Microenvironment filtering and plant competition jointly structure trait distributions across co-occurring individuals

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A B S T R A C T

The prevailing role of environmental filtering in community assembly has been widely corroborated at large spatial scales. However, how environmental filtering and plant competition collectively determine trait distributions among coexisting individuals at within-community scales remains an unresolved question. We measured four leaf and wood traits of 2700 co-occurring plants and soil physicochemical and topographic variables across individual locations within a 1 ha subtropical forest in eastern China. Multiple linear regression and variance partitioning analyses were conducted to test the relative effects of microenvironment properties and plant competition on trait distributions (e.g., mean, range, variance, skewness, and kurtosis) at four within-community spatial scales. The joint explanatory power of microenvironment properties and plant competition on trait distributions significantly enhanced with increase of spatial scales. The relative effects of plant competition on trait distributions were more pronounced at smaller scales, and the relative effects of microenvironment properties on trait distributions were remarkable at larger scales. Plant competition at smaller scales and microenvironment filtering at larger scales generated both convergence and divergence of four functional traits. Fertile soils selected for plants with large leaf area and high leaf phosphorus but low nitrogen contents and wood density. Steep and convex locations supported plants with large leaf area and low leaf nitrogen and phosphorus contents, and low wood density. Wet soils supported plants with high leaf nitrogen content and wood density, and low leaf phosphorus content. Acidic soils selected for plants with small leaves and high leaf nitrogen and phosphorus contents. These results provide strong evidence that relative to plant competition, microenvironment filtering is also a predominant driver of individual-level functional diversity and species assemblages at within-community scales. Our study highlights that simultaneously accounting for the consequences of microenvironment heterogeneity and plant competition on trait distributions is crucial for better understanding community assembly of locally co-occurring individuals.

1. Introduction

One of the most significant challenges in community ecology is to explain patterns of plant diversity across communities (Gaston, 2000; Lebrija-Trejos et al., 2010; Whittaker and Niering, 1975). Among the many processes that contribute to plant diversity distribution, two distinct non-random processes, i.e., environmental filtering and competitive exclusion, are assumed to play key roles in structuring species assemblages (Keddy, 1992; Kraft et al., 2015). In general, environmental filtering leads to convergent plant diversity distribution at broad spatial scales (Cadotte and Tucker, 2017). By contrast, competitive exclusion leads to divergent diversity distribution at local scales (Gross et al., 2013). There is mounting null model-based evidence that environmental filtering plays a main role at broad spatial scales, whereas competitive exclusion plays a dominant role at neighbourhood scales for structuring community (Chalmandrier et al., 2013; Kraft et al., 2008; Šímová et al., 2015). However, the relative contributions of these two non-random processes on community assembly have rarely been quantified at fine spatial scales, such as the scale of neighbourhood within communities (Adler et al., 2013; Pescador et al., 2020).

Within-community scale environmental heterogeneity is widespread in natural forest communities (de Bello et al., 2013; Richardson et al., 2012), and has significant consequences for tree growth (Pontara et al., 2016; Zhang et al., 2016) and species composition (Frelich et al., 2003). The examination of the relative effects between microenvironment filtering and competitive exclusion (hereafter, plant competition) on trait distributions across coexisting plants can improve our understanding of how community assembly is simultaneously driven by subtle variations in microenvironment properties and plant competition (Bergholz et al., 2017; Lang et al., 2010). The relative effects between microenvironment filtering and plant competition on species assemblages depend on the spatial distance between focal plants and their neighbours. The competition strength of focal plants is greater with their nearest neighbours than with those that are more distant (Gross et al., 2009). Edaphic properties, and soil water and nutrient availability may be altered by small variations in micro-topography (Price et al., 2014). As such, soil properties are more heterogeneous in the areas between focal plants and their distant neighbours than their nearest neighbours (Wiegand et al., 2007). We therefore hypothesize that, concurrent with plant competition, microenvironment properties are also a predominant driver of species assemblages within communities (as shown conceptually in Fig. 1).

