


## Environmental conditions are the dominant factor influencing stability of terrestrial ecosystems on the Tibetan plateau

Liang Ren <sup>1,2</sup>, Jiaxuan Huo<sup>1,2</sup>, Xiang Xiang<sup>1,2</sup>, Yingping Pan<sup>1,2</sup>, Yuanqiao Li<sup>1,2</sup>, Yuanyuan Wang<sup>1,2</sup>, Dehui Meng<sup>1,2</sup>, Cheng Yu<sup>1,2</sup>, Yang Chen<sup>3</sup>, Zichao Xu<sup>4</sup> & Yongmei Huang<sup>1,2</sup>✉

Ecosystem stability is essential for the sustainable provision of diverse ecosystem services. However, the factors that maintain ecosystem stability and their relative importance on the Tibetan Plateau, a region sensitive to climate change, remain unclear. Here, we combined data from ground-based biodiversity surveys at 143 sites from 2019 to 2021 with the temporal stability of ecosystems derived from remote sensing data from 2000 to 2020 to disentangle mechanisms of diversity–stability relationships. We further quantified the impact of biodiversity (taxonomic, functional, and phylogenetic diversity) and environmental context (spatial location, climate, and soil conditions) on temporal stability. Our results show that the stability of a typical ecosystem on the Tibetan Plateau is mainly regulated by environmental factors, and the environmental context can directly affect the stability of the ecosystem rather than indirectly through biodiversity. These findings are critical for adaptation measures and prioritizing conservation areas for future climate change scenarios.

<sup>1</sup>State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University, Faculty of Geographical Science, Beijing 100875, China.

<sup>2</sup>School of Natural Resources, Beijing Normal University, Faculty of Geographical Science, Beijing 100875, China. <sup>3</sup>Institute of Remote Sensing Science and Engineering, Faculty of Geographical Science, Beijing Normal University, Beijing 100875, China. <sup>4</sup>School of Resources and Environment, University of Electronic Science and Technology of China, Chengdu 611731, China. ✉email: [yhuang@bnu.edu.cn](mailto:yhuang@bnu.edu.cn)

The stability of terrestrial ecosystems in a changing environment is a growing concern, as it is essential to ensure the sustainable provision of various ecosystem functions and services in the face of increasing climate change and biodiversity loss<sup>1–3</sup>. Ecosystem stability is a multidimensional concept encompassing resistance, resilience, invariance, and persistence<sup>4–7</sup>. Nonetheless, empirical studies in recent years have mainly concentrated on the temporal stability of ecosystem functions<sup>8,9</sup>, which are often depicted by invariance in above-ground biomass or productivity over time<sup>2,10</sup>. Plant diversity contributes to the stability of ecosystems, as proven in experimentally assembled communities<sup>10,11</sup>, but the stability of natural communities may be driven by both biotic and abiotic factors<sup>12,13</sup>. The extent to which these factors affect the temporal stability of ecosystems remains unclear. Furthermore, the lack of insights into the underlying mechanisms may hinder the prediction of terrestrial ecosystem feedback under future climate change<sup>14</sup>, as well as the development of guiding policies for ecosystem stability<sup>15</sup>.

Two primary hypotheses regarding the mechanisms through which biotic factors maintain temporal stability exist. First, the diversity hypothesis suggests that communities with high diversity tend to include species that respond differently to environmental changes (manifested as temporal asynchrony)<sup>13,15,16</sup>. The compensatory dynamics between these species can enhance community stability, which increases with increasing plant diversity<sup>9,10,17</sup>. Although this hypothesis has received widespread attention due to statistical support<sup>18</sup>, the consistency of this diversity-stability relationship in natural communities is currently under debate, as many empirical tests in assembled communities demonstrate high evenness. However, the mass ratio hypothesis (also known as the dominance effect)<sup>19</sup> suggests that dominant species in a community have a strong influence on ecosystem functioning (including temporal stability)<sup>20</sup>, and has been confirmed in numerous investigations in natural communities, particularly in those with low evenness<sup>14,21,22</sup>.

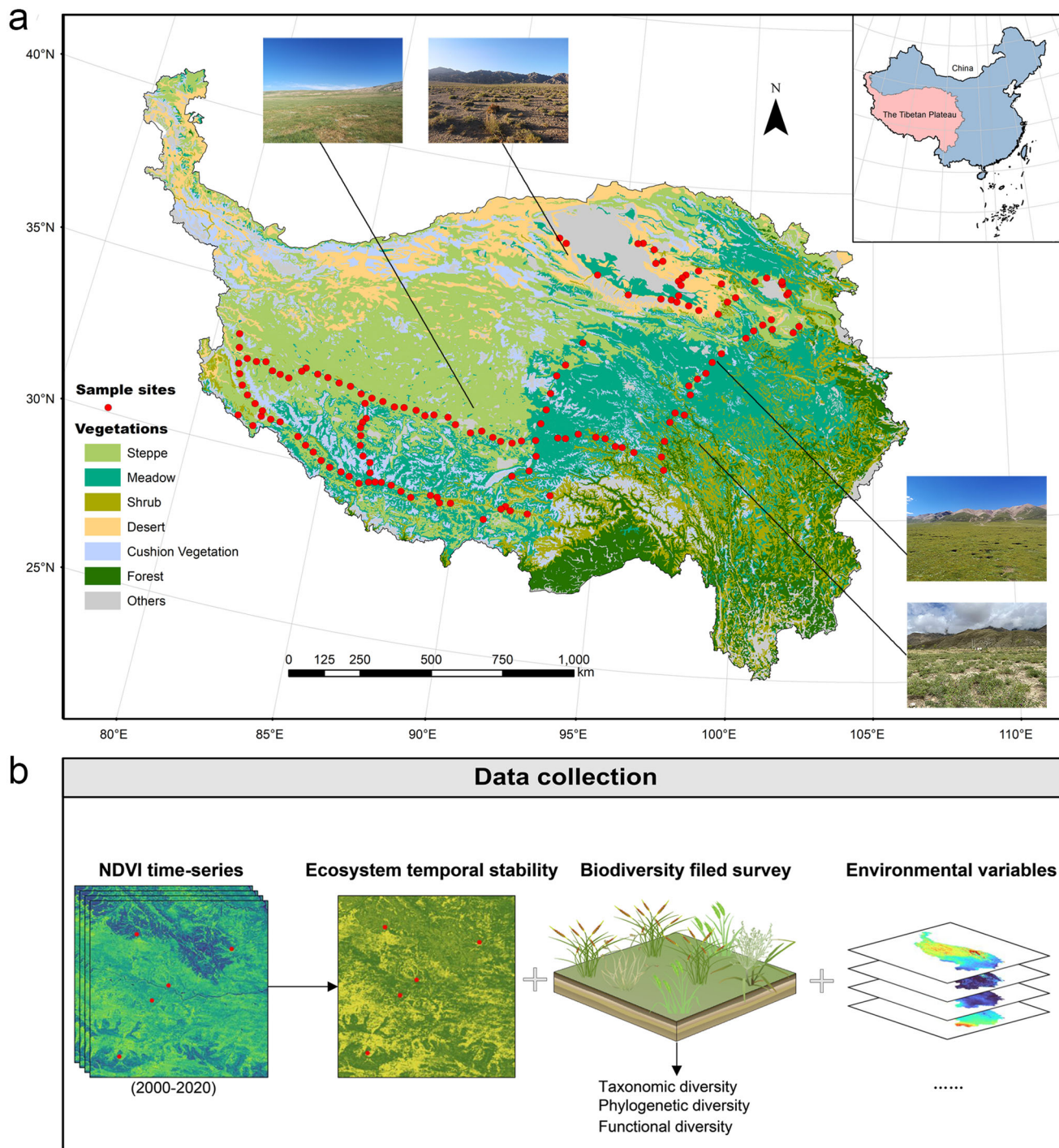
As both mechanisms may affect plant communities together, quantifying biotic factors from different perspectives can help to better predict the temporal stability of ecosystems. Simple metrics, such as species richness (SR), Simpson's diversity index (D), and species evenness<sup>20</sup>, are often used to assess the impact of species taxonomic diversity on temporal stability. Moreover, ecological strategies associated with growth may strongly influence temporal stability<sup>23</sup>, in which conservative species with slow growth rates, resource uptake and tissue turnover ('slow' species) tend to be more stable than exploitative species with the opposite strategy ('fast' species)<sup>24–26</sup>. This difference in strategy can be characterized by plant functional traits that are largely related to the leaf economics spectrum<sup>27</sup>. Slow species typically exhibit low specific leaf area, high leaf dry matter content (LDMC), low leaf nitrogen concentration (LNC), and low leaf phosphorus concentration (LPC); the opposite is true for fast species<sup>28,29</sup>. Metrics of functional diversity, such as functional richness and weighted means of key traits in communities, have been useful in explaining ecosystem stability<sup>1,26,30</sup>. Furthermore, phylogenetic diversity has a strong positive correlation with ecosystem stability, as shown in many analyses<sup>12,31,32</sup>. Although taxonomic, functional, and phylogenetic diversity may play important roles in the mechanisms that maintain community stability, few studies have comprehensively examined the relative importance of different biodiversity facets in maintaining the temporal stability of natural communities.

