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Functional diversity and soil nutrients regulate the interannual variability in gross primary productivity

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Authorship

P.Y. and N.H. designed and conducted the research (collected the datasets); P.Y. analyzed the data and wrote the manuscript; M.F.M., W.Z. C.L., and N.H. commented on the details of the manuscript drafts. All the authors have made substantial contributions to the writing of the manuscript.

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Abstract Global change, encompassing rising temperatures and an increase in extreme precipitation events, has influenced vegetation photosynthesis; this can be seen in the gross primary productivity (GPP) of terrestrial ecosystems, which, over time affects the global carbon cycle. The impact of climate on interannual variability in GPP (GPP_{IAV}) has been extensively explored in the literature. Other changing factors driven by global change, such as biodiversity and soil nutrient availability, are vital in predicting the future of the biosphere. However, the roles of these factors remain unclear. We combined *i*) data from 454 community plots collected using standard protocols from 2013 to 2019 across China, *ii*) plant trait data and phylogenetic information of more than 2,500 plant species, and *iii*) soil nutrient data that we measured. Using these data from 72 "real-world" ecosystems located across a range of environmental conditions and species pools, we investigated the role of environmental factors including temperature, precipitation and soil nutrients and multifaceted diversity (i.e., species richness, hypervolume-based functional diversity, and phylogenetic diversity) in mediating the magnitude of GPP_{IAV} using multi-model averaging and structural equation modeling. We found that soil nutrients and functional diversity are the main determinants of the magnitude of GPP_{IAV} and that climate effects are predominantly mediated by multifaceted diversity. We provide strong evidence that ecosystems with higher biodiversity have less variable annual biomass production and decrease the extent of GPP_{IAV} through compensatory effects across diverse ecosystems. Nutrient-rich ecosystems are likely to buffer the impact of climate variability on ecosystem carbon uptake better than nutrient-poor ecosystems. Our results demonstrate that biodiversity plays a crucial role in buffering the effects of environmental variability on carbon uptake in terrestrial ecosystems.

Keywords: Biodiversity, climate change, compensatory effect, gross primary productivity, hypervolume, interannual variation, soil nutrients

1. Introduction

The interannual variability of gross primary productivity (GPP_{IAV}) in terrestrial ecosystems is an important feature of the global C cycle (Ballantyne et al., 2012). It has a major impact on ecosystem C balance and ultimately affects the C sink, which is of paramount importance in predicting the future of the biosphere under the current changing climate (Piao et al., 2020, Fernández-Martínez et al., 2019). Global change is not only restricted to climate change, including rising global temperatures and changing rainfall regimes, but is also related to different factors causing biodiversity loss. Both climate change and biodiversity loss threaten ecosystem function stability; for example, they affect the stability of ecosystem biomass production, consequently affecting the GPP_{IAV}, ultimately affecting the ecosystem services they underpin. Changes in climatic conditions, such as rainfall shifts over years, will lead to variations in ecosystem productivity between different years (Yao et al., 2018, Fernández-Martínez et al., 2020, Li and Xiao, 2020).

The concentrations of soil nutrients, such as N and P, are also important abiotic factors, besides climatic factors, that may affect the magnitude of the GPP_{IAV} (Fernández-Martínez et al., 2020, Fernández-Martínez et al., 2014). Across broad environmental gradients, from desert steppes to forests, nutrient-rich ecosystems have higher ecosystem productivity than nutrient-poor ecosystems (Roy et al., 2001). This directly reduces the interannual variability (IAV) in productivity (Piao et al., 2020). With increasing nutrient levels along broad environmental gradients, ecosystems can potentially host more species, increasing their diversity, which results in an increase in ecosystem productivity due to the diversity–productivity relationship (Oehri et al., 2017). Thus it also reduces the magnitude of the GPP_{IAV} via indirect effect. However, the direct and indirect effects of soil nutrients on GPP_{IAV} are still poorly understood.

Given that a substantial body of evidence from ecological research has demonstrated that biodiversity stabilizes ecosystem productivity over time (Craven et al., 2018, García-Palacios et al., 2018, Oehri et al., 2017, Isbell et al., 2015), higher diversity is understood to reduce the magnitude of GPP_{IAV} (Chapin III, 2003, Richardson et al., 2007, Zhang et al., 2016, Zhou et al., 2016). It is now widely accepted that ecosystems with high diversity have higher resistance (productivity deviates slightly from average levels during disturbances) and/or resilience (productivity returns to average levels rapidly after disturbances), which reduces their variation in productivity over time (Isbell et al., 2015, Craven et al., 2018, Musavi et al., 2017, WangIsbell et al., 2021). Evidence from single ecosystem types also clearly demonstrates the important role of species richness (Musavi et al., 2017) and functional traits (García-Palacios et al., 2018) in stabilizing ecosystem production functions. However, compared with that of climatic factors, the role of multifaceted diversity (i.e. taxonomic diversity, functional diversity, and phylogenetic diversity) in the GPP_{IAV} has not been fully elucidated. In particular, most of the current research focuses on a single vegetation type, such as forests (Wales et al., 2020, Guo et al., 2021, Dolezal et al., 2020) or grasslands (Isbell et al., 2015, Cadotte et al., 2012, Loreau and De Mazancourt, 2013); studies that span multiple vegetation types are required.

