; Wu et al., 2019). The biomass of each sample plot was calculated for the years 2005, 2009, 2013, and 2017, since using multi-year measurement intervals can reduce short-term anomalous fluctuations in forest ecosystem functioning caused by climatic extremes (Von Gadow & Hui, 1999). Specifically, gamma stability (γ_S), alpha stability (α_S) and spatial asynchrony (ω) in the metacommunity was calculated as:

$$\gamma_S = \sum_k \mu_k / \sqrt{\sum_{k,l} \nu_{kl}} \quad (1)$$

$$\alpha_S = \sum_k \mu_k / \sum_k \sqrt{\nu_{kk}} \quad (2)$$

$$\omega = \sum_k \sqrt{\nu_{kk}} / \sqrt{\sum_{k,l} \nu_{kl}} \quad (3)$$

where μ_k and ν_{kk} denote the temporal mean and variance of forest productivity in the community k , and ν_{kl} denotes the covariance of the forest productivity between community k and l . Spatial asynchrony (ω) captured the asynchronous temporal dynamics among local communities in response to environmental fluctuations, and was defined as the ratio of gamma stability to alpha stability.

2.4. Statistical analysis

All analyses were conducted in R unless specified otherwise (R Core Team 2021, version 4.1.0). We tried two modeling approaches to evaluate the environmental heterogeneity-biodiversity relationship and the environmental heterogeneity-stability relationship, including linear mixed models (LMMs) and generalized additive mixed models (GAMMs; Fig. 3; Supporting Information Appendix S1: Fig. S4;). GAMMs were used because of its capacity to capture complex and non-linear relationships. The largest possible df was set to 5 for each smoother ($k = 5$), so that these results were visually better rendered and overfitting problems were avoided. We seek to understand ecosystem stability patterns through the study of multiple spatial extents ($N = 5$ to 10). Therefore, LMMs and GAMMs were used with spatial extent as random factors. The function *lme* in the “nlme” package was used to construct the linear mixed model (Pinheiro et al., 2017). The *tab_model* function of the “sjPlot” package was used to calculate conditional R^2 (Lüdecke, 2018). The *gam* function of the “mgcv” package was used to fit generalized additive mixed models (Wood & Wood, 2015). The explanatory variables were standardized (average = 0 and standard deviation = 1) at each spatial extent for normality and linearity (Cadotte, 2015). The variables of diversity, stability, and asynchrony were log (base 10) transformed to linearize the relationships before analysis (Wilcox et al., 2017). More importantly, the log-transformation allows the variation of gamma stability to be fully explained by alpha stability and spatial asynchrony (Wang et al., 2021). To avoid multicollinearity effects, we made sure that the variance inflation factor (VIF) of all predictive variables was less than five (Coelho de Souza et al., 2019).

GAMMs were used to show the total percentage (%) of deviance explained (DE); the Akaike Information Criterion (AIC) values for the analyses of theoretical components of the metacommunity stability (alpha stability and spatial asynchrony) as a function of environmental heterogeneity and biodiversity measures (Table 2), are calculated as follows:

$$y_i = a + f_1(x_i) + f_2(c_i) + \dots + f_n(v_i) + \varepsilon_i \quad (4)$$

where a is an intercept parameter, x_i , c_i , and v_i are explanatory variables, y_i is response variable, and the f_j are smooth functions, and the ε_i are independent $N(0, \sigma^2)$ random variables.

A variety of diagnostic methods were used to test the contribution of alpha diversity and beta diversity. Three model comparisons were made using GAMMs (Table 3), as follows:

Model Comparisons 1:

$$f_1(EH) + f_2(\alpha) \text{ versus } f_1(EH) \quad (5)$$

Model Comparisons 2:

$$f_1(EH) + f_2(\beta) \text{ versus } f_1(EH) \quad (6)$$

Model Comparisons 3:

