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The essential role of biodiversity in the key axes of ecosystem function

Running title: Effects of biodiversity on ecosystem functioning

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Abstract

Biodiversity is essential for maintaining the terrestrial ecosystem multifunctionality (EMF). Recent studies have revealed that the variations in terrestrial ecosystem functions are captured by three key axes: the maximum productivity, water use efficiency, and carbon use efficiency of the ecosystem. However, the role of biodiversity in supporting these three key axes has not yet been explored. In this study, we combined the *i*) data collected from more than 840 vegetation plots across a large climatic gradient in China using standard protocols, *ii*) data on plant traits and phylogenetic information for more than 2,500 plant species, and *iii*) soil nutrient data measured in each plot. These data were used to systematically assess the contribution of environmental factors, species richness, functional and phylogenetic diversity, and community weighted-mean (CWM) and ecosystem traits (i.e. traits intensity normalized per unit land area) to EMF via hierarchical partitioning and Bayesian structural equation modeling. Multiple biodiversity attributes accounted for 70% of the influence of all the variables on EMF, and ecosystems with high functional diversity had high resource use efficiency. Our study is the first to systematically explore the role of different biodiversity attributes, including species richness, phylogenetic and functional diversity, and CWM and ecosystem traits, in the key axes of ecosystem functions. Our findings underscore that biodiversity conservation is critical for sustaining EMF and ultimately ensuring human well-being.

Keywords: biodiversity-ecosystem functioning, functional trait, functional diversity, multifunctionality, mass ratio hypothesis, phylogenetic diversity, productivity, resource use efficiencies

Introduction

The functioning of ecosystems is based on multiple processes governing carbon, water, and energy cycling, which support ecosystem services and are closely related to the well-being of human societies(Hu et al., 2021; Jing et al., 2015). Recent ecosystem functioning research, focusing on carbon, water, and energy fluxes across major terrestrial biomes, has revealed that this set of ecosystem functions could be captured by three main axes (Migliavacca et al., 2021). The first axis reflects maximum ecosystem productivity (GPP_{max}), second axis reflects ecosystem water use strategies with a significant contribution of water use efficiency (WUE), and third axis represents ecosystem carbon use efficiency (CUE). These findings greatly improved our understanding of complex natural ecosystems and provided a new avenue to develop metrics of ecosystem multifunctionality (EMF) (Manning et al., 2018). However, light use efficiency (LUE) has not been included in these three main axes of ecosystem functions, despite being an important indicator for characterizing ecosystem resource use efficiency and a key parameter in various earth system models and remotely sensed products to assess ecosystem productivity (Gitelson et al., 2015). Focusing on a few simple and easily measurable ecosystem functions such as GPP_{max}, WUE, CUE, and LUE allows us to explore most of the across-site variability in ecosystem functioning and clarify the potential direct and indirect effects of environmental factors and biodiversity on EMF.

Ecosystem functioning depends on the environmental conditions and diversity and traits of the species that constitute an ecological community (Bruelheide et al., 2018). On the one hand, environmental conditions, including climatic and soil factors, can directly influence ecosystem functions, particularly in the context of intensified global environmental change of the Anthropocene. For example, the imbalance in precipitation among years (i.e. the changes in amount and frequency) affects the WUE of an ecosystem (Felton et al., 2020). On the other hand, environmental factors regulate species composition and affect ecosystem attributes, thereby indirectly affecting ecosystem functions (Fernández-Martínez et al., 2021). For example, climate change may lead to diversity loss (Mori et al., 2021) and a shift in functional components (Chapin et al., 2003; Suding et al., 2008), which would in turn affect the functioning of ecosystems and their carbon sink capacity (Chapin et al., 2003; Jing et al., 2022; Mori et al., 2021). Although the relationship between key ecosystem functions, environmental factors, and vegetation structural attributes (such as leaf area index) have been investigated by Migliavacca et al. (2021), the direct and indirect effects of environmental factors and biodiversity on the key axes of ecosystem functioning have not been explored to date.

Biodiversity is multifaceted and affects ecosystem functioning in two non-exclusive ways: through complementarity and selection effects (Liu et al., 2020). The complementarity effects usually refer to the increase in niche differentiation within a community reducing the competition among species and leading to greater complementarity in resource use, thereby ultimately enhancing ecosystem functioning. Species richness (i.e., the number of species in a community) is widely used as a proxy for diversity to characterize complementarity in research devoted to exploring biodiversity–ecosystem function relationships. However, the current consensus is that the contributions of different species are not equal, and therefore, species richness alone cannot adequately represent the effect of diversity on ecosystem functioning (Brun et al., 2019; Gross et al., 2017). Other facets of diversity, including phylogenetic diversity (reflecting the presence of different evolutionary lineages) and functional diversity (reflecting the variety of functions and resource use strategies), contain more information about the dissimilarities among species (Huang et al., 2020). Ecosystems with high diversity are more likely to have more dissimilar species, and these co-occurring species may contain dissimilar information, such as opposing traits and contrasting evolutionary histories (Brun et al., 2019). Such ecosystems may exploit different resources or the same resources on different spatial or temporal scales, leading to an increased overall resource utilization efficiency (Barry et al., 2019). There is no doubt that all the mentioned diversity measures, including species richness, functional diversity, and phylogenetic diversity, reflect niche differentiations and reduction in interference competition and can therefore be used to represent compensatory effects (Le Bagousse-Pinguet et al., 2019). Therefore, simultaneously evaluating the effects of these different diversity attributes on the key axes of ecosystem functions is necessary.

Selection effects, in which a well-performing species with a particular combination of characteristics becomes the dominant species and plays a positive role in ecosystem functioning (such as resource use efficiency), are also crucial. From a functional trait perspective, community-weighted mean (CWM) traits, which reflect the dominance of plants with particular traits at the expense of others, based on the mass ratio hypothesis have been used to identify the selection effects (Jing et al., 2021; Van de Peer et al., 2018). CWM traits reflect the dominance of particular trait values in a community and are closely related to the mass ratio hypothesis that the effect of a plant species on ecosystem function is proportional to its biomass (Garnier et al., 2004; Grime, 1998). This hypothesis was originally intended to explain functions related to biomass production and carbon cycling (Garnier et al., 2004). Indeed, the CWM trait value reflects the central behavior of an ecosystem or community. For example, high CWM of the concentrations of leaf nutrients, particularly nitrogen, typically indicate a community dominated by individuals of fast-growing acquisitive species with high photosynthetic rates (Garnier et al., 2016; Wright et al., 2010). However, ecosystems are complex adaptive systems with scale emergent properties. Therefore, it is difficult to predict ecosystem-level functions by only using CWM trait values (He et al., 2019). For example, predicting ecosystem productivity variations along elevation gradients with CWM values of leaf nutrient concentrations alone is challenging (Enquist et al., 2017). Fortunately, ecosystem traits or plant community traits per unit of land area, containing more community context information, such as biomass allocation and community size, appear to be a better proxy for dominant effects (Jing et al., 2021). Therefore, using community-level traits may provide valuable insights into how individual-level functional traits scale up to influence ecosystem-level multifunctionality and the roles they play in key ecosystem functions. Additionally, although manipulative experimental studies are valuable for determining the causality underlying biodiversity–EMF relationships, observational studies are also important. This is because they rely on natural climatic variations across multiple sites to explore how climate and biodiversity affect EMF, thereby reflecting the actual situation in “real-world” ecosystems (Baeten et al., 2013).

To investigate how environmental factors and biodiversity simultaneously influence EMF, we combined comprehensive data collected from 840 community plots, plant traits and phylogenetic information for 2,500 plant species, and soil data collected in 72 sites from 8 different biomes across China together with ecosystem functioning data. We used hierarchical partitioning and Bayesian structural equation modeling (SEM) to answer the following questions: 1) Are all multiple biodiversity attributes (species diversity and functional and phylogenetic diversity) related to the EMF key axis? 2) What are the relative contributions of environmental factors and multiple biodiversity attributes in driving EMF? 3) How do environmental factors and multiple biodiversity attributes directly and indirectly affect EMF?

