



# Consistent stabilizing effects of plant diversity across spatial scales and climatic gradients

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**Biodiversity has widely been documented to enhance local community stability but whether such stabilizing effects of biodiversity extend to broader scales remains elusive. Here, we investigated the relationships between biodiversity and community stability in natural plant communities from quadrat (1 m<sup>2</sup>) to plot (400 m<sup>2</sup>) and regional (5–214 km<sup>2</sup>) scales and across broad climatic conditions, using an extensive plant community dataset from the National Ecological Observatory Network. We found that plant diversity provided consistent stabilizing effects on total community abundance across three nested spatial scales and climatic gradients. The strength of the stabilizing effects of biodiversity increased modestly with spatial scale and decreased as precipitation seasonality increased. Our findings illustrate the generality of diversity–stability theory across scales and climatic gradients, which provides a robust framework for understanding ecosystem responses to biodiversity and climate changes.**

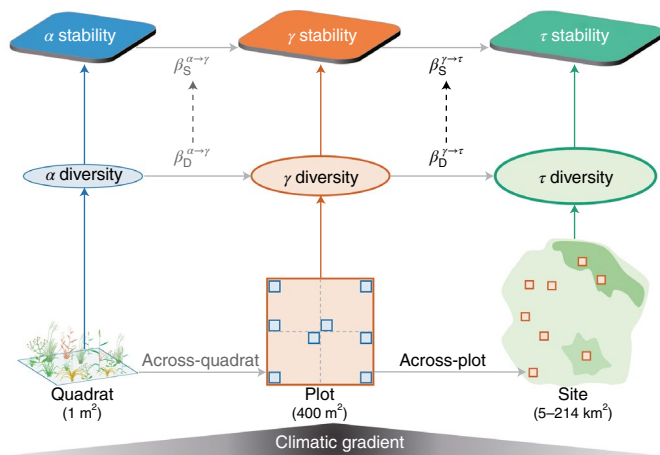
Reliable provisioning of ecosystem functions and services is a key objective that encompasses many of society's sustainability goals<sup>1</sup>. The diversity–stability relationship (DSR)—a research paradigm that has flourished during the past decades<sup>2–5</sup>—provides a framework for exploring how biodiversity and other drivers (for example, climate) regulate the stability of communities or ecosystems. While stability is a multidimensional concept<sup>3,6</sup>, recent studies have focused primarily on the temporal stability of ecosystem functions, for example the invariability of total productivity or biomass over time, and have shown that temporal stability generally increases with biodiversity<sup>7–9</sup>. The stabilizing effects of biodiversity are due to asynchronous responses of species to environmental fluctuations (insurance effects<sup>7,10</sup>) and/or more stable population dynamics<sup>11,12</sup>. However, previous studies have mostly considered ecosystems at local scales (for example, several to hundreds of square metres)<sup>13,14</sup>. It remains elusive to what extent the DSR theory applies to broader scales with larger environmental heterogeneity<sup>15–17</sup>. Clarifying the scale and environmental dependency of DSRs is essential for sustainable ecosystem management in the face of global biodiversity loss and environmental changes<sup>10,18,19</sup>.

Recent metacommunity theory postulates that positive DSRs can extend to broad spatial scales because the spatial turnover of biodiversity ( $\beta$  diversity) could provide spatial insurance effects for regional community dynamics<sup>20,21</sup>, just as local biodiversity ( $\alpha$  diversity) does for local communities<sup>7</sup>. This theory was built upon temporal stability measured by the ratio of the temporal mean to the standard deviation, which is also the stability metric we adopt in this paper. The stabilizing effect of  $\beta$  diversity provides the key to scaling up DSRs from local to broad scales. A strong stabilizing effect of  $\beta$  diversity can lead to stronger DSRs at broad scales than

those at local scales, whereas a weak stabilizing effect of  $\beta$  diversity may weaken or even blur DSRs at broad scales<sup>20,21</sup>. Metacommunity models predict that the stabilizing effect of  $\beta$  diversity increases when the spatial correlation of population dynamics increases<sup>20</sup>. Thus, the stabilizing effects of  $\beta$  diversity may be weak at local scales, where demographic stochasticity leads to a low spatial correlation of populations, and also weak at very large scales, where environmental correlation decreases as distance increases<sup>22</sup>. However, the scale dependence of  $\beta$  diversity effect has not yet been examined in empirical studies.

Several recent empirical studies have found positive DSRs across scales using data from different taxa, such as plants<sup>22–27</sup>, birds<sup>28</sup> and fishes and invertebrates<sup>29</sup>. In particular, many studies have confirmed the stabilizing effects of  $\beta$  diversity<sup>22,24–29</sup>, although neutral effects have also been reported<sup>30,31</sup>. However, a challenge for empirically testing DSR across spatial scales is that nested data at increasingly larger scales are rare. As a result, past empirical investigations of broader-scale stability have mostly used artificial aggregation of separate local communities, where the local communities represent replicates within a previous experiment or observational study<sup>22,25,27,30,31</sup>. Aggregating separate local communities rather than sampling at nested spatial scales potentially overlooks the influences of environmental heterogeneity and dispersal among local communities and might introduce non-independence for statistical analyses. The aggregation approach was used in particular in recent studies on plant communities<sup>22,25,27,30,31</sup>, which plays a key role in providing the primary productivity that supports all living organisms on land and has been the dominant system for studying DSR<sup>8,16</sup>. In addition to using aggregated communities, existing studies on plant DSRs across scales were mostly conducted

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**Fig. 1 | Biodiversity and ecosystem stability across multiple spatial scales along climatic gradients.** The spatial survey design of plant abundance and diversity from the NEON includes sampling at  $\alpha$  (1 m<sup>2</sup> quadrat),  $\gamma$  (400 m<sup>2</sup> plot) and  $\tau$  (5–214 km<sup>2</sup> site) scales at 36 sites across 16 ecoclimatic domains in the USA<sup>44</sup>. We define biodiversity (number of species) and community stability (ratio of mean community cover to its interannual standard deviation) at  $\alpha$ ,  $\gamma$  and  $\tau$  scales. We further define  $\beta$  diversity both across quadrats within a plot ( $\beta_D^{\alpha \rightarrow \gamma} = \gamma \text{ diversity} / \alpha \text{ diversity}$ ) and across plots within a site ( $\beta_D^{\gamma \rightarrow \tau} = \tau \text{ diversity} / \gamma \text{ diversity}$ ). We similarly define  $\beta$  stability at these two levels, which measures spatial asynchrony of community dynamics across quadrats and plots, respectively. Theory predicts that species diversity can increase stability at respective scales (indicated by arrows). Across sites, climatic factors (for example, precipitation and temperature) may influence species diversity, ecosystem stability and their relationships at different scales.

within a small spatial extent of up to 10 ha (but see ref. <sup>27</sup>). This restricts our understanding of the scale dependence of plant DSRs in natural, spatially interacting communities over broad spatial extents.

Environmental factors can also regulate biodiversity and stability, as well as their relationships<sup>32,33</sup>. It is well established that species diversity in various taxa increases with temperature and precipitation, creating a declining pattern of diversity from the Equator to the Poles<sup>34–36</sup>. Environmental factors also influence ecosystem stability by imposing external perturbations that alter ecosystem functions directly<sup>37–39</sup> or indirectly by shaping community diversity and composition<sup>14,40,41</sup>. Moreover, environmental factors may alter DSRs by modulating the strength of the stabilizing effect of biodiversity<sup>20,22,25,42</sup>. On the basis of a global experimental network, a recent study showed that nutrient addition weakened DSRs in grasslands at both local and broader scales<sup>25</sup>. Despite these advances, clarifying the environmental dependence of DSRs is still in its infancy and requires further investigation, particularly along natural environmental gradients.

Here, we use an extensive dataset of terrestrial plant communities collected between 2013 and 2020 from the National Ecological Observatory Network (NEON) to investigate the scale and climatic dependence of DSRs<sup>43</sup>. The dataset consists of 36 terrestrial sites in the United States, located across 16 ecoclimatic domains that vary in climate, vegetation and landforms (Extended Data Fig. 1). Each site contains 6–33 sampling plots (of 400 m<sup>2</sup>) distributed over a spatial extent from 5 to 214 km<sup>2</sup>, and each sampling plot contains eight 1 m<sup>2</sup> quadrats<sup>44</sup>. Within each quadrat, plant species richness and abundance (cover) were recorded annually for 4–8 yr following a standard protocol (Fig. 1). In total, the dataset contains >6,000 plant species from 7,560 quadrats and 945 plots across 36 sites. Such a standardized, hierarchical sampling of natural communities across

a continent provides a new opportunity for testing DSRs across spatial scales and climatic gradients.

On the basis of a spatial partitioning framework<sup>24</sup>, we define consistent measures of biodiversity and community stability at three nested spatial scales: quadrat ( $\alpha$ ), plot ( $\gamma$ ) and site ( $\tau$ ), where biodiversity was quantified by species richness and stability was calculated as the temporal stability of total community abundance (summed species cover) at each scale (Methods; Extended Data Fig. 2). We define  $\beta$  diversity at two levels, namely across-quadrat  $\beta$  diversity ( $\beta_D^{\alpha \rightarrow \gamma}$ ) as the ratio of  $\gamma$  diversity to  $\alpha$  diversity and across-plot  $\beta$  diversity ( $\beta_D^{\gamma \rightarrow \tau}$ ) as the ratio of  $\tau$  diversity to  $\gamma$  diversity (Fig. 1). Similarly, we define  $\beta$  stability at two levels, namely across-quadrat  $\beta$  stability ( $\beta_S^{\alpha \rightarrow \gamma}$ ) as the ratio of  $\gamma$  stability to  $\alpha$  stability and across-plot  $\beta$  stability ( $\beta_S^{\gamma \rightarrow \tau}$ ) as the ratio of  $\tau$  stability to  $\gamma$  stability (Fig. 1). These two metrics quantify the spatial asynchrony among quadrats within a plot and among plots within a site, respectively<sup>24</sup>.