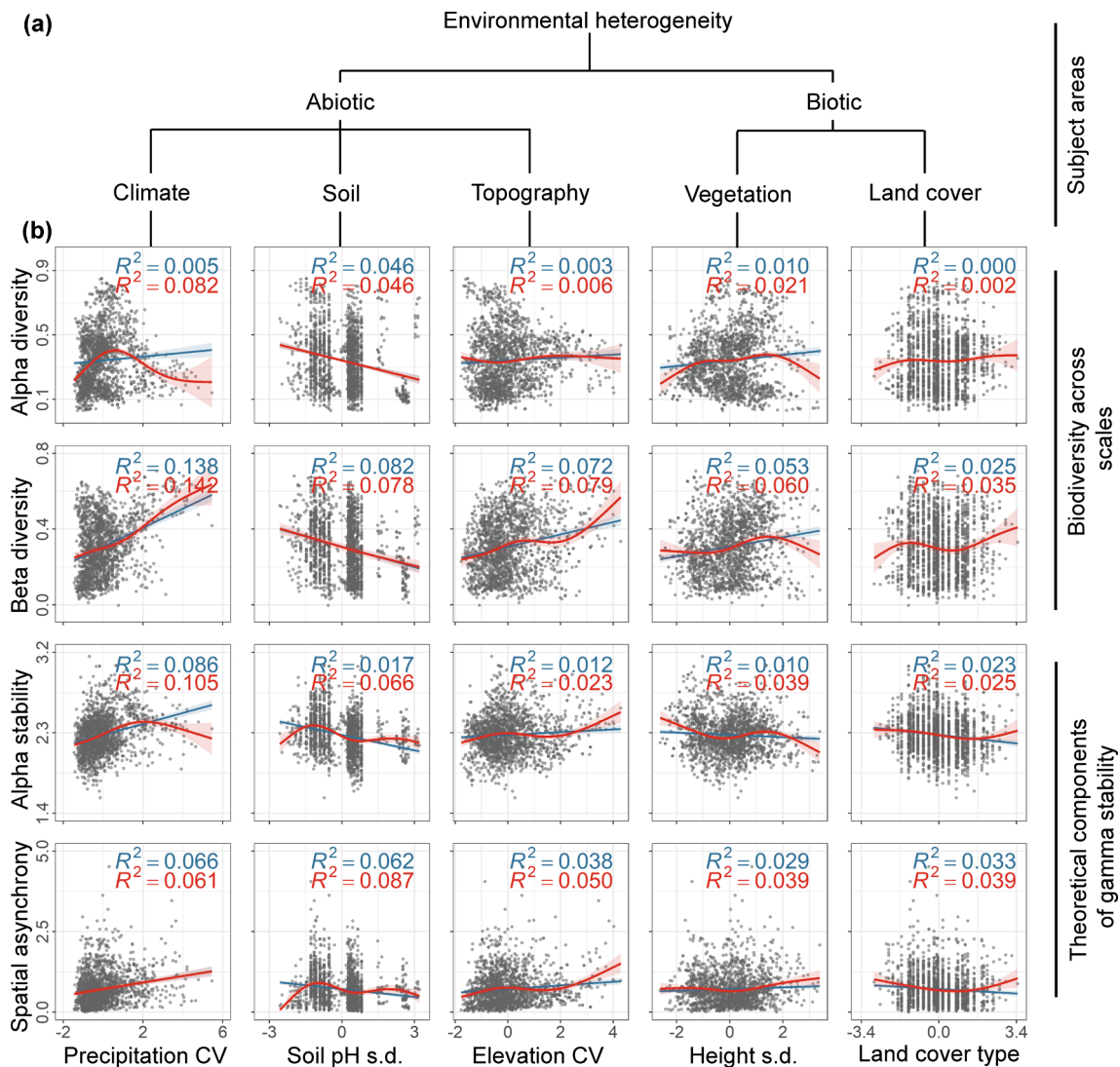


Fig. 3. The relationship between environmental heterogeneity and biodiversity, as well as between environmental heterogeneity and stability across scales. (a) Environmental heterogeneity in a forest ecosystem is represented by five subject areas: precipitation CV, soil pH s.d., elevation CV, tree height s.d., land cover type. (b) The relationship between each facet of environmental heterogeneity and alpha diversity, beta diversity, alpha stability, spatial asynchrony, respectively. The red line and R^2 values were estimated using the generalized additive mixed models (GAMMs), representing significant overall relationships (non-linear fixed effects) at multiple spatial extents, and shaded areas represent 95 % confidence intervals. The blue line and R^2 values were estimated using the line mixed models (LMMs), representing significant overall relationships (linear fixed effects) at multiple spatial extents, and shaded areas represent 95 % confidence intervals. Solid lines represent the significant paths ($p < 0.05$) and dashed lines indicate non-significant paths ($p > 0.05$). The following abbreviations were used: s.d., standard deviation; CV, coefficient of variation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$f_1(EH) + f_2(\alpha) + f_3(\beta) \text{ versus } f_1(EH) + f_2(\alpha) \quad (7)$$