Recent analyses have shown that environmental factors, such as climate variability and water availability, have important effects on ecosystem stability<sup>1,26</sup>, particularly at broad spatial scales. For example, a study on North American grasslands showed that the

biotic mechanisms that maintain community stability shift along a precipitation gradient<sup>33</sup>. Inter- and intra-annual variability in precipitation also has a modulating effect on ecosystem stability, and may influence primary productivity and temporal stability by filtering the functional traits and diversity of plant communities<sup>34,35</sup>. Similarly, soil properties have been shown to affect ecosystem stability, either by altering aboveground plant diversity<sup>1,16</sup> or by altering soil biota indirectly<sup>8,36,37</sup>. Additionally, anthropogenically driven environmental changes can lead to declines in ecosystem stability through mechanisms that are dependent on or independent of plant diversity<sup>38–40</sup>. Overall, biodiversity and ecosystem stability vary widely across climatic regimes, geographic regions and ecosystem types<sup>41,42</sup>, and this dependence on environmental context has severely hampered our understanding of various biotic and abiotic drivers and how they affect ecosystem temporal stability.

Known as the third pole of the Earth, the Tibetan Plateau is highly sensitive to climate change<sup>43,44</sup>. It has experienced more rapid warming than the global average in recent decades<sup>45</sup> with increasing interannual variations in precipitation, leading to overall vegetation growth, despite significant spatial heterogeneity<sup>46</sup>. Changes in biomass production and community characteristics caused by climate change suggest that they may have a potential impact on ecosystem stability on the Tibetan Plateau<sup>47</sup>, which has been explored in only few studies. The results of short-term manipulative experiments showed that warming significantly reduced the temporal stability of community biomass in alpine grasslands compared with the insignificant effect of precipitation change<sup>14</sup>. Meanwhile, a 20-year experimental observation conducted in alpine meadows did not find that climate change had a significant effect on the temporal stability of community biomass<sup>48</sup>. These results also suggest that communities maintain temporal stability through asynchronism at the local scale. Furthermore, asynchrony is an important mechanism for maintaining the temporal stability of communities at the local scale. However, this provides very limited knowledge to the multivariate driving mechanisms of community stability in natural ecosystems, especially for diverse typical ecosystems distributed along the broad climate and soil gradients of the Tibetan Plateau.

In this study, we sought to comprehensively assess the contributions of biotic and abiotic drivers to temporal stability across typical ecosystems (alpine meadows, steppes, shrubs, and deserts) on the Tibetan Plateau, based on a regional biodiversity observation dataset. Specifically, we first obtained the community structure and individual plant functional traits at 143 sites from ground field surveys, from which multifaceted biodiversity indices (taxonomic diversity, functional diversity, and phylogenetic diversity) were calculated (Fig. 1). They were then combined with various environmental covariates (e.g., climatic conditions and soil properties) and with the Landsat-derived temporal stability of the ecosystem obtained at the corresponding locations. We hypothesized that the temporal stability of ecosystems on the Tibetan Plateau is directly influenced by both biotic and abiotic factors (Fig. 2); however, the strength of the different factors varies by ecosystem. The following questions were explored: (a) Does ecosystem temporal stability differ among typical ecosystems on the Tibetan Plateau? (b) What are the relative strengths of biotic and abiotic factors in stabilizing ecosystems? and (c) How do various ecological factors directly and indirectly affect ecosystem temporal stability? The results showed that while the typical ecosystems on the Tibetan Plateau exhibited comparable levels of temporal stability, the underlying factors that maintained the stability of the ecosystems varied greatly. Abiotic factors such as climate and soil conditions were found to play a more important role compared to biotic factors, directly influencing the stability of the ecosystem to a large extent.



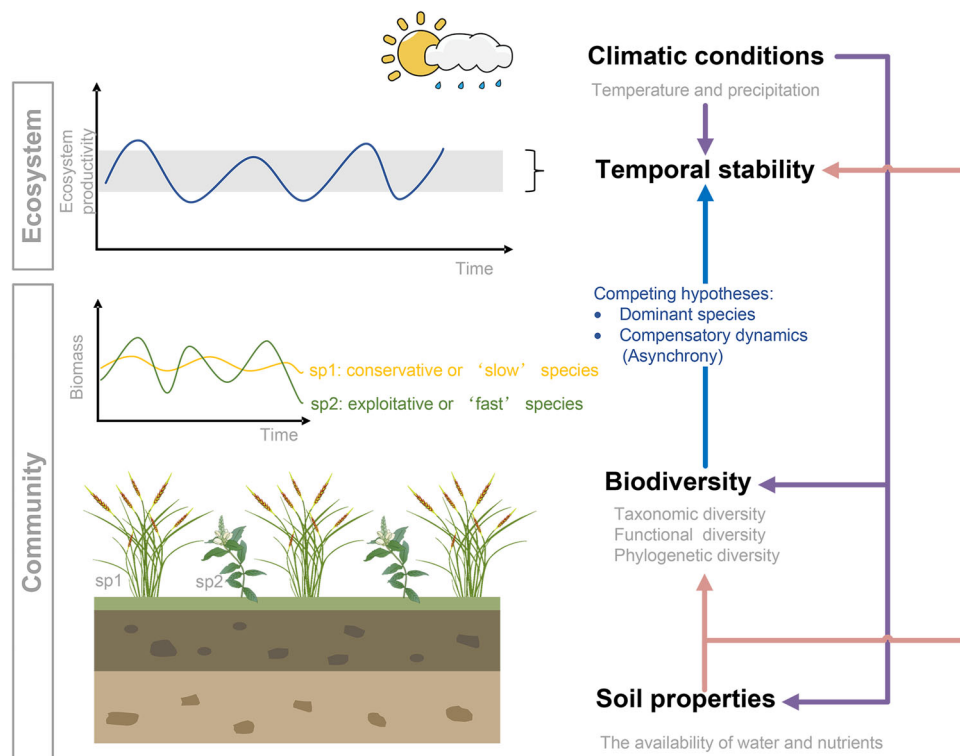
**Fig. 1** The location of the 143 sampling sites and the data collection process for each site. **a** Sampling sites spanned different vegetation types on the Tibetan Plateau, as shown on the background adapted from vegetation map of the People’s Republic of China (1: 1,000,000)<sup>53</sup>. **b** At each site, ecosystem stability was calculated and relevant biotic and abiotic data were collected. Community illustration icons are from Integration and Application Network, University of Maryland Center for Environmental Science (<https://ian.umces.edu/imagelibrary/>), which are available under a CC-BY 4.0 license (<https://creativecommons.org/licenses/by/4.0>).