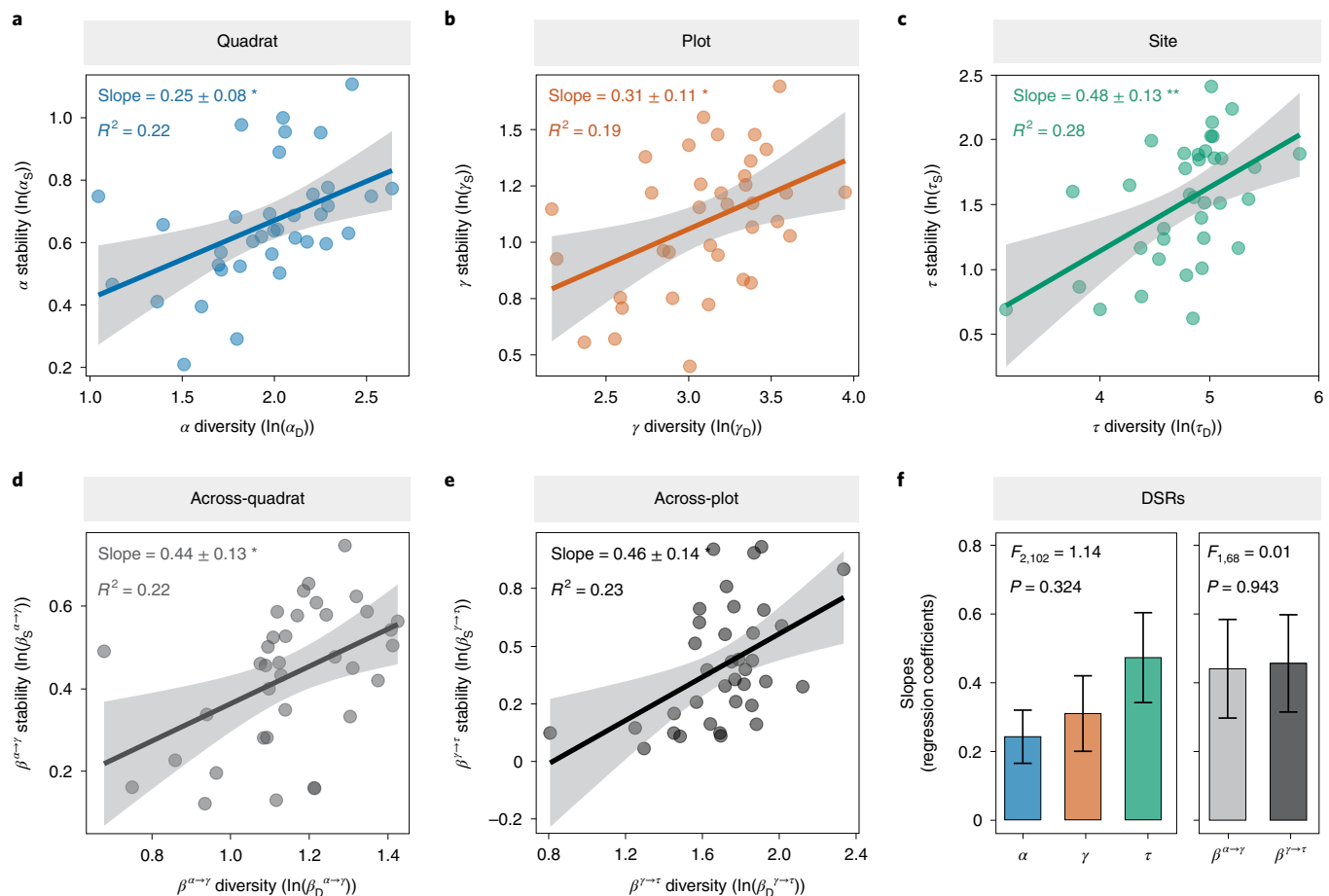
We address three questions: (1) does biodiversity provide consistent stabilizing effects across spatial scales from quadrat ( $\alpha$ ) to plot ( $\gamma$ ) to site ( $\tau$ )? (2) how do climatic factors (precipitation and temperature) affect biodiversity and stability across spatial scales? and (3) do the stabilizing effects of biodiversity—quantified as the log–log slope of DSRs—change with spatial scale and climatic conditions?

## Results

Community stability increased with plant species diversity at the quadrat ( $\alpha$ ), plot ( $\gamma$ ) and site ( $\tau$ ) scales, demonstrating consistently positive DSRs across spatial scales (Fig. 2, Extended Data Figs. 3–6 and Supplementary Tables 1 and 2). At the quadrat scale,  $\alpha$  diversity increased  $\alpha$  stability (Fig. 2a,  $F_{1,34} = 9.77$ ,  $R^2 = 0.22$ ,  $P = 0.004$ ) by increasing species asynchrony within quadrats (Supplementary Fig. 1b and Table 4,  $F_{1,861} = 89.90$ ,  $P < 0.0001$ ), rather than by influencing the stability of individual species (Supplementary Fig. 1a and Table 4,  $F_{1,861} = 0.48$ ,  $P = 0.488$ ). Across quadrats,  $\beta$  diversity ( $\beta_D^{\alpha \rightarrow \gamma}$ ) increased spatial asynchrony ( $\beta_S^{\alpha \rightarrow \gamma}$ ) within a plot (Fig. 2d,  $F_{1,34} = 9.44$ ,  $R^2 = 0.22$ ,  $P = 0.004$ ). At the plot scale, the stabilizing effects of  $\alpha$  and  $\beta$  diversity led to a positive relationship between  $\gamma$  diversity and  $\gamma$  stability (Fig. 2b,  $F_{1,34} = 7.93$ ,  $R^2 = 0.19$ ,  $P = 0.008$ ). Across plots,  $\beta$  diversity ( $\beta_D^{\gamma \rightarrow \tau}$ ) increased spatial asynchrony ( $\beta_S^{\gamma \rightarrow \tau}$ ) within a site (Fig. 2e,  $F_{1,34} = 10.39$ ,  $R^2 = 0.23$ ,  $P = 0.003$ ). Overall, these stabilizing effects of biodiversity across scales led to a positive relationship between  $\tau$  diversity and  $\tau$  stability at the site scale (Fig. 2c,  $F_{1,34} = 13.02$ ,  $R^2 = 0.28$ ,  $P = 0.001$ ). These results were robust after controlling for the potential confounding effects of climatic factors using partial regression analyses (Extended Data Fig. 3), by excluding woody species from our analyses (Extended Data Fig. 4) or using only sites with longer records (Extended Data Figs. 5 and 6).

The log–log slopes of DSRs increased modestly from quadrat ( $\alpha$ ) to plot ( $\gamma$ ) and further to site ( $\tau$ ) scales but statistical tests revealed no significant difference (Fig. 2f,  $F_{2,104} = 1.14$ ,  $P = 0.324$ ). Similarly, the log–log slopes of DSRs did not differ between across-quadrat and across-plot  $\beta$  scales (Fig. 2f,  $F_{1,68} = 0.01$ ,  $P = 0.943$ ). Compared with the DSR slope at the  $\alpha$  scale, those at across-quadrat and across-plot  $\beta$  scales were relatively higher but non-significant (across-quadrat  $\beta$  versus  $\alpha$ :  $F_{1,68} = 1.32$ ,  $P = 0.254$ ; across-plot  $\beta$  versus  $\alpha$ :  $F_{1,68} = 1.87$ ,  $P = 0.176$ ). The coefficients of determination of DSRs, that is, proportions of variance in community stability explained by plant diversity, were also similar and exhibited no clear trend across different spatial scales ( $R^2 = 0.19$ – $0.28$ ). Similar results were found after controlling for effects of climatic factors, by excluding woody species or using sites with longer records (Extended Data Figs. 3–6 and Supplementary Tables 1 and 2).

We constructed a structural equation model (SEM) to elucidate the direct and indirect effects of biodiversity and climatic factors on community stability across scales (Fig. 3, Extended Data Figs. 2 and 8 and Supplementary Tables 5–7). The SEM confirmed that plant



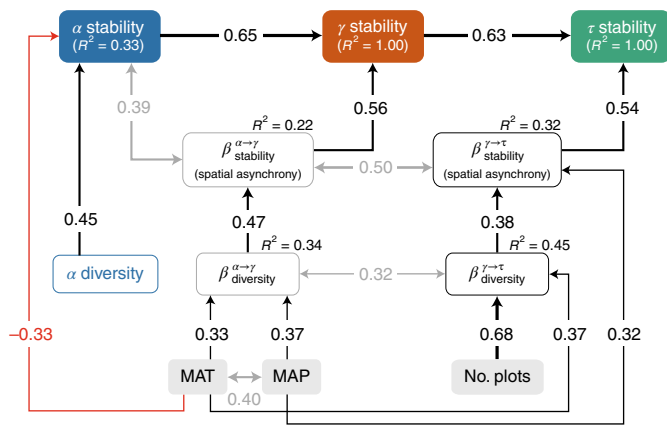
**Fig. 2 | The DSRs across multiple spatial scales. a–f.** Shown are the log–log relationships between  $\alpha$  diversity and  $\alpha$  stability at the quadrat scale (**a**,  $F_{1,34} = 9.77$ ,  $R^2 = 0.22$ ,  $P = 0.004$ ), between  $\gamma$  diversity and  $\gamma$  stability at the plot scale (**b**,  $F_{1,34} = 7.93$ ,  $R^2 = 0.19$ ,  $P = 0.008$ ), between  $\tau$  diversity and  $\tau$  stability at the site scale (**c**,  $F_{1,34} = 13.02$ ,  $R^2 = 0.28$ ,  $P = 0.001$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_S^{\alpha \rightarrow \gamma}$  across quadrats (**d**,  $F_{1,34} = 9.44$ ,  $R^2 = 0.22$ ,  $P = 0.004$ ), between  $\beta_D^{\gamma \rightarrow \tau}$  and  $\beta_S^{\gamma \rightarrow \tau}$  across plots (**e**,  $F_{1,34} = 10.39$ ,  $R^2 = 0.23$ ,  $P = 0.003$ ) and a comparison of regression slopes across scales using ANCOVA (**f**,  $F_{2,102} = 1.14$ ,  $P = 0.324$  among quadrat, plot and site scales;  $F_{1,68} = 0.01$ ,  $P = 0.943$  between across-quadrat and across-plot scales). In **a–e**, lines represent the overall relationships between biodiversity and community stability from the best-fit linear regression models (LMs) and shaded areas are the error bands and denote 95% confidence intervals. Significance levels are indicated as follows:  $^*P \leq 0.05$  and  $^{**}P \leq 0.001$ . In **f**, bars and error bars are regression coefficients and standard errors from LMs ( $n = 36$  for all) in **a–e**, respectively. Note that in **f**, pairwise comparisons between quadrat, plot and site levels are non-significant ( $P > 0.1$  for all). More information about the fitted models and partial regression models is provided in Extended Data Fig. 3 and Supplementary Tables 1 and 2.

diversity consistently enhanced community stability across multiple spatial scales. Climatic factors influenced community stability both directly and indirectly through plant diversity. Specifically, as mean annual precipitation (MAP) increased,  $\beta$  diversity across quadrats ( $\beta_D^{\alpha \rightarrow \gamma}$ ) and spatial asynchrony across plots ( $\beta_S^{\gamma \rightarrow \tau}$ ) both increased, which contributed to increasing  $\tau$  stability at the site scale. As mean annual temperature (MAT) increased,  $\beta$  diversity, both across quadrats ( $\beta_D^{\alpha \rightarrow \gamma}$ ) and across plots ( $\beta_D^{\gamma \rightarrow \tau}$ ), increased, which in turn increased  $\beta$  stability at these levels and provided stabilizing effects. However, such stabilizing effects were balanced by a reduced  $\alpha$  stability as MAT increased, resulting in a weak net effect of MAT on  $\gamma$  stability and  $\tau$  stability (Fig. 3). Overall, diversity and stability at  $\beta$  (both across-quadrat and across-plot) and  $\tau$  scales all increased along the gradient of MAP, whereas  $\beta$  diversity (both across-quadrat and across-plot) increased and  $\alpha$  stability decreased, along the gradient of MAT (Extended Data Fig. 7 and Supplementary Tables 8–11). Additionally, across-plot  $\beta$  diversity ( $\beta_D^{\gamma \rightarrow \tau}$ ) also increased with the number of plots within each site but not with the average distance between plots (Supplementary Tables 12 and 13).