The possible mechanism by which biodiversity reduces the variability in ecosystem biomass production such as GPP_{IAV} is through the compensation effect (WangIsbell et al., 2021). Studies on the leaf economics spectrum predict that fast-growing species namely, resource-acquisitive species with faster growth rates, resource uptake, and tissue turnover would have higher resilience to disturbance because of their rapid recovery. In contrast, slow-growing species, which are conservative species with slower growth rates, resource uptake, and tissue turnover, would have higher resistance to environmental stress (Reich, 2014, Craven et al., 2018, Li et al., 2021). Compared with communities with low diversity, communities with high diversity have more diverse ecological strategies (increasing their *portfolio effects*). They also have a higher ability to resist disturbances and weaken the impact of climate change on ecosystem production, thus reducing the GPP_{IAV} (Tilman and Downing, 1994, Schnabel et al., 2019, WangIsbell et al., 2021, García-Palacios et al., 2018). However, biodiversity is not simply equal to the number of species, but also includes functional and phylogenetic diversity, which encompass different diversity components and better reflect the differences in ecological strategies among the species in a community (Brun et al., 2019, Craven et al., 2018). Additionally, the mass ratio hypothesis states that ecosystem function is largely dependent on the trait values of the main contributors to plant biomass and is therefore better expressed as community weighted mean (CWM) trait values. The dominant effect based on the mass ratio hypothesis can also influence the $\mathrm{GPP}_{\mathrm{IAV}}$ to increase plant resistance to climatic variability by the selection of slower species (Craven et al., 2018, Garnier et al., 2004). However, a community dominated by fast species may also increase the stability of ecosystem production through higher resilience, and ultimately reduce the $\mathrm{GPP}_{\mathrm{IAV}}$ (Craven et al., 2018, Majeková et al., 2014). Therefore, the final net effect of the dominant effect across multiple ecosystems can be relatively low because the opposing effects of slow yet more resistant and fast and more resilient communities may cancel each other out.

The aim of the present study was to assess the relative importance of climate factors, soil nutrients, and multifaceted diversity on the $\mathrm{GPP}_{\mathrm{IAV}}$ at large scales across multiple vegetation types , and to reveal the change pattern of $\mathrm{GPP}_{\mathrm{IAV}}$ and its main drivers along different vegetation types across a wide range of environmental conditions. We combined field survey data from a large scale ecosystem investigation with high-quality GPP data derived from a satellite near-infrared reflectance dataset. The data included 1) data from 454 plant community plots surveyed across China from 2013 to 2019, 2) trait and phylogenetic information of more than 2,500 plant species, and 3) measured plot soil nutrient data (Fig. 1; Table S1). Monthly GPP and climate data were used to reflect temporal variability in productivity and climate over long time scales from 2000–2018. A multi-model averaging procedure was performed to evaluate the relative importance of climate factors, soil nutrients, and biodiversity, including CWM traits, species richness, functional diversity, and phylogenetic diversity for the $\mathrm{GPP}_{\mathrm{IAV}}$. We hypothesized that (1) a large proportion of the effect of climate variability on the

GPP_{IAV} can be attributed to diversity as an indirect effect, (2) species-rich ecosystems with high functional diversity reduce GPP_{IAV} through the compensation effect, and (3) ecosystems with higher soil nutrients can “buffer” the disturbance of climate variability on biomass production with higher functional diversity, directly and indirectly reducing the GPP_{IAV}.

2. Materials and methods

2.1. Study region and sites

We conducted our study across China, one of the most biodiverse countries in the world (McNeely et al., 1990). Based on the vegetation distribution of terrestrial ecosystems in China, we investigated 72 natural ecosystems and set up approximately 1,000 plots from 2013 to 2019. The plots were far away from areas with the main human disturbances according to standard sampling and plant community composition survey protocols (He et al., 2019). The 72 sites spanned a range of 50 degrees in longitude (78.46–128.89 °E) and 35 degrees in latitude (18.75–53.33 °N; Table S1) and encompassed deciduous needle-leaf forests, evergreen needle-leaf forests, deciduous broad-leaved forests, evergreen broad-leaved forests, meadows, sparse grasslands, steppes, sparse shrubbery, and desert steppes. The mean annual temperatures for these sites ranged from −3.8 °C to 22.2 °C, and the mean annual precipitation ranged from 25 mm to 1,785 mm (Table S1; Fig. 1). The soil types varied considerably in terms of nutrient concentration, from black earth with high organic content in cold temperate zones to tropical red soils with low organic content (Liu et al., 2018). We collected plant community structure data using the quadrat method and collected samples during the peak period of plant growth from July to August (four 30 m × 40 m for forest, six 10 m × 10 m for shrubland, and eight 1 m × 1 m for grassland). We set up plots within an area of approximately 1 × 1 km for the community structure survey and sampling. We plotted species accumulation curves using the ***vegan*** R package to check the representation of the field survey. Detailed site information has been reported in previous studies (Zhang et al., 2020, Zhao et al., 2020, He et al., 2019); these details are provided in Appendix S1.

2.2. Functional traits and diversity

Functional traits include size traits that reflect plant size and light competitiveness and economic traits that reflect leaf photosynthesis capacity and nutrient economies (Diaz et al., 2015, Maynard et al., 2021). The GPP_{IAV} reflects the fluctuations in the ecosystem-level photosynthetic capacity. We selected five representative traits, including three economic traits namely, specific leaf area (SLA, cm^2/g), leaf N concentration (LN, mg/g), and leaf P concentration (LP, mg/g), and two size traits, leaf area (LA, cm^2), and leaf dry mass (LM, g). All of these are closely related to the plant light competitiveness and photosynthetic capacity of the ecosystem. More detailed trait measurements and calculations are shown in Appendix S2 as well as in other peer-reviewed papers published by our group (He et al., 2020, Zhang et al., 2020, Zhao et al., 2020). We also used the average number of species within each plot (i.e., species richness) to represent taxonomic diversity as a fundamental driver of other diversity measures.

