

Latitudinal patterns of forest ecosystem stability across spatial scales as affected by biodiversity and environmental heterogeneity

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Abstract :

Our planet is facing a variety of serious threats from climate change that are unfolding unevenly across the globe. Uncovering the spatial patterns of ecosystem stability is important for predicting the responses of ecological processes and biodiversity patterns to climate change. However, the understanding of the latitudinal pattern of ecosystem stability across scales and of the underlying ecological drivers is still very limited. Accordingly, this study examines the latitudinal patterns of ecosystem stability at the local and regional spatial scale using a natural assembly of forest metacommunities that are distributed over a large temperate forest region, considering a range of potential environmental drivers. We found that the stability of regional communities (regional stability) and asynchronous dynamics among local communities (spatial asynchrony) both decreased with increasing latitude, whereas the stability of local communities (local stability) did not. We tested a series of hypotheses that potentially drive the spatial patterns of ecosystem stability, and found that although the ecological drivers of biodiversity, climatic history, resource conditions, climatic stability, and environmental heterogeneity varied with latitude, latitudinal patterns of ecosystem stability at multiple scales as affected by biodiversity and environmental heterogeneity. In particular, α diversity is positively associated with local stability, while β diversity is positively associated with spatial asynchrony, although both relationships are weak. Our study provides the first evidence for the latitudinal pattern of the temporal stability of naturally assembled forest metacommunities across scales as affected by biodiversity and environmental heterogeneity. Our findings suggest that the preservation of plant biodiversity within and between forest communities and the maintenance of

heterogeneous landscapes can be crucial to buffer forest ecosystems at higher latitudes from the faster and more intense negative impacts of climate change in the future.

Keywords : climatic history, resource conditions, climatic stability, forest productivity, spatial asynchrony, temporal stability, latitude, spatial scales

1. Introduction

Forests play a central role in protecting biodiversity and sequestering carbon, and are also considered an important natural solution to help mitigate climate change (Anderegg et al., 2020; Gibson et al., 2011; Luysaert et al., 2008). The ability of forests to maintain ecosystem functioning over time, especially in the face of environmental change, that is, temporal stability (hereafter “stability”), has gradually become a major focus of theoretical and empirical research on forest ecology and management (Jucker et al., 2014; Morin et al., 2014; Qiao et al., 2022; Schnabel et al., 2021). Climate change poses a variety of serious threats to tree survival, forest growth and sustainability (Bonan, 2008; Chausson et al., 2020; Gadow et al., 2021; Schnabel et al., 2019). However, its impact is uneven across the globe, leading to spatial differences in ecosystem functioning (Burrows et al., 2011; Choat et al., 2012; Loarie et al., 2009). For instance, the higher the latitude within a given region, the faster and more intense may the impacts of climate warming be expected (Antao et al., 2021; IPCC, 2014). Yet, there is still a lack of knowledge about how the stability of ecosystem functioning varies with latitude. Filling this knowledge gap could provide important insights for more effective designs and management solutions for forested landscapes, especially in areas most threatened by climate change (Anderegg et al., 2020; Astrup et al., 2018; Gadow et al., 2007).

Several studies have reported a decline in ecosystem functioning with latitude, which is in parallel with broad-scale patterns of biodiversity (Begon & Townsend, 2020; Gillman et al., 2015; Lieth & Whittaker, 2012; Tiegs et al., 2019). In contrast, the relationship between the temporal stability of ecosystem functioning and latitude is much less explored. The few existing studies conducted at local scales show that moths at higher latitudes tend to exhibit lower stability and more synchronous species dynamics (Antao et al., 2021), and that the biodiversity-stability relationship of zooplankton varies with latitude (Shurin et al., 2007). Currently, the threats of increasing environmental changes and human pressures on ecological communities occur from local to regional scales, calling for a better understanding of ecosystem stability at multiple spatial scales, which are more relevant to management and conservation (Gonzalez et al., 2020; Isbell et al., 2017; Wang et al., 2019). The multiscale theory of stability shows that the stability of regional communities (γ s, i.e. regional stability or γ stability) can be partitioned into the stability of local communities (α s, i.e. local stability or α stability) and asynchronous dynamics among local communities (β s, i.e. spatial asynchrony) (Wang et al., 2019; Wang & Loreau, 2014). However, it remains unknown how the multiscale nature of ecosystem stability changes with latitude and which ecological drivers shape this latitudinal pattern.

Among hypothesized stabilizing mechanisms, biodiversity has been intensively studied in local-scale experiments which have demonstrated that local community diversity (α_D , i.e. α diversity) stabilizes ecosystem functioning (Bai et al., 2004; Hautier et al., 2015; Jucker et al., 2014; Tilman et al., 2006). In recent years, the study of the biodiversity and stability relationship has been extended from a single local spatial scale to broader spatial scales (Wang & Loreau, 2016).

The multiscale theory of stability assumes that α diversity and species turnover across space (β_D , i.e. β diversity) are expected to enhance gamma stability mainly through its positive effects on local stability and spatial asynchrony, respectively (Wang & Loreau, 2014, 2016), since α diversity and β diversity can provide insurance effects for local and regional community dynamics by increasing species and spatial asynchrony, respectively (Liang et al., 2022; Wang & Loreau, 2016). There is mounting evidence from experimental studies on manipulated systems of positive biodiversity-stability relationships at multiple spatial scales (Hautier et al., 2020; Liang et al., 2021; Wang et al., 2019; Wang et al., 2021; Zhang et al., 2019). Given that the planet is facing significant changes in biodiversity across scales (Dee et al., 2022; Van der Plas, 2019), there has been a growing interest in returning to real-world ecosystems to understand whether and how biodiversity stabilizes ecosystem functioning in natural ecosystems and at broader scales (Catano et al., 2020; Liang et al., 2022; Patrick et al., 2021; Qiao et al., 2022). Unlike real-world ecological communities, experimental communities are usually established in a homogeneous environment at relatively small spatial extents (Albrecht et al., 2021; Hautier & Van der Plas, 2022). This limits the understanding of ecosystems in heterogeneous environments (Chase et al., 2019; Gonzalez et al., 2020), removes non-target species to prevent immigration, restricts the role of species dispersal and species sorting at landscape level (Leibold et al., 2017; Loreau et al., 2003), and typically assembles species randomly to simulate a random loss of diversity in the local species pool whereas species loss in natural ecosystems is not random (Genung et al., 2020). However, to date, not much is known about the changes in biodiversity and ecosystem stability across scales along broad natural gradients in naturally assembled communities, which limits our understanding of the

scale dependence of the stabilizing effects of biodiversity in real-world ecosystems.

Over the past decade or so, given the ongoing global environmental changes, concerns have been raised about the interaction between ecosystem stability and drivers that are related to environmental change (Garcia-Palacios et al., 2018; Grman et al., 2010; Hautier et al., 2014; Hautier et al., 2015; Ma et al., 2017; Oliver et al., 2010; Qiao et al., 2022; White et al., 2022). Specific environmental drivers might be important for plant community assembly processes, and thus ecosystem functioning and its long-term sustainability at a broader scale, and might exhibit significant spatial differences along natural gradients (Burrows et al., 2011; Loarie et al., 2009; Nishizawa et al., 2022). We identify four environmental drivers that can influence ecosystem stability: (i) Climatic history of a region is an important abiotic factor that may influence system processes and the response of ecosystem functioning to climatic perturbations (He et al., 2022; White et al., 2022). Ecosystem stability at the landscape scale is known to be associated with climatic history (White et al., 2022). Species occurring in areas that regularly experience extreme climatic events may develop adaptive signatures that may contribute to maintaining stable ecosystem functioning during future extreme events (Craine et al., 2013). (ii) Resource conditions, such as temperature and precipitation, which represent the conditions of heat and water in a region, are crucial for stabilizing ecosystem functioning, and relevant evidence has been presented in numerous studies (Gillman et al., 2015; Kicklighter et al., 1999; La Pierre et al., 2011; Ma et al., 2017). (iii) Climatic stability (i.e. inverse of variability) during the growing season is another important abiotic factor that can influence species richness and community stability (Gherardi & Sala, 2015). The invariability of mean temperature and total precipitation during the growing

season was found to affect community functioning by reducing species richness and species asynchrony in a temperate grassland (Zhang et al., 2018). (iv) Environmental heterogeneity is believed to be a major factor in maintaining stable ecosystem functioning at the landscape level (Wang et al., 2019; Wilcox et al., 2017). Heterogeneous landscapes offer a wide range of resources and microclimates, which can buffer the impact of climate change and produce more stable population dynamics (Oliver et al., 2010; Qiao et al., 2022; Wang & Loreau, 2016). However, existing studies generally focus on the role of only one or two of these environmental drivers on ecosystem stability, risking a potentially biased understanding of their stabilizing effects in naturally assembled communities at the local and larger spatial scales.