To further understand how the stabilizing effects of biodiversity may vary across climatic gradients, we fitted DSRs at  $\alpha$ , across-quadrat  $\beta^{\alpha \rightarrow \gamma}$  and  $\gamma$  scales across different plots in each site. In line with our site-level analyses (Fig. 2), diversity generally increased stability at  $\alpha$ ,  $\beta^{\alpha \rightarrow \gamma}$  and  $\gamma$  scales across plots within sites, with positive DSRs occurring in 86%, 69% and 72% of all 36 sites at respective scales (Fig. 4a–c and Supplementary Table 3). We then extracted the log–log slopes of DSRs in each site and examined their relationships with climatic factors. Results showed that, as precipitation seasonality increased, the positive DSRs weakened at both  $\alpha$  (Fig. 4d,  $F_{1,34} = 11.76$ ,  $P = 0.002$ ) and  $\gamma$  scales (Fig. 4f,  $F_{1,34} = 5.63$ ,  $P = 0.024$ ). But the slopes of DSRs at the three scales did not change along the gradients of MAP, MAT and temperature seasonality ( $P \geq 0.1$  for all; Supplementary Tables 8–11).

## Discussion

In an era of global change and rapidly increasing human impacts, understanding what contributes to stability in the functions and services (for example, food and carbon sequestration) provided by plant communities is relevant to society. While plant diversity



**Fig. 3 | The SEM depicting the relationships among climatic factors, species diversity and ecosystem stability across multiple spatial scales.** Shown are the final SEM with significant pathways ( $P \leq 0.05$ ) and the standardized path correlation coefficients (the values). Black and red arrows denote positive and negative associations, respectively, and grey arrows indicate correlations.  $R^2$  is the proportion of variance explained by the model. Fisher's  $C = 72.394$ ; d.f. = 66;  $P = 0.275$ ; Akaike information criterion (AIC) = 126.394;  $n = 36$ . Note that diversity and stability metrics are log-transformed. No. plots, number of plots within a site. Information about the a priori SEM and the unstandardized direct effects are provided in Extended Data Fig. 2 and Supplementary Table 5, respectively.

has been widely documented to enhance stability in local ecosystems, research has just started to reveal how such stabilizing effects extend to larger regions<sup>22,25–27,30</sup> (see also other taxa<sup>28,29</sup>). By leveraging extensive in situ plant community data surveyed from 36 NEON terrestrial sites across the United States, our analyses demonstrate consistently positive DSRs across spatial scales and climatic gradients. Our study distinguishes itself from recent studies on this topic in three major aspects. First, our analyses investigated DSRs across plant metacommunities in natural landscapes, rather than aggregates of separated local communities<sup>22,25,27,30,31</sup>. Second, we investigated DSRs across a nested hierarchy of three spatial scales, instead of two as in previous studies on plants<sup>22,25,26,30,31</sup> and other taxa<sup>28,29</sup>. This allows a better examination of the scale dependence of plant DSRs across vastly different spatial scales (from 1 m<sup>2</sup> to 400 m<sup>2</sup> to 5–214 km<sup>2</sup>). Third, we tested how the stabilizing effects of plant diversity at different scales vary along natural climatic gradients (the interaction between diversity and climate), taking advantage of the hierarchical sampling design of NEON spanning broad climatic conditions.

Our analyses reveal consistent stabilizing effects of plant diversity at various scales from quadrat ( $\alpha$ ) to plot ( $\gamma$ ) and site ( $\tau$ ) in natural communities (Figs. 2 and 4). These stabilizing effects are due to  $\alpha$  diversity within quadrats and  $\beta$  diversity both across quadrats ( $\beta^{\alpha \rightarrow \gamma}$ ) and across plots ( $\beta^{\gamma \rightarrow \tau}$ ), consistent with the predictions of metacommunity theory<sup>20,21</sup>. The stabilizing effects of  $\alpha$  diversity and  $\beta$  diversity across quadrats and across plots can be understood from their insurance effects by increasing asynchrony among species within quadrats, among quadrats and among plots, respectively. Thus, in line with recent findings showing positive DSRs at local and larger scales using aggregated communities<sup>22,25,27,28,30,31</sup>, our results demonstrate the stabilizing effects of plant diversity across three spatial scales in natural landscapes.

Moreover, our analyses reveal comparable or even stronger stabilizing effects of  $\beta$  diversity than those of  $\alpha$  diversity (Fig. 2 and Extended Data Figs. 3–6). This result contrasts with findings from previous studies using aggregated communities at small spatial extents (up to 10 hm<sup>2</sup>) in a single biome (grasslands), which

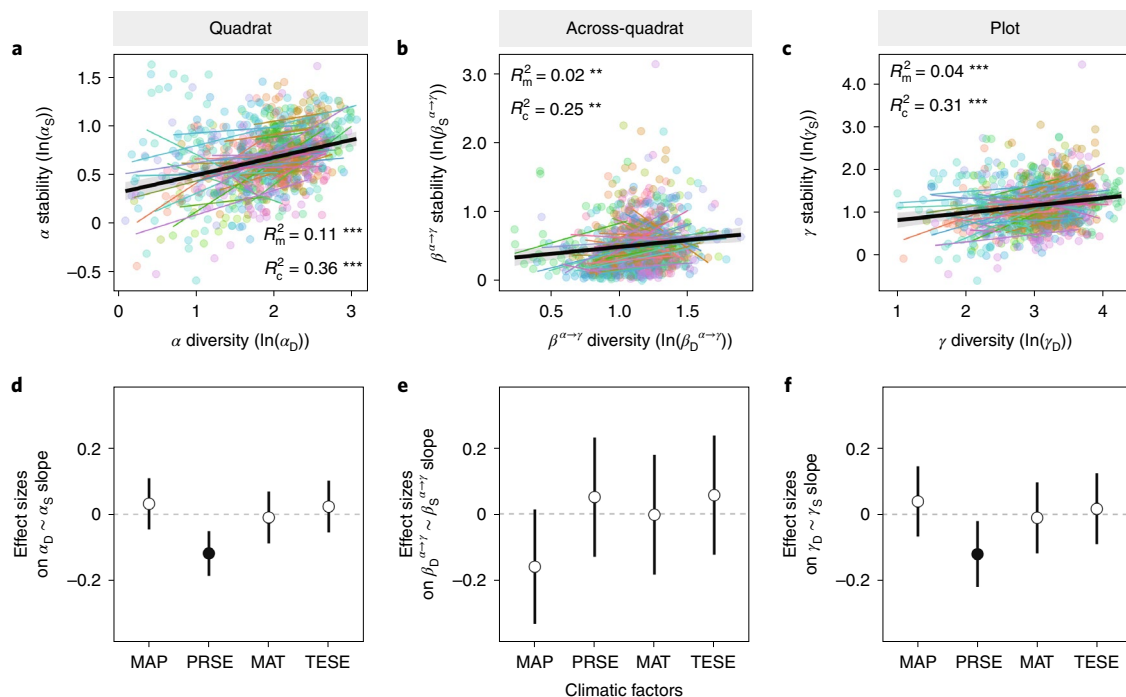
showed generally weaker effects of  $\beta$  diversity than  $\alpha$  diversity<sup>22,30,31</sup>. The relatively stronger stabilizing effect of  $\beta$  diversity in our study might be explained by the broader spatial extent (5–214 km<sup>2</sup>) and the greater heterogeneity considered, which allows a larger gradient of  $\beta$  diversity (Supplementary Fig. 6). The sampling design of NEON spans different land covers and biomes (Extended Data Fig. 1), characterized by dissimilar vegetation across a multitude of successional states with different associated life histories and traits<sup>44</sup>. This greater heterogeneity is likely to contribute to stronger spatial insurance effects than in grassland communities at small extents. In line with this explanation, two recent regional-scale studies reported significantly stronger stabilizing effects of  $\beta$  diversity than  $\alpha$  diversity in aggregated communities of forests across northeastern China<sup>27</sup> and birds across North America<sup>28</sup>. The stronger stabilizing effects of  $\beta$  diversity in our study led to relatively steeper DSR slopes from quadrat to plot and site scales, although this increase was modest and statistically non-significant (Fig. 2). Again, such a trend of increasing DSR slopes is consistent with the results of the regional-scale study on forests<sup>27</sup>, while contrasting with those carried out at small spatial extents in grasslands<sup>22,23</sup>. Overall, our results provide strong evidence for consistently positive DSRs across spatial scales but modest support for a positive scale dependence of DSRs.

Focusing on a single spatial scale, recent studies showed that climatic factors could influence ecosystem stability directly<sup>14,26,37</sup>, indirectly (for example, by changing species diversity<sup>14,40,41</sup>) or interactively (by modulating DSRs<sup>25,33,42</sup>). Our results extend these findings to a multiscale context. In particular, precipitation can influence ecosystem stability across scales via all aforementioned pathways. By increasing  $\beta$  diversity and  $\beta$  stability (both across quadrats and plots), an increased MAP results in a higher stability at the site scale (Fig. 3). This result corroborates previous findings that grassland stability increases with precipitation<sup>22</sup> and extends them to broader scales. Moreover, we found that a higher precipitation seasonality weakened the stabilizing effects of plant diversity at both  $\alpha$  and  $\gamma$  scales (Fig. 4). In sites with high precipitation seasonality, population dynamics are likely to be mainly driven by precipitation fluctuations, which causes high synchrony among species<sup>33,45</sup>. Such a high species synchrony could weaken the insurance effects of species diversity on stability<sup>7,11</sup>. Compared with precipitation, temperature influenced stability directly and indirectly but not interactively. The direct effect of temperature by decreasing  $\alpha$  stability (see also ref. <sup>39</sup>) was balanced by its indirect effect through increasing  $\beta$  diversity across quadrats and plots, resulting in a weak net effect on  $\tau$  stability at the site scale.

While the NEON dataset provides an opportunity to test DSRs across scales and climatic gradients, some caveats should be mentioned. First, we calculated temporal stability using total community abundance (total cover) as a proxy for ecosystem function. Although previous studies on stability reported consistent results using abundance and biomass/productivity<sup>25,30</sup>, we cannot assess their consistency (using abundance versus biomass) in our study due to a lack of relevant data. Second, the NEON dataset covers a relatively short observational period, which also differs among sites (4–8 yr)<sup>44</sup>. Previous studies suggested that the length of time series might influence the estimate of temporal stability<sup>46–48</sup>. However, our additional analyses suggest that time-series length had no effect on diversity, stability and their relationships in our study (Fig. 2, Extended Data Figs. 5 and 6 and Supplementary Tables 1, 2 and 14). Third, our analyses did not include some potentially relevant covariates due to a lack of information, such as soil properties that may vary within and across sites, dispersal processes that may interact with both diversity and the environment<sup>21</sup> and species functional traits that underpin the stabilizing effects of diversity<sup>49</sup>.