Methods

Study sites and vegetation inventory data

Field data were collected in 72 sites located in eight biome types spanning a range of 50 degrees of longitude (78.46–128.89 °E) and 35 degrees of latitude (18.75–53.33 °N) across China (Figure 1), including boreal forests/taiga; deserts & xeric shrublands; flooded grasslands & savannas; montane grasslands & shrublands; broadleaf & mixed forests; temperate conifer forests; temperate grasslands, savannas & shrublands; and tropical & subtropical moist broadleaf forests. The 72 typical natural ecosystems investigated included deciduous needle-leaf forests, evergreen needle-leaf forests, deciduous broad-leaved forests, evergreen broad-leaved forests, meadows, sparse grasslands, steppes, sparse shrubbery, and desert grassland. Our data set included representative sites of all zonal vegetation in China and covered all climatic belts and biogeographic regions with highly varying environmental conditions (the mean annual temperature and precipitation range from –4.75 to 22.85 °C and from 53.50 to 2274.20 mm, respectively; Appendix S1 Table S1) and total vascular plant species richness (ranges from 2 to 90 species per site, average = 16). The soils have large variations in nutrient concentrations (e.g., the soil nitrogen concentration [%] ranges from 0.01 to 0.94; Appendix S1 Table S1), ranging from black earth with high organic content in cold temperate zones to tropical red soils with low organic content (Liu et al., 2018).

To ensure that the surveyed sites are free of human interference, they were generally set up in nature reserves or nearby long-term monitoring sites near ecological stations. We collected plant community data using the quadrat method (from July to August in four 30 m × 40 m plots in forests, six 10 m × 10 m plots in shrublands, and eight 1 m × 1 m plots in grasslands; Appendix S1 Text S1), and individual plant samples were collected during the peak period of plant growth (Appendix S1 Text S1 and Text S2). Although differences in vegetation types result in different plot areas for field surveys, the species accumulation curve shows that our field survey is adequate and representative, implying that it is sufficient to represent the local biodiversity (Appendix S1 Figure S1). Detailed site information has been previously reported (Zhang et al., 2020; Zhao et al., 2020) and is provided in Appendix S1 Text S1. For each site, we extracted growing season precipitation (GSP) and temperature (GST) from CHELSA v.2.1 (https://chelsa-climate.org/downloads/) based on the coordinates.

Soil nutrients in each plot in all sites were measured using standardized protocols. Specifically, topsoil samples (0–10 cm) were collected using a soil auger after removing the surface litter and were combined to obtain a composite sample per plot to account for soil heterogeneity. All visible roots and organic debris were manually removed. The samples were ground to a fine powder using a ball mill (MM400 Ball Mill; Retsch, Haan, Germany) and an agate mortar grinder (RM200; Retsch). Soil carbon and nitrogen concentrations were measured using a Vario MAX CN Elemental Analyzer (Elemental, Hanau, Germany). Finally, we calculated the average concentrations of nutrients (soil total C and N) and the C/N ratio in each site, representing the nutrient status of the site. We used the first principal component (PC) of the soil nutrient variables (soil total C and N and C/N) to represent the nutrient status of each site (Appendix S1 Table S2).

Ecosystem functions

Ecosystem carbon, water, and energy cycling-related functions are captured by GPP_{max}, WUE, and CUE (Migliavacca et al., 2021). Considering the importance of LUE in earth system models, we estimated ecosystem multifunctionality using GPP_{max}, WUE, CUE, and LUE. All data related to ecosystem gross primary productivity (GPP [g C m^2 year^{-1}]; GPP_{max}, ecosystem-scale maximum daily photosynthetic CO_2 uptake [g C m^2 day^{-1}]) used in this study are from a vegetation photosynthesis model with a spatial resolution of 0.05° × 0.05° (Zhang et al., 2017). The model is a satellite-based vegetation photosynthesis model used to estimate GPP over the photosynthetically active period of vegetation (Xiao et al., 2004). It exhibited superior performance in site-level validation across a wide range of biomes compared to other models (such as the MOD17 algorithm and the greenness and radiation model), particularly in China, and is therefore suitable for large-scale studies across multiple biomes(Liu et al., 2014; Zhang et al., 2017). However, there is an evident scale mismatch between the plant diversity data based on field surveys (1 km × 1 km) and the productivity data based on vegetation photosynthesis models (5.5 km × 5.5 km). Therefore, to ensure the reliability of the results, we carried out a quantitative assessment of the scale mismatch problem. The results show that the spatial heterogeneity caused by the scale mismatch does not affect the robustness of our results (Appendix S1 Text S3 and Figure S2).

WUE represents the ecosystem-scale water use efficiency (g C L^{-1}) and can be computed using the formula reported by Migliavacca et al. (2021):

$$WUE = GPP\sqrt{VPD}/ET$$

where *VPD* is vapor pressure deficit (hPa), collected from CHELSA v.2.1 (https://chelsa-climate.org/downloads/), and *ET* is actual evapotranspiration (mm $year^{-1}$), obtained from Elnashar et al. (2021). We also calculated the water use efficiency as *WUE = GPP/T*, where *T* represents vegetation transpiration (mm $year^{-1}$) and transpiration data downloaded from https://www.nature.com/articles/s41597-020-00693-x (Niu et al., 2020). Despite showing slight numerical differences, the results of the two methods exhibited high collinearity across diverse ecosystems (Appendix S1 Figure S3). Considering that only focusing on vegetation transpiration and ignoring land surface evaporation may underestimate the impact of plant diversity on ecosystem-level WUE, we adopted the former equation to characterize WUE in the main analysis.

CUE represents the carbon use efficiency at the ecosystem level (%). CUE was predicted using boosted regression tree (BRT) models. Combining the strengths of regression trees (models that link responses to their predictors through recursive binary segmentation) and boosting (an adaptive method for combining multiple simple models to improve prediction performance), BRT models achieve high predictive accuracy (Elith et al., 2008). We collected global 325 site-year R_e and GPP data from eddy flux observations through a literature search (Chen et al., 2019; Chen et al., 2015; Xu et al., 2014), matched these with the coordinates (Appendix 1 Figure S4), and calculated CUE as follows:

$$CUE = 1 - (R_e/GPP)$$

where R_e is ecosystem respiration (g C m^2 year^{-1}). All data used in this study are provided as supplementary material (Appendix S5). Using the same coordinates, we then extracted 21 site-level environmental variables (including 19 bioclimatic variables, growing season length, and saturation vapor pressure deficits) from CHELSA v.2.1 (https://chelsa-climate.org/downloads/) and used these data to construct a BRT model to predict R_e as the response variable. BRTs were built using the R package gbm (Greenwell et al., 2020). The optimal hyperparameter values were identified using the caret package (Kuhn et al., 2012) through 10-fold cross-validation and a grid search spanning a range of values for four hyperparameters: interaction depth (2–5), total number of trees (1,000–5,000), learning rate (0.1–0.001), and the minimal number of observations in each terminal node (5, 10). The optimal model ($R^2 = 0.98$) was used to predict R_e at the 72 study sites.

LUE represents light use efficiency (g C MJ^{-1}) and is defined as *GPP/PAR* according to Fernández-Martínez et al., (2014), where *PAR* stands for the incident photosynthetically active radiation (MJ m^{-2} yr^{-1}) and was extracted from Ren et al., (2018).