**Results**

**Ecosystem stability and its relationship to individual predictor variables.** The mean value of temporal stability did not vary significantly among the four ecosystems on the Tibetan Plateau (range of 3.63–4.42). However, the two stability components differed significantly (Fig. 3). Ecosystems with higher mean NDVI values also exhibited higher standard deviations of NDVI, consistently ranking as alpine meadows >shrubs >steppes >deserts.

Analysis of the detrended temporal stability showed similar results.

The correlation analysis showed that the temporal stability of the four ecosystems was not significantly influenced by the same driving factors (Fig. 4), although some factors were highly correlated (Supplementary Fig. 1). Notably, soil properties had a broad effect on temporal stability in all ecosystems except for alpine meadows, which only showed significant correlations with



**Fig. 2 Schematic representation of how climate, soil, and biodiversity affect the temporal stability of an ecosystem.** Lines with different colors indicate distinct effects. Plant graphics were obtained from the Integration and Application Network, University of Maryland Center for Environmental Science (<https://ian.umces.edu/imagelibrary/>), which are available under a CC-BY 4.0 license (<https://creativecommons.org/licenses/by/4.0>).

latitude (and LPC and TS when analyzing detrended temporal stability) (Fig. 4). Despite the weak relationships between indicators of biodiversity and temporal stability, SR showed a positive trend towards temporal stability, LNC and LPC showed a negative trend towards temporal stability, and the role of functional indices, such as functional richness, varied among ecosystems. Additionally, some factors were strongly correlated with both components of temporal stability, but decoupled from temporal stability itself. For instance, all the considered soil variables were significantly correlated with the components of temporal stability within the alpine meadow ecosystems.

**Relative importance of biotic and abiotic drivers for ecosystem stability.** Among the three competing models, the full model was the best (Supplementary Tables 1 and 2) and could explain 42% to 59% of the variation in the detrended temporal stability across different ecosystems on the Tibetan Plateau (Supplementary Fig. 2). After the model averaging procedure, the best subset of each full model for the four typical ecosystems was used to assess the relative importance of biotic and abiotic variables on ecosystem stability (Fig. 5). For the alpine meadows, the spatial factor showed a large effect (accounting for 44% of the variance), although the effect of no factor was significant (Fig. 5a). For desert ecosystems, soil variables explained most of the variance in temporal stability (77%), and soil sand content exhibited a significant positive correlation with ecosystem stability (Fig. 5b). Biotic variables were the most important factors for the temporal stability of shrubs (86% of the variance), and CWM\_PC2 showed a significant negative correlation with ecosystem stability (Fig. 5c). For the steppes, the relative effect of soil variables was the highest (37%), and soil sand content and latitude were significantly and positively associated with ecosystem stability (Fig. 5d). Although some variables were not significant in the figure, the average estimates of variables from all models in the

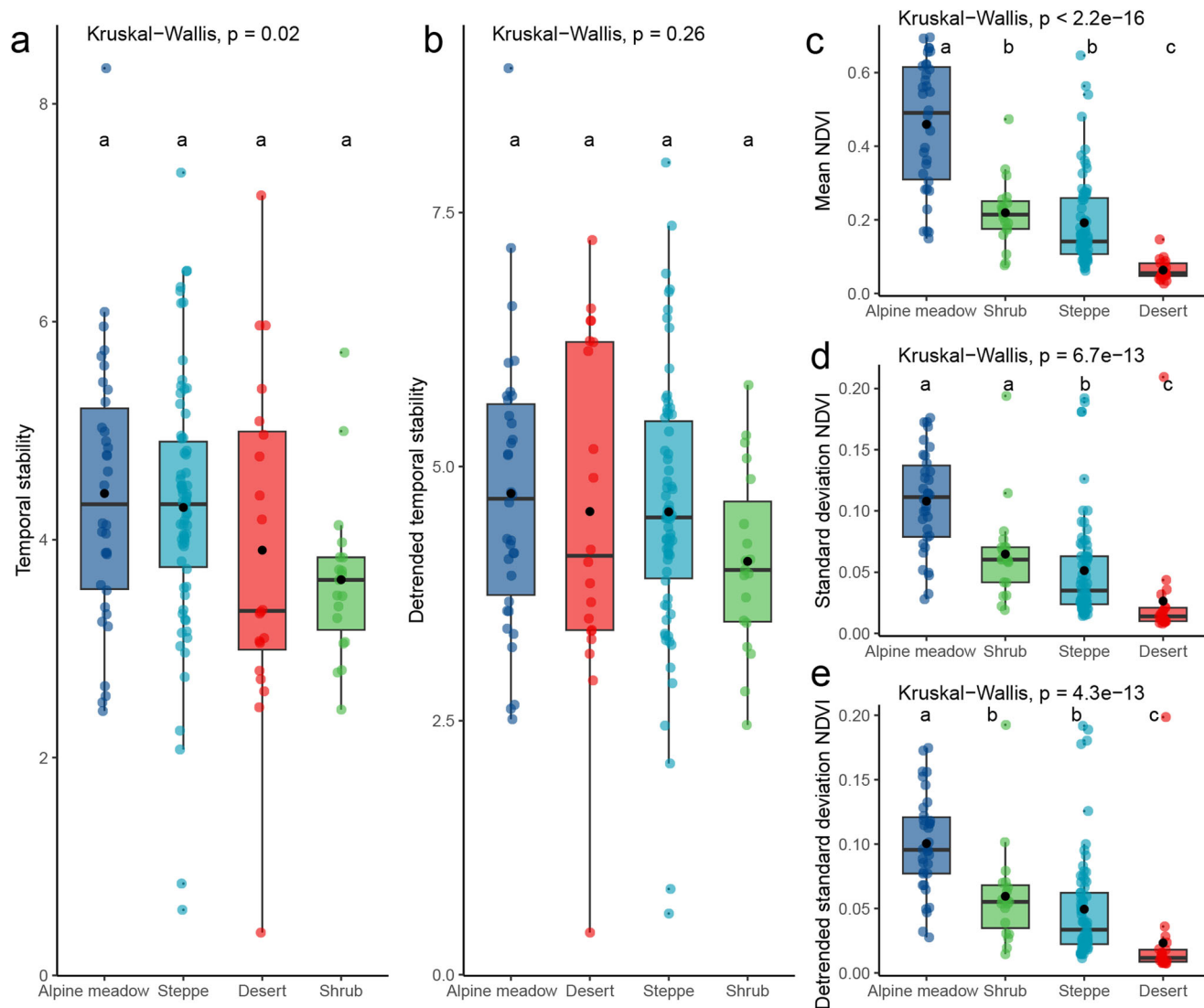
best subset were shown here, which are usually conservative estimates. These variables may not be unimportant because they are mechanistically related to temporal stability and can be significant in a certain best model.