Several decades of research have resulted in a mature theory of DSRs. But to make DSRs a relevant tool for ecosystem management,





**Fig. 4 | The DSRs within sites and their dependencies on climatic factors. a–f.** Shown are the log–log relationships between  $\alpha$  stability and  $\alpha$  diversity at the quadrat scale (**a**,  $F_{1,861} = 78.94$ , slope =  $0.18 \pm 0.02$ ,  $P < 0.0001$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_S^{\alpha \rightarrow \gamma}$  across quadrats (**b**,  $F_{1,861} = 10.57$ , slope =  $0.20 \pm 0.06$ ,  $P = 0.0012$ ), between  $\gamma$  stability and  $\gamma$  diversity at the plot scale (**c**,  $F_{1,861} = 20.49$ , slope =  $0.17 \pm 0.04$ ,  $P < 0.0001$ ) and how their log–log slopes are affected by climatic factors (**d–f**). In **a–c**, coloured points and lines correspond to values and fitted DSRs with each site and black lines represent the overall relationships between plant diversity and community stability across all sites from linear mixed-effects models (LMMs). Shaded areas are the error bands and denote 95% confidence intervals and significance levels are as follows: \*\* $P \leq 0.001$  and \*\*\* $P \leq 0.0001$ . The marginal ( $R_m^2$ ) and conditional ( $R_c^2$ )  $R$ -squared represent fractions of variance explained by ‘fixed effects’ and ‘fixed + random effects’, respectively. In **d–f**, centres and error bars are standardized regression coefficients and their 95% confidence intervals, respectively, between each climatic factor and the log–log slopes of  $\alpha_D \sim \alpha_S$  at the quadrat scale (**d**,  $P = 0.429, 0.812, 0.002$  and  $0.559$  for MAP, MAT, PRSE and TESE, respectively), those of  $\beta_D \sim \beta_S$  at the across-quadrat scale (**e**,  $P = 0.079, 0.976, 0.584$  and  $0.542$  for MAP, MAT, PRSE and TESE, respectively) and those of  $\gamma_D \sim \gamma_S$  at the plot scale (**f**,  $P = 0.476, 0.848, 0.024$  and  $0.763$  for MAP, MAT, PRSE and TESE, respectively), respectively ( $n = 36$  for all). Filled dots indicate significant effects ( $P \leq 0.05$ ). PRSE, precipitation seasonality; TESE, temperature seasonality. Information about the fitted LMMs and bivariate relationships is provided in Supplementary Tables 3 and 8–11.

it is essential to extend the spatial scale at which they are studied and to clarify how they may be modulated by climatic conditions<sup>4,15,17,18</sup>. Using an extensive dataset of plant communities, our study demonstrates consistent stabilizing effects of plant diversity across spatial scales and climatic gradients in natural communities. By showing that the stabilizing effects of biodiversity at broad scales are at least as strong as those at local scales, our findings highlight the importance of preserving biodiversity at broad scales. Also, our results reveal that climate change can influence ecosystem stability via multiple pathways, particularly through its interaction with biodiversity, an issue that requires future research<sup>42</sup>. Overall, our study illustrates the generality of diversity–stability theory across scales and climatic gradients. This theory thus provides a robust framework for understanding ecosystem sustainability in the face of biodiversity and climate changes.

## Methods

**The NEON plant dataset.** Our study was based on plant community survey data from the NEON: plant presence and percentage cover, RELEASE-2021 (DP1.10058.001); <https://doi.org/10.48443/abge-r811>. The dataset was accessed from <https://data.neonscience.org> on 4 February 2021<sup>43</sup>. A standardized sampling protocol is designed to monitor plant diversity and abundance across spatial and temporal scales<sup>44</sup>. Specifically, at each of the 47 NEON terrestrial sites (covering 5–214 km<sup>2</sup>), multiple plots (20 × 20 m<sup>2</sup>) were established, each composed of eight quadrats (1 × 1 m<sup>2</sup>). Within each quadrat, the identity and abundance (estimated cover) of each species have been recorded by NEON field ecologists on a yearly basis between 2013 and 2020. Further details of the sampling design are available in ref. <sup>44</sup>.

Because the NEON plant data did not encompass species-level biomass or productivity data, we calculate the temporal stability (or invariability) using species cover data at all spatial scales. This stability metric indicates the temporal stability of vegetation status in a fluctuating environment and has been used as a proxy for the stability of ecosystem function (for example, biomass or productivity)<sup>25,30,41</sup>. The datasets were collected during the growing season between 2013 and 2020. As different sites were established at different times, we used data from 36 NEON sites with at least 4 yr of records to achieve a reliable estimate of temporal stability. Among these 36 sites, 24 had  $\geq 5$  yr of records and 14 had  $\geq 6$  yr of records. In total, >6,000 plant species were encountered in 7,560 quadrats (1 m<sup>2</sup>) within 945 plots (400 m<sup>2</sup>) from the 36 NEON sites (5–214 km<sup>2</sup>) across the United States (Extended Data Fig. 1). The growth form of the plant species (woody versus herbaceous) is designated following the Carolina Vegetation Survey Protocol<sup>50</sup>.

**The ecoclimatic data.** We extracted the climate data at the site level from the WorldClim Global Climate database (v.1.4; <http://www.worldclim.org/>)<sup>51</sup>. We used four climate variables from the WorldClim database, namely MAP, MAT, precipitation seasonality (coefficient of variation) and temperature seasonality (standard deviation × 100). These ecoclimatic variables are correlated with each other across the 36 sites (Extended Data Fig. 1 and Supplementary Fig. 4), especially between MAT and temperature seasonality. As climatic variables were measured in different units, they were normalized using the z-scores (original values minus the mean and then divided by standard deviation) before statistical analyses.

**Biodiversity and stability across multiple scales.** Within each NEON site, we define diversity and stability at multiple spatial scales. We first calculated plant diversity (number of plant species) at three scales: quadrats of 1 m<sup>2</sup> ( $\alpha$ ), plots of 400 m<sup>2</sup> ( $\gamma$ ) and sites of 5–214 km<sup>2</sup> ( $\tau$ ). The  $\alpha$  diversity represents the mean number of quadrat-level plant species averaged across all quadrats and plots within the site;  $\gamma$  diversity denotes the mean number of plot-level plant species averaged across all

plots within the site;  $\tau$  diversity is the total number of plant species observed within the site. We then define  $\beta$  diversity at two levels, namely across-quadrat  $\beta$  diversity ( $\beta_D^{\alpha \rightarrow \gamma}$ ) as the ratio of  $\gamma$  diversity to  $\alpha$  diversity and across-plot  $\beta$  diversity ( $\beta_D^{\gamma \rightarrow \tau}$ ) as the ratio of  $\tau$  diversity to  $\gamma$  diversity.

Within each site, we also calculated community stability by the inverse of the coefficient of variation (the ratio of mean to standard deviation) and calculated the mean stability at quadrat ( $\alpha$  stability), plot ( $\gamma$  stability) and site ( $\tau$  stability) scales as follows<sup>24</sup>:

$$\alpha \text{ stability}(\alpha_S) = \frac{\sum_{i,k,m} \mu_{i,k,m}}{\sum_{k,m} \sqrt{\sum_{i,j} v_{ij,kk,mm}}}, \quad (1)$$

$$\gamma \text{ stability}(\gamma_S) = \frac{\sum_{i,k,m} \mu_{i,k,m}}{\sum_m \sqrt{\sum_{i,j,k,l} v_{ij,kl,mm}}}, \quad (2)$$

$$\tau \text{ stability}(\tau_S) = \frac{\sum_{i,k,m} \mu_{i,k,m}}{\sqrt{\sum_{i,j,k,l,m,n} v_{ij,kl,mm}}}. \quad (3)$$

where  $\mu_{i,k,m}$  and  $v_{ij,kl,mm}$  denote the temporal mean and variance of the cover of species  $i$  in local quadrat  $k$  in plot  $m$ , respectively, and  $v_{ij,kl,mm}$  denotes the covariance between species  $i$  in local quadrat  $k$  in plot  $m$  and species  $j$  in local quadrat  $l$  in plot  $n$ . We then define  $\beta$  stability at two levels, namely across-quadrat  $\beta$  stability ( $\beta_S^{\alpha \rightarrow \gamma}$ ) and across-plot  $\beta$  stability ( $\beta_S^{\gamma \rightarrow \tau}$ ), as the weighted mean of spatial asynchrony across quadrats and plots, respectively<sup>24</sup>:

$$\text{Across - quadrat } \beta \text{ stability}(\beta_S^{\alpha \rightarrow \gamma}) = \frac{\sum_{k,m} \sqrt{\sum_{i,j} v_{ij,kk,mm}}}{\sum_m \sqrt{\sum_{i,j,k,l} v_{ij,kl,mm}}}, \quad (4)$$

$$\text{Across - plot } \beta \text{ stability}(\beta_S^{\gamma \rightarrow \tau}) = \frac{\sum_m \sqrt{\sum_{i,j,k,l} v_{ij,kl,mm}}}{\sqrt{\sum_{i,j,k,l,m,n} v_{ij,kl,mm}}}. \quad (5)$$

These two metrics of  $\beta$  stability characterize the spatial asynchrony of community dynamics and serve as scaling factors from smaller to larger spatial scales. By definition we have:  $\beta_S^{\alpha \rightarrow \gamma} = \gamma_S/\alpha_S$ ;  $\beta_S^{\gamma \rightarrow \tau} = \tau_S/\gamma_S$  (ref. <sup>24</sup>). Also, we can partition  $\alpha$  stability into species stability and species asynchrony<sup>11,52</sup>. Specifically, species stability is defined as the mean of local population stability weighted by species abundance (for example, cover) within quadrats and species asynchrony is defined as the ratio of  $\alpha$  stability to species stability, which captures the temporal incoherence in population dynamics among species within quadrats<sup>24</sup>. More details about the definitions and interpretations of these stability and asynchrony indices can be found in ref. <sup>24</sup> (Supplementary Figs. 2 and 3 and Table 4).

We note that each diversity or stability metric defined above represents the site-level average at the respective scale, so each site has only one value of diversity or stability at each scale (Supplementary Fig. 5). To further test DSRs across plots within sites and their dependence on climatic factors, we also calculated plot-level averages of diversity and stability at  $\alpha$ ,  $\beta^{\alpha \rightarrow \gamma}$  and  $\gamma$  scales ( $n=945$ ). For each plot within each site, these metrics were obtained, respectively, using equations (1), (2) and (4) by fixing the subscript 'm' to the respective plot (that is, without taking the sum over the dimension 'm'). All diversity and stability metrics are log-transformed (using natural logarithm base e, denoted as 'ln') to standardize the effect sizes in statistical analyses.

**Statistical analyses.** To examine the relationships between plant diversity and community stability (DSRs) at different scales ( $\alpha$ ,  $\gamma$ ,  $\tau$ ,  $\beta^{\alpha \rightarrow \gamma}$  and  $\beta^{\gamma \rightarrow \tau}$ ), we ran linear regression models (LMs) to fit DSRs across sites ( $\geq 4$  yr observations:  $n=36$ ) and extracted their log-log slopes. We then performed an analysis of covariance (ANCOVA) to test whether DSR slopes differ among spatial scales from  $\alpha$  to  $\gamma$  and  $\tau$  levels, as well as between across-quadrat and across-plot  $\beta$  scales ( $\beta^{\alpha \rightarrow \gamma}$  and  $\beta^{\gamma \rightarrow \tau}$ ). To test the robustness of our results, we conducted three analyses. First, we examined DSRs using partial linear regression models (p-LMs) to exclude potential confounding effects of climatic factors (MAP and MAT). Second, we recalculated diversity and stability and refitted DSRs by removing woody plant species in our dataset. Third, we ran above LMs and p-LMs using sites with records of  $\geq 5$  yr ( $n=24$ ) or  $\geq 6$  yr ( $n=14$ ) to account for the across-site variation in time-series length.