Ecosystem multifunctionality

Several methods have been recently used to investigate the relationship between biodiversity and multifunctionality, three of which are the most frequently used: the single function approach, averaging approach, and multiple threshold approach. Considering that each approach has its strengths and weaknesses (Jing et al., 2020), we used all three methods to calculate the multifunctionality. Specifically, *i*) the single function approach uses individual ecosystem functions that are independently related to biodiversity for analysis; *ii*) the averaging approach combines a collection of different ecosystem functions (*f*) into a single multifunctionality index (*M*) that quantifies the average level of standardized multiple ecosystem functions (Equation 1); *iii*) the multiple threshold approach is derived from the single threshold method (see Equation 2) and captures different thresholds that simultaneously exceed the maximum observed value of each function and evaluates whether more (or fewer) functions are simultaneously present at a high (or low) level (Byrnes et al., 2014; Hu et al., 2021). The multiple threshold multifunction can be calculated as the number of functions that exceeded the maximum value of each function for a series of consecutive thresholds (from 1% to 99% with 1% intervals).

$$M = \frac{1}{F}\sum_{i=1}^{F} g\big(r_i(f_i)\big) \tag{1}$$

$$M = \sum_{i=1}^{F}\big(r_i(f_i) > t_i\big) \tag{2}$$

where F represents the number of measured functions, f_i represents the measured value of function i, r_i is a mathematical function that converts f_i to be positive when necessary, g represents the standardization (mean = 0, SD = 1) of all measured values, and t_i represents the threshold value. For Equation 2, different thresholds can be selected for different functions as required.

Overall, the multifunctionality data for the study sites effectively reflected the patterns across several key axes of ecosystem functions at the global level (Figure 1c and d). As this study focused on a limited number of ecosystem functions and aimed to distinguish direct from indirect effects of environmental factors, we report the results for the single function and averaging approaches. These two approaches are straightforward and interpretable ways to measure an ecosystem’s ability to simultaneously sustain multiple functions (Jing et al., 2015). All selected single functions were positively correlated with the EMF index (Appendix Figure S5). The results of the multiple threshold method are presented in Appendix S1.

Biodiversity measures

CWM traits We used five leaf traits measured at the individual level (for more details, see Appendix S1 Text S2), including two size traits (leaf area [LA, cm^2], leaf dry mass [LM, g]) and three economic traits (specific leaf area [SLA cm^2/g], leaf N concentration [LNC, mg/g], and leaf P concentration [LPC, mg/g]). Variations in these traits are controlled by climatic and soil factors (Joswig et al., 2022), and these traits are closely related to ecosystem carbon, water, and energy cycling (Garnier et al., 2016). All trait values were log-transformed and subjected to PC analysis using the R package vegan (Oksanen et al., 2013). The first PC axis was used to represent the CWM traits, capturing 53% of the variations in these five traits (Appendix S1 Figure S6a).

Ecosystem traits Based on the CWM traits, the ecosystem traits can be calculated using the following formula:

$$Trait_{ecosystem} = \sum_{i=1}^{n} Trait_i \times LMI_i = Trait_{cwm_{biomass}} \times LMI \quad (3)$$

where i and n are the species i and the number of species in the community, respectively; LMI is the LM index, that is, the LM per unit land area (kg m^{-2}). We standardized (mean = 0, SD = 1) all four ecosystem traits, including leaf area index (LAI, m^2 m^{-2}), LMI (g m^{-2}), and LNC and LPC per unit land area (LNI and LPI, g/m^2), and we used the first PC axis as a measure of ecosystem trait (Appendix S1 Figure S6b).

Functional diversity We used kernel density n-dimensional hypervolumes (Blonder et al., 2018) to calculate functional dispersion as a measure of functional diversity (Blonder et al., 2014; Mammola et al., 2020). Dispersion is calculated as the average pairwise distance of a sample of stochastic points in the trait space and similar to the dispersion of a phylogenetic or functional tree (Laliberté et al., 2010). Hypervolume-based functional dispersion reflects the average difference between the trait space centroid and random points within the boundaries of the hypervolume (Mammola et al., 2020). All five CWM traits were log-transformed and scaled before creating the hypervolume (Blonder et al., 2018). We first built the hypervolumes with species abundance data and a species × traits matrix using the kernel.build function in the BAT R package (Blonder et al., 2018; Mammola et al., 2019; Mammola et al., 2020). We used the recommended settings of high-dimensional gaussian kernel density estimation to estimate the stochastic points that determine the hypervolume shape and volume (Mammola et al.,2019; Mammola et al., 2020). Then, we used the kernel.dispersion function to calculate functional dispersion (Blonder et al., 2018; Mammola et al., 2019; Mammola et al., 2020).

Phylogenetic diversity We used the mean phylogenetic distance (MPD) to represent the phylogenetic diversity. MPD is calculated as the mean phylogenetic distance (i.e., branch length) between all pairs of species within a community, reflecting the phylogenetic structuring throughout the phylogeny. We used the R package Taxonstand based on The Plant List (*http://www.theplantlist.org*) to correct and confirm the names of the species found in the 72 sites. We constructed a phylogenetic tree using the V.PhyloMaker package with PhytoPhylo megaphylogeny as the backbone (Jin et al., 2019; Qian et al., 2015; Tsirogiannis et al., 2016). We then used the PhyloMeasures package to calculate the MPD.

Species richness We used the average number of species across all plots within each site to represent taxonomic diversity (i.e., species richness) as a fundamental driver of the other diversity measures.

Statistical analysis

Data analyses were conducted on site-level (n = 72) since data on the ecosystem functioning (i.e., the response variable in the data analyses) were only available at this level. The CWM traits, ecosystem traits and other diversity measures were therefore averaged per site. Relationships between environmental factors, biodiversity, and EMF (including individual ecosystem functions) were assessed using Pearson's r and linear regression models fitted with ordinary least squares. Model assumptions were checked by visually inspecting residual plots for homogeneity and quantile–quantile plots for normality. GSP was log10-transformed to account for a nonlinear response. We used partial regressions to detect relationships between environmental factors and multiple biodiversity attributes and EMF after controlling for the effects of the other covariates within a model (James et al., 2013). The interaction between the variables was not significant; therefore, we fitted the models using only the main effects. All variables were standardized (z-score, mean = 0, SD = 1) prior to analysis to interpret parameter estimates on a comparable scale.

Hierarchical partitioning We evaluated the relative importance of the predictors under consideration as the drivers of EMF via the hierarchical partitioning method. This method employs a quantitative framework that unifies commonality analysis and hierarchical partitioning to estimate the overall importance of individual predictors, and it is implemented in the rdacca.hp package (Lai et al., 2022). This method indicates the partial effects, including individual R^2 and relative importance, of each explanatory variable (i.e., GSP, soil nutrients, species richness, functional diversity, phylogenetic diversity, CWM traits, and ecosystem traits) based on hierarchical partitioning (Lai et al., 2022). Hierarchical partitioning does not consider potential interactions between factors but determines the contribution of a given explanatory variable to EMF by examining each possible model structure containing a given predictive variable, thereby avoiding the increase or decrease in the variance explained by any given predictor variable and the problem of multicollinearity among predictor variables (Conner et al., 2009). It is well known that correlations exist between environmental factors and the multiple biodiversity attributes of an ecosystem under a given environmental condition (Joswig et al., 2022); thus, this approach is suitable for our data. The significance level (*P*-value) of the individual contribution of each explanatory variable was obtained by permutation tests using the permu.hp function in the R package rdacca.hp (Lai et al., 2022). The true value of each individual contribution was compared with the reference distribution under the null hypothesis generated by randomly rearranging the data multiple times (Legendre et al., 2012).