To fill this gap, we developed a set of permanent forest plots distributed over a large temperate forest region. This observational infrastructure enables us to perform a more comprehensive multiscale analysis of the spatio-temporal dynamics of changes in forest ecosystem functioning, including an analysis of the relationships between ecosystem stability at multiple scales (that is, spatial asynchrony, local stability, and regional stability) and latitude. We also evaluate the biodiversity-stability relationship from local to larger spatial scales, and study the effects of biodiversity, geography, and a set of environmental drivers on ecosystem stability at multiple scales. Specifically, we addressed the following three questions relating to natural forest community assembly across large ecological gradients: (i) is forest ecosystem stability at local and larger spatial scales negatively associated with latitude? (ii) are the biodiversity-stability relationships at local and regional spatial scales positive? (iii) which potential drivers affect the latitudinal pattern of ecosystem stability across scales? We expect that this study improves our

understanding of how multiscale ecosystem functioning is changing over time and space, and thus provides important insights about the consequences of global environmental change and associated loss of species diversity in different geographical regions.

2. Materials and methods

2.1 Study site

We used an extensive data set of permanent forest plots distributed in the Chinese provinces of Inner Mongolia, Liaoning, Jilin, and Heilongjiang, a study area located in Northeast Asia (Supporting Information Appendices S1 and S2). The database includes 262 plots, each containing four 100 m² circular subplots (Supporting Information Appendix S3). The distance between any two adjacent subplots is 15 m. The latitudinal range of these plots extends from 39 to 54° N (a range of 15°). The total land area of the investigated region is approximately 700 000 km², of which more than one-third is covered by temperate broadleaf and mixed coniferous forests (FAO & UN, 2020; Olson et al., 2001). Rainfall ranges from 363.8 to 1,073.7 mm year⁻¹, and the temperature ranges from -5.6 to 9.8°C (Fick & Hijmans, 2017).

2.2 Calculation of productivity and temporal stability

All individual trees ≥ 5 cm stem diameter at breast height in the subplots were mapped, identified and measured (Supporting Information Appendix S4). The aboveground biomass of each tree was calculated based on species-specific allometric models in the county or district where the tree was located, using wood density (in grams per cubic centimeter) and diameter at breast height as variables (Fang et al., 2014; Wu et al., 2019). The incremental cores of each tree were taken at a height of 1.3 m in the summer of 2017 (Supporting Information Appendix S1). We calculated

aboveground biomass in 2005, 2009, 2013 and 2017. Forest productivity was quantified as the increase in biomass per ha between consecutive years derived from incremental cores and then used to calculate temporal stability (del Río et al., 2022; Dolezal et al., 2020).

Each 100 m² subplot represents the local (α) spatial scale. The four subplots within each site represent the regional (γ , or larger) spatial scale (Wang et al., 2019; Wang & Loreau, 2014). Following Tilman et al. (2006) and Hautier et al. (2020), stability at multiple scales was quantified as temporal invariability of aboveground biomass productivity after detrending data. At the regional scale, regional stability (γ_S) was the temporal stability of total productivity in four subplots in each regional community at each site. At the local scale, local stability (α_S) was the temporal stability of productivity averaged across four local subplots in each regional community at each site. Spatial asynchrony (β_S) was defined as the ratio between regional stability to local stability.

The relevant equations are:

$$\gamma_S = \sum_i \mu_i / \sqrt{\sum_{i,j} v_{ij}} \quad (1)$$

$$\alpha_S = \sum_i \mu_i / \sum_i \sqrt{v_{ii}} \quad (2)$$

$$\beta_S = \sum_i \sqrt{v_{ii}} / \sqrt{\sum_{i,j} v_{ij}} \quad (3)$$

where μ_i and v_{ii} are the temporal mean and variance of productivity of local community i , and v_{ij} is the covariance of productivity between local communities i and j (Loreau & de Mazancourt, 2008; Wang et al., 2019).

2.3 Quantification of biodiversity and environmental drivers

Biodiversity was measured at the local and regional spatial scale. Species diversity was measured as 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, α diversity (α_D) was measured as the inverse of a weighted average of Simpson indices in local subplots, weighted by the relative forest biomass stock of local subplots. γ diversity (γ_D) was measured as the inverse of Simpson index at regional plots. Following the multiplicative framework, β diversity (β_D) was defined as the ratio of γ diversity to α diversity (Wang & Loreau, 2014, 2016).

Following White et al. (2022), the climatic history was quantified based on the probability of the occurrence of extreme climate events. We extracted the daily temperature and daily precipitation measurements from 1961-2004 for the geographic coordinates of each plot using a gridded dataset with a resolution of 1×1 km (Qin & Zhang, 2022) (Supporting Information Appendix S5). Extreme precipitations and temperatures were both defined by the "fat tail" measure, which represents the range of extreme climates relative to the central part of the data: $(Q_{0.975} - Q_{0.025}) / (Q_{0.875} - Q_{0.125})$, where Q_x represents the x quantile of the distribution (Schmid & Trede, 2003; White et al., 2022). The period 2005-2017 is the observation time of changes in forest productivity for this study. Thus, the period 1961-2004 was used to assess the impact of the climatic history rather than the contemporary climate, and to avoid overlap with the data on current resource conditions (White et al., 2022). Resource conditions were computed based on the conditions of temperature and precipitation affecting tree survival and forest growth (Ma et al., 2017; Valencia et al., 2020). We extracted the monthly mean temperature and monthly total precipitation from the WorldClim2 dataset with a resolution of 1×1 km for the years 2005-2017 based on the geographical coordinates of each plot (Fick & Hijmans, 2017) (Supporting Information Appendix S6). The mean annual temperature and mean annual precipitation of the

observation period were used to represent the conditions of temperature and precipitation, respectively. Climatic stability was quantified using the inter-annual temperature stability and inter-annual precipitation stability during the growth period (Zhang et al., 2018). We screened for monthly mean temperatures and monthly total precipitation during the local plant growing months (May, June, July, August and September) from 2005-2017 (Fick & Hijmans, 2017) (Supporting Information Appendix S7). Similar to community stability, the inverse of the interannual coefficient of variation of temperature and precipitation over the plant growing season is used to define the temperature and precipitation stability. Environmental heterogeneity of the regional communities was represented as the difference among local communities (Heidrich et al., 2020; Stein et al., 2015). The standard deviations of the individual stand-basal areas ($\text{m}^2 \text{ha}^{-1}$) of the entire region were used to quantify environmental heterogeneity which is known to be a good predictor of terrestrial species diversity and ecosystem processes at broader scales (Enquist et al., 2009; Pretzsch & Schütze, 2016).

2.4 Statistical Analysis

All statistical analyses were performed using the R software unless specified otherwise (R Core Team 2021, version 4.1.0). Linear regression analysis (LRA) was used to assess the relationships between latitude and ecosystem stability at multiple scales. We also used this approach to assess the latitudinal gradients of each predictor variable used in this study, including climatic history, resource conditions, climatic stability, environmental heterogeneity, α_D and β_D . Adjusted R^2 values in the linear relationship between predictor variables and ecosystem stability were calculated to assess how much stability was explained by each individual predictor variable. LRA was used to

test whether the linear relationships between γ_D and γ_S , α_D and α_S , β_D and β_S , latitude and γ_S were significant. Partial LRA was run by extracting the residuals and testing the relationship between the residuals and each individual predictor variable. Before conducting the statistical analyses, all explanatory and stability variables were naturally log-transformed to meet the normality requirements of data analysis.