To explore the effects of climatic factors on community stability at different spatial scales both directly and indirectly by influencing plant diversity among 36 NEON sites, we fitted an SEM using the R package piecewiseSEM<sup>53</sup>. In light of metacommunity theory<sup>24</sup>, we initiated a SEM that characterized the potential effects of climatic factors on  $\alpha$  stability, spatial asynchrony both across quadrats ( $\beta_S^{\alpha \rightarrow \gamma}$ ) and across plots ( $\beta_S^{\gamma \rightarrow \tau}$ ) by altering  $\alpha$  diversity,  $\beta$  diversity both across quadrats ( $\beta_D^{\alpha \rightarrow \gamma}$ ) and plots ( $\beta_D^{\gamma \rightarrow \tau}$ ), which propagated to  $\gamma$  stability and further

to  $\tau$  stability (Extended Data Fig. 2). We also included the number of plots within each site and the average distance between plots as covariates, which may influence the across-plot  $\beta$  diversity and stability<sup>21,24</sup>. Because MAT and temperature seasonality are strongly negatively correlated (Supplementary Fig. 4a;  $R^2=0.61$ ,  $P<0.0001$ ), we included MAT, MAP and precipitation seasonality in our initial model. On the basis of this initial SEM, we fitted the model and used Shipley's test of  $d$ -separation to examine if any pathway was missing and should be added<sup>53</sup>. We obtained a final SEM by omitting non-significant pathways and variables (for example, precipitation seasonality). We also examined the robustness of this final SEM by re-introducing temperature seasonality and performing the test of  $d$ -separation to evaluate whether temperature seasonality had any additional effect. This test reported no missing pathways, suggesting no effect of temperature seasonality.

To assess how DSRs may change along climatic gradients, we first calculated the log-log slopes of DSRs at  $\alpha$ ,  $\beta^{\alpha \rightarrow \gamma}$  and  $\gamma$  scales using plot-level averages of diversity and stability within each site and then tested their relationships with climatic factors. To account for possible spatial autocorrelation across plots, we fitted DSRs within each site using generalized linear models with an exponential autocorrelation function (corExp(form= $\sim$ latitude + longitude)). Using plot-level diversity and stability metrics, we also conducted two analyses to test consistency between plot-level and site-level analyses. First, we applied linear mixed-effects models (LMMs) to assess the overall DSRs at  $\alpha$ ,  $\gamma$  and  $\beta^{\alpha \rightarrow \gamma}$  scales across 36 sites. Because different sites contain different numbers of plots (for example, 6–33) and these plots belong to different vegetation types (for example, the National Land Cover Database Vegetation Type Name, nlcdClass), we set the nlcdClass nested within site as a random factor and included corExp(form= $\sim$ latitude + longitude|siteID/nlcdClass) to characterize spatial autocorrelation across plots. The LMMs were conducted using the R package nlme<sup>54</sup>. Second, we fitted a sub-SEM to characterize the direct and indirect effects of climatic factors on plot-level  $\alpha$ ,  $\beta^{\alpha \rightarrow \gamma}$  and  $\gamma$  stability. The initial model is similar to the one in Extended Data Fig. 2 but without  $\beta_S^{\gamma \rightarrow \tau}$  and  $\tau$  diversity and stability. Again, we fitted this SEM using LMMs, including the nlcdClass nested within site as a random factor and the spatial autocorrelation function as specified above. We obtained the final SEM by omitting non-significant pathways and variables.

All analyses were programmed in R v.3.6.0 (ref. <sup>55</sup>).

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

Raw datasets are available from the NEON (<https://data.neonscience.org/data-products/DP1.10058.001>). The data used in this study are available via GitHub ([https://github.com/mwliang/NEON\\_stability](https://github.com/mwliang/NEON_stability)).

## Code availability

R code of all analyses is available at GitHub ([https://github.com/mwliang/NEON\\_stability](https://github.com/mwliang/NEON_stability)).

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## Author contributions

M. Liang and S.W. conceived the idea, analysed the data and wrote the first draft. B.B., L.M.H., Y.H., L.J., M. Loreau, S.R., E.R.S. and P.L.Z. contributed to the development and revision of the manuscript.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41559-022-01868-y>.

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41559-022-01868-y>.

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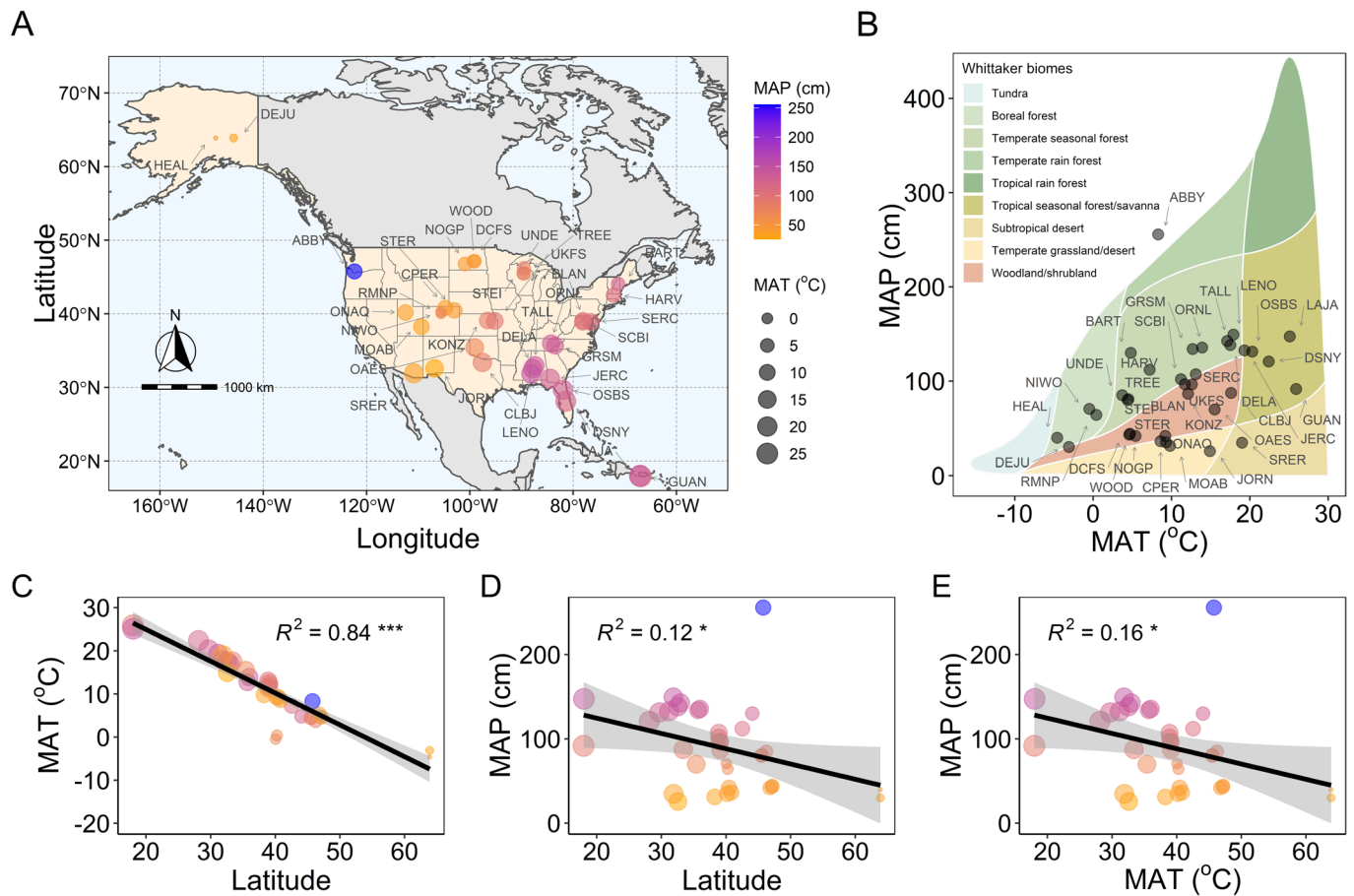
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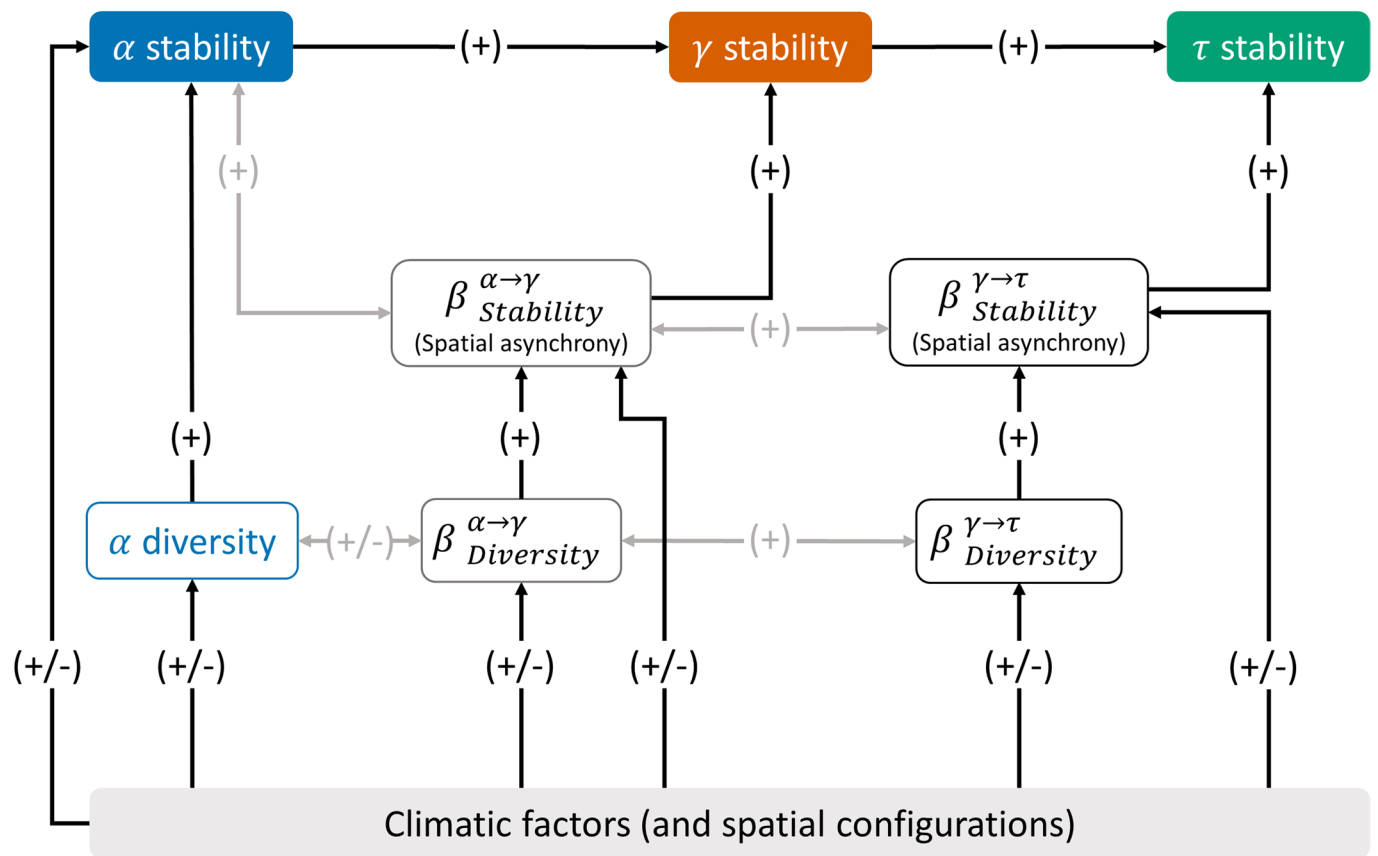
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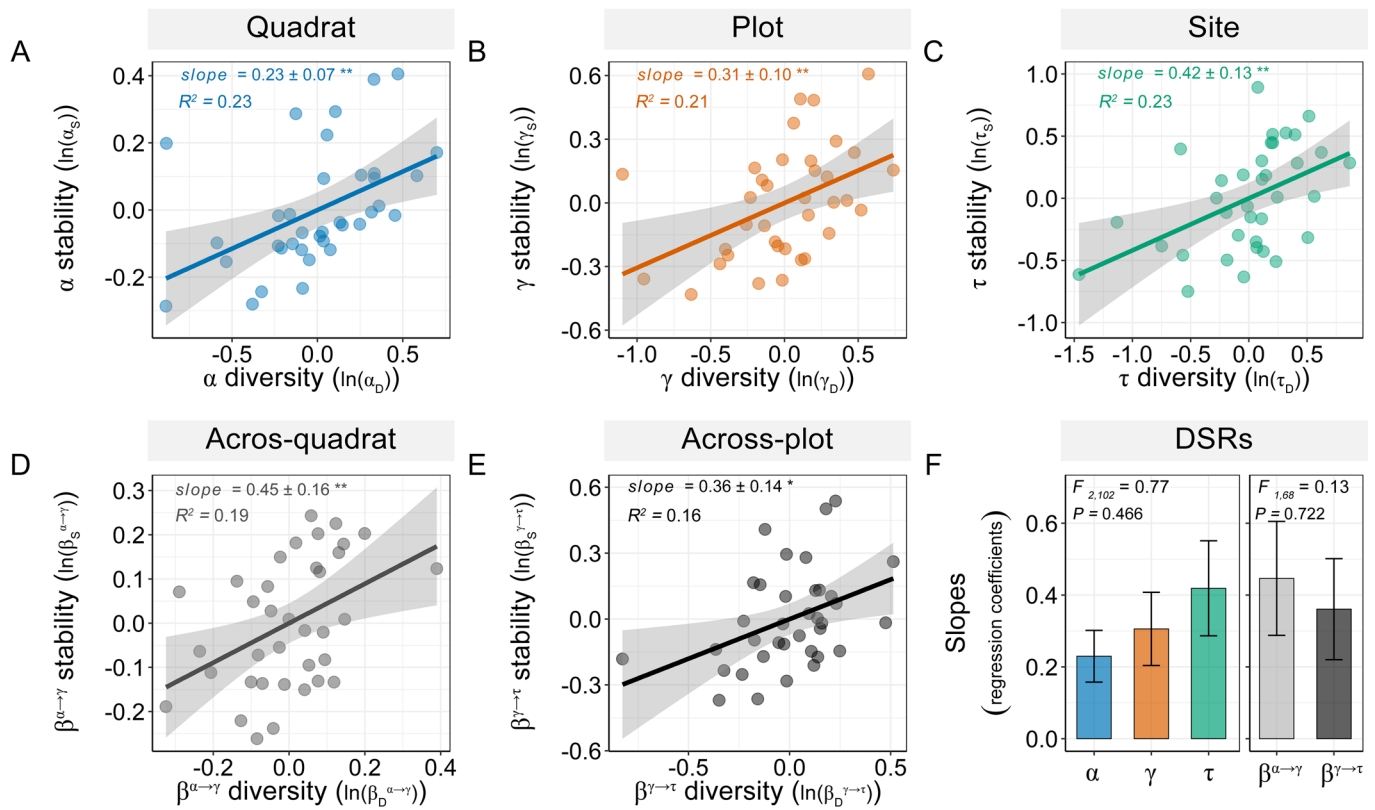


