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Environment shapes tree community traits in China's forests

Running title: Trait-environment relationships in China's tree communities

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

Z.T. and H.Z. conceived the ideas of the study; Q.G. and H.Z. collected the data; S.N.S. contributed trait data; H.Z. and Y.G. analyzed the data; H.Z., Y.Y. and Z.T. led the writing and revision of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Climate data are publicly available in WorldClim (<https://www.worldclim.org/>). Soil data are publicly available in China Soil Database (<http://globalchange.bnu.edu.cn/home>). Plant trait data were accessed from the China Plant Trait Database (Wang et al., 2018) and TRY Database (<https://try-db.org>, accessed April 2019). Community traits data associated with this study are available at <https://doi.org/10.6084/m9.figshare.19754758.v1>

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Abstract

Question: Environmental filtering plays an important role in plant community assembly. To what extent does the broad-scale environment influence the functional composition of woody plants in China's forests? Is there stronger trait convergence under harsher environmental conditions?

Location: China.

Methods: We characterized community traits and their relationships to climate and soil, using a dataset with 1,312 plots of tree communities composed of 1,591 tree

species and ten functional traits across China. Using quadratic models, we explored how community traits change with different environmental factors.

Results: Trait spectra at the species level and the community level were significantly correlated, and the first two principal components captured 74.5% of the variation in community-weighted mean traits (CWMs). The trait spectra showed a clear elevational pattern and varied along climate and soil gradients. Compared to random expectations, the multi-trait functional diversity showed a divergence pattern on poor soils at the plot scale.

Conclusions: Two well-known dimensions, the leaf economics spectrum and size-related spectrum, could be extended from the species level to the community level. Environment, especially climate conditions, drive the trait spectra and their elevational patterns at broad scale, indicating environmental filtering might shape the trait composition of tree communities in China. However, stronger environmental filtering does not occur under harsher environmental conditions.

KEYWORDS

Community assembly, environmental filtering, forests, functional composition, functional diversity, functional traits, macroclimate

1. Introduction

Functional traits represent the plant strategies for adapting to varied environments and are useful for predicting community assembly processes (Violle et al., 2014). The niche-based processes of community assembly such as environmental filtering and limiting similarity can be revealed by studying the patterns of functional trait composition and diversity within and across communities (McGill et al., 2006; Kraft et al., 2008; Mason et al., 2013; Kraft et al., 2014). The composition and diversity of functional traits within a community could be characterized adequately using the

dominance (Lavorel et al., 2007) and variation (Ricotta & Moretti, 2011; Enquist et al., 2015) in trait values within a given community.

Two well-known dimensional spectra of plant trait variation, the size-related spectrum and the leaf economics spectrum, have been found in global plant species (Diaz et al., 2016). The two-dimensional spectra may also be applied at the community level (Bruehlheide et al., 2018). However, community functional composition is driven not only by species identity but also by their relative abundances within the community. Trait combinations at the community level can be different from the trade-offs at the species level. Some studies have reported stronger correlations among functional traits at the community level than at the species level (Dominguez et al., 2012; Jiang et al., 2017). The dominant traits within a community are expected to indicate the optimal strategy under certain environmental conditions (Shipley et al., 2011; Enquist et al., 2015); therefore, environmental filters shape the covariation among the traits of the species in a community. However, community mean traits may also decouple traits covariation at the species level because of the combinations of various strategies within a community that facilitate species co-existence (Ben-Hur et al., 2012). A comparison of trait spectra at the species level and community level might provide insight into the processes of community assembly (de la Riva et al., 2016).

Linking community traits to the environment is important for developing a predictive framework for ecosystem functioning and community assembly (Lavorel & Garnier, 2002). It is recognized that the environment regulates community trait covariation and its geographic patterns (Perez-Ramos et al., 2012; Guerin et al., 2022). A global-scale analysis found that environmental filtering dominates the plant community assembly and revealed relatively strong relationships between the environment and tree community traits (Wieczynski et al., 2019). It is commonly acknowledged that the dominance of and variation in trait values reflect the optimum and intensity of environmental filtering, respectively. The relationships between

dominant traits and the environment should reflect the selection towards locally optimal phenotypes; therefore, species with trait values close to the community average traits are more likely to be present (Laliberté et al., 2013; Muscarella & Uriarte, 2016).

In addition, the relative importance of environmental filtering in shaping functional composition may vary along environmental gradients. In this sense, the stress-dominance hypothesis (SDH) suggests that abiotic filtering is more intense in extreme environments than in other environments, leading to stronger trait convergence under harsher environmental conditions (Coyle et al., 2014). However, the observed shifts in trait values along different abiotic gradients are often inconsistent, implying that abiotic factors regulate traits in idiosyncratic ways (Kermavnar & Kutnar, 2020). Moreover, trait may also diverge in a harsh environment, posing challenges to the statement that the intensity of abiotic filtering increases towards extreme environmental conditions (Grime, 2006; Bernard-Verdier et al., 2012). One reason is that environmental constraints might act more strongly on multivariate traits than on a single trait (Kraft et al., 2015; Muscarella & Uriarte, 2016). Alternatively, species interactions such as competition and facilitation that lead to trait divergence can obscure the effect of environmental filtering (Mayfield & Levine, 2010; McIntire & Fajardo, 2014). To better assess the effect of the environment on community assembly, analyses using extensive locally measured traits and in situ community data along multiple environmental gradients are needed.