We calculated the CWM values for the five leaf traits (LA, LM, SLA, LN, and LP) using the *vegan* R package (Oksanen et al., 2013). We then calculated several functional diversity indices, including functional richness, dispersion, and evenness, based on kernel density n-dimensional hypervolumes (Blonder et al., 2018, Mammola and Cardoso, 2020). In stead of using distance-based functional trees, n-dimensional hypervolumes represent the functional space of a species or community as a Hutchinsonian niche, which is an abstract Euclidean space defined by a set of independent axes corresponding to individual or species traits. This technique shows considerable application potential in the field of trait-based ecology (Mammola and Cardoso, 2020), especially given that the Hutchinsonian hypervolume is a foundational concept in many fields of ecological and evolutionary research (Blonder et al., 2014). This approach does not require transforming the data into dissimilarities, but relies on the raw position of an individual or species within a multidimensional space (Mammola and Cardoso, 2020, Blonder et al., 2018), while accounting for possible empty spaces within some extreme trait values (Blonder, 2016). To eliminate size-dependent trait biases and remove the influence of different units and scales, we log-transformed and then scaled (mean = 0, SD = 1) all five traits before creating the hypervolume (Blonder et al., 2018). We built the hypervolume with species abundance data and a species × traits matrix using the ***kernel.build*** function of the BAT package in R. We used the recommended settings of high-dimensional kernel density estimation (***method* = *gaussian***) to estimate the stochastic points that determine the shape and volume of the hypervolume (Mammola, 2019, Mammola and Cardoso, 2020). We used the ***kernel.alpha***, ***kernel.dispersion***, and ***kernel.evenness*** functions to calculate the **functional richness**, **divergence**, and **regularity**, respectively. We used a combination of these three indices as a proxy for functional diversity.

We used the R package *Taxonstand* based on The Plant List database (*http://www.theplantlist.org*) to correct and confirm the names of the species found in our 72 sites. We constructed a phylogenetic tree with all these species using the *V.PhyloMaker* package with the *PhytoPhylo* megaphylogeny as its backbone (Jin and Qian, 2019, Tsirogiannis and Sandel, 2016, Qian and Jin, 2015). Further, we calculated three commonly used indices to represent the phylogenetic diversity using the *PhyloMeasures* package, including *i*) Faith's index (PD, sum of branch lengths in the minimum spanning subtree for a given set of species, reflecting the evolutionary distances between species), *ii*) the mean pairwise distance (MPD, mean phylogenetic distance [branch length] among all pairs of species within a community, reflecting the phylogenetic structuring across the whole phylogeny), and *iii*) the mean nearest taxon distance (MNTD, mean distance between each species within a community and its nearest neighbor, reflecting the phylogenetic structure closer to the tips). We used a combination of these three indices of phylogenetic diversity as a proxy for overall phylogenetic diversity, after which we assessed its impact on the GPP_{IAV} (Tsirogiannis and Sandel, 2016, Webb, 2000).

2.3. Soil nutrients

We determined all the soil nutrients in each plot using standard protocols (Liu et al., 2018). We used a soil auger to collect soil samples (0–10 cm) from each plot after removing the surface litter layer. To reduce soil heterogeneity, we combined the soil samples (30–50 random points in each plot) collected within each plot into a composite sample. We then sieved the composite soil samples through a 2-mm mesh and air-dried them; all the visible roots and organic debris were separated by hand. We ground the samples into a fine powder using a ball mill (MM400 ball mill, Retsch, Germany) and an agate mortar grinder (RM200, Retsch, Haan, Germany). We measured the total C and N concentrations in the soil using an elemental analyzer (Vario MAX CN Elemental Analyzer, Elemental, Hanau, Germany). We measured the total P concentration using molybdenum antimony spectrophotometry and a continuous flow analyzer (AutoAnalyzer3 Continuous-Flow Analyzer; Bran Luebbe, Germany). The soil pH was measured an Ultrameter-2 pH meter (Myron L. Company, Carlsbad, CA, USA). We calculated the average concentration of nutrients and pH of the samples from each site to represent the site nutrient status.

2.4. Interannual variation in climate and productivity

We downloaded the data on the long term global monthly GPP product from 2000 to 2018 (228 months) from *https://doi.org/10.6084/m9.figshare.12981977.v2* with a spatial resolution of 5.5 km (satellite-based near-infrared reflectance [NIR_V]. The GPP data product, hereafter GPP_{NIRv}, was used to determine the GPP_{IAV} across different sites (WangZhang et al., 2021). The near-infrared reflectance of vegetation is strongly correlated with solar-induced chlorophyll fluorescence a direct index of photons intercepted by chlorophyll as well as with site-level and globally gridded estimates of GPP (Badgley et al., 2017). This dataset has been verified and found to outperform similar GPP products in capturing seasonal variability in productivity (WangZhang et al., 2021). Therefore, we used this product to investigate the variation in GPP over the last two decades (Fig. 1c).

We calculated the $\mathrm{GPP}_{\mathrm{IAV}}$ using the coefficient of variation (CV), the most commonly used index in the research field of the diversity-ecosystem stability relationship. The CV was calculated as the mean value divided by the standard deviation of annual GPP.

We downloaded the high-resolution grids of climate data from 2000–2018 from CHELSA V2.1 (https://chelsa-climate.org/downloads/), with a 1 km spatial resolution. We calculated the multiyear mean value of the climate variables per site including mean annual temperature (MAT), mean annual precipitation (MAP), and IAV in temperature and precipitation using the same method used for calculating the $\mathrm{GPP}_{\mathrm{IAV}}$. All ecosystem productivity and climate (including temperature and precipitation) data were extracted according to the latitude and longitude coordinates of each site. As there was a spatial scale mismatch between the field areas surveyed (1 km × 1 km) and the remote sensing data GPP (5.5 km × 5.5 km), we quantitatively assessed whether the spatial heterogeneity would cause GPP data to be insufficiently representative of the surveyed area (Appendix S3). We used a validation method from García-Palacios et al. (2018) to verify that the spatial mismatch does not affect the robustness of the results of our study (Figure S1).