Multiple linear regression models were used to evaluate the effects of multiple predictors considered to affect ecosystem stability at multiple spatial scales. Before the multiple regression analysis, we removed the predictors whose variance inflation factors (VIF) value was more than five, such as extreme temperatures, mean annual temperature, and γ_D , to avoid the problem of multicollinearity (Coelho de Souza et al., 2019). Hence, five environmental variables (extreme precipitations, precipitation stability, temperature stability, mean annual precipitation, and vegetation heterogeneity), two diversity variables (α_D and β_D), two geographic variables (latitude and longitude), and two stability variables (α_S or/and β_S) were included in the multiple regression model for predicting ecosystem stability across geographical scales. The predictor variables were standardized (average = 0 and SD = 1). The relative effect of each predictor was obtained by calculating the ratio of the standardized regression coefficients of the predictor variables to the sum of all absolute coefficients (Gross et al., 2017). The relative importance of predictors was grouped into seven identifiable variance fractions: climatic history, climatic stability, resource conditions, environmental heterogeneity, ecosystem stability, geography, and biodiversity (Yuan et al., 2021).

Piecewise structural equation modeling (pSEM) was used to illustrate the different pathways

by which the above drivers affect regional stability and its two theoretical components. We developed a pSEM framework based on a priori knowledge about the mechanisms driving stability at multiple scales (Supporting Information Appendix S8). We first used a principal component analysis (PCA) on the variables representing climatic history, resource conditions, and climatic stability, separately. Then we used the first component PC1 (with an explanation of 64.52%-88.13%; Supporting Information Appendix S9) to reduce some of the complexity and avoid too many paths in the model. The pSEM was estimated using the R package “piecewise” (Lefcheck, 2016). Fisher's C statistics and Akaike information criterion (AIC) were used to evaluate the overall fitness of pSEM. When the model had a Fisher's C statistic with $p > 0.05$, it was assumed that the fit was adequate (Shipley, 2009). Before constructing pSEM, all explanatory variables were standardized (average = 0 and standard deviation = 1) to obtain standardized path coefficients.

3. Results

The results show that regional stability (γ_S) and spatial asynchrony (β_S) decreased with latitude (Fig. 1abd, $p < 0.05$), but local stability was not significantly related to latitude (Fig. 1d and Supporting Information Appendix S10, $p > 0.05$). γ_S was positively related to vegetation heterogeneity, local stability (α_S), β_S and α_D after controlling the effect of latitude (Fig. 1c, $p < 0.05$). β_S was positively related to vegetation heterogeneity, α_S , α_D , and β_D after controlling the effect of latitude (Fig. 1f, $p < 0.05$). A similar pattern emerges for biodiversity, as α and β diversity also decreased with latitude (Fig. 2h and Supporting Information Appendix S10). A large number of environmental drivers decreased with increasing latitude, including extreme temperatures, mean annual precipitation, mean annual temperature, temperature stability, and

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vegetation heterogeneity. Only extreme precipitations and precipitation stability increased with latitude (Fig. 2a-g). Among the predictors considered, α_D and vegetation heterogeneity explained most of γ_S and α_S , while β_S is explained by an array of factors (Fig. 2i and Supporting Information Appendix S10). The relationships between γ_D and γ_S , α_D and α_S , β_D and β_S were positive and significant (Fig. 3abc, $p < 0.001$). After controlling for the effect of α_D , α_S was further positively associated with vegetation heterogeneity and β_S , and negatively associated with β_D (Fig. 3d, $p < 0.05$). After controlling for the effect of α_D , α_S was positively associated with vegetation heterogeneity and β_S , and negatively associated with β_D (Fig. 3e, $p < 0.05$). After controlling for the effect of β_D , β_S was positively associated with extreme precipitations, mean annual temperature, mean annual precipitation, precipitation stability, vegetation heterogeneity and α_S , and negatively associated with extreme temperatures and latitude (Fig. 3f).

The multiple linear regressions models explained 100%, 14.7%, and 18.6% of the variations in γ_S , α_S and β_S , respectively (Fig. 4). Biodiversity, geography and ecosystem stability are the important predictive variables for α_S and β_S , explaining a larger fraction of the total variation. Biodiversity and geography were selected as the best predictors of α_S (explaining 31.8% of the variation) and β_S (explaining 25.3% of the variation), respectively. The relationship between climate history, resource conditions, climatic stability and ecosystem stability is not significant. As expected from theory, regional stability was fully explained by local stability and spatial asynchrony (Fig. 4a, Fig. 5, and Supporting Information Appendix S11). Alpha stability and spatial asynchrony showed a positive correlation (the standardized direct effect was 0.26, $p < 0.001$). Consistent with our hypotheses, α_D had positive associations with local stability (standardized path

coefficient of indirect effects 0.27, $p < 0.001$) while β_D is positively associated with spatial asynchrony (the standardized indirect effect was 0.17, $p < 0.001$). Spatial asynchrony decreases with increasing latitude (the standardized direct effect was -0.22, $p < 0.001$) as well as local stability and spatial asynchrony through environmental heterogeneity and biodiversity. However, although climate history, resource conditions and climatic stability are affected by geographical factors, their effects on biodiversity and stability are not significant ($p > 0.05$).

4. Discussion

4.1 Negative latitudinal gradients in the stability of naturally assembled regional communities

Exploring what potential drivers are associated with the ability of ecological communities to maintain functioning over time has long been a central issue of ecology and conservation biology (Bai et al., 2004; Loreau 2022; McCann, 2000; Tilman et al., 1996). Several theoretical and empirical studies have demonstrated that certain ecological drivers affect the functioning and stability of ecosystems (Hautier et al., 2014; Isbell et al., 2015; Tilman et al., 2006). These studies refer mainly to the local scale, whereas land management decisions are often made at the landscape level. In addition, there is a growing awareness that studies of natural ecosystems provide an opportunity to identify the factors associated with sustainable ecosystem functioning in real-world ecosystems (Hautier & Van der Plas, 2022). Given that threats to biodiversity and ecosystem properties from global-scale environmental change are likely to vary spatially in the future (Antao et al., 2021; IPCC, 2014). In this study, we tested the relationship between latitude and the temporal stability of forest productivity across scales using a network of permanent forest plots spanning a

wide ecological and geographic gradient. As expected, we found that the stability of regional forest productivity is decreasing with increasing latitude. These results are consistent with growing evidence for reduced aboveground wood production, seed production, and temporal stability of local insect communities with increasing latitudes (Antao et al., 2021; Gillman et al., 2015; Moles et al., 2009). According to the multiscale theoretical framework of stability, spatial asynchrony and local stability are the two components that fully explain regional stability. Potential environmental drivers might indirectly influence regional stability through their effects on spatial asynchrony and local stability, which is supported by the results of the structural equation model in this study (Fig. 5). Our study shows that spatial asynchrony was significantly negatively associated with latitude, while local stability was not. This implies that the drivers of negative latitudinal gradients of spatial asynchrony are important factors in shaping latitudinal patterns of regional stability.

4.2 Biodiversity and stability relationships at multiple scales in natural forests are positive but weak

Our study provides evidence that a positive relationship between biodiversity and stability dominates at multiple spatial scales in natural forest communities. Specifically, we found that α diversity was significantly and positively associated with local stability, which is consistent with other theoretical and empirical studies (Hautier et al., 2015; Loreau 2022; Tilman & Downing, 1994; Yachi & Loreau, 1999). Higher tree diversity may increase the asynchronous temporal response exhibited by different species to their shared local environment, or through overyielding, ultimately enhancing the stability of ecosystem functioning in local communities (Jucker et al., 2014; Schnabel et al., 2019; Yachi & Loreau, 1999). We also found that β diversity was

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significantly and positively associated with spatial asynchrony. Theoretical studies suggest that β diversity is positively associated with spatial asynchrony, based on the fact that higher variation and dissimilarity in species composition among communities are expected to increase asynchronous community responses to environmental fluctuations (Hautier et al., 2020; Wang & Loreau, 2016). Most experimental studies have reported positive relationships between β diversity and spatial asynchrony (Hautier et al., 2020; Liang et al., 2021; Wang et al., 2021), although non-significant relationships have also been reported (Zhang et al., 2019). Previous studies at local scales have reported that positive relationships between biodiversity and stability were common but weak in natural systems (Houlahan et al., 2018). We also observed such evidence in our natural forests at local and larger spatial scales. Some evidence from local communities suggests that functional and phylogenetic diversity may be of greater predictive power for ecosystem functioning and its stability than taxonomic diversity (Cadotte et al., 2008; Craven et al., 2018; Qiao et al., 2021). In addition, since the stability trend of forest ecosystems is mainly determined by the woody part of the vegetation and the species composition changes relatively slowly, it is common to use incremental core data to calculate the temporal stability of forests, which can indicate the temporal stability of the state of a forest in a fluctuating environment (del Río et al., 2022; Dolezal et al., 2020). However, the effects of forest recruitment and mortality on community stability remain poorly known. Based on previous experience involving the role of forest demographics in biodiversity-ecosystem function relationships, it is expected that over time, forest growth, recruitment, and mortality have the potential to affect biodiversity and stability relationships through changes in species composition (Poorter et al., 2017; van der Sande et al.,

2017). Therefore, future studies of biodiversity-stability relationships across spatial scales should consider multiple facets of biodiversity and the demographic process, providing a new perspective for understanding and predicting these relationships.