Bayesian structural equation modeling We examined the direct and indirect effects of environmental factors (i.e., GSP and soil nutrients) and multiple biodiversity attributes (i.e., species richness, functional diversity, phylogenetic diversity, CWM traits, and ecosystem traits) on EMF using Bayesian piecewise SEM (Appendix S1 Figure S7). Although both ecosystem and CWM traits showed good predictive power in hierarchical partitioning, owing to the high collinearity between the two (r > 0.70; Appendix S1 Figure S4) and to reduce model complexity, we established two alternative models (one including only ecosystem traits and one including only CWM traits) and reported the one with the best goodness of fit. For both models, we not only included pathways through which environmental factors affect functional and phylogenetic diversity via species richness but also included pathways through which environmental factors directly impact these measures of diversity. This is because several studies have established that these diversity measures have independent ecological significance as different aspects of biodiversity (Díaz et al., 2022) and are directly regulated by environmental factors (Anacker et al., 2012; Le Bagousse-Pinguet et al., 2019; Li et al., 2019; Wieczynski et al., 2019). In other words, species richness is decoupled from community composition, and changes in composition can still lead to changes in functional diversity and/or phylogenetic diversity with no change in species richness. As there was no significant correlation between GST and EMF, we excluded it from the SEM analysis. We rechecked collinearity before model construction using the variance inflation factor (VIF), which was below 5 for all explanatory variables included and far below the problematic collinearity threshold (VIF > 10) (Lüdecke et al., 2021). All SEM models fitted in this study were created in the Stan computational framework (http://mc-stan.org/) using the brms package (Bürkner et al., 2017) and run with two Markov chain Monte Carlo (MCMC) chains with 10,000 iterations and a warm-up of 1,000 runs. The accuracy of the MCMC results is reliable and robust as (1) visual inspection showed that it was stable and converged toward a common target, (2) all Rhat values (the ratio of the effective sample size to the overall number of iterations, with values close to one indicating convergence) were below 1.01 and effective sample sizes were > 5,000 for all coefficient estimates, and (3) there were no divergent transitions after warm-up (Appendices S2 and S3). The estimate of a coefficient is considered significant when its confidence interval does not include zero. As all variables were standardized before analysis, the obtained parameter estimates (standardized path coefficient, hereafter, β_{std}) were the standardized direct effects, and the standardized indirect effects were obtained by multiplying the direct effects.

We used the leave-one-out cross-validation information criterion (LOOIC) and expected log predictive density (ELPD) for model verification using the loo package (for LOOIC and ELPD; smaller and larger values are indicative of a better fit, respectively) (Vehtari et al., 2017). We performed posterior prediction checks using the bayesplot package (Gabry et al., 2018). The validation results for all models are provided in Appendices S2 and S3. We used the Pareto shape to diagnose abnormal observation points for each constructed SEM (Vehtari et al., 2017). Notably, very few (1–2) observations were diagnosed as being of poor quality; however, the results did not substantially change after removing the outliers, further demonstrating the reliability of the data (field surveys for 72 ecosystems based on uniform standards) We report the results including all observations. The described main analysis was repeated for individual ecosystem functions, including GPP_{max}, WUE, CUE, and LUE (Appendix S4).

Results

1) Bivariate relationships between multiple biodiversity attributes and EMF

Our results showed that GSP, soil nutrients, and multiple biodiversity attributes were positively correlated with EMF (Table 1; Figure 2; Appendix S1 Figure S5). There was no significant correlation between GST and EMF ($P > 0.05$; Figure 2). Partial regressions revealed substantial relationships between ecosystem traits and CWM traits and EMF (Appendix S1 Figure S8). However, the strength of the relationships between multiple biodiversity attributes and individual ecosystem functions varied widely (Table 1; Table 2; Appendix S1 Figure S9–12). Specifically, multiple biodiversity attributes had robust relationships with GPP_{max} and LUE (Appendix S1 Figure S9 and S12), moderate relationships with WUE (Appendix S1 Figure S10), and weak relationships with CUE (only those with CWM traits and ecosystem traits were significant; Appendix S1 Figure S11). Notably, ecosystem traits and individual ecosystem functions showed consistent significantly positive relationships, although the strength of the relationships varied (Figure 3). LUE was closely correlated with GPP_{max} of the key axis of ecosystem function (Figure 1d), and variations in both were well captured (Table 2). Additional analyses revealed that CWM traits were positively correlated with ecosystem traits (Appendix S1 Figure S13); however, this relationship was strongly influenced by the selected traits (Appendix S1 Figure S14). CWM traits were poorly correlated with ecosystem traits when both were based on leaf nutrient concentration (Appendix S1 Figure S14), whereas CWM traits and ecosystem traits were positively correlated when both were based on leaf size and dry mass (Appendix S1 Figure S14).

2) Relative contributions of multiple biodiversity attributes to EMF

Ecosystem traits, CWM traits, functional and phylogenetic diversity, and species richness were selected as significant predictors of EMF, indicating that both selection (i.e., the mass ratio effect) and compensatory effects influence the key axes of ecosystem functions (Table 1). Moreover, the mass ratio effects represented by ecosystem traits and CWM traits ($R^2 = 0.34$; Table 1) on the key axis of ecosystem functions were stronger than the compensatory effects represented by the diversity index (i.e., species richness, functional diversity, and phylogenetic diversity; $R^2 = 0.21$; Table 1). Specifically, hierarchical partitioning results showed that biodiversity indicators were strongly associated with EMF, representing key axes of ecosystem functions, and that ecosystem traits had the highest individual contribution among all predictors (22.48% of the total R^2; Table 1). Species richness alone explained only a small portion of the EMF variations ($R^2 = 0.05$; Table 1); however, the inclusion of other multiple biodiversity attributes increased the effect of biodiversity on EMF by 10-fold (up to 0.50 of the total R^2; Table 1). Although the individual contribution of multiple biodiversity attributes in individual ecosystem functions greatly varied, ecosystem traits and CWM traits were the two most robust predictors of individual ecosystem functions (15.42–46.19% and 14.77–40.08%, respectively, of the total R^2; Table 2).

3) Effects of environmental factors and multiple biodiversity attributes on EMF

SEM with ecosystem traits explained 73% of the variations in EMF (Figure 4a), and SEM with CWM traits explained 76% of the variations in EMF (Appendix S1 Figure S15). However, SEM with ecosystem traits representing the dominant effect had a better goodness of fit (LOOIC = 572.9 ± 45.1, ELPD = –286.4 ± 22.6; Figure 4a) than the model where CWM traits represented the dominant effect (LOOIC = 635.50 ± 46, ELPD = –317.8 ± 23; Appendix S1 Figure S12). Ecosystem traits had the significantly highest direct effect on EMF, with a β_{std} of 0.45, whereas GSP exerted the highest indirect effect on EMF, with a β_{std} of 0.28 (Figure 4b). Notably, as expected, in addition to directly affecting EMF, environmental factors indirectly affected EMF through multiple biodiversity attributes (phylogenetic diversity, CWM traits, and ecosystem traits; Figure 4b and Appendix S1 Figure S15). In addition, the interpretation of SEM (i.e., R^2) with individual ecosystem functions greatly varied, ranging from 0.85 (for LUE) to 0.16 (for CUE); however, the indirect effects of environmental factors through multiple biodiversity attributes were also evident in individual ecosystem functions (Appendix S4). Similarly, strong, positive effects of multiple biodiversity attributes on EMF were observed via the multiple threshold approach (Appendix S1 Figures S16 and S17).

Discussion

Our results provide insights into the roles of multiple biodiversity attributes in sustaining multiple ecosystem functions. More specifically, we comprehensively investigated the key roles of multiple diversity attributes in the key axes of ecosystem functions. Collectively, these attributes, including species richness, phylogenetic diversity, functional diversity, CWM traits, and ecosystem traits, explained up to 59% of EMF across a wide range of geographical settings, including large climatic differences and soil nutrient conditions. The simultaneous effects of multiple biodiversity attributes on multiple functions emphasize the necessity to shift from studying biodiversity from a taxonomic perspective to using a more multidimensional perspective to better grasp the complex effect of biodiversity on terrestrial ecosystem functions and prevent the underestimation of the consequences of biodiversity loss on ecosystem functions. The need to consider multiple biodiversity attributes has recently been demonstrated and highlighted in the studies of ecosystem productivity (Brun et al., 2019) and carbon, nitrogen, and phosphorus cycling in ecosystems (Le Bagousse-Pinguet et al., 2019). Our results extend this field of research by highlighting how multiple biodiversity attributes simultaneously affect several key axes of ecosystem functions.