**Direct and indirect effects of biotic and abiotic factors on ecosystem stability.** The direct or indirect effects of biotic and abiotic variables on ecosystem stability were considered within different ecosystems of the Tibetan Plateau. PLS-PM analysis showed that the variance explained by the model for detrended temporal stability across ecosystems ranged from 27% to 60% (Fig. 6), indicating that the key variables were able to account for most of the stability of typical ecosystems. For alpine meadows and shrubs, ecosystem stability was mainly directly influenced by climatic conditions (standardized path coefficient: 0.51 vs.  $-0.73$ ; Fig. 6a, c). In deserts, ecosystem stability was significantly and directly influenced by soil properties (standardized path coefficient:  $-0.58$ ; Fig. 6b). For steppes, ecosystem stability was significantly influenced by a combination of climatic conditions, soil properties, and CWM fast-slow (standardized path coefficients: 0.40,  $-0.50$ ,  $-0.24$ ; Fig. 6d).

In general, the results of the PLS-PM analysis showed that both the direct and indirect effects of abiotic factors had a surprisingly important impact on ecosystem stability compared to biotic factors (Supplementary Fig. 3). Additionally, latitude is only important in alpine meadows and steppes that span a large geographic range, and considering latitude in the PLS-PM of deserts and shrubs greatly reduces the goodness of fit (Supplementary Fig. 4).

## Discussion

**Regional specificity of ecosystem stability on the Tibetan Plateau.** Our results showed that the temporal stability of diverse



**Fig. 3 Differences of stability and its components among ecosystems.** Differences among ecosystems in temporal stability (a), detrended temporal stability (b) and their components, mean of NDVI (c), standard deviation of NDVI (d) and detrended standard deviation of NDVI (e) are shown. The upper side of the box indicates the upper quartile, the lower side indicates the lower quartile, the black horizontal line represents the median, and the black dot represents the mean. Colored scatter indicates samples from alpine meadows ( $n = 34$ ), deserts ( $n = 20$ ), shrubs ( $n = 19$ ), and steppes ( $n = 70$ ). The results of Kruskal-Wallis test between groups are marked in the figure, and different letter marks indicate significant differences ( $P < 0.05$ ).

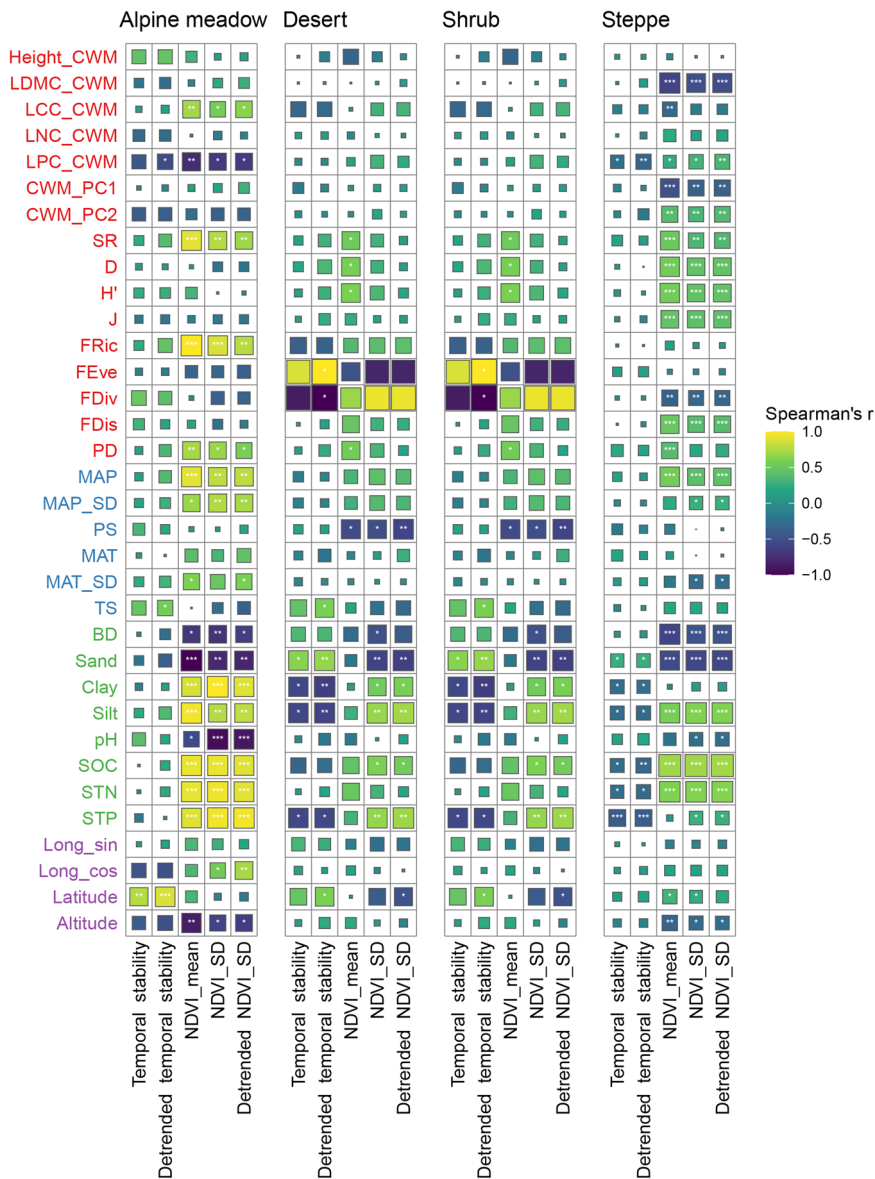
ecosystems on the Tibetan Plateau was strongly affected by biotic and abiotic factors of varying strength (Figs. 4 and 6), but did not differ significantly among ecosystems (Fig. 3). Ecosystems on the Tibetan Plateau are at a low level of stability. Previous global-scale studies using remote sensing indices have shown that shrublands and grasslands are the two least stable biomes over time compared to other natural biomes<sup>41</sup>, and that alpine regions worldwide are highly sensitive to climate variability<sup>49</sup>, which reflects the sensitivity and specificity of the Tibetan Plateau.