Here, we gathered a large dataset, including the vegetation survey data of 1,312 forest plots combined with ten functional traits for 1,591 tree species in China. By linking species and trait data to ten environmental factors, we explored the consistency of community trait-environment relationships. This study addresses the data gap in Asia for previous global trait-environment studies (e.g., Brulheide et al., 2018; Wicznski et al., 2019). We addressed the following questions: (1) How do trait spectra differ between the species and the community level? We expected a size-

related spectrum and leaf economics spectrum at both the community and the species level, and stronger covariation between functional traits for the community-weighted mean traits compared to the cross-species traits. (2) How do community mean traits change with different environmental factors? We expected that climate and soil factors would jointly drive trait composition by selecting for certain optimum trait values. (3) Does multi-trait functional diversity show stronger convergence under extreme rather than benign environments? We expected traits convergence under harsh environmental conditions according to the stress-dominance hypothesis.

2. Materials and methods

2.1 Plot data

We used a local community assembly dataset including 1,312 forest plots investigated during 1997~2008, each with an area of 600 m² (20×30 m). These plots were collected from 46 well-protected mountains across China (Figure 1). Along the elevational transects of each mountain, plots were placed at an interval of 50–100 m. All tree stems with diameter at breast height (DBH) of ≥ 3 cm were identified and measured in each plot. Our dataset covered a wide environmental gradient from temperate to tropical latitudes and from arid to humid regions, with elevations spanning from 160 to 4,250 m. The forest types ranged from boreal forests in the north to subtropical evergreen forests in the center to tropical rainforests in the south (Fang et al., 2012). The details of the plot investigation were described in previous studies (Tang et al., 2012; Fang et al., 2012). The checklist of the tree communities was matched with the Plant List by the R package ‘plantlist’ (Zhang, 2018). In total, 1,591 tree species were recorded in all plots.

2.2 Climate and soil data

We gathered site-specific climate and soil data using publicly available high-resolution raster layers (Appendix S1). Five climate variables, i.e., mean annual temperature (MAT), annual temperature range (TAR), annual precipitation (AP),

coefficient of variation of annual precipitation (CV.P), and solar radiation (SR), were extracted from WorldClim (V2.1, resolution at 30×30 arc second, mean during 1970-2000, Fick & Hijmans, 2017) by the geographic coordinates of the plots.

Five soil variables collected from 0-30 cm, i.e., soil pH, cation exchange capacity (CEC), soil organic carbon (SOC), soil nitrogen (TN) and soil phosphorus (TP), were extracted from the China Soil Database (resolution at 30×30 arc second, Shangguan et al., 2013). SOC, TN and TP were weighted by the depth×bulk density of the different layers, while PH and CEC were weighted by the depth of the different layers. We examined the correlations between the environmental variables to detect potential collinearity (Appendix S2). PCA was performed on the environmental factors. We extracted the first two components that represented 65.2% of the overall variation and were rotated by "varimax" to simplify the information for each axis. Factor loadings and plot scores of the second component were multiplied by -1 (Appendix S3). PC1 represents soil conditions under which a higher score indicates more fertile soil (high SOC, TN, TP and CEC), and PC2 represents climate conditions under which a higher score indicates a benign climate (warm, moist and stable environment).

2.3 Trait data

We selected ten functional traits (Table 1) that have been widely measured and investigated in previous studies related to plant growth, survival, and regeneration strategies (Diaz et al., 2016; Messier et al., 2017; Brulheide et al., 2018).

We sampled and measured the leaf dry matter content (LDMC), specific leaf area (SLA), height, leaf nitrogen (leaf N), and phosphorus (leaf P) and their ratio (N/P) of 405 species from 79 additional forest plots in 2013. The 79 plots occur on eight mountains and are evenly distributed across China (Figure 1). We randomly sampled at least three mature individuals of each species from each mountain to measure height. For each individual, we sampled at least five complete and mature leaves to

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measure SLA and at least ten leaves to measure leaf N and leaf P. Leaf area was measured from the scanned leaf. LDMC was weighed by drying at 65 °C. SLA was calculated by dividing the LDMC by leaf area. Leaf N was measured by a C/N element analyser (PE-2400 II), and leaf P was measured by the Mo-Sb colorimetry method (Bray & Kurtz, 1945). We then averaged each trait value across all sampled individuals ignoring their locations, and used the calculated species-mean trait values in the analysis. Based on previous studies (Violle et al., 2012; Des Roches et al., 2018; Maitner et al., 2021), intraspecific variation, which also contributes to community assembly, was ignored in the analysis due to the species number and geographic scope of our study.

Trait values that were not sampled in situ were further collected from the China Plant Trait Database (Wang et al., 2018) and TRY Database (Kattge et al., 2011). For taxa recorded at the genus level only in the database, we calculated the genus mean for the target trait. In total, traits collected from local and public databases covered 30.1%-77.4% of the species (Table 1).

We then filled the trait data gaps by the advanced Bayesian Hierarchical Probabilistic Matrix Factorization (BHPMF) method using the 'BHPMF' package (Schrodte et al., 2015; Fazayeli, 2017) in R. The BHPMF method is well-acknowledged to be reliable for sparse datasets (Fazayeli et al., 2014; Schrodte et al., 2015). We first standardized the species-mean trait values before gap-filling and used the information for phylogenetic groups to fill the gaps in the missing data at the species level. We removed all imputations with a standard deviation >1.5. Finally, we obtained ten gap-filled traits covering 95.2% of the species×trait combinations.