Key roles of community-weighted mean traits and ecosystem traits in sustaining EMF

Our study revealed the important roles of CWM traits and ecosystem traits in driving EMF, with even higher influence than that of abiotic factors such as GSP. Both CWM traits and ecosystem traits reflect the functional component of selection effect, according to the mass-ratio hypothesis (Jing et al., 2021). Specifically, the roles of species traits mentioned in selection effects in influencing ecosystem function were directly quantified here by CWM and ecosystem trait values and effectively summarized by mass ratio effects (i.e., ecosystem functioning is largely determined by the traits of dominant species) (Mokany et al., 2008). Briefly, if a community or ecosystem is strongly dominated by species with traits that indicate high productivity or efficient resource use (such as a large LA), the ecosystem can achieve its highest resource use efficiency and production potential. From this, we can further reasonably infer that species diversity is not as important as traits in this case (i.e., dominated by mass ratio effects). As our results show, species diversity may even have a negative relationship with EMF. Numerous previous studies, both in forests and grasslands, have found widespread mass ratio effects, which are typically even stronger than those of diversity (Finegan et al., 2015; Fotis et al., 2018; Garnier et al., 2004; Mokany et al., 2008). These studies provided direct evidence that the traits of dominant species play irreplaceable roles in promoting ecosystem functions, such as carbon uptake (Finegan et al., 2015; Fotis et al., 2018; Garnier et al., 2004) and nutrient cycling (Le Bagousse-Pinguet et al., 2019; Tardif et al., 2014). Our study further demonstrates the existence of mass ratio effects in driving ecosystem resource (such as light and water) use efficiency and GPP_{max}.

One of the most interesting findings is the strong association between ecosystem traits (i.e., traits per unit land area) and EMF. The ecosystem traits in this study were closely related to plant nutrient pools (e.g., total leaf nitrogen and phosphorus content) and leaf area index (see Appendix S1 Figure S6) and even directly reflected their magnitudes. Although the plant nutrient pool is not a direct measure of ecosystem function (i.e., ecosystem fluxes of energy and matter) (Farnsworth et al., 2017), it is an important attribute for its determination (e.g., decomposition, carbon sequestration, nitrification and nutrient recycling) (Hu et al., 2021; Jing, Prager, et al., 2022; Jing et al., 2015; Peters et al., 2019; Zhang et al., 2022a). LAI is also an important indicator that reflects the light interception ability of ecosystems and is closely related to the GPP_{max} (Zhang et al., 2022b). Several empirical studies have revealed that the plant nutrient pool and leaf area index are particularly relevant to the long-term net balance of energy and matter in the ecosystem (Jing et al., 2022; Jing et al., 2015) and actively maintain and promote ecosystem functions related to production (Jing et al., 2022). Therefore, higher ecosystem trait values mean that the vegetation per unit area of land has higher resource utilization efficiency and capacity, indicating that more productive and efficient species are selected and thereby considered as the drivers of EMF (He et al., 2019; He et al., 2022). Similarly, the study by Migliavacca et al. (2021) revealed the important roles of leaf area index, ecosystem scale foliar N content, and aboveground biomass in two key axes, GPP_{max} and CUE, which is consistent with our findings. The link between CWM traits and EMF has been widely reported and studied (Finegan et al., 2015; Fotis et al., 2018; Garnier et al., 2004; Grime, 1998); however, the link between EMF and ecosystem traits has been less well studied. The results of this study demonstrate that, in contrast to CWM traits, which rely heavily on the selection of traits, the relationship between ecosystem traits and ecosystem function is relatively robust as long as the selected traits can be standardized to unit land area.

In addition, an advantage of using ecosystem traits is that their relationship to ecosystem functioning quantified per unit land area is independent of the area as long as the surveyed quadrats are adequately representative of local biodiversity (see Appendix S1 Figure S18). Scaling theory in the biodiversity–ecosystem functioning field (Gonzalez et al., 2020; Isbell et al., 2017; Thompson et al., 2018) predicts that the contribution of each additional species to ecosystem function will increase with the sampling extent, under the premise that ecosystem function linearly increases with sampling extent (i.e., the functioning of large-scale ecosystems is the sum of the functioning of small-scale ecosystems). However, most ecosystem level functions, such as ecosystem productivity and resource use efficiency, are currently measured on a per unit land area basis. In per unit land area terms, functioning should be invariant to area. Hence, the strength (i.e., the slope) of the diversity-ecosystem function relationship could potentially weaken by increasing the sampling extent (Barry et al., 2021). As ecosystem traits are also quantified on a unit land area basis, similar to ecosystem functions (He et al., 2022), using them rather than diversity can prevent this dilemma. Their use would help us draw more objective conclusions about diversity–ecosystem function relationships.

Mechanisms underlying the effects of multifaceted diversity on EMF

In addition to CWM traits and ecosystem traits, diversity (particularly functional diversity and phylogenetic diversity) also plays a vital role in EMF (see Table 1). Numerous empirical and theoretical studies have revealed that diversity improves resource (such as light and water) use efficiency at the ecosystem level through compensatory effects(Barry et al., 2019; Milcu et al., 2014; Williams et al., 2021), which is consistent with our findings (Table S3). It is well known that differences between species may lead to more efficient light use in diverse ecosystems, a central premise for complementary effects (Niklaus et al., 2017; Williams et al., 2021). The results of the Jena grassland experiments also suggested that high functional diversity (based on leaf nitrogen) increases LUE and WUE by increasing the complexity of the community vertical structure (Milcu et al., 2014). Although evapotranspiration may be stronger in ecosystems with more species (Milcu et al., 2014), greater productivity (i.e., photosynthetic processes) is the dominant regulator of WUE (Hu et al., 2008; Niu et al., 2011). Therefore, ecosystems with high functional diversity tend to have a higher resource use efficiency (Milcu et al., 2014), which is consistent with our findings. In addition, the estimated effect of functional diversity on ecosystem functioning may be related to the type and quantity of the traits selected (Huang et al., 2020). In this study, we selected typical economic traits (leaf nutrient content and SLA) and size traits (leaf size), both of which are closely related to the vegetation primary production of the ecosystem (Garnier et al., 2016). This is also an indispensable reason why functional diversity has a significant effect on EMF.

In contrast with functional diversity, phylogenetic diversity does not depend on selected traits, but only on the phylogenetic history of the species within a community (Huang et al., 2020). Thus, phylogenetic diversity may reflect additional functional specialization axes that are captured neither by leaf nutrient content nor by size traits but by two basic characteristics that reflect plant resource utilization strategies (Srivastava et al., 2012). Specifically, phylogenetic diversity can effectively consider hidden traits that are particularly relevant to ecosystem functioning, such as those related to pathogen infection, pollination rates, mycorrhizal communities (Barry et al., 2019; Parker et al., 2015), or plant population strategies (Le Bagousse-Pinguet et al., 2019). Recent studies have revealed that communities with distant phylogenetic relationships exhibit greater compensatory effects (Huang et al., 2020). A study on drylands demonstrated a significant positive relationship between phylogenetic diversity and resource use efficiency (Le Bagousse-Pinguet et al., 2019). However, the plasticity of plant traits, such as their potential intraspecific variation, leads to functional diversity being malleable even without the changes in plant community composition, whereas phylogenetic diversity is not, at least until species composition changes. Therefore, the response of phylogenetic diversity to environmental changes may be delayed, which could be why it is not as important as functional diversity. Overall, our results confirm that the introduction of phylogenetic and functional diversity increases the contribution of diversity to EMF than using species richness alone.