where environmental heterogeneity includes five facets of environmental heterogeneity. The additional percentage of deviance explained (ΔDE), and adjusted coefficient of determination (ΔR_{adj}^2) was used to indicate the explanatory power induced by adding variables. We used the Akaike Information Criterion (AIC) of each model (base model + added variables) minus the AIC of the base model to quantify the difference in model fit (ΔAIC). This approach also approximates whether the reduction in total deviation caused by adding each biodiversity measure to the environmental heterogeneity model was significant (p -value) which was performed using the *anova.gam* function in the “mgcv” package (Burley et al., 2016). Latitude and longitude were included in the model to account for the potential effects of spatial autocorrelation between metacommunities (Gross et al., 2017; Maestre et al., 2012). The sinus and cosinus values of the longitude were used to avoid bias caused by the intrinsic circularity of longitude in the regression model (Le Bagousse-Pinguet et al., 2017).

The relative contribution (%) of five facets of environmental heterogeneity (EH), alpha diversity, and beta diversity were estimated with regard to alpha stability and spatial asynchrony (Fig. 4). These contributions were divided into combined contribution (proportion of variance that is explained by environmental heterogeneity, alpha diversity, and beta diversity) and unique contributions (proportion of variance that can be uniquely explained by a single predictor and excluding the contribution of longitude and latitude), which is determined by the deviance decomposition method.

3. Results

We found that most environmental heterogeneity-biodiversity relationships and environmental heterogeneity-stability relationships are non-linear (Fig. 3). The different facets of environmental heterogeneity varied greatly in explaining the variation in biodiversity and ecosystem stability (Fig. 3b). Specifically, climatic heterogeneity explained most of

Table 2

Total percentage (%) of deviance explained (DE) and Akaike information criterion (AIC) values for the analyses of alpha stability and spatial asynchrony as a function of environmental heterogeneity (EH) and biodiversity measures. The following abbreviations were used: Five-EH, five facets of environmental heterogeneity, including climatic heterogeneity, soil heterogeneity, topographic heterogeneity, vegetation heterogeneity, and land cover heterogeneity.

Response	Predictors	DE (%)	R ² _{adj}	AIC	ΔAIC
Alpha stability	Five-EH	34.3 %	0.333	-1063.508	135.807
	Five-EH	38.0 %	0.368	-1155.64	43.676
	Five-EH	36.5 %	0.354	-1116.999	82.316
	Five-EH	39.8 %	0.385	-1199.316	0
	α diversity	31.8 %	0.312	-1021.316	178.000
	β diversity	30.4 %	0.297	-982.8021	216.514
	α diversity	33.3 %	0.325	-1052.492	146.824
	β diversity	22.1 %	0.209	2351.42	116.293
Spatial asynchrony	Five-EH	22.1 %	0.209	2351.42	116.293
	Five-EH	22.7 %	0.213	2345.621	110.494
	Five-EH	27.1 %	0.257	2244.231	9.104
	Five-EH	27.8 %	0.263	2235.127	0
	α diversity	17.8 %	0.170	2424.354	189.227
	β diversity	22.1 %	0.213	2327.943	92.815
	α diversity	22.9 %	0.220	2317.572	82.445
	β diversity				

Table 3

Results for the generalized additive mixed models of alpha stability and spatial asynchrony. For each model comparison (i.e., base model *versus* base model + added variable). Five facets of environmental heterogeneity (EH) include: precipitation CV, pH s.d., elevation CV, height s.d., land cover type. ΔDE (%) is the average additional percentage of deviance explained by adding that variable. ΔAIC is the Akaike information criterion (AIC) values for each model (i.e., base model + added variable) minus the base model. ΔR²_{adj} is the average additional percentage of variance explained by adding that variable. The following abbreviations were used: Five-EH, five facets of environmental heterogeneity, including climatic heterogeneity, soil heterogeneity, topographic heterogeneity, vegetation heterogeneity, and land cover heterogeneity.