2.4 Community traits

For each plot and each functional trait, we calculated the community-weighted mean (CWM) and Rao's quadratic diversity (Rao's Q) to present the dominance and divergence of the community traits (Ricotta & Moretti, 2011), respectively:

$$CWM = \sum_{i=1}^S P_i X_i$$

$$\text{Rao's } Q = \sum_{i,j} d_{ij} P_i P_j$$

$$d_{ij} = \frac{1}{n} \sum_{k=1}^n (X_{ik} - X_{jk})^2$$

where S is the number of species within the plot and P_i and X_i are the relative abundance and mean trait value of the i^{th} species in the plot, respectively. d_{ij} is the trait dissimilarity between the i^{th} and j^{th} species using Euclidean distance divided by the number of traits (Botta-Dukat, 2005). n is the number of traits. Because a small number of plots contained species with missing trait data, a minimum of 991 (stem conduit density) and a maximum of 1,155 (height) plots were used to calculate the community traits. Compared with methods based on multidimensional spaces, Rao's Q , representing the expected dissimilarity between two species sampled at random, is concise and suitable for measuring the divergence of trait space and computationally advantageous (Botta-Dukat & Czucz, 2016; Mammola et al., 2021). Rao's Q was calculated for both single traits and multivariate traits by the package 'FD' in R (Laliberté & Legendre, 2010; Laliberté et al., 2014).

To determine whether a trait was convergent or divergent within the community compared to random expectations, we compared the observed and expected Rao's Q values for each trait under a null model (de Bello, 2012). To generate a null model for each plot, we changed the identity of the species by randomly sampling species for 999 times from all species pools while keeping species number and relative abundance in the actual observation unchanged. The standardized effect size (SES) was then calculated to measure the difference between the observed and modelled Rao's Q as:

$$SES = [Q_{obs} - \text{mean}(Q_{null})] / \text{Std}(Q_{null})$$

where Q_{obs} and $mean(Q_{null})$ are the observed and mean modelled Rao's Q, respectively, and $Std(Q_{null})$ is the standard deviation of the 999 modelled Rao's Q. A total of 130 plots with only one species were removed. Negative SES values indicate trait convergence while positive values indicate trait divergence. All Rao's Q were log-transformed before calculating the SES. If the observed Rao's Q was larger or smaller than 97.5% of Rao's Q of the null model, then we considered that the trait distribution within the community diverged or converged significantly compared to the null model. We did not calculate the SES of the CWM because theoretically, the mean CWM of the null model is equal for each plot when we randomly sample from the same species pool and the relationships between the SES of the CWM and the environment have no more information than the CWM-environment relationships.

2.5 Statistical analysis

Except LDMC and N/P, species traits and CWMs were natural logarithmic transformed before the analysis. To investigate key dimensions of trait variation, we performed a principal component analysis (PCA) for species traits and the CWMs. The first two axes were extracted and their eigenvalues were greater than 1. Kernel density estimation was further applied to estimate the occurrence probability of the species or plots in the trait space defined by the first two principal components. We conducted a PCA and kernel density estimation analysis following Diaz et al. (2016). Procrustes analysis was performed to compare the difference and relationship between the PCAs at the species level and the community level. Furthermore, we analyzed the elevational gradient of the first two principal components at the community level with linear mixed-effects model. Sampling sites, namely identity of the mountain area, were treated as random factor to correct the effects of latitude.

Empirical studies have found that trait-environment relationships can be nonlinear (Rolhauser et al., 2021). We considered a quadratic model to explore the CWM-environment relationships. We built a linear model and a quadratic model for

each CWM-environment relationship. We used the quadratic model if it had a $\Delta AIC < 2$, compared to the linear model, the linear model otherwise.

We calculated an SES for all trait combinations. A quadratic model was built to fit the SES-environment relationship following the same model selection process. Twenty percent plots at both ends and the middle of environmental gradients were extracted to test whether SES was equal to zero with a two-sided T test.

PCA, kernel density estimation, Procrustes analysis and linear mixed-effects model were performed in the packages ‘psych’ (Revelle, 2021), ‘ks’ (Duong, 2007), ‘vegan’ (Oksanen et al., 2020) and ‘lme4’ (Bates et al. 2015) in the R statistics, respectively.

3. Results

3.1 Trait spectra at the community level

In the trait spectra defined by the first two components, both the size-related spectrum and leaf economics spectrum stood out for species trait variation and community weighted mean traits. The first two principal components jointly accounted for 42.5% of the total variation in species traits and 74.5% of the total variation in CWMs (Figure 2, Appendix S4). The results of the Procrustes analysis showed that the CWMs were significantly related to species trait variation ($M^2=0.429$, $P=0.001$). However, the first two components captured more information of CWMs, and only the first component explained 55.4% of the variation. In the community-level PCA, size-related traits were highly related to PC1, and leaf economics traits were related to both PC1 and PC2.

The first two components of CWMs showed clear elevation patterns: PCA1 (conditional $R^2=0.83$, marginal $R^2=0.36$) and PCA2 (conditional $R^2=0.77$, marginal $R^2=0.14$) axis score decreased with increased elevation (Figure 3). In addition, because our data covered areas with freezing temperatures (negative MAT), we checked the position of these plots ($n=156$) in the trait spectra (Appendix S5).