2.5. Statistical analysis

To simplify model construction and avoid collinearity, which would disrupt robust parameter estimation, we first performed four principal component analyses to reduce the dimensions of the CWM trait values, functional diversity (functional richness, divergence, and regularity), phylogenetic diversity (PD, MPD, and MNTD), and soil nutrient values (soil total C, N, P, and soil pH). We adopted Kaiser's rule to temporarily retain the principal component axes (PCA) with eigenvalue > 1, and then finally reserve a PCA for each type of variable through the best subset selection procedure (Table S2). The first PCA explained 53% of the variability in CWM, 50% of the variability in functional diversity, 48% of the variability in phylogenetic diversity, and 61% of the variability in soil nutrients (Fig. S2). In addition, to assure normality of the response variable, the $\mathrm{GPP}_{\mathrm{IAV}}$ values were log-transformed before the analyses.

We used the multi-model averaging method based on the spatially controlled linear mixed effects model with random effects of vegetation type and locality to evaluate the effects of CWM traits, diversity, climate, and soil nutrients on GPP_{IAV}. We controlled for spatial autocorrelation by generating a spatial matrix with longitude and latitude coordinates of each locality for each site following an established approach (Kubelka et al., 2018) and incorporated it into the mixed effects model. In our statistical models, we set the vegetation type as a random factor to account for the inherent differences in productivity and temporal variability among different vegetation types. The rationality of the random factor setting in the full model was also checked from a statistical perspective using an intraclass correlation coefficient (ICC). This was calculated by dividing the random effect variance by the total variance (i.e., the sum of the random effect variance and the residual variance). We used the *relmatLmer* function of the *lme4qtl* package in R to fit the full model and then we used the "dredge" function in the Multi-Model Inference (*MuMIn*) R package to generate a complete set of submodels from the full model. We ranked all the possible models following the Akaike information criterion (AIC) and selected those models with ΔAIC values < 4 to calculate the average model using the *model.avg* function (Grueber et al., 2011). We standardized all the explanatory variables (mean=0, SD =1) prior to analysis using the z-score to interpret parameter estimates at a comparable scale. We checked the collinearity before model construction using the VIF; the VIF of all the variables was < 5, far from problematic collinearity thresholds (Lüdecke et al., 2021). We examined the residuals of the full model using the *Performance* package and did not find any deviations in the model assumptions. The interaction between the variables was not significant; therefore, we fitted the models using only the main effects.

We used piecewise structural equation modeling (SEM) to explore the direct and indirect effects of diversity, climate, and soil nutrients on the GPP_{IAV}. In order to maintain consistency and simplify the model construction, we also performed PCA analysis on climate variables (MAT, MAP and their IAV), finally retaining the first

PCA. As a confirmatory path analysis method (Shipley, 2009), piecewise SEM is a collection of regression models; it is a flexible framework that can contain different model structures, distributions, and assumptions. The core of its principle is the d-separation test (Lefcheck, 2016), which evaluates whether any necessary paths are missing from the model. This is necessary because the goodness-of-fit tests used in a standard SEM are inappropriate for a piecewise SEM (Shipley, 2013). We established a near-saturated initial model containing all the potential relationships between environmental factors, biodiversity, and the GPP_{IAV} based on a priori knowledge from the literature on the study of diversity-stability relationships. In this model, we also included direct paths from species richness to functional diversity and phylogenetic diversity. This is because according to existing studies, their variation can be directly attributed to the change of species richness in a community (Craven et al., 2018). The step AIC procedure of model selection method (Shipley, 2013) was used to select the model with the minimum AIC value, based on the initial structural equation model. The process selects and retains the most important paths and removes the majority of nonsignificant paths. We obtained the model that best fit our data. Given that the CWM traits has been found to have a weak effect on the GPP_{IAV} through the multi-model averaging procedure based on the mixed effects model, our final SEM did not include CWM trait. Furthermore, given that GPP_{IAV} is driven by its two fundamental components (GPP_{mean} and GPP_{SD}), we built a separate SEM to provide additional insight into the driving mechanisms of GPP_{IAV}. Based on the above analysis, we used a concise bar chart to show the regulatory effects of soil nutrients and functional diversity on the GPP_{IAV} among different vegetation types in the context of variability driven by environmental conditions.

3. Results

According to the model averaging procedure, soil nutrients (relative importance, RI = 1; $\Delta AIC \leq 4$, N = 25) and functional diversity (RI = 0.97; $\Delta AIC \leq 4$, N = 24) were the two most important factors explaining the variability in the GPP_{IAV} (Table 1).

Across all the sites, ecosystems with higher soil nutrients and functional diversity tended to have lower $\mathrm{GPP_{IAV}}$ values (Fig. 2).

The results from the SEM confirmed that soil nutrients and functional diversity had significant negative direct effects on the $\mathrm{GPP_{IAV}}$, with standardized path coefficients of −0.47 and −0.34, respectively (Fig. 2a). However, the SEM results also revealed the important role of climate factors (including MAT and MAP and their IAV) in species richness and functional diversity, which indirectly affects the $\mathrm{GPP_{IAV}}$ (Fig. 2b). The SEM approach highlighted that climate (negatively related to MAT and MAP and positively related to their IAV) had significant negative direct effects on species richness and functional diversity, with standardized path coefficients of −0.58 and −0.28, respectively (Fig. 2a). Ecosystems with higher MAT and MAP and less variable climate (IAV of MAT and MAP) had higher species richness, which ultimately reduced their $\mathrm{GPP_{IAV}}$ (Fig. 2). In addition to affecting the species richness, climate also affects functional and phylogenetic diversity. We found that climate had a significant direct impact on functional and phylogenetic diversity, with standardized path coefficients of −0.28 and −0.27, respectively (Fig. 2). Across all sites, warmer and wetter ecosystems had higher functional diversity, which ultimately reduced their $\mathrm{GPP_{IAV}}$ (Fig. 3; Fig. S5), whereas ecosystems with higher climate variability tended to have lower functional diversity, which ultimately increased their $\mathrm{GPP_{IAV}}$ (Fig. 3; Fig. S5).