Response	Base model	Added variable	ΔDE	ΔAIC	ΔR ² _{adj}	p-value
Alpha Stability	Five-EH	+ α diversity	3.62 %	-92.131	0.035	< 0.001
	Five-EH	+ β diversity	2.10 %	-53.491	0.020	< 0.001
	Five-EH + α diversity	+ β diversity	1.80 %	-43.676	0.017	< 0.001
Spatial asynchrony	Five-EH	+ α diversity	0.59 %	-5.799	0.004	< 0.05
	Five-EH	+ β diversity	4.96 %	-107.189	0.048	< 0.001
	Five-EH + α diversity	+ β diversity	5.08 %	-110.494	0.050	< 0.001

the variation in alpha diversity, beta diversity and alpha stability (Fig. 3b; $R^2 = 0.082$, $p < 0.001$; $R^2 = 0.142$, $p < 0.001$; $R^2 = 0.105$, $p < 0.001$). Soil heterogeneity explained most of the variation in spatial asynchrony (Fig. 3b; $R^2 = 0.087$, $p < 0.001$).

Our additive model revealed that the best model included the five facets of environmental heterogeneity (five-EH, that is, climatic heterogeneity, soil heterogeneity, topographic heterogeneity, vegetation heterogeneity, and land cover heterogeneity), alpha diversity, and beta diversity (Table 2) and explained a large percentage of the deviance in alpha stability (39.8 %) and spatial asynchrony (27.8 %). The combined five facets of EH, alpha diversity, and beta diversity explained 34.3 %, 31.8 % and 30.4 % of the deviance in alpha stability, respectively, and 22.1 %, 17.8 % and 22.9 % of the deviance in spatial asynchrony, respectively. Most of the deviance in alpha stability was explained by the five EH and alpha diversity, with alpha diversity explaining an additional 3.62 % of alpha stability relative to the deviance explained by the five EH combined (Table 3). Most of the deviance in spatial asynchrony was explained by beta diversity and the five EH, with beta diversity explaining an additional 4.96 % of spatial asynchrony relative to the deviance explained by the five EH combined (Table 3).

Alpha diversity had the highest percentage of the unique contribution to alpha stability (5.08 %), followed by vegetation heterogeneity (1.49 %). The unique contributions of individual EH were all below 2 % (Fig. 4a-b). Beta diversity had the highest percentage of the unique contributions to spatial asynchrony (3.31 %), followed by vegetation heterogeneity (1.94 %). Among the five EH, vegetation heterogeneity contributed most to alpha stability and spatial asynchrony (Fig. 4c). The unique contribution of most predictor variables to gamma stability through spatial asynchrony is greater than that through alpha stability (Fig. 4c-d). Beta diversity had the highest percentage of unique contribution to gamma stability (4.11 %), followed by vegetation heterogeneity (1.63 %), alpha diversity (1.48 %), topographic heterogeneity

(1.08 %), soil heterogeneity (0.99 %), climatic heterogeneity (0.88 %), and land cover heterogeneity (0.46 %) (Fig. 4d). The unique contribution of diversity within and among local communities combined (5.58 %; alpha diversity + beta diversity) to gamma stability was greater than that of the five EH (5.03 %; Fig. 4).

4. Discussion

Based on a large set of natural forest plots covering an extensive temperate forest region and using a multi-scale stability framework, we estimated the effect of the multiple facets of environmental heterogeneity and biodiversity on the stability of forest productivity across scales. Our results show that the relationship between environmental heterogeneity and biodiversity, as well as between environmental heterogeneity and stability across scales were mostly nonlinear (Hypotheses I and II). Both environmental heterogeneity and biodiversity were important drivers for determining the stability of natural forests at multiple spatial scales (Hypothesis III). The unique contribution of biodiversity to stabilizing ecosystem functioning at both local and landscape scales was greater than that of environmental heterogeneity, including climate, soils, topography, vegetation, and land cover. These findings highlight the important role of biodiversity in stabilizing forest ecosystem functioning.