3.2 CWM-environment relationships

In general, most CWM-environment relationships were better fitted with a quadratic model (Figure 4). Soil and climate conditions both correlated with the CWMs; however, the dominant factor was different for different traits. The CWM of SLA, leaf N and leaf P showed a weak relationship ($R^2 < 0.1$) with both soil and climate conditions. With an R^2 of 0.52, the leaf N/P exhibited the strongest relationship with climate. Climate explained more variance in the CWM of the leaf area, N/P, height and SSD, while soil properties explained more variance in that of the LDMC and SCD. The CWM of LDMC decreased, while that of the SCD increased, with increased soil fertility (high PC1). The CWM of N/P, leaf area, seed mass and SSD increased, while that of height and SCD decreased towards more benign climates (high PC2).

3.3 Trait SES-environment relationship

The majority of plots showed a random distribution of traits. For all traits except height and SCD, plots with significant convergence were more abundant than those with significant divergence (Appendix S6). Multivariate traits within the community showed different divergence/convergence patterns along the soil and climate gradients (Figure 5). In general, multivariate traits tended to diverge at both ends of the soil fertility gradient and converge in the middle of the soil fertility gradient. Trait space was more divergent in the middle of the climate gradient but showed a random pattern at the ends of the climate gradient. The variations in the SES of single traits along the soil and climate gradients are provided in Appendix S7.

4. Discussion

This study provides a comprehensive picture of the trait composition of tree communities in China at a large geographical extent. Two well-known trait spectra at the species level were extended to the community level. We found an elevational pattern of community trait spectra that may be driven by the environment, especially

climate. Broad-scale environmental filtering influences optimal strategies under given environmental conditions; however, our results do not support the stress-dominance hypothesis.

4.1 Community mean traits are highly coordinated

The first two components captured more information on CWM variation than on species trait spectra, indicating that CWMs are highly coordinated. The leaf economics spectrum and size-related spectrum were two main axes of trait variation at the species level, consistent with the results of previous global analyses (Diaz et al., 2016). Trait spectra at the species level and community level were significantly correlated, and the two spectra also existed in tree communities' trait space. The similarity between species-level and community-level trait spectra indicates the same drivers influence trait evolution and community composition (Bruehlheide et al., 2018).

However, the two spectra identified at the community level were not orthogonal. Leaf economics traits and size-related traits are also correlated at the community level (Golodets et al., 2009; de la Riva et al., 2016). Larger seed trees could be more abundant in conservative forests (high LDMC and high leaf N/P) because large seeds are advantageous of surviving in stressful habitats, reflecting tolerance–fecundity trade-offs (Muller-Landau, 2010).

Most variance in the CWMs was represented by the first principal component, which showed a clear elevation pattern. By selecting for certain optimum trait values, previous studies found that environmental filtering is an important driver of community-level trait spectra (Perez-Ramos et al., 2012; Jiang et al., 2017; Simova et al., 2017). Since our data covered a broad elevation gradient, the elevation pattern of the community trait spectra may have been shaped by climate and soil conditions covarying with elevation. For example, freezing temperatures could constrain trait expression (Appendix S5). Community resource economics traits are variable in freezing temperatures, but average size traits have a limited range (Thomas et al., 2020). Energy limitation constrains the investment to plant growth and places plants

at risk for embolism (Olson et al., 2018). A high SCD under a freezing limitation may indicate a strategy to maintain hydraulic safety in freezing temperatures. However, a high community mean height in freezing temperatures could result from forest vertical strata, which is discussed in the next section.

4.2 Climate and soil conditions together shape the community mean traits

A global analysis reported a relatively weak relationship between community traits and broad-scale environments (Bruehlheide et al., 2018), bringing into question the influence of broad-scale environments on plot-level traits. Although much of the variation in CWMs cannot be explained because local factors such as disturbance (Maire et al., 2012), topography (Opedal et al., 2015) and biotic interactions (Kraft et al., 2014) also contribute to trait composition, our results showed that most plot-level traits had distinct patterns along broad-scale environmental gradients, especially along climate gradient. A continental scale analysis in Australia (Guerin et al., 2022) and an analysis of the global tree community (Wieczynski et al., 2019) also showed that environmental factors are strong drivers of functional composition. It is important to note that we only considered woody plants in the tree communities, while Bruehlheide et al. (2018) included understorey plants, such as herbaceous plants and shrubs, in forests. The trait composition of the understorey layer is influenced by not only the environment (Cubino et al., 2021) but also canopy shading (Kermavnar et al., 2021). Recently, studies have also found variable trait-environment relationships between trees and herbs (Simova et al., 2018; Cheng et al., 2022). We think that considering trait composition, including the understorey layer, in forests blurs the effect of the broad-scale environment on trait composition of a tree community.

Most relationships can be fitted better with a quadratic model, indicating nonlinear trait-environment relationships (Rolhauser et al., 2021). Most CWMs monotonously changed along the environmental gradients of the survey but showed a variable response effect at the end of the gradients. This result indicates the need to study the trait-environment relationships under extreme environmental conditions (Bjorkman et

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al., 2018). Most size-related traits showed stronger correlations with climate conditions. Climate driving trait composition may be an important reason for the elevation pattern of the PCA1 axis score (highly related to size-related traits) at the community level. Most traits were weakly correlated with soil conditions. Given that in comparison to climate, soil variables are more heterogeneous at the local scale, one plausible explanation would be that the coarse soil data do not accurately reflect the plots' soil environments (Baldeck et al., 2013).