The composition and primary productivity of plant communities in alpine regions in response to climate change is of great interest<sup>46,50,51</sup>. However, neither diversity nor the two components of temporal stability (mean and standard deviation of productivity) could be substituted for monitoring temporal stability. Our results showed that some ecological variables affected both the mean and standard deviation of NDVI, but were decoupled from ecosystem stability (Fig. 4). This is similar to previous findings in community experiments<sup>26,52</sup>, in which biomass-promoting factors also increase the standard deviation of the biomass over time. Although manipulative experiments or long-term monitoring are more

direct means of studying climate change impacts<sup>14,47</sup>, their results are usually limited to specific habitats, and natural communities in different habitats may respond to climate change in very different ways across the vast spatial extent of the Tibetan Plateau<sup>48</sup>. Therefore, snapshot surveys were conducted on most of the Tibetan Plateau to detect shifts in the stability of different ecosystems along climatic or soil gradients. Biotic and abiotic factors served as predictor variables to explain 42–59% of the variation in ecosystem stability in this study (Fig. 5), whereas a previous study conducted on alpine grasslands on the Tibetan Plateau explained only 43% of the variation in ecosystem stability. In summary, this study establishes an important bridge between local field surveys and satellite remote sensing on a large spatial scale to assess ecosystem stability.

#### Role of different biodiversity aspects on ecosystems stability.

Both theoretical and experimental studies have demonstrated the positive effects of biodiversity on ecosystem stability. However, these studies focused more on forest<sup>41,53,54</sup> and grassland

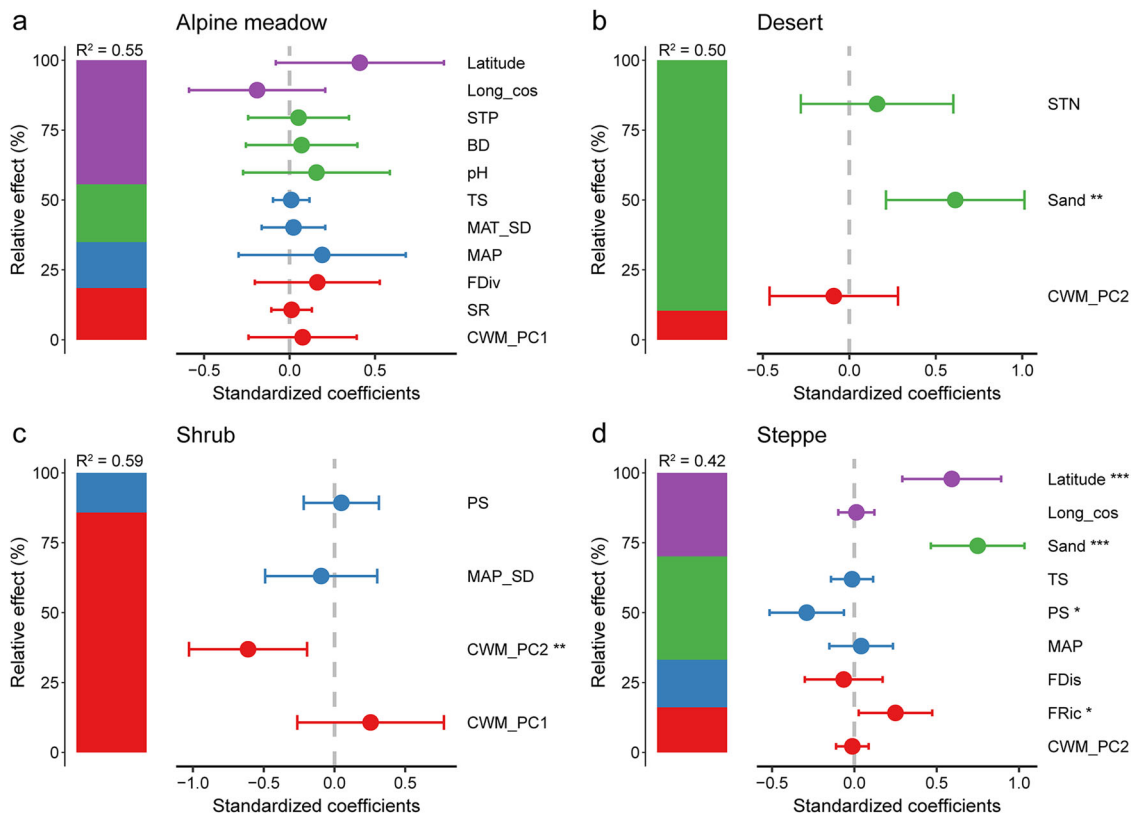


**Fig. 4 Correlations between ecosystem stability and its components and explanatory variables.** The size of the squares indicates the significance of Spearman’s correlation between explanatory variables, and the colors represent the different strengths of the correlations. Biotic variables include: Height\_CWM, LDMC\_CWM, LCC\_CWM, LNC\_CWM, LPC\_CWM (community-level weighted means of plant functional traits); CWM\_PC1 (the first principal component of the plant functional traits), CWM\_PC2 (the second principal component of the plant functional traits); SR (species richness), D (Simpson’s diversity index), H’ (Shannon-Wiener index), J (Pielou’s evenness index); FR<sub>ic</sub> (functional richness), FE<sub>ve</sub> (functional evenness), FD<sub>v</sub> (functional divergence), FD<sub>is</sub> (functional dispersion); PD (phylogenetic diversity). Abiotic variables include: MAP (mean annual precipitation), MAP\_SD (interannual precipitation variability), PS (intraannual precipitation variability), MAT (mean annual temperature), MAT\_SD (interannual temperature variability), TS (intraannual temperature variability); BD (soil bulk density), Sand (soil sand content), Silt (soil silt content), Clay (soil clay content), pH (soil pH), SOC (soil organic carbon), STN (soil total nitrogen), STP (soil total phosphorus); Long<sub>sin</sub> (sinus of longitude), Long<sub>cos</sub> (cosinus of longitude), latitude and altitude. \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

ecosystems<sup>10,16,55,56</sup>, and the limited studies on biodiversity contribution to ecosystem stability on the Tibetan Plateau are limited to alpine grasslands<sup>37,48,57</sup>. Our analysis reveals the relative importance of biotic and abiotic factors, among which biotic factors explain a high proportion (86%) of ecosystem stability of shrubs on the Tibetan Plateau, compared to a contribution of 10–18% in other typical ecosystems (Fig. 5). Similarly, although a variety of indicators that could affect ecosystem stability were selected to construct purely biotic predictive models, these models only had near abiotic or full model performance in shrub ecosystems ( $R^2 = 0.51$ ), with an  $R^2$  of only 0.06 to 0.23 in other

ecosystems (Supplementary Table 2). One possible explanation is that studies in which species diversity significantly contributed to ecosystem stability were conducted in areas with relatively high SR<sup>21</sup>, whereas most of our sample sites had low SR (mean = 8). This is supported by a study conducted by ref.<sup>37</sup> in alpine grasslands, in which plant diversity explained only 39% of the variation in temporal stability in their model.