By additionally including the two basic components of $\mathrm{GPP_{IAV}}$ (i.e. $\mathrm{GPP_{mean}}$ and $\mathrm{GPP_{SD}}$) in a separate SEM, we provided added insight into the mechanisms by which soil nutrients and diversity affect $\mathrm{GPP_{IAV}}$. Functional diversity reduce the $\mathrm{GPP_{IAV}}$ by increasing the $\mathrm{GPP_{mean}}$ and decreasing the $\mathrm{GPP_{SD}}$ with standardized path coefficients of 0.29 and −0.35, respectively, while the direct effect of soil nutrients on $\mathrm{GPP_{IAV}}$ may be influenced by its negative effects on the $\mathrm{GPP_{SD}}$ with a standardized path coefficient of −0.28 (Fig. S3).

Finally, the bar graph shows that the $\mathrm{GPP_{IAV}}$ increased with the decrease in soil nutrients and functional diversity across different vegetation types (Fig. 3). Although the first axis of the PCA with the CWM trait (positively correlated with soil C, N, and P; Fig. S4a) was not significantly correlated with GPP_{IAV} in forests, it was significantly negatively correlated with GPP_{IAV} in grasslands (Fig. S4).

4. Discussion

Our results supported our main hypothesis stating that ecosystems with higher diversity would have lower GPP_{IAV} because of compensation effects and that soil nutrients would buffer the impact of climate variability on the GPP_{IAV} through direct and indirect effects. However, the effect of biodiversity on the GPP_{IAV} was not directly promoted by species richness but by functional diversity, which includes information about the functional dissimilarity between species within the community.

4.1. Influence of multidimensional diversity on GPP_{IAV}

Our results provided strong evidence that biodiversity can stabilize ecosystem production and reduce the magnitude of the GPP_{IAV} (Fig. 2 and 3). Ecosystems with higher diversity tended to have lower GPP_{IAV}, which is consistent with the positive relationship between diversity and ecosystem stability according to the insurance hypothesis (García-Palacios et al., 2018). As numerous studies have shown, higher diversity of plant resource utilization strategies promotes higher asynchrony in species responses to environmental fluctuations, ultimately suppressing GPP_{IAV} (García-Palacios et al., 2018, Craven et al., 2018, Loreau and De Mazancourt, 2013, Morin et al., 2014). Over longer timescales, the response of vegetation to climate change can explain the IAV in ecosystem flux better than only the climate variables (Ma et al., 2011, Richardson et al., 2007). Climate change can affect the properties of ecosystem vegetation, leading to further variations in productivity (Chapin III, 2003). Although species richness can also partially characterize the role of diversity in the GPP_{IAV} (Musavi et al., 2017), using a multidimensional diversity measure that contains more information is a better choice because multiple diversity measures can reflect the impact of diversity, prevent the omission of dissimilar information among species, and prevent underestimations of the role of diversity (Craven et al., 2018, Dolezal et al., 2020). The multifaceted nature of diversity, beyond the number of species, is highly important for understanding ecosystem functions and stability (Craven et al., 2018, Mahaut et al., 2020, Brun et al., 2019, Dolezal et al., 2020). A negative relationship between diversity and the $\mathrm{GPP}_{\mathrm{IAV}}$ can predominantly be seen in compensation effects (Cardinale et al., 2012, Fernández-Martínez et al., 2020). The complementary effect promotes the temporal asynchrony of community species productivity and increases ecosystem resistance through the combination of species with diversified ecological strategies, both of which help reduce the $\mathrm{GPP}_{\mathrm{IAV}}$ (Loreau and De Mazancourt, 2013, Ammer, 2019).

Functional diversity has the strongest effect among different biotic factors on the $\mathrm{GPP}_{\mathrm{IAV}}$. A previous large-scale study on global drylands has also found that leaf trait diversity promotes ecosystem stability (García-Palacios et al., 2018). This suggests that niche differences between species are better captured by functional diversity. However, these niche differences were not captured by the species richness and phylogenetic diversity. Instead, species richness was found to affect the $\mathrm{GPP}_{\mathrm{IAV}}$ mainly through the pathway of functional diversity. Higher species richness means that an ecosystem has a greater probability of containing species with more ecological strategies (increasing their portfolio effects) due to niche differentiation (Craven et al., 2018), ensuring a stronger ability to resist disturbances and mitigate the effects of climate change on ecosystem production, thereby reducing the $\mathrm{GPP}_{\mathrm{IAV}}$ (Isbell et al., 2015). Additional analyses also provided evidence that functional diversity reduces $\mathrm{GPP}_{\mathrm{IAV}}$ by directly reducing the variability of biomass production over time (i.e. $\mathrm{GPP}_{\mathrm{SD}}$). This may be because an assemblage of species with high functional diversity increases ecosystem resistance, thus weakening the fluctuation of productivity over time in response to extreme climatic events (Isbell et al., 2015, Loreau and De Mazancourt, 2013). In contrast, functional diversity could also reduce the $\mathrm{GPP}_{\mathrm{IAV}}$ by directly increasing the production potential (i.e., $\mathrm{GPP}_{\mathrm{mean}}$). This is because the strong compensatory effect produced by higher functional diversity leads to improvements in resource availability, absorption, and use efficiency (Ammer, 2019). All of these vital processes involved in the complementary effects have been identified in forests (Morin et al., 2011, Jing et al., 2021) and grasslands (Grace et al., 2007, Huang et al., 2020), as well as above and below ground components (Ammer, 2019, Jing et al., 2021).