Effects of environmental factors on EMF via multiple biodiversity attributes

Our results underscore that environmental conditions, including climatic factors and soil nutrient status, influence EMF directly and indirectly by acting on plant traits and multiple biodiversity attributes, as revealed by several recent studies (Hu et al., 2021; Jing et al., 2015). We followed a macroecological approach to encompass numerous ecosystem types, spanning a large environmental gradient covering most of Earth's major biomes. Precipitation is an important factor driving ecosystem type gradients, such as changes from grassland to shrub and forest ecosystems along the precipitation gradient (Chapin et al., 2002). Accordingly, we found that precipitation during the growing season is an important environmental predictor of EMF. On the one hand, precipitation during the growing season directly determines the available water as a limiting resource in most ecosystems and has an effect on ecosystem productivity (Gherardi et al., 2019), which in turn affects the use efficiency of other resources, such as light. On the other hand, precipitation and water availability affect the plant traits in an ecosystem (i.e., response traits) (Suding et al., 2008), such as the vertical distribution of roots (B. Zhang et al., 2019) and anatomical traits related to hydraulic transport and WUE (Griffin-Nolan et al., 2018; Liu et al., 2018), thereby indirectly regulating the ecosystem resource use efficiencies.

The soil nutrient content affects the nutrients available to vegetation and directly regulates resource use efficiencies, such as CUE (Fernández-Martínez et al., 2014). A study in temperate forests by Xu et al. (2020) revealed that the availability of soil nutrients, particularly nitrogen, regulates forest resource use efficiency (WUE and LUE) by affecting the canopy photosynthetic capacity (i.e., maximum photosynthetic capacity). This is similar to the mechanism through which functional diversity improves resource utilization efficiency by increasing the magnitude of productivity. Simultaneously, increased soil nutrient contents imply that the ecosystem can accommodate more species, thereby improving EMF through compensation effects (Barry et al., 2019). In addition to the macroclimate factors evaluated in this study, microclimate factors, such as sub-canopy temperature, affect ecosystem functioning. For example, microclimate can directly affect species distribution and abundance in the ecosystem (Murphy et al., 2015), which in turn affects leaf physiological traits, such as canopy packing (Jucker et al., 2015). All these may affect the utilization of limited resources by the ecosystem and are worthy of further exploration.

Perspectives for future studies on biodiversity–EMF relationships

Our study provided evidence that biodiversity plays an important role in the key axes of ecosystem functions. However, this study has some limitations that need to be addressed in future studies. First, the robustness of the research results can be enhanced if the CUE data are derived from measured data based on flux observations. Future biodiversity surveys are expected to be combined with ecosystem-level flux observations to provide high-quality data on both biodiversity and ecosystem functions. This will help us better understand the linkages between ecosystem structure and function. Second, the effect of soil microbial diversity (i.e., belowground diversity) on resource use efficiency and maximum ecosystem productivity is a future research direction that cannot be ignored. Focusing only on aboveground diversity may obscure the relationship between diversity and EMF. Soil microbial diversity significantly affects the nutrient uptake in an ecosystem (Fleischer et al., 2019; Hu et al., 2021; Jing et al., 2015; Terrer et al., 2021), particularly in arid climates (Hu et al., 2021). Thus, it can be expected to play a significant role in resource use efficiency. For example, soil microorganisms decompose litter and soil organic matter through heterotrophic respiration (Tang et al., 2020), which affects the carbon cycle and CUE of the ecosystem. Despite these limitations, we revealed for the first time that the importance of ecosystem traits no less important than CWM traits This study provides an important indicator to facilitate the understanding of EMF from a trait perspective. Furthermore, we suggest that the standardization of traits to unit land area should be given more attention in the future to prevent underestimating the effect of plant traits in driving ecosystem processes and functions.

Author contributions

N.H. P.Y., and M.F.M. designed the research. P.Y. conducted the research (collected the datasets and analyzed the data). P.Y. wrote the manuscript. K.V.M., M.M., G.R. Y., and N.H. commented on the details of the manuscript drafts. All authors contributed substantially to revisions.

Competing interests

There are no conflicts of interest to declare

Data accessibility

The data that support the findings of this study are openly available in Figshare at: https://doi.org/10.6084/m9.figshare.22209718.v1.

Code accessibility

All the R packages used are described in the methods section. No new R package or function was created.

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Table 1 Independent effects of environmental factors and biodiversity measures on ecosystem multifunctionality (EMF) based on hierarchical partitioning.

Predictors	Unique effect[†]	Share effect	Importance (R^2)	Contribution (%)	*P*-value
GSP[‡]	0.013	0.12	0.13	16.70	0.003
GST	0.024	0.02	0.04	4.99	0.05
Soil nutrients	0.004	0.07	0.07	8.72	0.02
Species richness	-0.002	0.05	0.05	6.07	0.04
Functional diversity	0.003	0.09	0.09	11.40	0.007
Phylogenetic diversity	-0.001	0.08	0.07	9.29	0.014
CWM traits	0.027	0.14	0.16	20.42	0.001
Ecosystem traits	0.020	0.16	0.18	22.48	0.001
Total	0.088	0.71	0.80	100	

The table shows the results of variance partitioning in an independent-effects analysis; *P*-values are from permutation tests based on 999 randomizations.

[‡] GSP, growing season precipitation, GST, growing season temperature; CWM, community-weighted mean. CWM traits and ecosystem traits represent the first principal components of five CWM traits and four ecosystem traits, respectively.

Table 2 Relative importance of individual environmental variables and biodiversity measures in predicting individual ecosystem functions based on hierarchical partitioning.

	GPP_{max}[†]		WUE		CUE		LUE	
Predictors	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)	Importance (R^2)	Contribution (%)
GSP[‡]	$0.12^{**\S}$	14.83	0.09^{**}	13.34	0.011	9.05	0.18^{***}	21.35
GST	0.02	3.02	0.10^{**}	15.82	-0.010	-7.94	0.04^{*}	5.26
Soil nutrients	0.11^{**}	13.22	0.05	7.19	0.001	1.11	0.05^{*}	5.95
Species richness	0.04^{*}	5.52	0.04	6.27	-0.005	-4.21	0.08^{**}	9.65
Functional diversity	0.10^{**}	11.96	0.08^{*}	11.94	0.022	17.38	0.13^{**}	14.67
Phylogenetic diversity	0.11^{**}	13.53	0.07^{*}	11.06	-0.002	-1.75	0.05^{*}	5.76
CWM traits	0.12^{**}	14.77	0.12^{**}	18.96	0.051^{*}	40.08	0.16^{**}	18.42
Ecosystem traits	0.19^{***}	23.12	0.10^{**}	15.42	0.058^{*}	46.19	0.16^{**}	18.96
Total	0.81	100	0.64	100	0.13	100	0.85	100

[†] GPP_{max}, ecosystem-scale maximum photosynthetic CO_2 uptake (g C m^2 day^{-1}); CUE, carbon use efficiency at the ecosystem level (%); LUE, light use efficiency (g C MJ^{-1}); WUE, water use efficiency (g C L^{-1}).

[‡] GSP, growing season precipitation; GST, growing season temperature; CWM, community-weighted mean. "CWM traits" represents the first PC of CWM traits, which explains 53% of the variation in four CWM traits, and "ecosystem traits" represents the first PC of ecosystem traits, which explains 98% of the variation in five ecosystem traits.

[§] $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; P-values are from permutation tests based on 999 randomizations.