Many studies at the local scale have explored the biotic mechanisms by which plant communities stabilize productivity through species manipulation<sup>10,11,58,59</sup>. These suggest that mechanisms such as compensatory dynamics and species



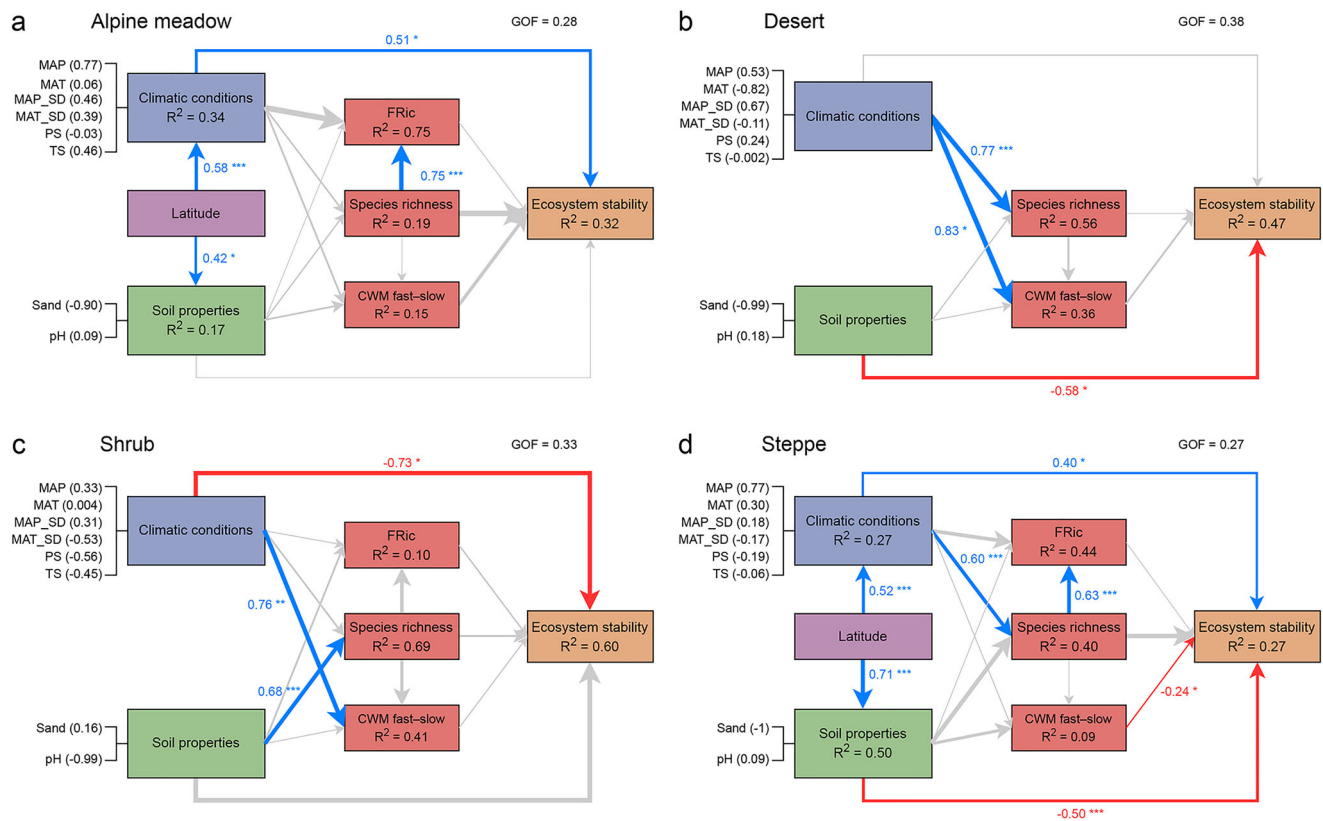
**Fig. 5 Relative effects of multiple predictors of detrended temporal stability.** Results of full models for alpine meadow (a), desert (b), shrub (c) and steppe (d) are shown. The standardized coefficients (model-averaged estimates) of the model predictors are shown with their associated 95% confidence intervals. The stacked bars show the relative importance (percentage of variance explained) of each type of predictors. The graphs show the best model selected based on the AICc. SR species richness, FR<sub>ic</sub> functional richness, FD<sub>iv</sub> functional divergence, FD<sub>is</sub> functional dispersion, CWM\_PC1 the first principal component of the plant functional traits, CWM\_PC2 the second principal component of the plant functional traits, MAP mean annual precipitation, MAP\_SD interannual temperature variability, PS intraannual precipitation variability, MAT\_SD interannual temperature variability, TS intraannual temperature variability, BD soil bulk density, Sand soil sand content, pH soil pH, STN soil total nitrogen, STP soil total phosphorus, Long\_cos cosine of longitude. \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

asynchrony have critical effects on temporal stability. However, our results are more inclined to support the dominant species effect; the function of the community, as suggested by the mass ratio hypothesis, is primarily influenced by dominant rather than rare species<sup>19</sup>. This is reflected by the generally better performance of the CWMs used in this study compared with other indicators of functional diversity in predicting ecosystem stability, especially in shrub ecosystems (Fig. 5c). Interestingly, CWM\_PC2 (i.e., CWM fast-slow, representing a component of the leaf economic spectrum) can have a significant negative impact on the ecosystem stability of shrubs; this negative correlation trend was also observed in deserts and steppes, although it was not significant. This is consistent with the expectation that fast species (with relatively high CWM\_PC2 values) are relatively unstable. Craven et al.<sup>26</sup> argued that the relationship between CWM\_PC2 and ecosystem stability may be site-specific. For example, fast species have the capacity for rapid recovery, and may thus maintain ecosystem stability in habitats with frequent disturbances. However, given the relatively low ecosystem stability of shrubs (Fig. 3), their ability to stabilize ecosystems may be limited. This presents issues, as the ongoing shrub invasion process on the Tibetan Plateau<sup>60,61</sup> may be accompanied by a decrease in regional ecosystem stability. However, this needs to be verified by subsequent studies.

**Environmental conditions determine ecosystem stability on the Tibetan Plateau.** Most local-scale studies have suggested that

environmental conditions indirectly regulate ecosystem stability, mainly through biotic factors<sup>62</sup>. However, some recent studies have shown that environmental conditions, such as water availability<sup>1,14,26</sup>, may have direct effects on ecosystem stability. Our model explained a large proportion of the variation in ecosystem stability in the alpine meadows, deserts, shrubs, and steppes (43%, 40%, 52%, and 36%, respectively), in which only abiotic factors were considered (Supplementary Table 2). In contrast, several studies that relied on climatic variables and/or taxonomic diversity to predict remotely derived ecosystem stability have explained a lower percentage, with 16% in natural mountain ecosystems in Switzerland<sup>63</sup>, 29% in natural dune grasslands in the Netherlands<sup>64</sup>, and 29–33% in multiple ecosystems worldwide<sup>65</sup>. From this perspective, ecosystem stability in the Tibetan Plateau is more dependent on the environmental variables than biodiversity.