Tree communities with high average leaf area, seed mass and SSD tend to be more prevalent in warm, moist and stable climates than in other climates. Plants can benefit from small leaves by maintaining temperature and water in cold and dry environments, while large-leaf plants have growth advantages under conditions when physiologically possible through wide leaf-to-air temperature differences to keep leaves at a more suitable temperature for photosynthesis (Wright et al., 2017). High carbon gains in benign environments lead to investment in seed (Murray et al., 2004). However, we found an unexpected result that tree communities with low average heights were abundant in warm and moist environments. Drought and cold environments are considered limitations to tree height (Olson et al., 2018). Species composition could lead to this result. Although maximum plant height is higher in warmer and wetter regions, such as those with tropical and subtropical forests, temperate and boreal forests generally contain less complex vertical strata and subcanopy species (Spicer et al., 2020), resulting in a higher abundance-weighted mean height. This scenario suggests that caution should be taken when simply extending trait-environment relationships from the species level to the community level.

Community mean leaf N/P showed a strong positive correlation with climate conditions, which is consistent with the soil substrate age N/P hypothesis that phosphorus limitation is strong in warm regions due to highly leached soils (Reich & Oleksyn, 2004). Community mean LDMC decreases with increased soil fertility. Soil

fertility influences plant investment in leaf dry matter (Hodgson et al., 2011). Soil fertility acts as a filter causing functional composition towards more conservative resource-use strategies, such as leaves with higher LDMC (Pinho et al., 2018). The community mean SCD is higher in fertile soil, which has rarely been discussed in previous studies. SCD is considered to reflect hydraulic safety and response to water availability (Poorter et al., 2010; Jupa et al., 2021). However, there is no clear conclusion linking SCD with soil fertility. Our result may imply the potential of SCD to indicate trees' resource-use strategies, which need to be studied in future works.

4.3 Community trait diversity along environmental gradients in relation to community assembly

Different null models can influence the ability to detect environmental filtering, and the unconstrained null model in our study tend to detect convergence patterns because it assumes that any species could colonize any site (de Bello, 2012). Despite this, we failed to find a more convergent trait space in harsh environmental conditions. Limited evidence for the stress-dominance hypothesis was also found in North American tree communities (Coyle et al., 2014).

Along different stress gradients, changes in assembly rules are different (Kermavnar & Kutnar, 2020). Trait space diverges in high fertility soils and shifts to convergence as soil fertility decreases, in line with the stress-dominance hypothesis. Abiotic filtering in harsh soil conditions plays a role in community assembly (Chapman & McEwan, 2018; Kermavnar & Kutnar, 2020). However, in the poorest soil at the survey scale, trait space showed a significant divergence pattern. Biotic processes, such as competition and facilitation, may conceal the influence of environmental filtering, resulting in trait divergence within communities (Gotzenberger et al., 2012; McIntire & Fajardo, 2014; Cadotte & Tucker, 2017). According to the stress gradient hypothesis, plants compete intensely in a benign environment but cooperate and facilitate more in a stressful environment (Callaway et

al., 2002; He et al., 2013). Facilitation in barren soil may be a potential cause of trait divergence.

SES showed a relatively weak relationship with climate conditions. Only in the middle of the climate gradient, did trait space show significant divergence. This result could have been related to the shift in vegetation types. The forest types are evergreen broad-leaved forests, mixed evergreen and deciduous broad-leaved forests, deciduous broad-leaved forests and evergreen coniferous forest along latitudinal gradient, and the pattern is related to climate (Ge & Xie, 2017; Ge et al., 2019). The middle of the climate gradient contains many plots of mixed evergreen and deciduous broad-leaved forests. It is well acknowledged that evergreen and deciduous trees differ greatly in functional traits (Li et al., 2021). In mixed forests, multiple strategy codominance, such as evergreen and deciduous, led to trait divergence. This result implies that the absolute dominance of a single strategy could lead to trait convergence (Mayfield & Levine, 2010). For the future, it might make sense to investigate the effects of climate within similar forest types, that might take away some of local variability and lead to a clearer climate signal.

5. Conclusions

Overall, we found evidence that the trait spectra at the community level is driven by environmental factors. Specifically, climate and soil conditions exhibited relatively strong relationships with the CWMs, indicating the effect of environmental filtering on trait composition of tree communities, and climate seems to be important. Broad-scale environmental filtering plays an important role in tree community assembly, but we did not find evidence of strong environmental filtering under extreme environmental conditions.

One caveat of the study is that we did not consider intraspecific trait variation. For some species and traits with strong plasticity, intraspecific variation also plays an important role in trait composition. Although collecting intraspecific data is laborious,

future work could consider intraspecific variation to capture more details related to trait composition and improve our understanding of trait-environment relationships.

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CONFLICT OF INTEREST

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AUTHORS' CONTRIBUTIONS

Z.T. and H.Z. conceived the ideas of the study; Q.G. and H.Z. collected the data; H.Z. and Y.G. analyzed the data; H.Z., Y.Y. and Z.T. led the writing and revision of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Climate data are publicly available in WorldClim (<https://www.worldclim.org/>). Soil data are publicly available in China Soil Database (<http://globalchange.bnu.edu.cn/home>). Plant trait data were accessed from the China Plant Trait Database (Wang et al., 2018) and TRY Database (<https://try-db.org>, accessed April 2019). Community traits data associated with this study are available at <https://doi.org/10.6084/m9.figshare.19754758.v1>

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Table 1. Plant traits and data coverage before gap-filling using the Bayesian Hierarchical Probabilistic Matrix Factorization (BHPMF) method.