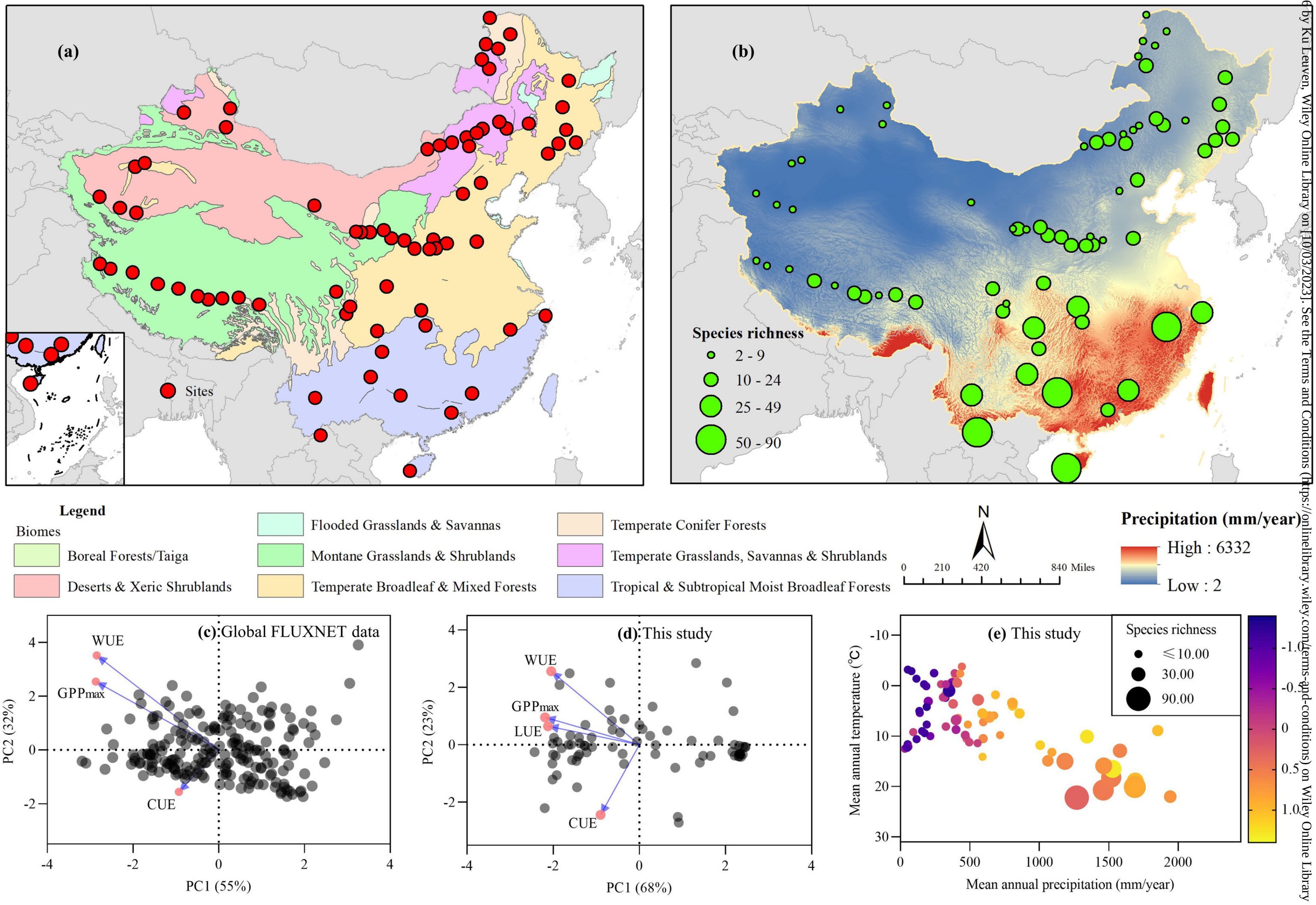
Figure Captions

Figure 1 Spatial distribution of the study sites across diverse biomes (a) and along a broad environmental gradient (b). The ecosystem types that were investigated included tropical forests, temperate forests, boreal forests, steppe, montane grasslands, and others across a wide environmental gradient. The data in panel (c) were derived from the Global FLUXNET data used by Migliavacca et al. (2021) to reveal the three key axes of terrestrial ecosystem functions. In panels b and e, circle size represents the species richness at each study site. In panel e, the color gradient of the circles indicates the changes in ecosystem multifunctionality (z-score, dimensionless) of the sites studied along the environmental gradient. Data for the division of biomes in panel a were obtained from the revised map of Ecoregions 2017 (Dinerstein et al., 2017) available at ecoregions2017.appspot.com. The spatial distribution map of the study sampling sites was created using ArcGIS software v10.8. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Figure 2 Relationships between ecosystem multifunctionality and environmental factors and multiple biodiversity attributes. "CWM trait" represents the first principal component (PC) of community-weighted mean (CWM) traits, which explains 53% of the variations in four CWM traits and "ecosystem trait" represents the first PC of ecosystem traits, which explains 98% of the variations in five ecosystem traits. Lines were fitted by ordinary least squares (lm function in R) after all variables were standardized (z-score, mean = 0, SD = 1).

Figure 3 Bivariate relationships between ecosystem traits and individual ecosystem functions, including (a) GPP_{max}, (b) LUE, (c) WUE, and (d) CUE. GPP_{max}, ecosystem-scale maximum photosynthetic CO_2 uptake (g C m^2 day^{-1}); WUE, water use efficiency (g C L^{-1}); CUE, carbon use efficiency at the ecosystem level (%); LUE, light use efficiency (g C MJ^{-1}). "Ecosystem trait" represents the first PC of ecosystem traits, which explains 98% of the variations in five ecosystem traits. All variables were standardized (z-score, mean = 0, SD = 1) prior to analysis.

Figure 4 Bayesian piecewise structural equation (SEM) models exploring the direct and indirect effects of environmental factors and biodiversity measures on ecosystem multifunctionality (EMF), which is related to carbon, water, and energy cycling of ecosystems. GSP, precipitation in the growing season. Ecosystem trait represents the first PC of ecosystem traits, which explains 98% of the variations in five ecosystem traits. Black arrows represent positive relationships, whereas red arrows represent negative relationships. Solid lines indicate significant effects, and dotted gray lines represent non-significant effects. For the leave-one-out cross-validation information criterion (LOOIC) and expected log predictive density (ELPD), smaller and larger values, respectively, indicate a better fit.