**Extended Data Fig. 1 | Geographic and climatic information of 36 NEON sites.** Shown are the geographic distribution across the United States (**A**), distribution in the Whittaker biomes (**B**), the mean annual temperature (**C**, MAT:  $F_{1,34} = 176.50$ ,  $P < 0.0001$ ) and mean annual precipitation (**D**, MAP:  $F_{1,34} = 4.70$ ,  $P = 0.037$ ) along the latitude gradient, as well as (**E**) their relationship between MAT and MAP (**E**,  $F_{1,34} = 6.43$ ,  $P = 0.016$ ). In (**A**–**B**), the abbreviation of the site name is provided in Appendix data 1. In (**C**–**E**), shaded areas are the error bands and denote 95% confidence intervals and significance levels are as follows: “\*”:  $P \leq 0.05$  and “\*\*\*”:  $P \leq 0.0001$ .

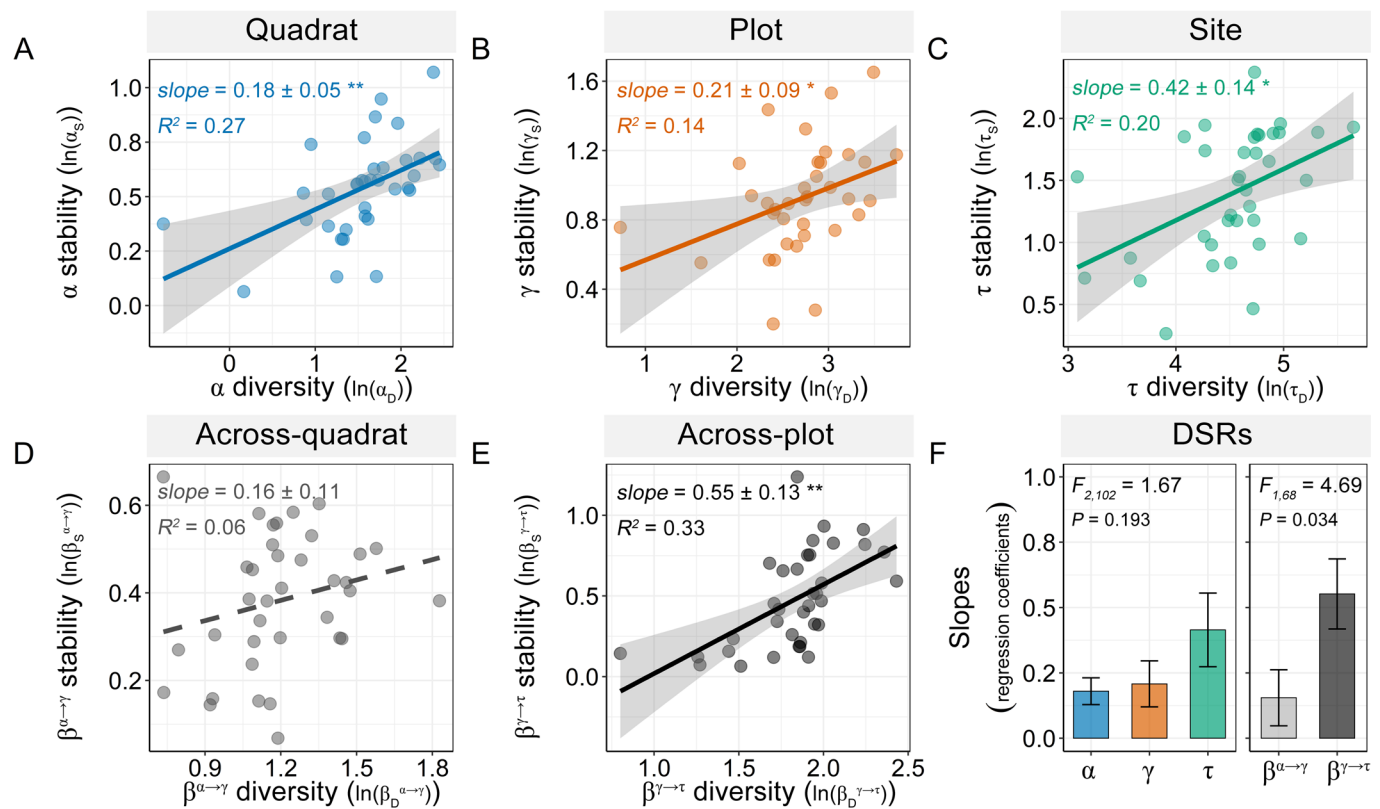




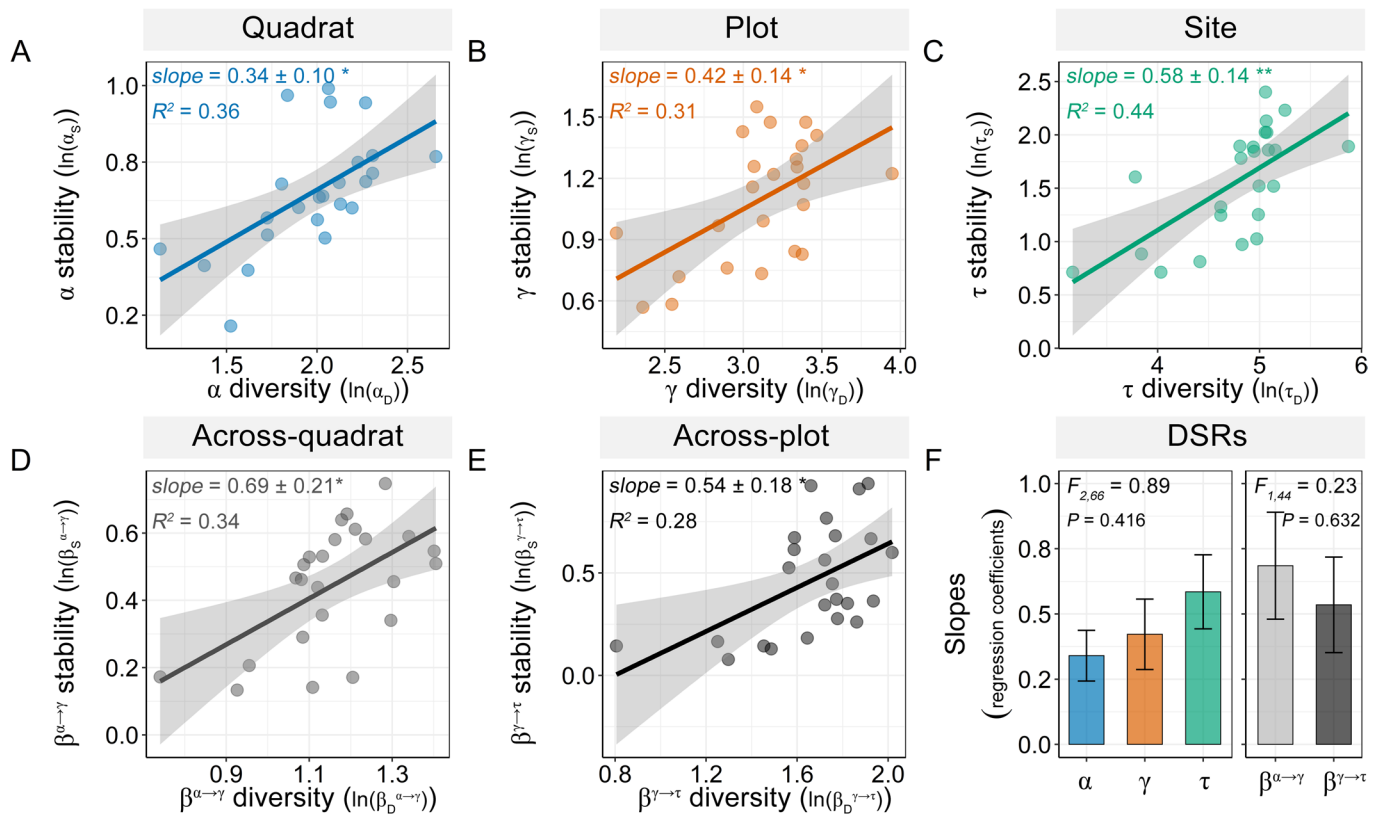
**Extended Data Fig. 2 |** A hypothesized structural equation modelling (SEM) illustrating the direct and indirect effects of climatic factors (as well as spatial configuration of plots) on biodiversity and stability at different scales. Details about the rationales of each pathway in the SEM are provided in Supplementary Table 15.