Our widely distributed forest plots with large ecological gradients allow us to test the relative contribution of the multiple facets of environmental heterogeneity and biodiversity to ecosystem stability from local to regional scales. Biodiversity contributes to the stability of forest productivity at least as much as environmental heterogeneity, including climate, soils, topography, vegetation, and land cover. Both theoretical and empirical studies have reported biodiversity to stabilize regional ecosystem functions through local and spatial “insurance” effects, respectively (Hautier et al., 2020; Wang and Loreau, 2016; Zhang et al.,

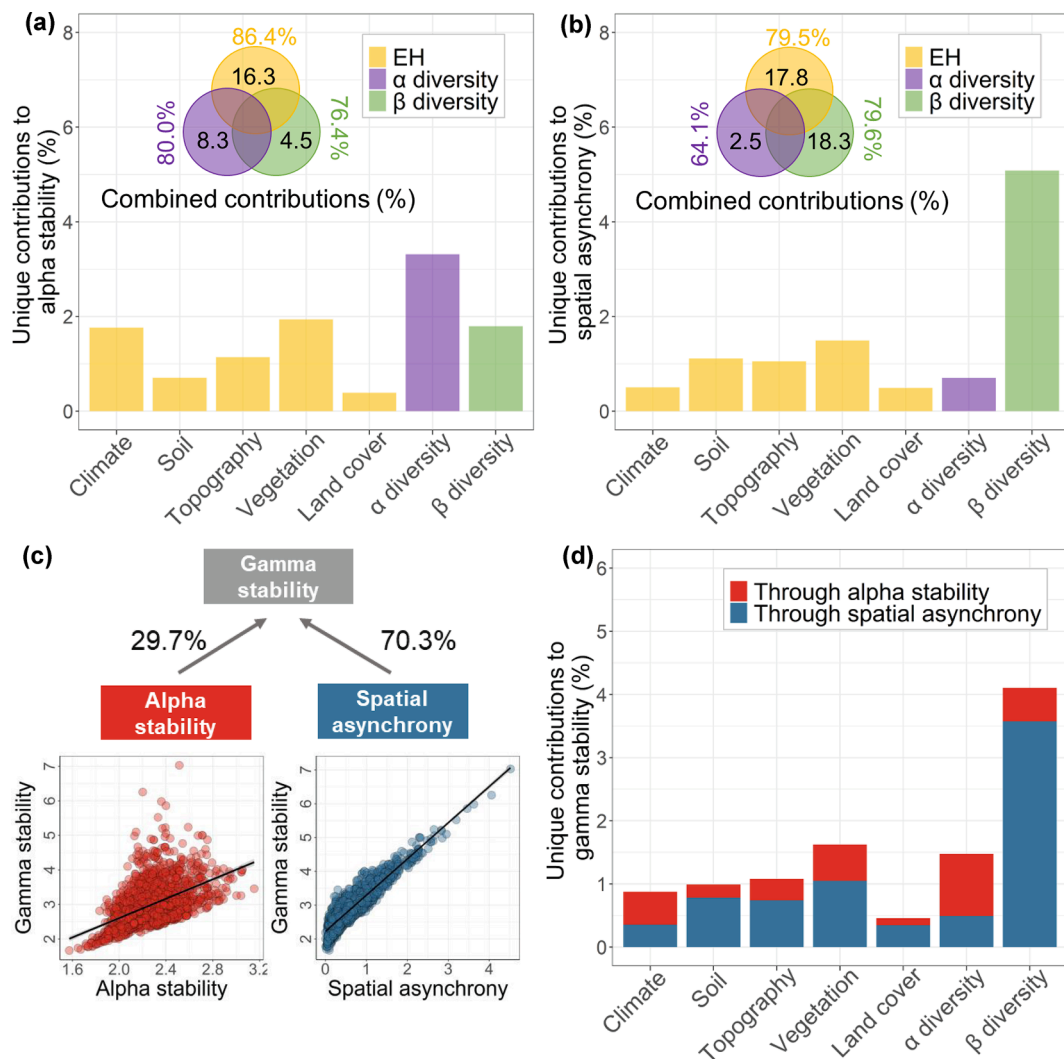


Fig. 4. Contribution (%) of environmental heterogeneity (EH), alpha diversity, and beta diversity to stabilize forest ecosystems from local to larger spatial scale. (a)-(b): Unique contributions (proportion of variance that a single predictor can uniquely explain) of environmental heterogeneity, alpha diversity, and beta diversity to alpha stability and spatial asynchrony, respectively. The Venn diagram in the upper left corner shows the combined contribution. (c): The relative contribution of alpha stability and spatial asynchrony to gamma stability. (d): Unique contributions of environmental heterogeneity, alpha diversity, and beta diversity to gamma stability through alpha stability and spatial asynchrony.