4.3 Latitudinal patterns of forest stability across scales are associated with environmental heterogeneity

Previous studies usually focus on relatively few ecological drivers which relate to environmental changes and evaluate their performance in predicting ecosystem stability. In the present study, we consider the link between a series of environmental drivers and latitudinal patterns on the temporal stability of forest productivity. We found that although most of the environmental drivers of climatic history, resource conditions, climatic stability, and environmental heterogeneity varied with latitude, only environmental heterogeneity is significantly associated with latitudinal patterns of forest ecosystem stability across scales. Environmental heterogeneity is generally considered to be particular relevance to conservation because of its ease of manipulation (Hopkins et al., 2007; Oliver et al., 2010). High environmental heterogeneity may increase available niche space and provide shelter for adverse resource conditions and extreme climates, thus promoting species diversity (Hughes & Roughgarden, 1998; Stein et al., 2014), since heterogeneous landscapes may provide a wider range of resources and microclimates, which can buffer communities from environmental changes and extreme events, resulting in more stable community dynamics (Collins et al., 2018; Oliver et al., 2010; Wilcox et al., 2017). Wang and Loreau (2016) used a dynamical model of competitive communities to report that environmental homogenization may lead to the destabilizing effect of biodiversity loss at multiple spatial scales that can be more severe. Our study

provides evidence of the positive effect of environmental heterogeneity on tree diversity and forest stability across scales in naturally assembled communities. Environmental heterogeneity that improves α and β diversity may therefore promote regional stability through local stability and spatial asynchrony. We advocate future investigations of the contributions of microclimate and resources within heterogeneous forest landscapes to the stability of ecosystem functioning, which would help to reveal the response mechanism of forest ecosystems to the negative effects of environmental homogenization.

Previous studies that evaluated the performance of different environmental drivers in predicting ecosystem stability have yielded inconsistent and even contradictory results. For example, White et al. (2022) using remotely sensed data at a landscape level (e.g. spatial extent of 10×10 km) found that vegetation stability was primarily associated with a history of extreme events and that these effects outweighed any positive effects of species richness. At a local level (e.g. spatial extent of 1×1 m), Zhang et al. (2018) et al found that the variability of precipitation decreased species asynchrony and stability in a long-term study of a temperate grassland ecosystem. The role of spatial extents and grain sizes of the research plots on the biodiversity-ecosystem functioning relationship and the biodiversity-ecosystem stability relationship is therefore receiving greater attention (Gonzalez et al., 2020; Qiao et al., 2021). Based on our results and previous experience involving the relationship between environmental drivers and ecosystem stability, the spatial extent and grain size are likely to affect the identification of important drivers affecting the latitude patterns of temporal stability. Therefore, embracing scale-dependence in future studies will contribute to a deeper understanding of complex biogeographic patterns and the

likely responses to the negative effects of global environmental change and species loss (Chase et al., 2018; Gonzalez et al., 2020).

5. Conclusions

Based on an extensive data set of permanent forest plots distributed over a large region of temperate forests, this study presents evidence about the negative latitudinal pattern of regional stability and spatial asynchrony of naturally assembled forest ecosystems. There are positive and significant relationships between biodiversity and stability at local and larger spatial scales in the observed natural forest ecosystems. A number of environmental drivers varied with latitude, yet latitudinal patterns of stability are most closely associated with biodiversity and environmental heterogeneity. Based on these results, we suggest that the preservation of forest diversity at local and larger spatial scales and the maintenance of heterogeneous landscapes are important for maintaining forest stability across scales in the region, especially at higher latitudes that are expected to be especially impacted by climate change in the future. The results of this study may contribute to more effective designs of forested landscapes in a changing environment.

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Authors' contributions

X.Q., S.W., and Y.H. conceived the idea of this study; X.Q. designed the research; C.Z., X.Z., and

K.v.G. designed the permanent plots; Y.G., N.Z., Z.Z., and X.Z. compiled the data and performed the literature search; X.Q. analyzed the data and wrote the first draft of the manuscript; T.L., S.W., Y.H., H.W., C.Z., and K.v.G. contributed through discussion, clarification and writing via multiple rounds of revision. All co-authors contributed substantially to the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability

The data that support the findings of this study are openly available in Figshare (<https://doi.org/10.6084/m9.figshare.21836586>).