**Extended Data Fig. 3 | The diversity – stability relationships (DSRs) across multiple spatial scales, based on partial regression models after controlling for the effects of climatic factors (N = 36 sites).** Shown are the log–log relationships between  $\alpha$  diversity and  $\alpha$  stability at the quadrat level (**A**,  $F_{1,34} = 10.2$ ,  $R^2 = 0.23$ ,  $P = 0.003$ ), between  $\gamma$  diversity and  $\gamma$  stability at the plot level (**B**,  $F_{1,34} = 9.00$ ,  $R^2 = 0.21$ ,  $P = 0.005$ ), between  $\tau$  diversity and  $\tau$  stability at the site level (**C**,  $F_{1,34} = 10.02$ ,  $R^2 = 0.23$ ,  $P = 0.003$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_S^{\alpha \rightarrow \gamma}$  across quadrats (**D**,  $F_{1,34} = 7.92$ ,  $R^2 = 0.19$ ,  $P = 0.008$ ), between  $\beta_D^{\gamma \rightarrow \tau}$  and  $\beta_S^{\gamma \rightarrow \tau}$  across plots (**E**,  $F_{1,34} = 6.57$ ,  $R^2 = 0.16$ ,  $P = 0.015$ ), and a comparison of regression slopes across scales using ANCOVA (**F**,  $F_{2,102} = 0.77$ ,  $P = 0.466$  among quadrat, plot, and site levels;  $F_{1,68} = 0.13$ ,  $P = 0.722$  between across-quadrat and across-plot levels), respectively. Lines represent DSRs from the partial linear regression models (p-LMs) after accounting for the effects of mean annual precipitation and mean annual temperature. Shaded areas are the error bands and denote 95% confidence intervals; and significance levels are as follows:  $^{**}$ :  $P \leq 0.05$  and  $^{***}$ :  $P \leq 0.001$ . In (**F**), bars and error bars are regression coefficients and standard errors from p-LMs ( $n = 36$  for all) in (**A** – **E**). Note that in (**F**), pairwise comparisons between quadrat, plot, and site levels are non-significant ( $P > 0.1$  for all). Information about the fitted models is provided in Supplementary Table 2.



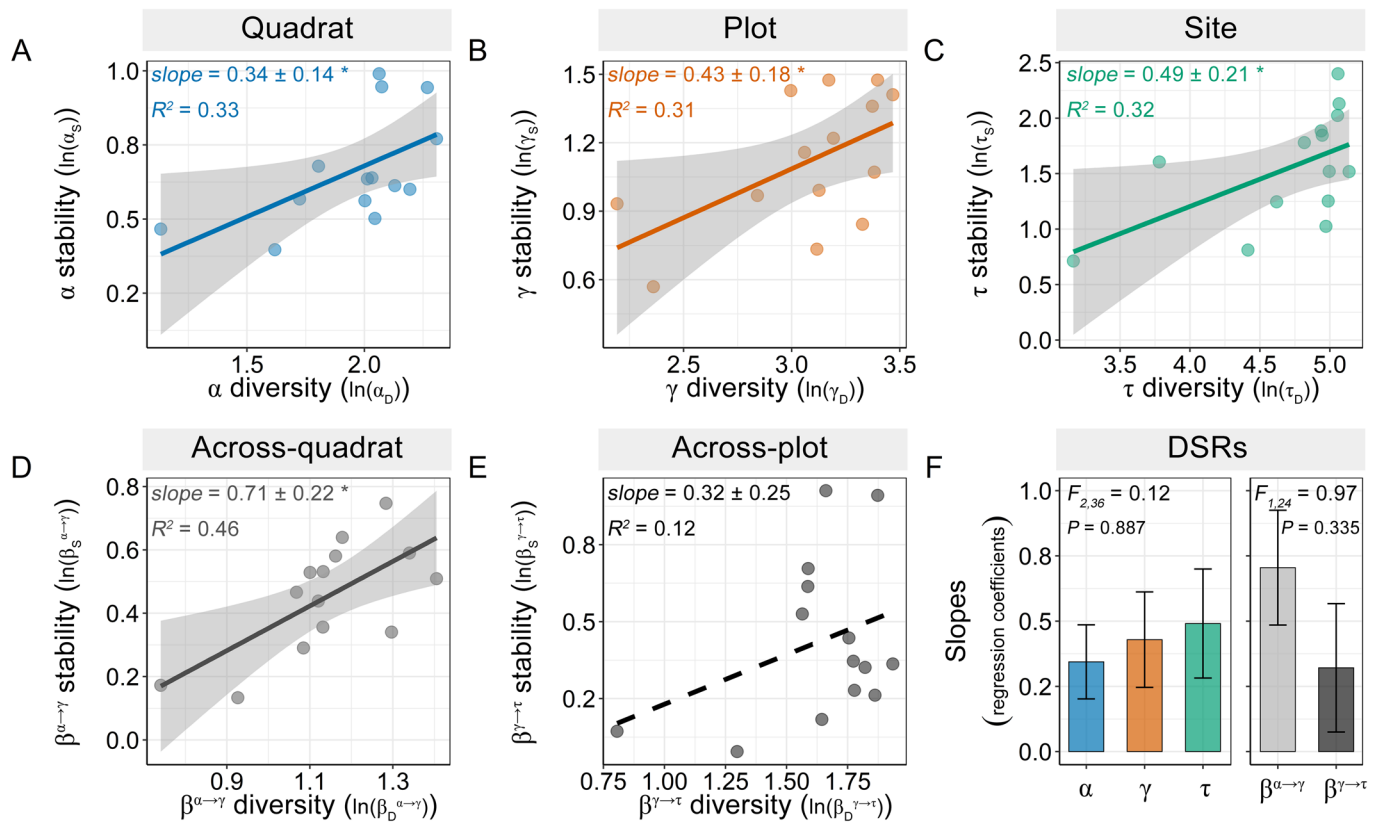
**Extended Data Fig. 4 | The diversity – stability relationships (DSRs) across multiple spatial scales, after excluding woody plant species (N = 36 sites).** Shown are the log–log relationships between  $\alpha$  diversity and  $\alpha$  stability at the quadrat level (**A**,  $F_{1,34} = 12.27$ ,  $R^2 = 0.26$ ,  $P = 0.001$ ), between  $\gamma$  diversity and  $\gamma$  stability at the plot level (**B**,  $F_{1,34} = 5.58$ ,  $R^2 = 0.14$ ,  $P = 0.024$ ), between  $\tau$  diversity and  $\tau$  stability at the site level (**C**,  $F_{1,34} = 8.67$ ,  $R^2 = 0.20$ ,  $P = 0.006$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_s^{\alpha \rightarrow \gamma}$  across quadrats (**D**,  $F_{1,34} = 2.09$ ,  $R^2 = 0.06$ ,  $P = 0.158$ ), between  $\beta_D^{\gamma \rightarrow \tau}$  and  $\beta_s^{\gamma \rightarrow \tau}$  across plots (**E**,  $F_{1,34} = 17.01$ ,  $R^2 = 0.33$ ,  $P = 0.0002$ ), and a comparison of regression slopes across scales using ANCOVA (**F**,  $F_{2,102} = 1.67$ ,  $P = 0.193$  among quadrat, plot, and site levels;  $F_{1,68} = 4.69$ ,  $P = 0.034$  between across-quadrats and across-plots levels). In (**A**–**E**), lines represent the overall relationships between biodiversity and community stability from the best-fit linear regression models (LMs), and shaded areas are the error bands and denote 95% confidence intervals. Significance levels are indicated as follows: \*\* $P \leq 0.05$  and \*\*\* $P \leq 0.001$ .  $R^2$  is the explained variance in LMs. In (**F**), bars and error bars are regression coefficients and standard errors from p-LMs ( $n = 36$  for all) in (**A**–**E**). Note that in (**F**), pairwise comparisons between quadrat, plot, and site levels are non-significant ( $P > 0.1$  for all).



**Extended Data Fig. 5 | The diversity – stability relationships (DSRs) across multiple spatial scales, using sites with  $\geq 5$  years records ( $N = 24$  sites).**

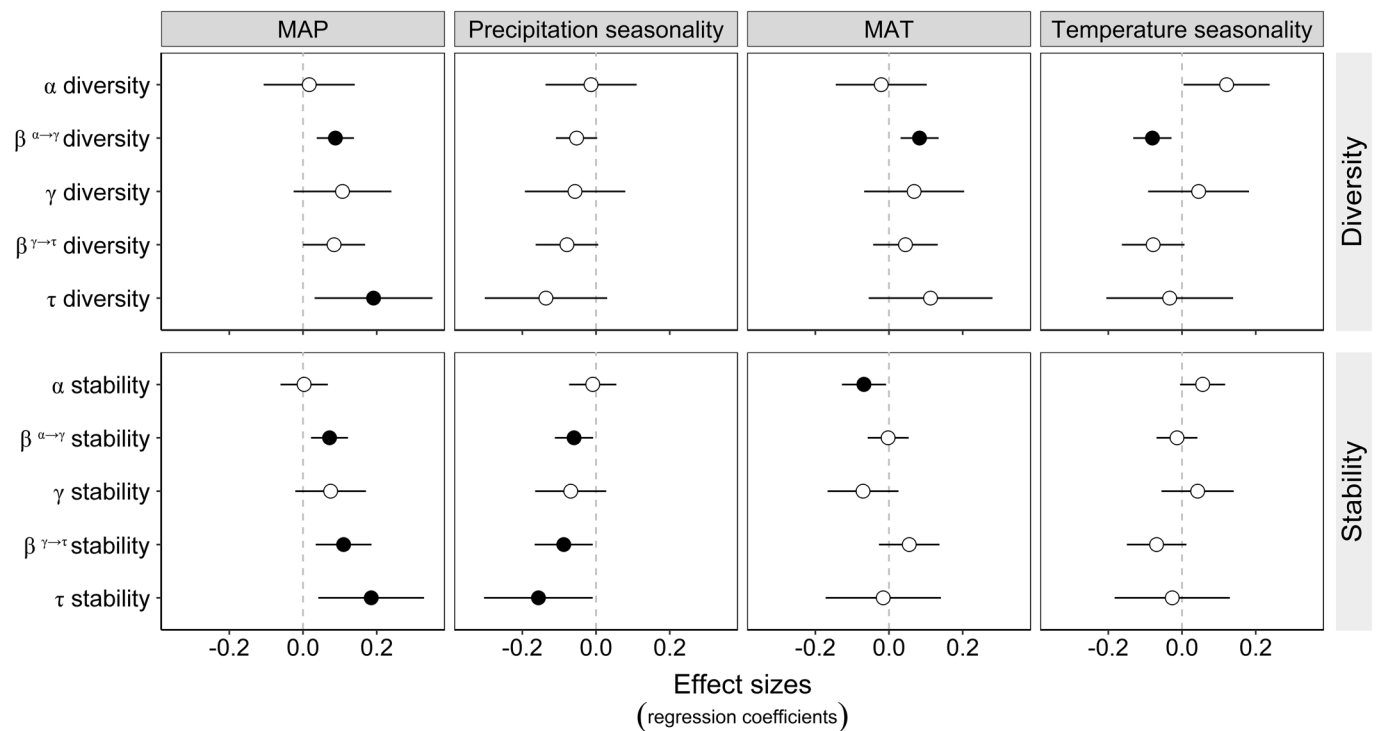
Shown are the log–log slopes between  $\alpha$  diversity and  $\alpha$  stability at the quadrat level (**A**,  $F_{1,22} = 12.34$ ,  $R^2 = 0.36$ ,  $P = 0.002$ ), between  $\gamma$  diversity and  $\gamma$  stability at the plot level (**B**,  $F_{1,22} = 9.79$ ,  $R^2 = 0.31$ ,  $P = 0.005$ ), between  $\tau$  diversity and  $\tau$  stability at the site level (**C**,  $F_{1,22} = 16.99$ ,  $R^2 = 0.44$ ,  $P = 0.001$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_s^{\alpha \rightarrow \gamma}$  across quadrats (**D**,  $F_{1,22} = 11.13$ ,  $R^2 = 0.34$ ,  $P = 0.003$ ), between  $\beta_D^{\gamma \rightarrow \tau}$  and  $\beta_s^{\gamma \rightarrow \tau}$  across plots (**E**,  $F_{1,22} = 8.51$ ,  $R^2 = 0.28$ ,  $P = 0.008$ ), and a comparison of regression slopes across scales using ANCOVA (**F**,  $F_{2,66} = 0.889$ ,  $P = 0.416$  among quadrat-, plot-, and site levels;  $F_{1,44} = 0.233$ ,  $P = 0.632$  between across-quadrats and across-plots levels). In (**A**–**E**), lines represent the overall significant relationships between biodiversity and community stability from the best-fit linear regression models (LMs), and shaded areas are the error bands and denote 95% confidence intervals. Significance levels are indicated as follows:  $^{**}$ :  $P \leq 0.05$  and  $^{***}$ :  $P \leq 0.001$ .  $R^2$  is the explained variance in LMs. In (**F**), bars and error bars are regression coefficients and standard errors from p-LMs ( $n = 36$  for all) in (**A**–**E**). Note that in (**F**), pairwise comparisons between quadrat, plot, and site levels are non-significant ( $P > 0.1$  for all). More information about the fitted models and partial regression models is provided in Supplementary Tables 1–2.