2019). Specifically, the local insurance effect is derived from the asynchronous responses of species with different functional traits to a local environment (Yachi & Loreau, 1999). The spatial insurance effect is derived from the asynchronous responses of local communities with different species compositions to a spatially correlated environment (Wang and Loreau, 2016). At the regional scale, environmental heterogeneity makes an important contribution to the stability of forest productivity (Fig. 4). Wang and Loreau (2016) used a dynamical model of competitive metacommunities and found that the stabilizing effect of biodiversity increases as spatial environmental correlation increases from the local to the regional scale. Our study estimated the relative contribution of biodiversity to regional stability and found that the stabilizing effect of each facet of environmental heterogeneity was lower than that of biodiversity from local to larger spatial scales (Fig. 4). Indeed, at the regional scale, the influence of the degree of spatial environmental heterogeneity on the stabilizing effect of biodiversity can be understood as: high environmental heterogeneity leads to spatial insurance effects. When environmental heterogeneity between local communities is low, homogeneous environments provide synchronous effects. The dissimilarity among local communities thus becomes important in providing

spatial insurance effects (Steiner et al., 2013; Wang and Loreau, 2016). This finding is relevant in the design of forested landscapes (Gadow, 2016; Gadow and Pukkala, 2008).

The relative contribution of the multiple facets of environmental heterogeneity to gamma stability through spatial asynchrony is greater than that through alpha stability (Table 2 and Fig. 4c and d). Wilcox et al. (2017) examined mechanisms of temporal stability across spatial scales in 62 plant communities from five continents, suggesting that environmental heterogeneity might be the key to maintaining the stability of ecosystem services at larger spatial scales. Our results show that five facets of environmental heterogeneity have an important contribution to regional stability through spatial asynchrony, which is consistent with Wilcox et al. (2017). We found that the unique contribution of different facets of environmental heterogeneity to ecosystem stability was quite different (Fig. 4). This may be due to the following reasons: 1) differences in resources and limitations in different regions, the main abiotic and biotic drivers of ecosystem functions are different. For example, mountains show sharp and foreseeable environmental change with elevation, so elevation is the main factor impacting ecosystem functioning in the alpine plant communities (Sanders & Rahbek, 2012). 2) Not every facet of environmental heterogeneity has

the full gradient length of heterogeneity in the real-world environment. Different facets of environmental heterogeneity have different lengths of the coverage gradient in our study area (Heidrich et al., 2020; Stein & Kreft, 2015), which may affect the relative importance of environmental heterogeneity to regional stability.

The results of our study show that among the various facets of environmental heterogeneity studied, vegetation heterogeneity made the highest unique contribution to spatial asynchrony, followed by soil heterogeneity (Fig. 4). Unlike grasslands and other ecosystems, the pronounced horizontal and vertical dimensions of vegetation in forest ecosystems can form complex habitats for various organisms (Heidrich et al., 2020). Vegetation heterogeneity reflects the variation of the microclimatic conditions in the forest. The availability of light and soil moisture are affected by the stand structure, resulting in different environmental conditions in the forest when compared to grasslands (Davies & Asner, 2014; Hardwick et al., 2015). This indirectly affects the biodiversity within the forest as well as multiple ecosystem processes and functions, including evaporation, decomposition, and vegetation productivity and its temporal stability (Ehbrecht et al., 2019; Schall et al., 2018). High abiotic heterogeneity, such as soil heterogeneity, is more likely to provide increased environmental gradients and resource availability. That in turn may increase niche space, and thus play an essential role in maintaining biodiversity and ecosystem functions (Kallimanis et al., 2010; Udy et al., 2021). However, the different facets of environmental heterogeneity are often closely linked (Stein et al., 2014; Stein & Kreft, 2015). For example, changes in topographic heterogeneity, usually lead to changes in temperature, precipitation, and species distribution, and thus to climatic and vegetation heterogeneity (Elsen et al., 2021; Stein & Kreft, 2015).

5. Conclusion

In this study, we examine the effects of environmental heterogeneity and biodiversity on stabilizing woody plant productivity across scales in a large temperate forest region. These effects are mostly nonlinear. Our results support the assumption that, at local and larger spatial scales, environmental heterogeneity and biodiversity are both important drivers that determine the stability of natural forests. Biodiversity contributes at least as much to the stability of forest productivity at multiple spatial scales as any one of the five facets of environmental heterogeneity investigated. Our results suggest that maintaining biodiversity at multiple spatial scales in heterogeneous landscapes is essential for stabilizing the functioning of natural forest ecosystems.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120695>.

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