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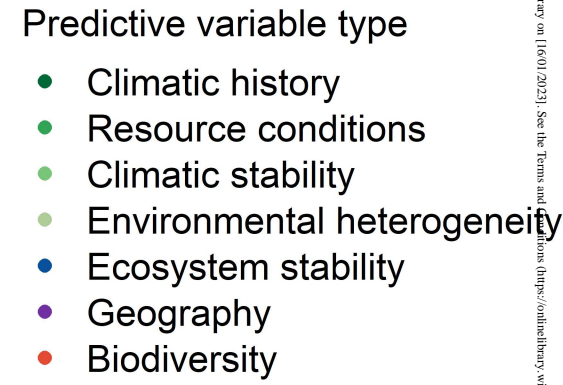
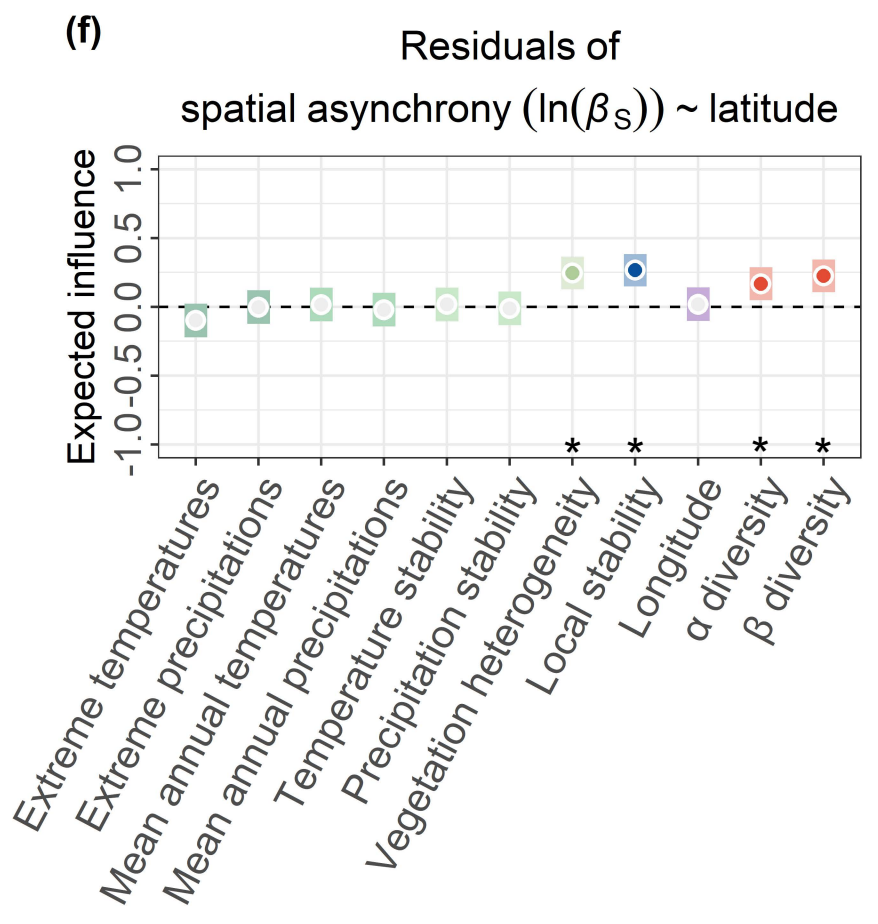
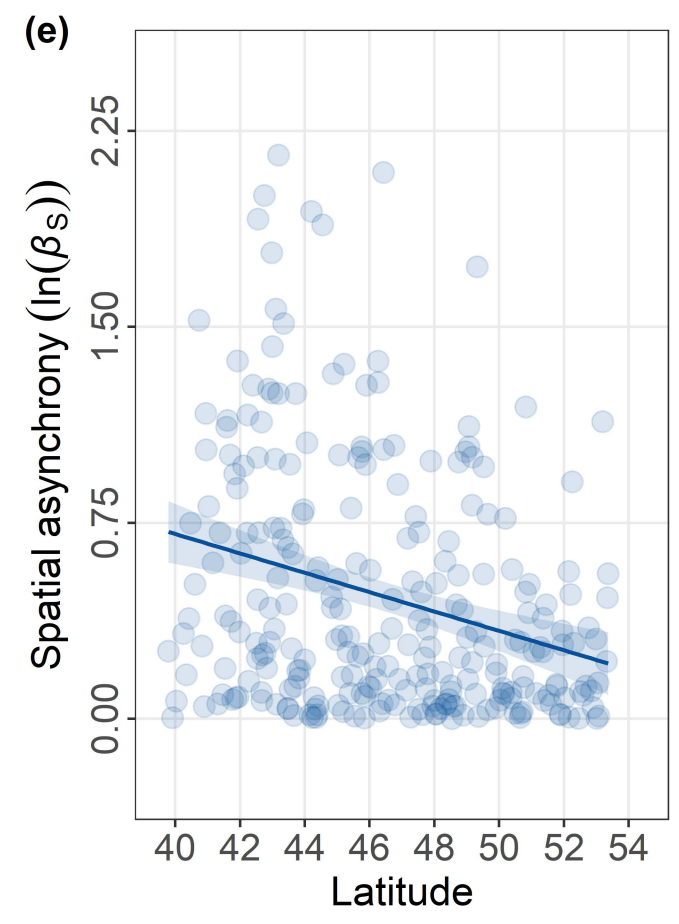
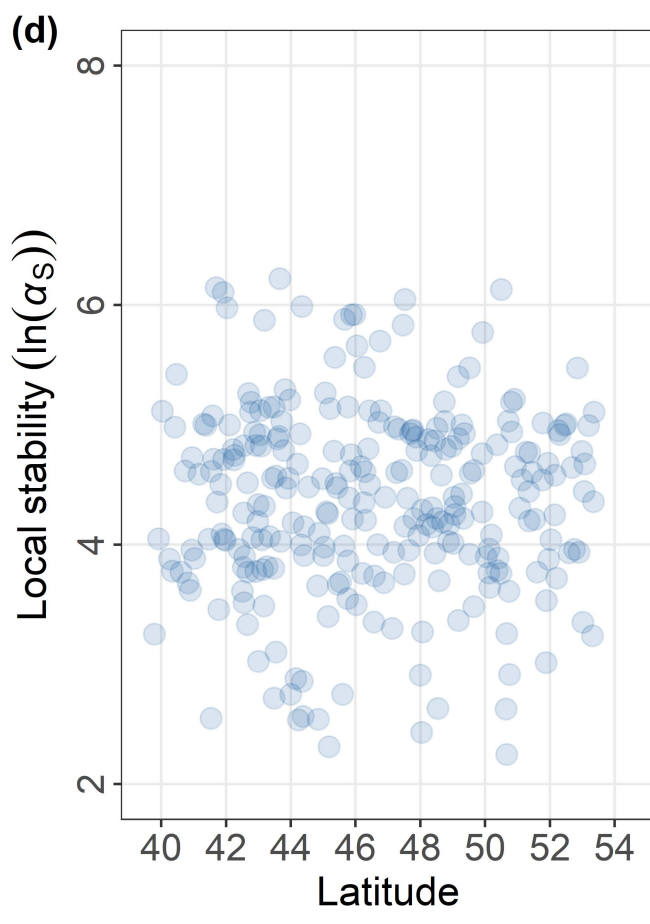
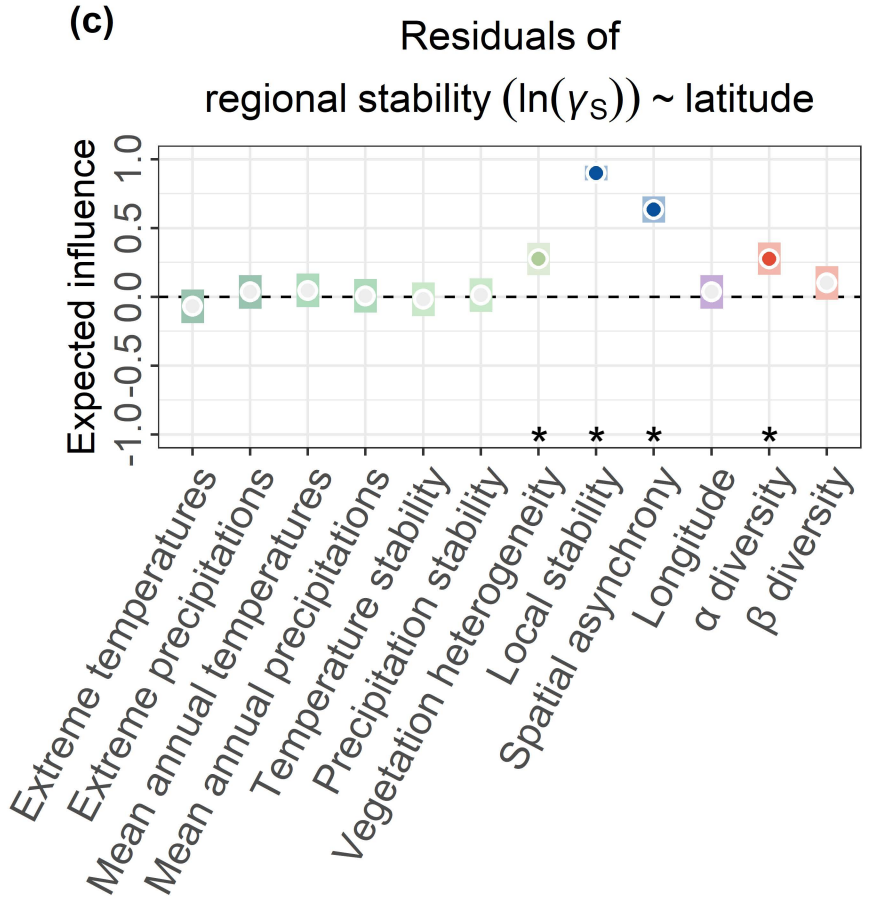
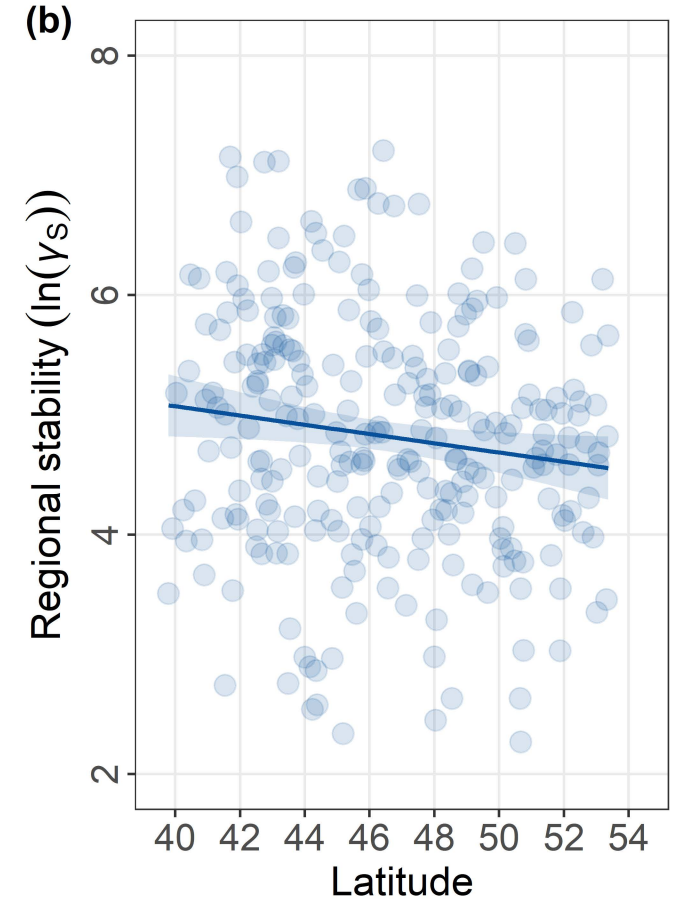
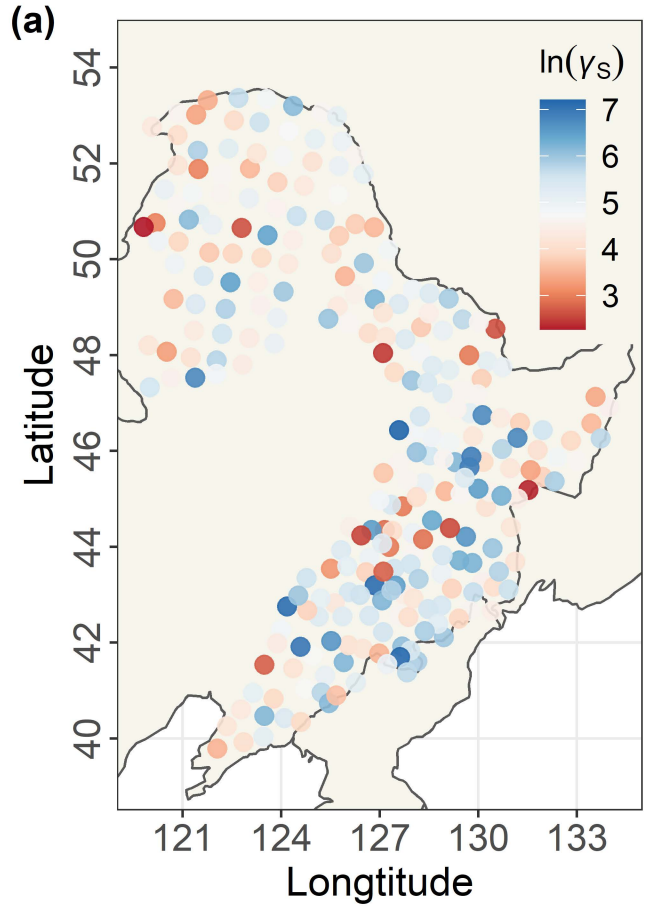
Fig. 1 Latitudinal gradient affecting forest ecosystem stability. (a) Spatial distribution of regional stability (γ_S). Relationships between latitude and (b) regional stability (γ_S , $F_{1,260} = 5.02, p < 0.05$); (d) local stability (α_S , $F_{1,260} = 0.01, p > 0.05$); (e) spatial asynchrony (β_S , $F_{1,260} = 22.46, p < 0.05$). Solid lines represent significant relationships with latitude ($p < 0.05$); blue shaded areas denote the 95% confidence interval of these relationships. No line was added when the relationship with latitude was not significant ($p > 0.05$). Linear relationship between (c) residuals of the regional stability-latitude relationship; (f) residuals of the spatial asynchrony-latitude relationship and each independent variable. Points and shades represent the estimated means and 95% confidence intervals of the model, respectively. Confidence intervals not overlapping with the dashed line ($x = 0$) and * indicate statistical significance ($p < 0.05$). Solid symbols indicate statistical significance ($p < 0.05$), hollow symbols no statistical significance ($p > 0.05$).