Trait (abbreviation, unit)	Functional significance	Group	Coverage	Mean (Range)
Specific leaf area (SLA, mm ² /mg)	Leaf economics spectrum, a trade-off between carbon gain and longevity (Wright et al., 2004).	Economics	63.4%	18(3.2-109.0)
Leaf N per mass (Leaf N, mg/g)		Economics	62.7%	18.7 (3.4-226.3)
Leaf P per mass (Leaf P, mg/g)		Economics	58.2%	1.9 (0.1-7.7)
Leaf dry matter content (LDMC, %)	Leaf construction costs (Hodgson et al., 2011).	Economics	51.0%	0.4 (0.1-0.8)
Leaf N/P (N/P)	Nutrient limitation (Gusewell, 2004).	Economics	38.3%	18.8 (2.7-50.6)
Leaf area (-, mm ²)	Water and energy balance (Wright et al., 2017).	Size	54.6%	6824.1 (2.4-112399.8)
Seed mass (-, mg)	Trade-off between fecundity and tolerance (Muller-Landau, 2010).	Size	49.4%	305.8 (0.01-100)
Height (-, m)	Resource acquirement and light competition (Westoby, 1998).	Size	77.4%	12.3 (0.2-75)
Stem specific density (SSD, g/cm ³)	Mechanical resistance, a trade-off between growth potential and mortality risk (Wright et al., 2010).	Size	42.2%	0.5 (0.2-0.9)
Stem conduit density (SCD, mm ⁻²)	Hydraulic safety (Poorter et al., 2010).	Size	30.1%	152 (3-520)

Figure captions

Figure 1. Distribution of forest plots in China. A total of 1,312 forest plots (black dots) were collected from 46 well-protected mountains during 1997~2008. Seventy-nine additional forest plots (red triangles) were surveyed for trait data collection in 2013.

Figure 2. Trait spectra defined by the first two principal components at the (a) species level and (b) community level. Functional traits except LDMC and N/P were log-transformed. Each dot indicates a species or plot in (a) and (b), respectively. Vectors represent factor loadings in PCAs. Red arrows indicate leaf economics traits and blue arrows indicate size-related traits. The colour gradient indicates the regions of highest (red) to lowest (white) occurrence probability of species or plots in the trait space defined by PC1 and PC2, with contour lines indicating 0.5, 0.95 and 0.99 quantiles. (c) Procrustes analysis rotating species-level PCA to fit community-level PCA. SLA: specific leaf area; LDMC: leaf dry matter content; Leaf N: leaf nitrogen per mass; Leaf P: leaf phosphorus per mass; N/P: leaf N/P; SSD: stem specific density; SCD: stem conduit density.

Figure 3. Elevation pattern of (a) PC1 (conditional $R^2=0.83$, marginal $R^2=0.36$) and (b) PC2 (conditional $R^2=0.77$, marginal $R^2=0.14$) of community-weighted mean (CWM) traits. Lines represent the fitting of linear mixed-effects models; Shadows represent 95% confidence intervals. Sampling sites treated as random factors are shown in different colours.

Figure 4. Variation in community weighted mean (CWM) traits along soil and climate gradients. CWMs except LDMC and N/P are log-transformed. A higher PC1 score indicates a fertile soil, and a higher PC2 score indicates a benign climate. The black line represents the fitting of the linear or quadratic model with a confidence interval of 0.95. All regressions are significant ($P<0.05$). SLA: specific leaf area; LDMC: leaf dry matter content; Leaf N: leaf nitrogen per mass; Leaf P: leaf

phosphorus per mass; N/P: leaf N/P; SSD: stem specific density; SCD: stem conduit density.

Figure 5. Standardized effect size (SES) of multivariate traits (Rao's Q) along (a) soil and (b) climate gradients. A higher PC1 score indicates a fertile soil, and a higher PC2 score indicates a benign climate. $SES > 0$ represents divergence and $SES < 0$ represents convergence. Black dots indicate significant divergence/convergence patterns. The black line represents the fitting of the quadratic model with a confidence interval of 0.95. Both regressions are significant ($P < 0.05$). Boxplot of SES of 20% plots at the low, middle and high end of the (c) soil and (d) climate gradient. A two-sided T test is used to test whether SES is equal to zero (** $p < 0.01$, * $p < 0.05$, ns $P > 0.05$).

Figure 1.