Unlike phylogenetic diversity, which describes only the differentiation of information between species over their evolutionary history (Huang et al., 2020, Cadotte et al., 2012), functional diversity is closely related to the traits measured in this study (Huang et al., 2020). Although we selected functional traits closely related to ecosystem production (Garnier et al., 2016, Perez-Harguindeguy et al., 2016), this does not guarantee the inclusion of all the necessary information (Huang et al., 2020, Barry et al., 2019). Our results showed that the role of CWM traits representing the dominant effect on GPP_{IAV} was highly pronounced in grassland ecosystems (with forest ecosystems excluded), but less so across multiple ecosystems. It implies that conclusions drawn from studies conducted in one ecosystem-type are worthy of further investigation in other ecosystem-types by employing a macroecology approach (McGill, 2019); new phenomena may emerge once the scale of study is changed.

Management, including thinning, and disturbance, such as grazing can directly affect the primary production of an ecosystem and, subsequently, the GPP_{IAV} (Musavi et al., 2017). Site age, including forest age, is also a potential factor affecting the GPP_{IAV} (Musavi et al., 2017). As succession progresses, forests may develop more diverse canopy and root structures, allowing for more complementary use of nutrients and water and reducing the impact of environmental change on production (Musavi et al., 2017). In addition, atmospheric nitrogen deposition in the Anthropocene has increased the bioavailable nitrogen in terrestrial ecosystems (Zhu et al., 2021), which may also affect GPP_{IAV}. Firstly, nitrogen deposition especially its dry deposition component can be absorbed by plants through stomata, leaf cuticle and bark in the canopy to stimulate photosynthetic capacity (Yan et al., 2019), positively affecting GPP (Zhu et al., 2021), and ultimately indirectly inhibiting GPP_{IAV}. Secondly, nitrogen deposition especially the wet deposition component can directly change the soil nutrient state (Yan et al., 2019, Zhu et al., 2016). The increase of available nutrients in the soil will enhance the resilience of ecosystems against climate extremes, and thus directly buffer the GPP_{IAV}.

4.2. Effects of soil nutrients on interannual variation in ecosystem productivity

Consistent with our initial hypothesis, our results indicated that soil nutrients "buffer" the impact of climate variability on biomass production and reduce the magnitude of the GPP_{IAV}. The soil nutrient status in an ecosystem directly affects its biomass production (Vicca et al., 2012) and determines the magnitudes of biomass production and accumulation (Fernández-Martínez et al., 2014). A study examining temperate forests (Xu et al., 2020) has shown that soil nutrients, including nitrogen availability, regulate the photosynthetic capacity of the vegetation canopy, which has an important effect on the magnitude of productivity. Ecosystems with higher biomass and productivity often have higher stability (Guo et al., 2021, Wales et al., 2020, Craven et al., 2018). However, additional analyse showed that soil nutrients inhibited GPP_{IAV} primarily by attenuating productivity fluctuations over time (i.e. GPP_{SD}) rather than by increasing productivity potential (i.e. GPP_{mean}). This may be because the soil nutrient content is not equivalent to the soil nutrients available to plants, so the relationship between soil nutrient content and GPP_{mean} is not significant. In addition, nutrient-rich ecosystems tend to have higher net C uptake (Fernández-Martínez et al., 2014), which means that they can accommodate more species according to species-energy relationships (Craven et al., 2020). Thus, soil nutrients may also affect GPP through their indirect role in diversity.

Knowledge about the key effects of soil nutrients on the stability of ecosystem C uptake is crucial, especially given the human-induced alterations in soil nutrient status and biogeochemical cycles in many regions worldwide (Yu et al., 2019, Zhu et al., 2016). Fertile soils will generally support more diverse plant communities by providing a wider range of niches and imposing more relaxed ecological constraints on growth (Yuan et al., 2019). This implies that soil nutrients are also expected to directly affect

GPP_{IAV}. However, it is worth noting that soil total C, N, and P content does not equate to available nutrient content that is directly available to plants. The available nutrients in the soil depend both on the available (or unavailable) forms of N and P and the corresponding soil texture variables, including sand, silt, and clay contents and soil pH. Only labile nitrogen (such as NH_4^+–N and NO_3^- –N) can be utilized by the fine roots of plants and soil pH that is too high or too low will inhibit the absorption of soil nutrients by plants. Therefore, our use of soil total N and P to represent overall N and P levels can only be taken as rough estimates of soil fertility and quality. A precise assessment of the relationship between the soil available nutrients and the GPP_{IAV} is necessary in the future.

4.3. Inspiration for future studies on ecosystem C cycle

We undertook a holistic, multi-site assessment of how climate, soil nutrients, and multifaceted diversity including species richness and functional and phylogenetic diversity affect the GPP_{IAV} across a geographic and climatic gradient. The Earth's vegetation cover is critical for maintaining the global C cycle and balance, but global change is increasingly changing Earth's natural vegetation by reducing its cover area and changing its attributes (Chapin III, 2003, Isbell et al., 2013). This has a profound impact on the C balance in terrestrial ecosystems, especially given the key role of the GPP_{IAV} in the IAV of net C uptake (Piao et al., 2020). It is insufficient to determine how plant functional traits and diversity affect the global C cycle, especially at large scales. With the advancement of remote sensing technology, it has become possible to directly retrieve data on functional diversity at the grid level and explore the relationship between functional diversity and ecosystem functioning (Garnier et al., 2016). Based on high-quality data, our findings provide strong evidence that the diversity of functional traits affects the stability of ecosystem gross C uptake. Although the direct role of climate cannot be ignored, considering the key role that vegetation plays in the entire terrestrial C cycle, the effects of biodiversity (including phylogenetic, functional, and taxonomic diversity) and plant functional traits on the terrestrial C cycle should be studied in more detail in the future. Moreover, studies focusing on a single ecosystem type need to be extended to include a range of diverse ecosystem types to reach more general conclusions. Combining observations from high-tech remote sensing instruments with those from eddy-covariance towers distributed in various biomes worldwide may represent an important approach for assessing these effects.