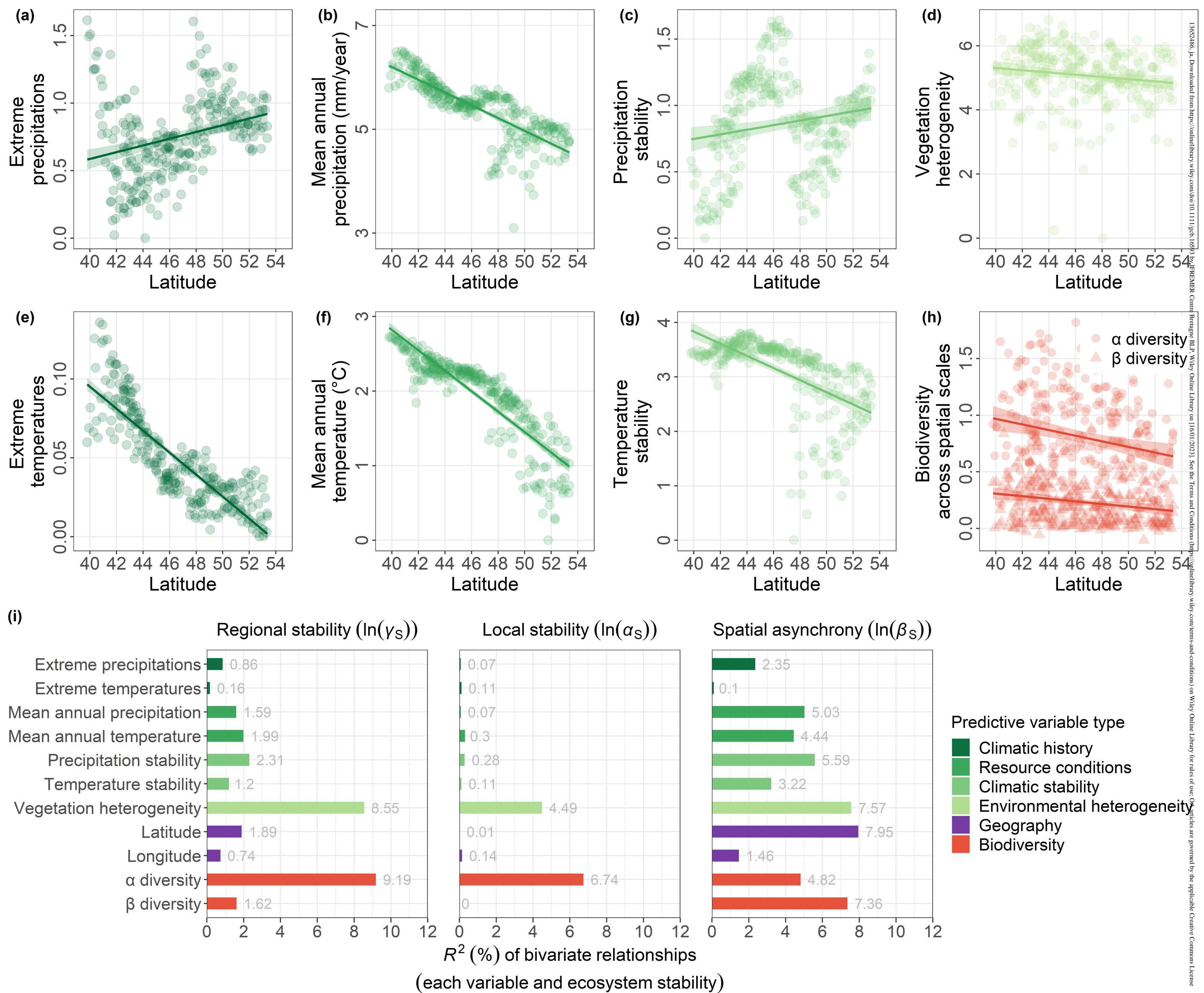
Fig. 2 Relationships between environmental drivers and latitude (a-h) and R^2 values of linear regression models between predictor variables and stability (i). All relationships in (a-h) are significant ($p < 0.05$). Solid lines denote significant relationships, shaded areas represent the 95% confidence interval of these relationships. In (i), R^2 values (%) are provided as grey texts in the graph.

Fig. 3 Biodiversity-stability relationship across spatial scales. (a) γ diversity-regional stability relationship ($R^2 = 0.08$, $F_{1,260} = 22.33$, $p < 0.001$); (b) α diversity-local stability relationship ($R^2 = 0.06$, $F_{1,260} = 18.80$, $p < 0.001$); (c) β diversity-spatial asynchrony relationship ($R^2 = 0.07$, $F_{1,260} = 20.66$, $p < 0.001$). Linear relationship between (d) residuals of the regional stability- γ diversity relationship; (e) residuals of the local stability- α diversity relationship and (f) residuals of the spatial asynchrony- β diversity relationship and each predictive variable. In (a-c), the respective areas represent the 95% confidence intervals. The fitted regression is significant at $p < 0.05$. In (d-f), points and shades represent the estimated means and 95% confidence intervals, respectively. Confidence intervals not overlapping with the dashed line ($x = 0$) and * indicate statistical significance ($p < 0.05$). Solid symbols indicate statistical significance ($p < 0.05$), hollow symbols no statistical significance ($p > 0.05$).