Results on regional and global scales suggest that long-term average background biogeographic conditions directly determine patterns of ecosystem stability<sup>1,42</sup>, which is consistent with our findings. In particular, soil properties representing water and nutrient availability were important for interpreting ecosystem stability (Figs. 5 and 6). Recent studies on grasslands spanning 5 global climate regions<sup>16</sup> and 72 natural ecosystems across China have shown similar results<sup>66</sup>. Thus, inconsistencies may exist between studies that assume large environmental gradients, manipulative experiments, or plot monitoring. The latter often assumes that the compensatory dynamics or dominance effects of



**Fig. 6** The most parsimonious path model illustrating the direct and indirect effects of biotic and abiotic factors on ecosystem stability. Partial least squares path models for alpine meadow (**a**), desert (**b**), shrub (**c**) and steppe (**d**) are shown. The model explores the effects of latitude, climatic conditions, soil properties, species richness, FR<sub>ic</sub> (functional richness) and CWM fast-slow (also called CWM\_PC2, the second principal component of the plant functional traits) on detrended temporal stability. Blue and red lines indicate positive and negative significant relationships, respectively, and gray lines indicate insignificant relationships; the thickness of the line represents the strength of the causal relationship, supplemented by a standardized path coefficient. Each number in parentheses indicates the loading value of the indicator to the latent variable. R<sup>2</sup> indicates the total variation of a dependent variable is explained by independent variables; GOF indicates the goodness of fit of the entire model. MAP mean annual precipitation, MAP\_SD interannual precipitation variability, PS intraannual precipitation variability, MAT mean annual temperature, MAT\_SD, interannual temperature variability; TS, intraannual temperature variability; Sand, soil sand content; pH, soil pH. \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

organisms can effectively buffer the effects of environmental change<sup>47,48,56</sup>; however, this may be because small sample sizes limit the understanding of multiple abiotic factors under natural conditions<sup>42</sup>.

In the present study, four typical ecosystems were found to be modulated by abiotic factors in different details. The environmental conditions were divided into spatial, climatic, and soil factors, and the ecosystem stability of the alpine meadows and steppes showed a clear spatial dependence, where latitude was considered an important predictor of ecosystem stability (Fig. 5). However, latitude is not a simple proxy for MAT or MAP because it is highly correlated with other environmental factors, including temperature seasonality and soil pH (Supplementary Fig. 1). PLS-PM analysis showed that latitude strongly modulated the linear combination of climatic and soil factors in the alpine meadows and steppes, indicating that latitude was a confounding factor. The results also showed that MAP and temperature variability had a greater impact on the stability of alpine meadows, whereas temperature variability was hardly significant in the steppes. Moreover, ecosystem stability in deserts and steppes was positively modulated by soil sand content (Fig. 5), which has been demonstrated in studies on global dryland ecosystems<sup>1</sup>. Soil sand content may be related to biological mechanisms that were not considered in this study. Perennial plants growing in water- and nutrient-limited environments may have greater resistance to stress by relying

on a deep and extensive root system to maintain stability<sup>10</sup>, which deserves attention in future studies.

Finally, we argue that the patterns of different ecosystem responses to environmental change increase the difficulty in predicting ecosystem stability on the Tibetan Plateau in the context of climate change. Climate averaging states, climate variability, and soil properties jointly control community assembly and ecosystem function at different scales. Ecosystem function changes must be explored in conjunction with scenarios beyond simple increases or decreases in temperature or precipitation, and the interactions between global change factors and other predictors must be fully considered<sup>67</sup>.

## Methods

**Study area.** The Tibetan Plateau is an extremely unique ecological region with a typical plateau climate that is characterized by low temperatures, strong solar radiation, and limited precipitation<sup>68</sup>. In this study, 143 sites on the Tibetan Plateau were surveyed from July to August in 2019, 2020, and 2021 (Fig. 2). Considering vegetation types and road accessibility, we designed systematic survey routes across the northern, central, and southwestern regions of the plateau. The spatial distances between the sites were controlled at approximately 40 km (80 km when the vegetation difference was small). These routes covered typical ecosystems and climatic regions of the Tibetan Plateau, except for forests in the southeast and depopulated zones in the northwest. The mean annual temperatures of the study sites ranged from -6.19 °C to 7.70 °C, and the annual precipitation ranged from 33.34 to 669.70 mm. The investigated ecosystems were classified into four types according to the dominant species: (1) alpine meadow ecosystems, mostly *Kobresia pygmaea* meadows; (2) steppe ecosystems, mainly *Stipa purpurea* alpine steppes, as



well as *Stipa caucasica* subsp. *glareosa* desert steppes and *Neotrinia splendens* temperate steppes; (3) shrub ecosystems, typically *Sophora moorcroftiana* and *Caragana versicolor* shrubs; and (4) desert ecosystems, typically *Haloxylon ammodendron* and *Oreosalsola abrotanoides* deserts.

**Sampling and measurement.** The most representative vegetation was selected at each site for the community species composition surveys by randomly setting up a  $1 \times 1$  m quadrat on a relatively homogeneous plot for a meadow or steppe ecosystem, a  $5 \times 5$  m quadrat for woody plants for a desert or shrub ecosystem, and a nested  $1 \times 1$  m quadrat for herbaceous plants (if present). Thereby, we obtained the cumulative number of species in the quadrats (species richness) and the absolute and relative coverage of each species.

We collected and measured five plant functional traits for species with relatively dominant cover, including LDMC, LNC, LPC, leaf carbon concentration, and plant height, referring to handbooks for standardized measurements of plant functional traits<sup>69,70</sup>. These traits characterize key aspects of plant form and function<sup>27,71</sup> and have been linked to ecosystem stability in other studies<sup>1,26</sup>.

**Multiple facets of biodiversity.** We considered taxonomic, functional, and phylogenetic diversity to describe different facets of biodiversity; however, rather than prespecifying which indices were important, indices for subsequent analysis based were selected based on their correlation with ecosystem stability. Specifically, we used SR, D, Shannon-Wiener index ( $H'$ ) and Pielou's evenness index ( $J$ ) to describe taxonomic diversity, which can be calculated using the R package "vegan." Phylogenetic diversity was measured based on Faith's approach, and calculated using the R package "picante"<sup>72</sup>. We calculated diversity indicators based on the five functional traits, namely functional richness ( $FR_{ic}$ ), functional evenness ( $FE_{ve}$ ), functional divergence ( $FD_N$ ), functional dispersion ( $FD_{is}$ ), and calculated community-weighted means (CWMs), using the R package "FD"<sup>73</sup>.

Plant functional traits were not available for all species in our dataset, and data imputation considering phylogenetic information and trait correlations was performed by combining data from our field surveys with the TRY database<sup>74,75</sup>. Given that previous studies have shown the feasibility of using plant cover data from field surveys and trait data from the TRY database to calculate CWMs<sup>1,76</sup>, trait interpolation is deemed feasible and allows for a more accurate calculation of the functional diversity metrics. Furthermore, the CWMs before and after interpolation were highly correlated and similarly distributed (Supplementary Fig. 5).

Supplementary Note 1 provides more information on the interpolation calculation.

According to the theory of plant form and function spectrum<sup>71</sup> and leaf economics spectrum<sup>27</sup>, the five traits involved in this study are functionally closely related; therefore, we could perform principal component analysis on the five CWMs. Using the "principal" function in the R package "psych," we extracted the first two principal components, which together account for 65% of the variance among the CWMs (Supplementary Fig. 6). The first principal component (abbreviated as CWM\_PC1) is negatively correlated with plant height and positively correlated with leaf carbon concentration, reflecting the trade-off between plant size and leaf structure across species. The second principal component (abbreviated as CWM\_PC2) is positively correlated with LNC and LPC and negatively correlated with LDMC, which can be considered a quick-return end described by the leaf economics spectrum<sup>27</sup>. It is also referred to as CWM fast-slow, and is expected to have a negative impact on temporal stability.