Data accessibility

Ecosystem primary productivity and climate data come from databases that are freely available databases as described in methodology; The plant trait data that support the findings of this study will be made available in the dedicated repository of ***Figshare*** upon publication. Plant occurrence data are available from the corresponding author upon reasonable request.

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Table 1 Results of model analyses averaging the effects of diversity, climate, and soil nutrients on the interannual variability (IAV) of gross primary productivity.

Type of variable	Predictors	Estimate[†]	CI	RI	N
	Intercept	−2.46	−4.71~ −0.20		
Diversity	Species richness	0.077	−0.086 ~ 0.46	0.41	12
	Functional diversity	**−0.38**	**−0.70~ −0.08**	**0.97**	**24**
	Phylogenetic diversity	−0.002	−0.39 ~ 0.36	0.12	4
	CWM traits[‡]	0.014	−0.12 ~ 0.33	0.14	4
Climate	Mean annual temperature	0.009	−0.26 ~ 0.42	0.11	4
	IAV of temperature	0	−0.19 ~ 0.19	0.11	4
	Mean annual precipitation	−0.18	−0.84 ~ 0.10	0.49	13
	IAV of precipitation	0.002	−0.26~ 0.30	0.11	4
Soil	**Soil nutrients**	**−0.38**	**−0.55 ~ −0.21**	**1**	**25**

[†] The table shows standardized parameter estimates, 95% confidence interval (CI) values, and relative importance (RI) values derived from weighted averaging of parameter estimates over the best-fit models (for models with ΔAICc < 4). Boldface indicates that the variable's RI is greater than the threshold of 0.8, usually indicating that the variable is very important, whereas N indicates the number of models that contain the corresponding variables.

[‡] CWM traits represent the first principal component axis of community weighted mean traits, including specific leaf area [SLA, cm^2/g], leaf N concentration (LN, mg/g), and leaf P concentration [LP, mg/g], and two size traits, namely leaf area (LA, cm^2), and leaf dry mass (LM, g); functional diversity represent the first principal component axis of functional richness, divergence, and regularity; phylogenetic diversity represent the first principal component axis of Faith index, mean pairwise distance, and the mean nearest taxon distance; soil nutrients represent the first principal component axis of soil pH, soil total C, N, and P concentrations (%).

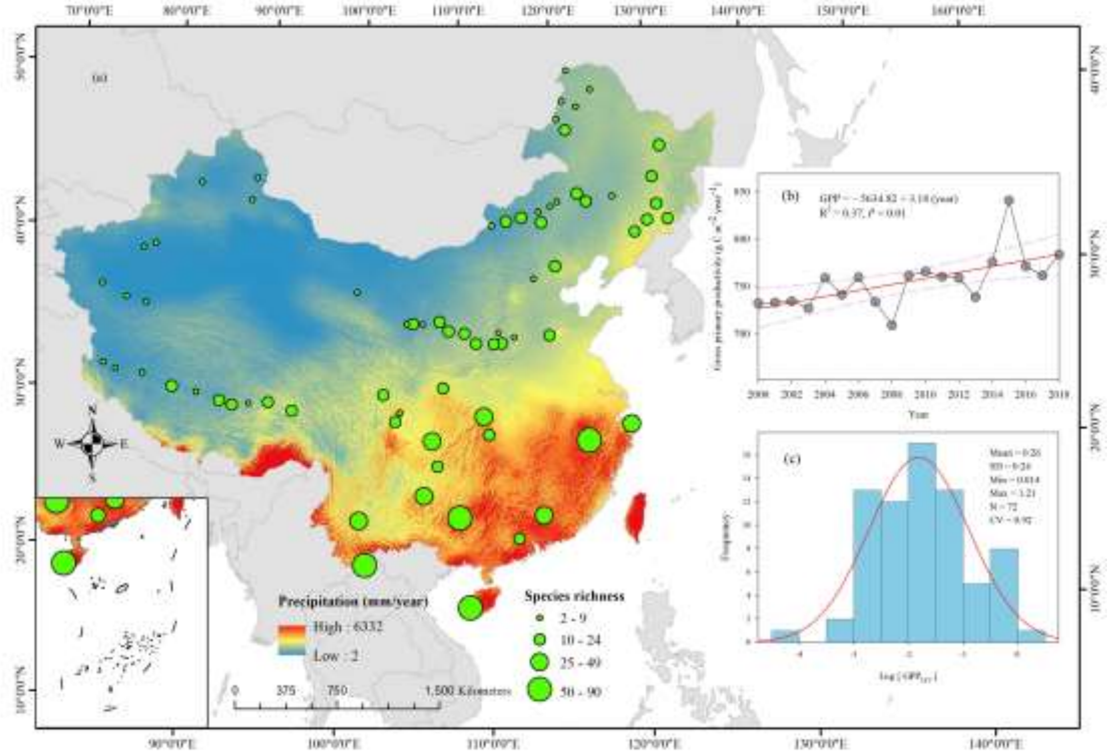

Fig. 1 (a) Map of sampling site distribution, (b) changes in gross primary productivity (GPP) over time from 2000 to 2018, and (c) frequency distribution of the interannual variability of GPP (GPP$_{IAV}$) in 72 sites across China. In panel c, the red line shows the normal distribution of GPP$_{IAV}$ (after logarithmic transformation) in the 72 sites fitted by the Gaussian function; the data passed the normality test (Shapiro–Wilk, P = 0.22).