Community trait distributions can be regulated by both abiotic and biotic filters (Gao et al., 2014; Jeffers et al., 2015; Mitchell et al., 2017). The distribution of trait values for a given community depends on which ecological processes primarily play out in structuring species assemblages (Souza et al., 2016). Within communities, if microenvironment properties and plant competition are two simultaneous drivers of community assembly, these two ecological processes are expected to result in both trait convergence and divergence (Adler et al., 2013; Gross et al., 2013; Cadotte and Tucker, 2017), as reflected by the shift patterns of mean, range, variance, skewness, and kurtosis (Fig. 1). Specifically, as a result of the filtering processes, microenvironment heterogeneity shifts

the mean and restricts the range and the variance of trait values, but increases the skewness (i.e., more asymmetric) and the kurtosis (i.e., more leptokurtic) of trait values (Cornwell et al., 2006; Le Bagousse-Pinguet et al., 2017). Conversely, plant competition spread the variance of trait values at a given trait range but decreases the skewness (i.e., more symmetric) and the kurtosis (i.e., more platykurtic) of trait values (Cornwell and Ackerly, 2009; Schamp et al., 2008).

Therefore, we predict that community trait distributions associate with both plant competition and microenvironment properties, if they are strong within-community drivers of species assemblages (Fig. 1). Since competition strength correlates negatively with the spatial distance between focal plants and their neighbours (Newbery and Stoll, 2020), we expect that trait variations between focal plants and their nearest neighbours (i.e., at neighbourhood scale) can be explained much more by plant competition than by microenvironment properties. Alternatively, we expect that trait variations of co-occurring plants within communities are attributable to the subtle fluctuations of microenvironment properties.

To test the above predictions, we measured four leaf and wood traits across 2700 co-occurring plants and 10 microenvironment variables relevant to soil physicochemical and topographic properties at the individual's location, within a 1 ha subtropical evergreen broadleaved forest in Zhejiang Province, eastern China. The highest priority for this individual-based measurement was to examine the relative effects of microenvironment properties on trait distributions in the presence of plant competition at within-community scales (Adler et al., 2013). For this study, we calculated five trait distributions (i.e., mean, range, variance, skewness, and kurtosis) for each trait across co-occurring individual plants at four fine spatial scales. Multiple linear regression and variance partitioning analyses were used to test the relative effects of microenvironment properties and plant competition on trait distributions. Specifically, we were interested in addressing the following questions: i) how microenvironment properties (physicochemical and
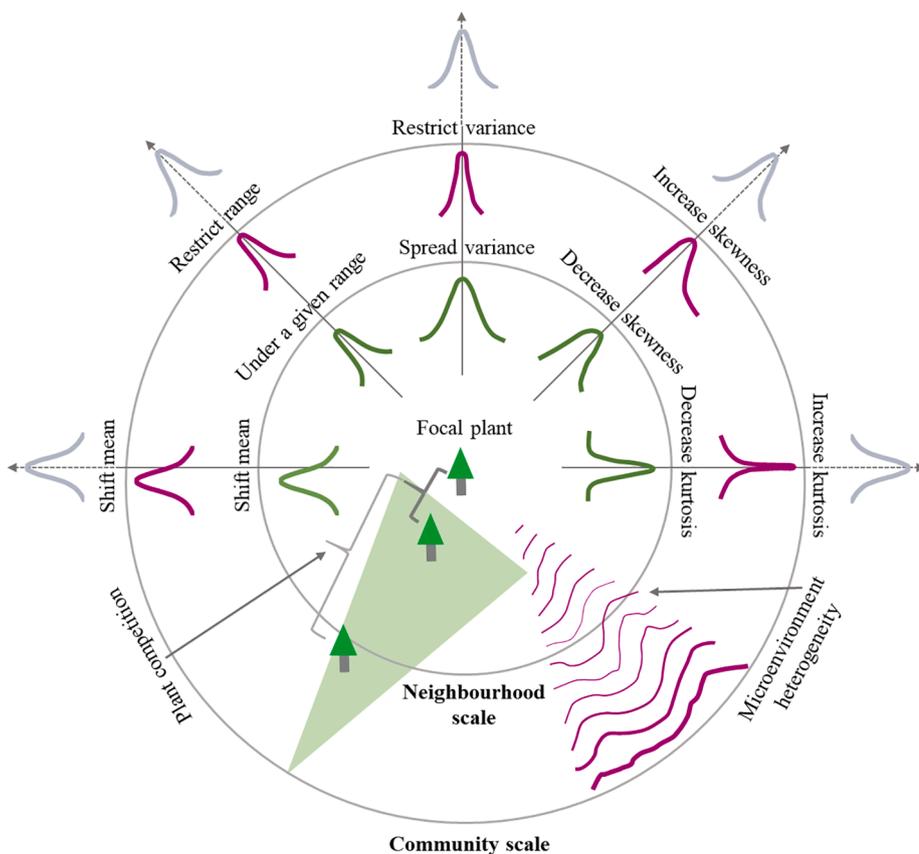