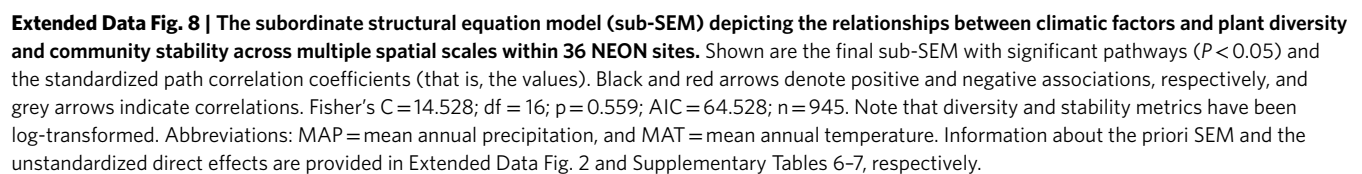




**Extended Data Fig. 6 | The diversity – stability relationships (DSRs) across multiple spatial scales, using sites with  $\geq 6$  years records ( $N = 14$  sites).**

Shown are the log–log slopes between  $\alpha$  diversity and  $\alpha$  stability at the quadrat level (**A**,  $F_{1,12} = 5.84$ ,  $R^2 = 0.33$ ,  $P = 0.033$ ), between  $\gamma$  diversity and  $\gamma$  stability at the plot level (**B**,  $F_{1,12} = 5.46$ ,  $R^2 = 0.31$ ,  $P = 0.038$ ), between  $\tau$  diversity and  $\tau$  stability at the site level (**C**,  $F_{1,12} = 5.52$ ,  $R^2 = 0.32$ ,  $P = 0.037$ ), between  $\beta_D^{\alpha \rightarrow \gamma}$  and  $\beta_s^{\alpha \rightarrow \gamma}$  across quadrats (**D**,  $F_{1,12} = 10.29$ ,  $R^2 = 0.46$ ,  $P = 0.008$ ), between  $\beta_D^{\gamma \rightarrow \tau}$  and  $\beta_s^{\gamma \rightarrow \tau}$  across plots (**E**,  $F_{1,34} = 1.70$ ,  $R^2 = 0.12$ ,  $P = 0.216$ ), and a comparison of regression slopes across scales using ANCOVA (**F**,  $F_{2,36} = 0.120$ ,  $P = 0.887$  among quadrat-, plot-, and site- levels;  $F_{1,24} = 0.970$ ,  $P = 0.335$  between across-quadrats and across-plots levels). In (**A**–**E**), solid lines represent the overall significant relationships between biodiversity and community stability from the linear regression models (LMs), and shaded areas are the error bands and denote 95% confidence intervals; a dashed line denotes insignificant ( $P > 0.05$ ). Significance levels are indicated as follows: ‘\*’:  $P \leq 0.05$ .  $R^2$  is the explained variance in LMs. In (**F**), bars and error bars are regression coefficients and standard errors from p-LMs ( $n = 36$  for all) in (**A**–**E**). Note that in (**F**), pairwise comparisons between quadrat, plot, and site levels are non-significant ( $P > 0.1$  for all). More information about the fitted models and partial regression models is provided in Supplementary Tables 1–2.





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- ☒ ☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
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### Software and code

Policy information about [availability of computer code](#)

#### Data collection

Our study was based on plant community survey data from the National Ecological Observatory Network (NEON). Plant presence and percent cover, RELEASE-2021 (DP1.10058.001). <https://doi.org/10.48443/abge-r811>. Dataset was accessed from <https://data.neonscience.org> on February 4th, 2021. A standardized sampling protocol is designed to monitor plant diversity and abundance across spatial and temporal scales. Specifically, at each of the 47 NEON sites (5-214 km<sup>2</sup>), multiple plots (size: 20 m × 20 m) were established, within which eight quadrats (1 m × 1 m) were established. For each quadrat, the identity and abundance (estimated cover) of each species have been recorded by NEON field ecologists on a yearly basis between 2013 and 2020.

#### Data analysis

R code of all analyses is available at GitHub ([https://github.com/maoweiliang/NEON\\_stability](https://github.com/maoweiliang/NEON_stability)).

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Raw datasets are available at the National Ecological Observatory Network (<https://data.neonscience.org/data-products/DP1.10058.001>). The data used in this study are available via GitHub ([https://github.com/maoweiliang/NEON\\_stability](https://github.com/maoweiliang/NEON_stability)).



# Field-specific reporting

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## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Our study investigates the relationship between plant species diversity and community stability across multiple spatial scales and along broad environmental gradients. To do so, we used plant community survey data from the National Ecological Observatory Network (NEON). Plant presence and percent cover, RELEASE-2021 (DP1.10058.001). <a href="https://doi.org/10.48443/abge-r811">https://doi.org/10.48443/abge-r811</a> . Dataset was accessed from <a href="https://data.neonscience.org">https://data.neonscience.org</a> on February 4th, 2021.
Research sample	Because different NEON sites were established at different time, we used data from those sites with at least 4-year observations (finally 36 sites were selected) to achieve a reliable estimate of temporal stability. The datasets have been collected in the growing season between 2013 and 2020. In total, more than 6,000 plant species have been monitored in 7,560 quadrats (1 m <sup>2</sup> ) within 945 plots (400 m <sup>2</sup> ) from the 36 NEON sites across the United States.
Sampling strategy	<p>Within each NEON site, plant species abundance were available at quadrats of 1 m<sup>2</sup> (<math>\alpha</math>), plots of 400 m<sup>2</sup> (<math>\gamma</math>), and sites of 5-214 km<sup>2</sup> (<math>\tau</math>) scales. We calculated species diversity and stability at each of these scales. To compare the relationships between plant diversity and community stability (DSRs) at different scales, we ran linear regression models (LM) to extract the log-log slopes of DSRs and calculated the averaged slopes within each site (N = 36). We then performed the analysis of covariance (ANCOVA) to test the differences of DSR slopes among spatial extents from quadrat to plot and further to site levels. We also performed the linear partial regression models by first running LMs between each diversity/stability variable and abiotic factors (mean annual temperature and precipitation) and then extracting the residuals of diversity/stability and testing their relationships using LMs.</p> <p>Moreover, because different sites contain the different number of plots (e.g., 5~33) and belong to different vegetation types (e.g., the National Land Cover Database Vegetation Type Name, nlcdClass), the number of plots and vegetation types may have confounded effects when comparing diversity, stability, and their relationships among sites. Thus, to test the robustness of our results, we applied linear mixed-effects models (LMMs) to assess the diversity-stability relationships at <math>\alpha</math>, <math>\beta^*(\alpha \rightarrow \gamma)</math>, and <math>\gamma</math> scales, with the nlcdClass nested within site as a random factor.</p> <p>Lastly, the environmental variables are highly associated with the geospatial coordinates across NEON 36 sites, indicating geographically environmental conditions of the sites (e.g., drier vs. wetter, colder vs. warmer). To test the effects of the mean and seasonality of temperature and precipitation on different diversity and stability metrics, we fitted multiple LMs (N=36). Also, we fit a structural equation modeling to explore direct and indirect effects of environmental factors on stability at different spatial scales via influencing species diversity.</p>
Data collection	The identity and abundance (estimated cover) of each species have been recorded by NEON field ecologists in 7,560 quadrats (1 m <sup>2</sup> ) within 945 plots (400 m <sup>2</sup> ) from the 36 NEON sites.
Timing and spatial scale	All quadrats and plots are sampled annually in all 36 sites during 2013 and 2020 (at least 4 years during this period). The 36 sites are geographically distributed from 18.0 to 63.9 degrees N and from 66.9 to 149.2 degrees W in the United States.
Data exclusions	As different sites were established at different time, we used data from 36 NEON sites with at least 4-year observations to achieve a reliable estimate of temporal stability. Sites with less than 4-year observations were excluded.
Reproducibility	Not applicable because observational data were used. Codes for statistical analyses are available at GitHub (see above).
Randomization	We considered the allocation of the 36 sites as a random process, which should not cause any systematic bias for our analysis. Although the sites were located across large gradients of environmental factors which might confound the relationship between diversity and stability, we have used linear partial regression models (to exclude the effects of environmental factors on diversity and stability) to test the robustness of our results. Such partial regression models demonstrated consistent positive effects of biodiversity on stability at multiple spatial scales.
Blinding	Not applicable because the dataset is derived from field surveys on natural plant communities, rather than a randomized experiment (e.g. randomized controlled trials).
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	This study involves the analysis of existed publicly available dataset NEON, which collected data from 36 sites across 20 states in the US between 2013 and 2020. According to the sampling protocols ( <a href="https://data.neonscience.org/data-products/DP1.10058.001">https://data.neonscience.org/data-products/DP1.10058.001</a> ), site conditions such as temperature, precipitation, and etc. have been recorded along the way, and all relevant field condition data can be successfully accessed in the supplementary data.
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Location	The 36 NEON sites were geographically located at from 18.0 to 63.9 degrees N and from 66.9 to 149.2 degrees W in 20 states of the US. Their coordinates are provided in the supplementary data.
Access & import/export	According to the NEON documents ( <a href="https://data.neonscience.org/data-products/DP1.10058.001">https://data.neonscience.org/data-products/DP1.10058.001</a> ), the NEON Field Operations Manager and the Lead Field Technician have primary authority to access the field and conduct sampling in safe conditions.
Disturbance	Not applicable.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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