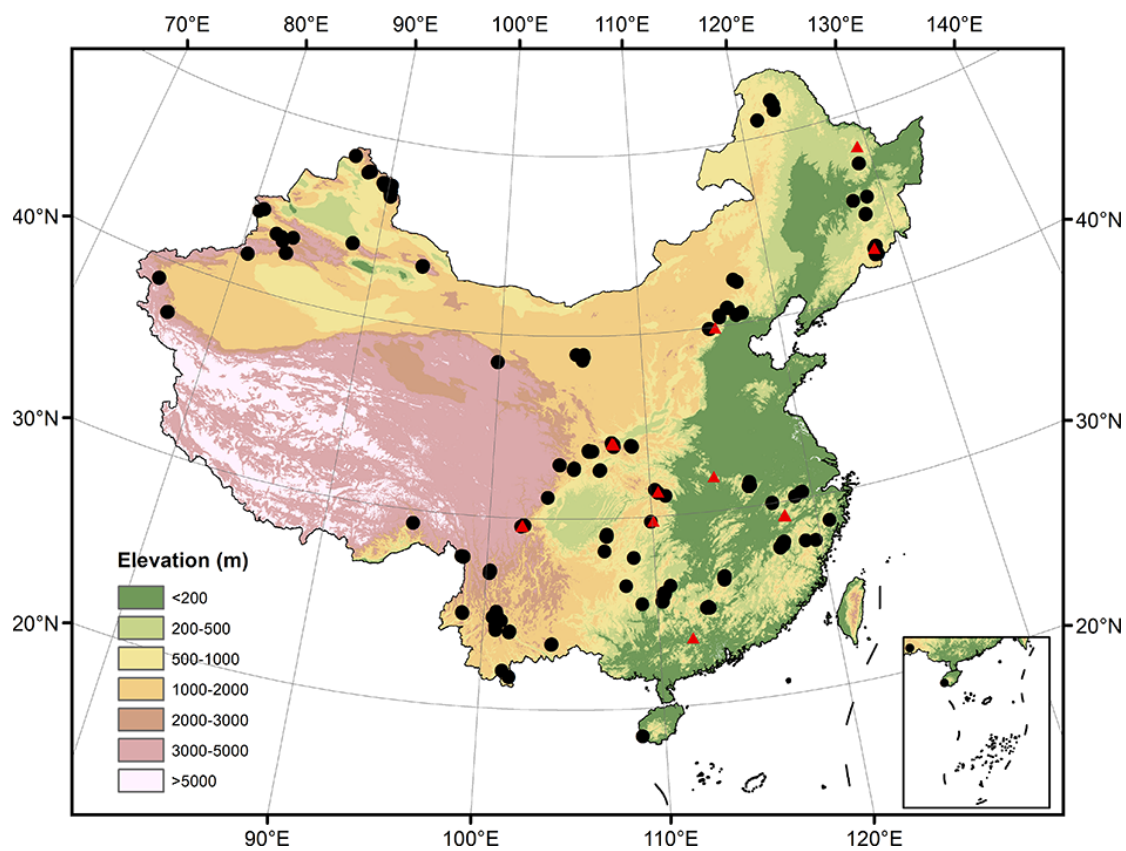


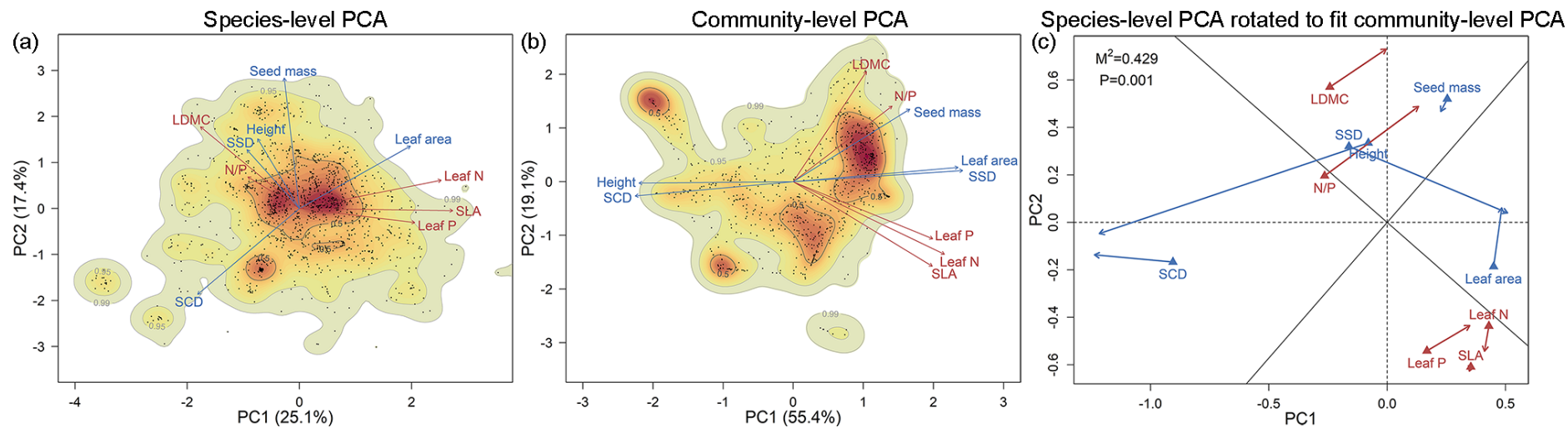
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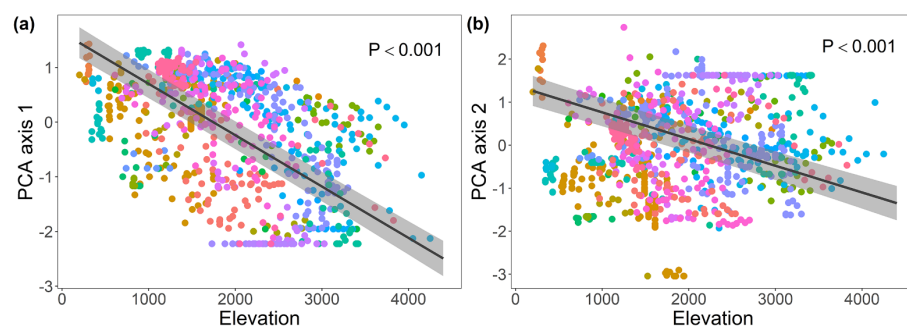
Figure 3.