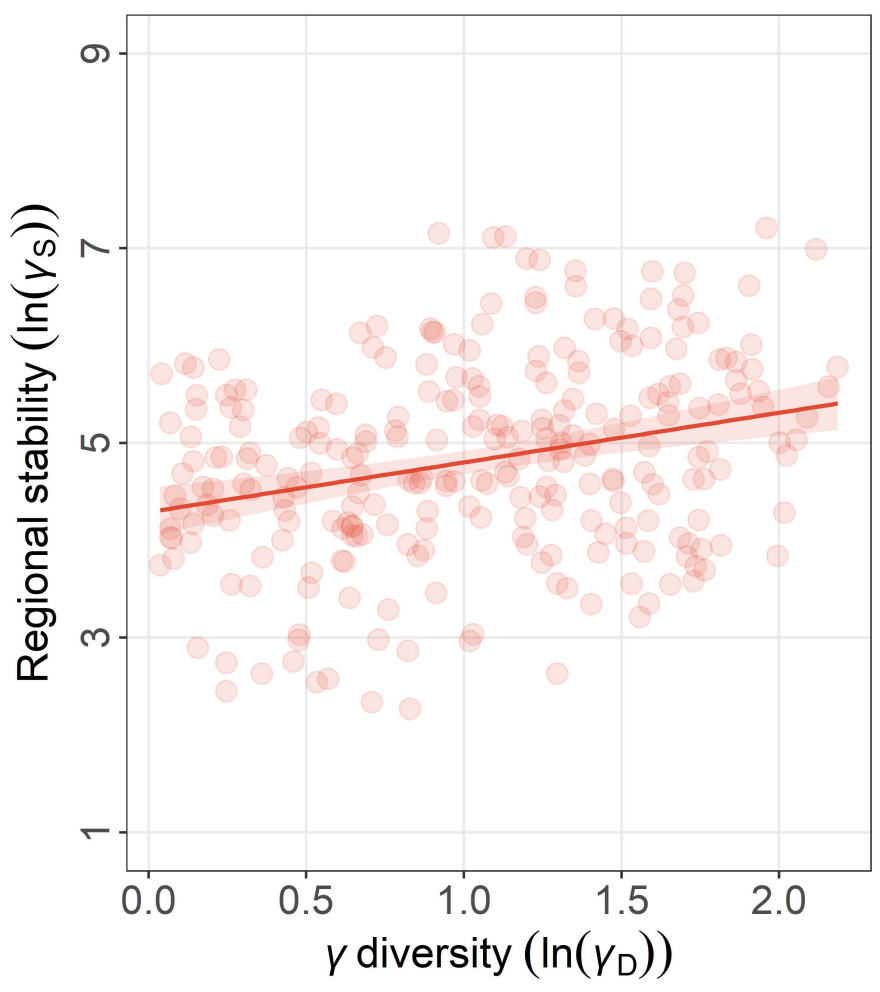
Fig. 4 Effects of geography, biodiversity and environmental drivers on ecosystem stability across spatial scales. (a) Regional stability; (b) local stability and (c) spatial asynchrony. On the left, points and shades represent the standardized regression coefficients of model predictors and 95% confidence intervals, respectively. Confidence intervals not overlapping with the dashed line ($x = 0$) and * indicate statistical significance ($p < 0.05$). Solid symbols indicate statistical significance ($p < 0.05$), hollow symbols no statistical significance ($p > 0.05$). On the right, the relative importance of each predictor variable type (expressed as the percentage of explained variance) and the adjusted R^2 of the models are shown.

Fig. 5 Final piecewise Structural Equation Models (pSEMs) exploring the relationships between geography, biodiversity, environmental drivers, and stability across scales. Single-headed arrows represent causal pathways while double-headed arrows correspond to co-varying variables. Black and red solid arrows represent significant positive and negative coefficients ($p < 0.05$), respectively. Grey dashed arrows represent non-significant coefficients ($p > 0.05$). Model test statistics are: Fisher's $C = 71.84$, $df = 64$, $p = 0.234$, $AIC = 147.84$. Numbers correspond to standardized regression coefficients. The width of the arrows scale with the magnitude of the standardized regression coefficients. The percentages next to the endogenous variables represent the variance explained by each model (R^2). The multiple-layer rectangles indicate the first component from the PCA. '↑' and '↓' in rectangles represent the positive and negative relationships between adjacent variables and the corresponding PC1, respectively. Extre-tem, extreme temperatures; Extre-pre, extreme precipitations; Mea-tem, mean annual temperature; Mea-pre, mean annual precipitation; Sta-tem, temperature stability; Sta-pre, precipitation stability.