**Ecosystem temporal stability.** Temporal stability ( $S$ ) is defined as  $\mu/\delta$ , where  $\mu$  is the mean value of an ecosystem property for a time period and  $\sigma$  is its standard deviation over the same interval<sup>10</sup>. Since ecosystem properties generally show directional changes over time<sup>26</sup>, as seen in Huang and Xia<sup>41</sup>, detrended temporal stability ( $S_d$ ) was also calculated for each site, defined as  $\mu/\delta_d$ . Detrending was performed by linear regression of the mean value of an ecosystem property against the year, where  $\delta_d$  is the standard deviation of the residual for each regression. Landsat satellite-derived normalized difference vegetation index (NDVI) was used as a proxy for vegetation productivity, and serves as an essential ecosystem property in studies of arid and semi-arid ecosystems<sup>1,41,64</sup>. Although some studies have used enhanced vegetation index to avoid oversaturation in areas of high vegetation productivity<sup>37,41</sup>, our study hardly covered such areas and included deserts with very low vegetation productivity, where the NDVI usually performs better<sup>77</sup>. Temporal stability was calculated as the ratio of the mean annual NDVI calculated from 2000 to 2020 to the standard deviation of the annual NDVI over that period.

The annual NDVI for each site was obtained from the dataset of 30 m annual maximum NDVI over China from 2000 to 2020<sup>78</sup>. This dataset synthesized all available Landsat 5/7/8 images for the entire year. It was preprocessed (eliminating the effects of geometry, clouds, aerosols, etc.), and linear interpolation and Savitzky-Golay filtering was used to smooth the data and reduce the effect of noise on the composite NDVI maximum<sup>79,80</sup>. Compositing the annual maximum NDVI allows different cycles of vegetation growth across different ecosystems<sup>1</sup> to be accounted for, and avoids the problem of too few pixels when compositing for short periods (e.g., during the growing season). Plots from the field surveys were matched one-by-one to individual pixels in Landsat data (30 m resolution) by

recorded locations, which was proven to be a feasible method in previous studies using ground surveys of  $30 \times 30$  m<sup>1</sup> or  $100 \times 100$  m<sup>37</sup> matched to MODIS data (250 m resolution).

**Climatic, soil, and spatial variables.** Monthly climatic conditions (mean air temperature and total precipitation) from 2000 to 2020 from the 1 km monthly temperature and precipitation dataset for China were gathered<sup>81–86</sup>. Six climatic variables affecting ecosystem stability were calculated: mean annual temperature (MAT), mean annual precipitation (MAP), interannual temperature variability (standard deviation of annual mean temperature, MAP\_SD), intraannual temperature variability (coefficient of variation of monthly temperature, TS), interannual precipitation variability (standard deviation of total annual precipitation, MAP\_SD), and intraannual precipitation variability (coefficient of variation of monthly precipitation, PS). Soil variables were the properties of layers 0–5 extracted from the basic soil property dataset of high-resolution China soil information grids<sup>87–89</sup>, including soil bulk density, sand content, silt content, clay content, soil organic carbon content, soil total nitrogen content, soil total phosphorus content, and soil pH. Because of the potential effects of spatial autocorrelation, the longitude, latitude, and altitude of each site were also considered as explanatory variables<sup>1,90</sup>. The cosine and sine of the longitudes were used to avoid bias caused by the intrinsic circularity of the longitude<sup>1</sup>.

**Statistical analyses.** Kruskal–Wallis nonparametric tests were used to compare differences in temporal stability, detrended temporal stability, and their components across ecosystems to account for the non-normal distribution of some data (Fig. 3). Spearman's correlation analysis was used to explore the strength of association between any two variables (Fig. 4; Supplementary Fig. 1). Given that temporal stability and detrended temporal stability were qualitatively similar and that the relationship between explanatory variables and detrended temporal stability was more pronounced, only results for detrended temporal stability (hereafter referred to as ecosystem stability) were shown in the other analyses.

Multiple linear regression was used to construct models to predict ecosystem stability, and a multi-model inference method was used for model selection<sup>91</sup>. Before constructing any linear model, a Box–Cox transformation was used for non-spatial variables to reduce skewness (enhance normality)<sup>92,93</sup>. Variance inflation factors (VIF) were also calculated by iteratively removing explanatory variables with strong multicollinearity (e.g., clay content, silt content, and altitude) until  $VIF < 10$ <sup>94–96</sup>. To obtain the best predictions of ecosystem stability and test the relative importance of the contributions of biotic and abiotic factors, three types of models were developed: (1) abiotic models (including only climatic, soil, and spatial variables); (2) biotic models (including only biodiversity metrics); and (3) full models (including all possible explanatory variables). The best subset of models was selected separately using a procedure based on the modified Akaike information criterion (AICc;  $\Delta AICc < 2$ ), which was performed using the "dredging" function in the R package "MuMIn." Considering the  $R^2$  and AICc values of the models, the most convincing model was selected. In most cases, more than one best model was selected, and formed a subset of the best models (Supplementary Tables 1 and 2); therefore, the standardized coefficients of the explanatory variables were obtained by model averaging. The full model outperformed the other two types of models, and their prediction performance in Supplementary Fig. 2, along with comparison of all models in Supplementary Table 2. Variance decomposition was performed based on the method described by ref. 97 to obtain the relative effects of spatial, climatic, soil, and biotic factors. Additionally, to determine if spatial autocorrelation was explained by the multiple regression model, the Moran's I autocorrelation index was calculated for the residuals of the best model using the R package "ape." The results show that the Moran's I of alpine meadows, deserts, shrubs and steppes were  $-0.03$  ( $P = 0.95$ ),  $-0.09$  ( $P = 0.58$ ),  $-0.11$  ( $P = 0.58$ ) and  $-0.01$  ( $P = 0.45$ ), respectively, indicating little spatial autocorrelation.

To clarify the direct and indirect drivers of ecosystem stability, the partial least squares path model (PLS-PM) was performed using the R package "plspm"<sup>98</sup>. This approach has advantages over ordinary structural equation models. For example, it requires a smaller sample size and does not impose distributional assumptions on the data, making it suitable for exploratory analysis. Considering the comparability among ecosystems and goodness of fit of the model, only the most critical variables were selected to construct the PLS-PM. Adding unimportant variables or setting unreasonable paths can reduce the overall model's goodness of fit and  $R^2$  for ecosystem stability; for example, considering the latitude in the model for deserts and shrubs is redundant (Supplementary Fig. 4). Therefore, the model was built based on a priori knowledge, as detailed in Supplementary Note 2. All the analyses outlined above were performed in R v.4.1.2<sup>99</sup>.

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

## Data availability

Data generated and analyzed in this study are publicly available in the Figshare repository: <https://doi.org/10.6084/m9.figshare.22689649>.

**Code availability**

The code that supports the findings of this study is openly available at: <https://doi.org/10.6084/m9.figshare.22689649>.

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## Author contributions

L.R. conceived and designed the main conceptual ideas of this work, processed the laboratory experiments, performed data analysis, and wrote the manuscript. J.H., X.X., Y.W., and Y.H. contributed to field investigation. Y.P., Y.L., Y.W., D.M., and C.Y. assisted laboratory analysis. Y.C. and Z.X. provided advice on remote sensing data. Y.H. supervised the study, contributed to the revising of the manuscript, and contributed to the funding resources.

## Competing interests

The authors declare no competing interests.

## Additional information

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**Correspondence** and requests for materials should be addressed to Yongmei Huang.

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