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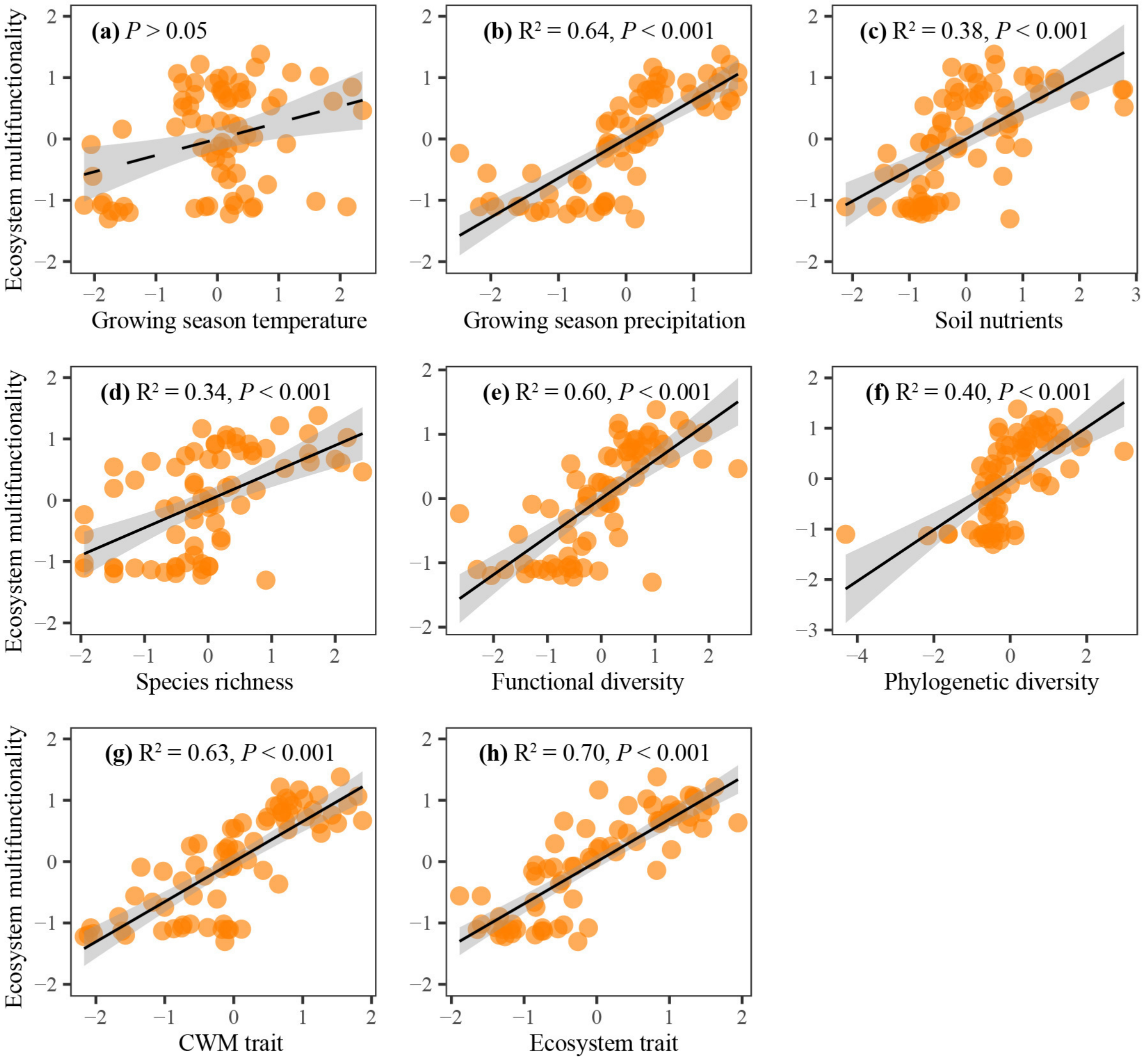

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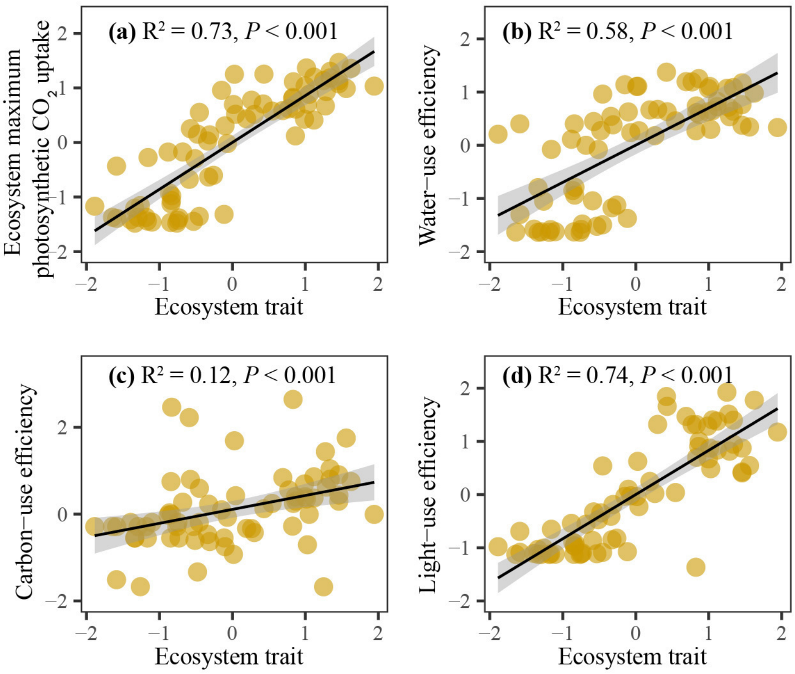

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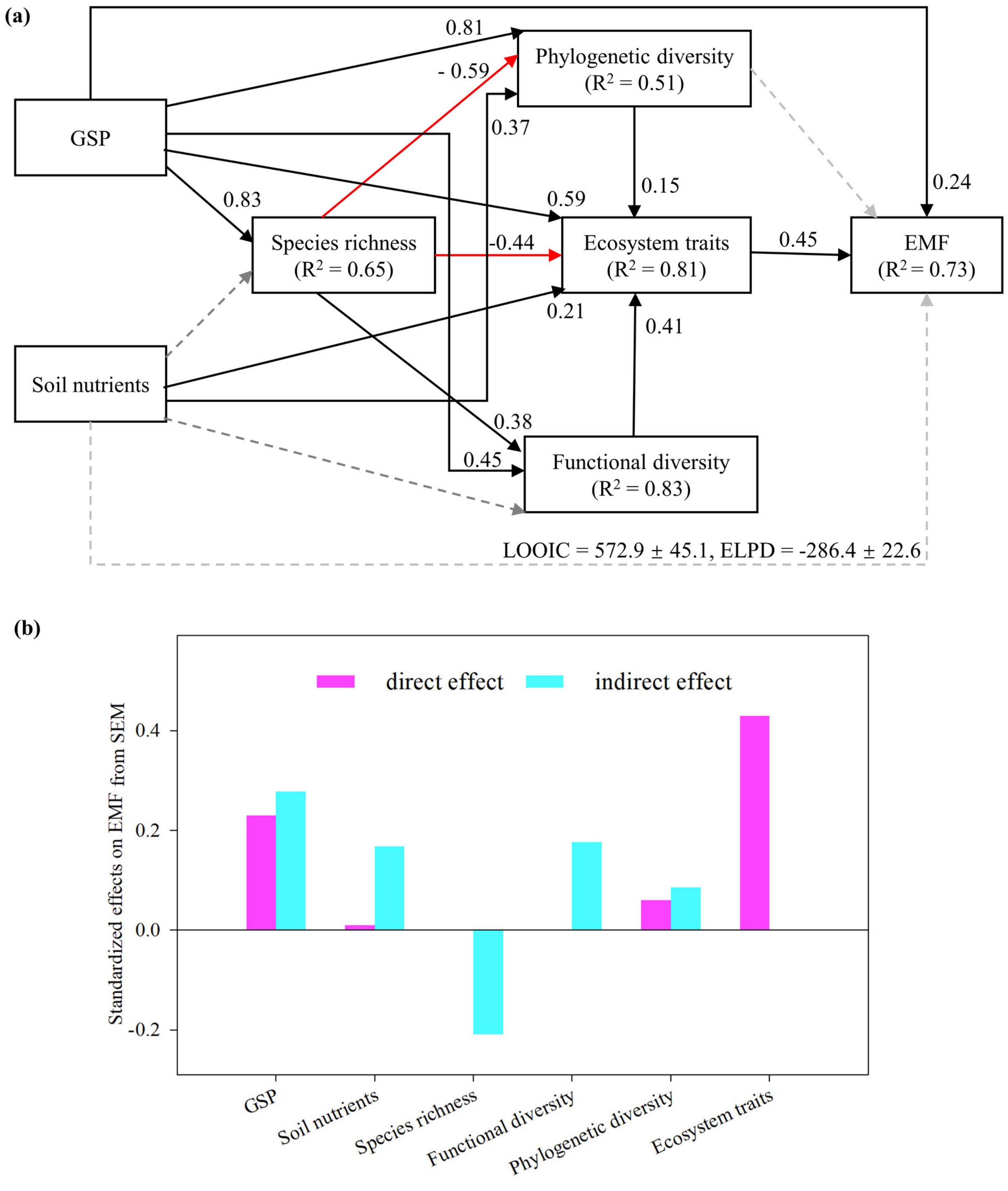

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