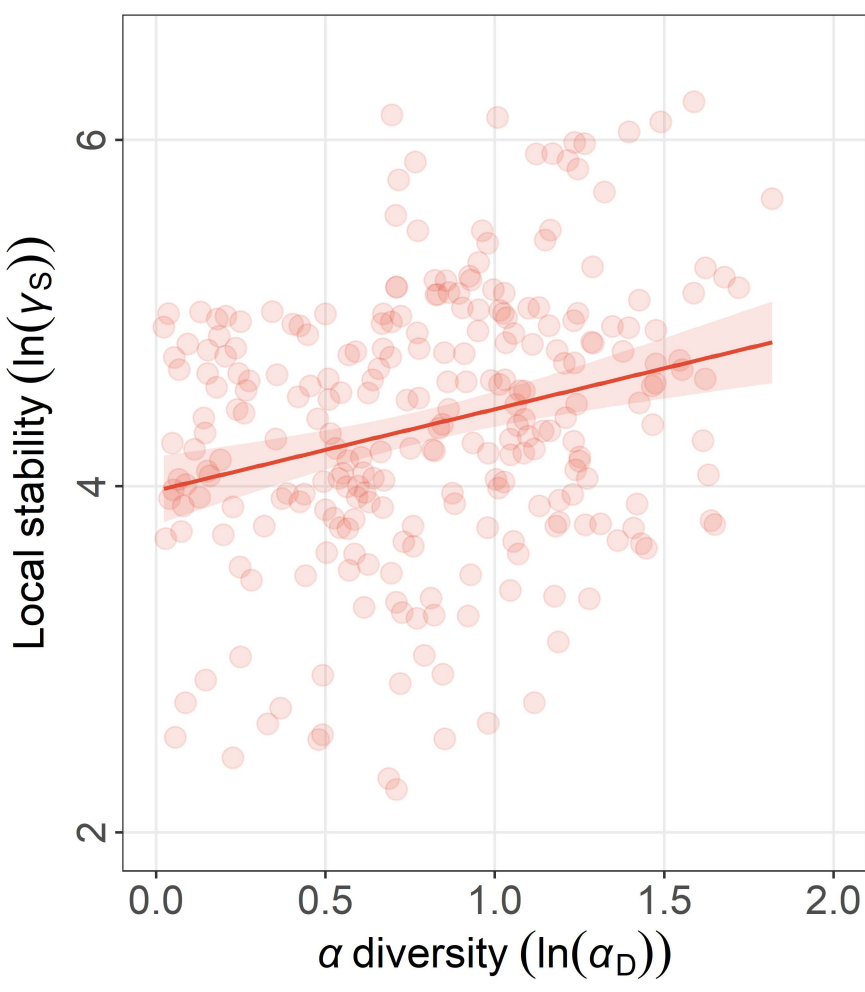




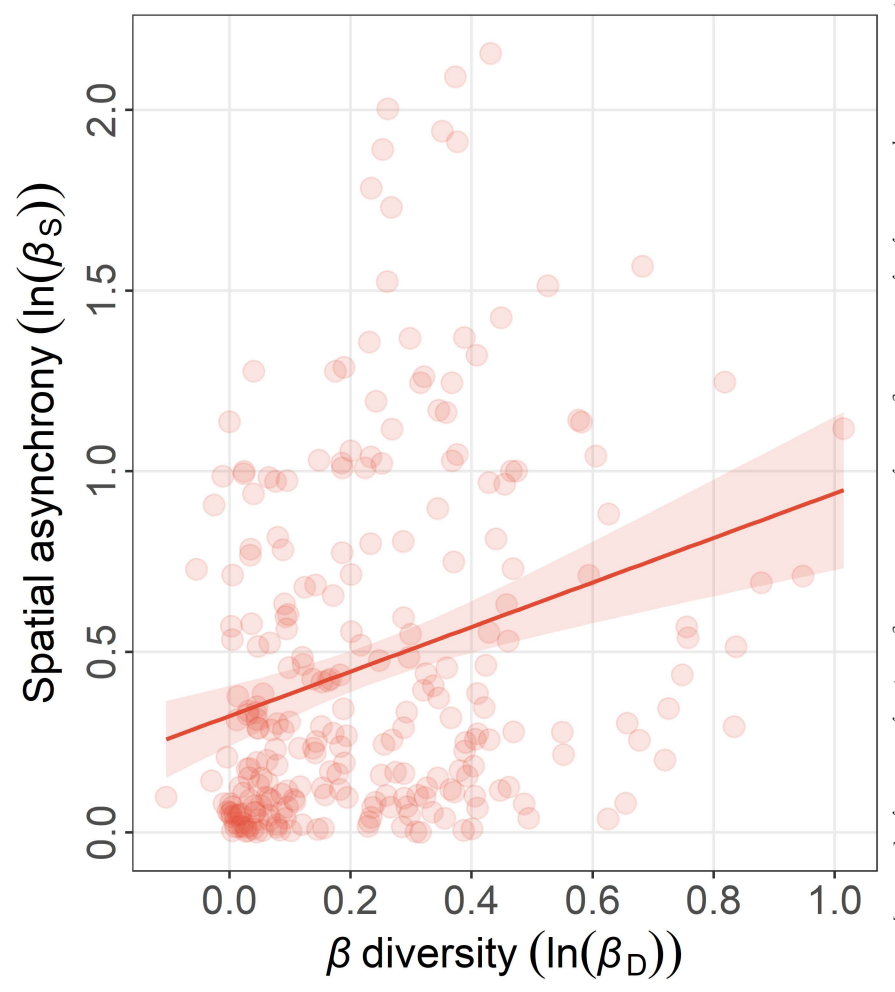
(a) Relationship between regional stability ($\ln(\gamma_S)$) & γ diversity ($\ln(\gamma_D)$)



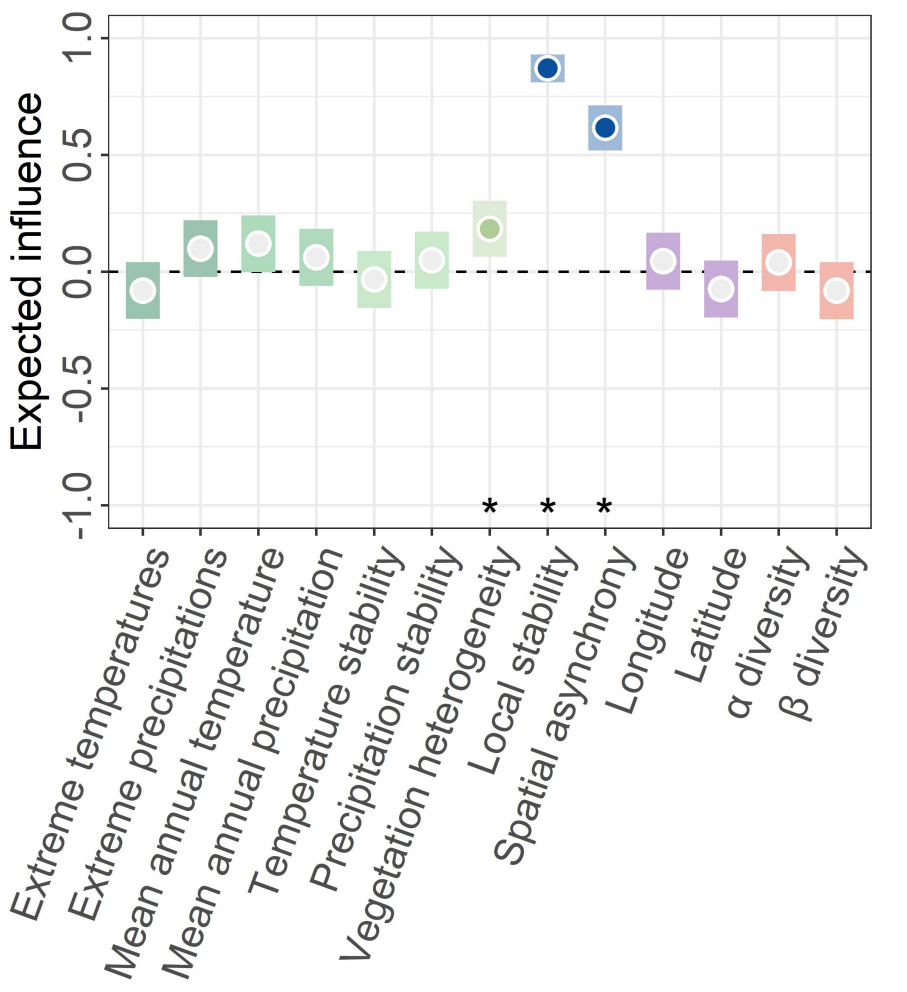
(b) Relationship between local stability ($\ln(\alpha_S)$) & α diversity ($\ln(\alpha_D)$)



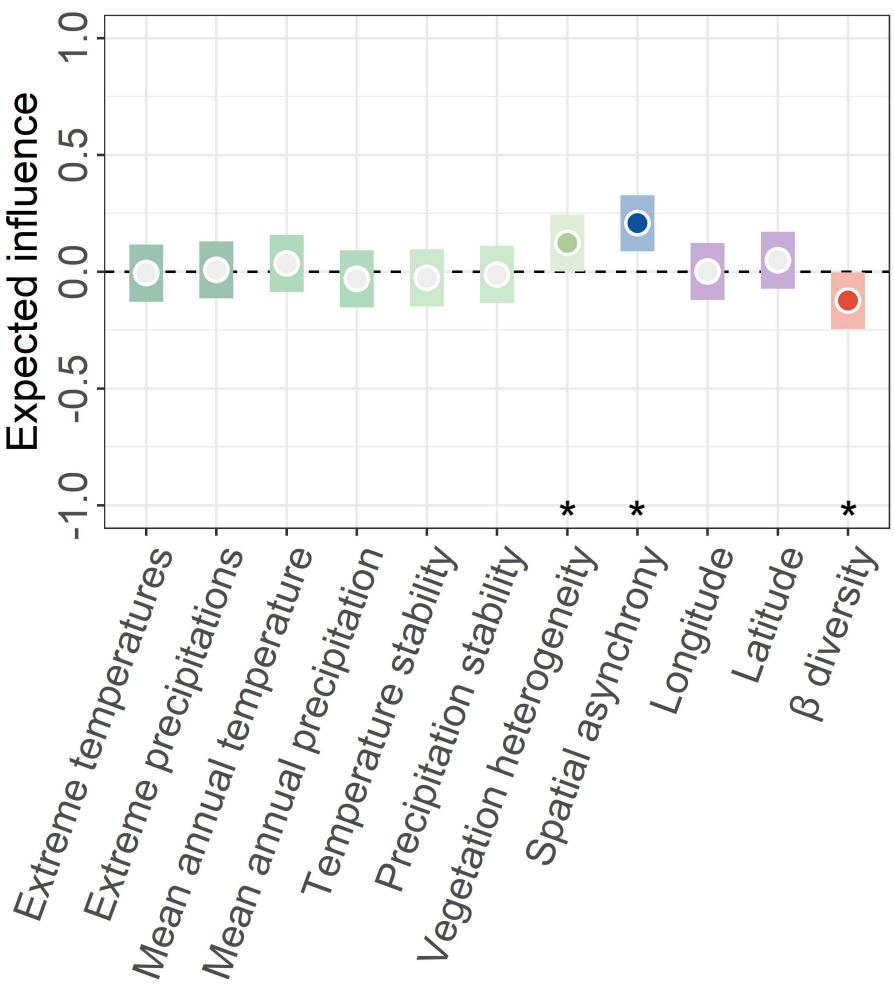
(c) Relationship between spatial asynchrony ($\ln(\beta_S)$) & β diversity ($\ln(\beta_D)$)



(d) Residuals of regional stability ($\ln(\gamma_S)$) ~ γ diversity ($\ln(\gamma_D)$)



(e) Residuals of local stability ($\ln(\alpha_S)$) ~ α diversity ($\ln(\alpha_D)$)



(f) Residuals of spatial asynchrony ($\ln(\beta_S)$) ~ β diversity ($\ln(\beta_D)$)