Figure 4.

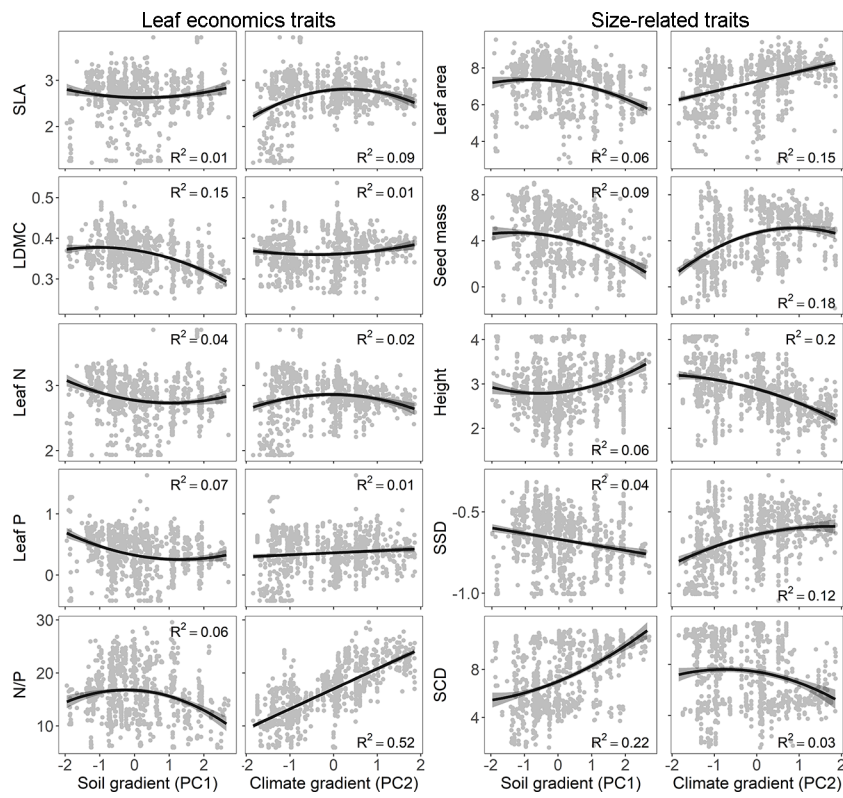
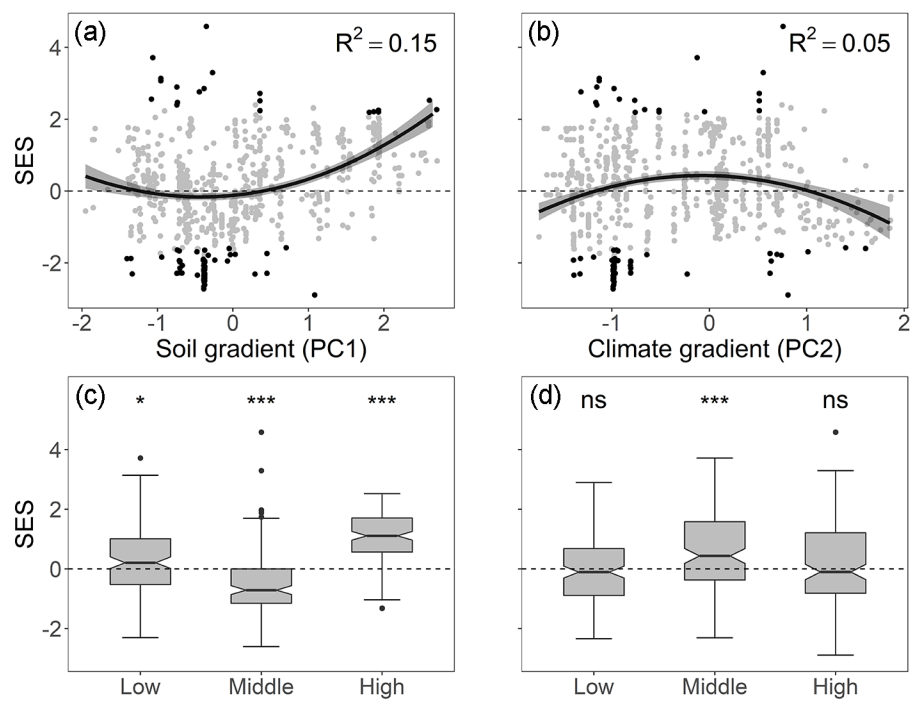


Figure 5.

Supporting information

Appendix S1. Environmental data and data source used in this study

Appendix S2. Correlation between the environmental variables

Appendix S3. Factor loadings of the first two principal components of the environmental factors.

Appendix S4. Factor loadings of the first four principal components of species traits and community-weighted mean (CWM) traits

Appendix S5. Position of plots with the freezing temperatures in community trait spectra

Appendix S6. Proportion of plots with significantly divergent or convergent trait diversity

Appendix S7. Standardized effect size (SES) of single trait along soil and climate gradients.

Appendix S8. List of references contained in TRY dataset.