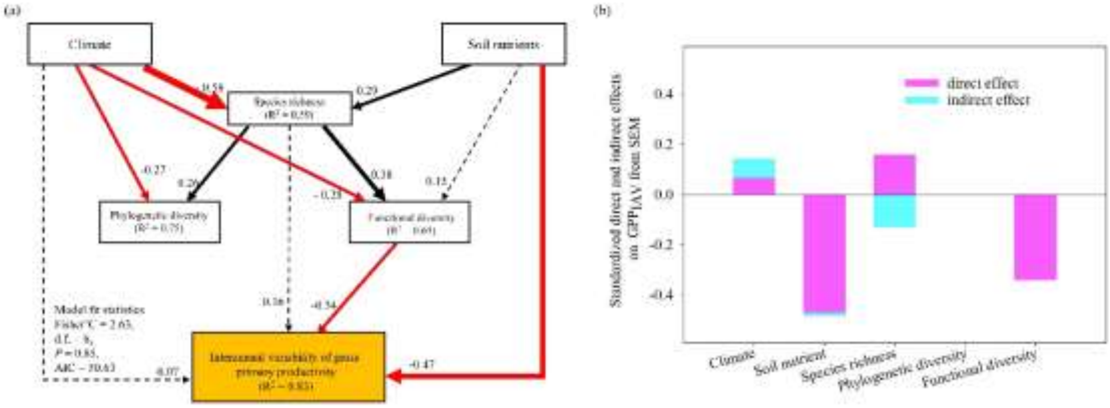

Fig. 2 Piecewise structural equation model revealing the direct and indirect effects of multiple abiotic and biotic factors on the interannual variability in gross primary productivity (GPP$_{IAV}$) across the 72 sites. Black arrows indicate positive effects, whereas red arrows indicate negative effects; solid lines indicate statistically significant effects, and dashed lines indicate non-significant effects; the width of each significant path is proportional to its standardized path coefficient. Climate represents the first principal component axis of mean annual temperature (°C), mean annual precipitation (mm year^{-1}), and their interannual variability; soil nutrients represent the first principal component axis of soil pH, soil total C, N, and P concentrations (%); functional diversity represent the first principal component axis of functional richness, divergence, and regularity; phylogenetic diversity represent the first principal component axis of Faith's index, the mean pairwise distance, and the mean nearest taxon distance. All explanatory variables were standardized (z-score, mean = 0, SD = 1) prior to analysis.

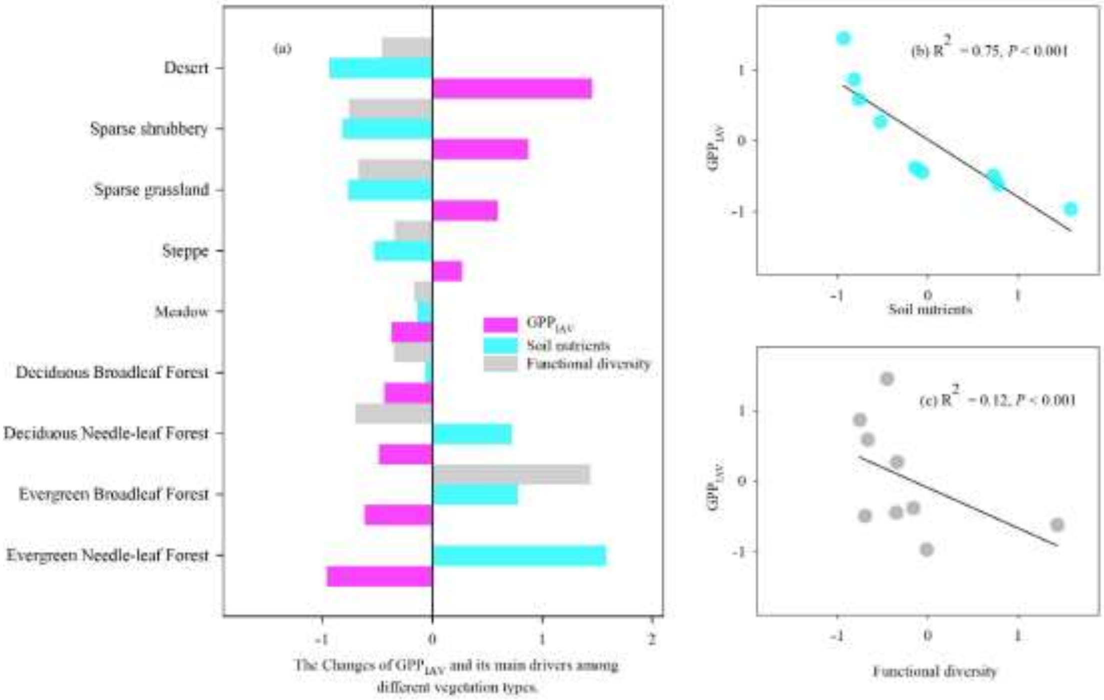

Fig. 3 (a) The pattern of interannual variability in gross primary productivity (GPP_{IAV}), soil nutrients, and functional diversity among different vegetation types, and (b–c) the bivariate relationship between GPP_{IAV} and soil nutrients and functional diversity. Each point in panels b and c represents the mean value for each vegetation type. Soil nutrients represent the first principal component axis of soil pH, soil total C, N, and P concentrations; functional diversity represents the first principal component axis of functional richness, divergence, and regularity. All variables were standardized (z-score, mean = 0, SD = 1) to eliminate dimensions and facilitate their comparison.