Fig. 1. Schematic representation of shifts in trait distributions under the simultaneous effects of microenvironment filtering and plant competition at the scale of within-community. The outer circle represents the boundary of a given community, and the inner circle represents the neighbourhood scale where a focal plant and its nearest neighbours strongly interact. The green inverted triangle from outer circle to inner circle indicates that competition of a focal plant increases from its distant neighbours to nearest neighbours. The purple lines formed triangle indicates that microenvironment heterogeneity decreases from community scale to neighbourhood scale. The Gaussian curve represents trait distribution patterns. The grey curves outside of the outer circle represent the standard normal distribution. The purple curves around the outer circle represent trait distributions shaped by microenvironment filtering, i.e., shift trait mean, restrict trait range and variance, increase trait skewness and kurtosis. The green curves around the inner circle represent trait distributions structured by plant competition, i.e., shift trait mean, keep a constant under a given trait range as a result of microenvironment filtering, spread variance of trait values, decrease trait skewness and kurtosis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

topographic variables) and plant competition intensity vary with spatial scale within communities? and ii) what are the relative effects between microenvironment filtering and plant competition on trait distributions within communities?

2. Materials and methods

2.1. Study site

This research was conducted in a subtropical forest in Tiantong National Forest Park (29°48′ N, 121°47′ E), located in Zhejiang Province of eastern China. The climate of this region is subtropical monsoon. The mean annual temperature is 16.2 °C, and mean annual precipitation is 1374.7 mm (Song, 1995). The vegetation within the Park is characterized as a subtropical evergreen broadleaved forest (EBLF), which has been severely disturbed over the last century, with only small intact and semi-intact tracts remaining around the Tiantong Buddhist Temple. The mainly loam-textured soils of this region belong to Ferralsols, with pH values ranging from 4.0 to 4.5. The parental material is composed of Mesozoic sediments and intrusive acidic rocks, including quartzite and granite (Yan et al., 2018).

A spatially mapped 20 ha (500 m × 400 m) forest dynamic plot was established in the intact area of the Park from 2009 to 2010 following the protocol of the CTFS-ForestGEO Network (Condit, 1998). A 1 ha functional trait plot was selected in the dynamic plot for the mapping of individual-based woody plant traits (Fig. S1). The topography of this functional trait plot was very heterogeneous and rugged, with a convex-concave degree changing from –3.8 to 2.1, with elevations ranging from 321 to 442 m, and slopes varying from 23.2 to 36.8°.

The west and east sides of the functional trait plot runs through two north–south oriented valleys, with the interior area spanning two small northwest-to-southeast oriented ridges, approximately 100 m apart (Fig. S1). The soil physicochemical properties changed substantially across the plot, and the coefficients of variation in soil total carbon, nitrogen, phosphorus contents, and soil humus depth were 12.9, 11.7, 29.8, and 16.0%, respectively. The soil water content per volume (SWCV) and soil bulk density varied from 24 to 33%, and 0.7 to 1.0 g. cm^{-3}, respectively (Table S1).

The species composition shifted considerably with variable physicochemical and topographic properties. The valley area was mostly occupied by deciduous species (e.g., *Choerospondias axillaris*) in the canopy layer, and wet-resistant evergreen species such as *MaChilus leptophylla* and *Lithocarpus harlandii* in the sub-canopy layers, whereas the evergreen species *Eurya loquaiana* dominated in the understory. In very steep slopes and ridge areas, the community was generally dominated by deciduous species, such as *Litsea elongate* and *Lindera glauca*. The stem density was 395 ± 52 individuals per 0.1 ha over the functional trait plot.

All woody plants with a diameter at breast height (DBH, tree diameter at 1.3 m above root collar) of ≥ 1 cm in the functional trait plot were tagged, identified, measured, and geo-referenced from August 2009 to September 2013. There were a total of 2,700 stems belonging to 68 species, 47 genera, and 29 families. Evergreen species dominated the community and accounted for 80% of the individual plants.

2.2. Trait measurements

Four functional traits that represent the key dimensions of the leaf and wood economics spectra were measured in this study. Over the summer seasons (i.e., June to August) from 2010 to 2013, the specific leaf area (SLA), leaf nitrogen content (LNC) and phosphorus content (LPC), and twig wood density (TWD) were measured for 2,700 individuals in the functional trait plot. SLA is a key trait of the leaf economics spectrum that strongly relates to leaf carbon assimilation and energy exchanges (Wright et al., 2004). LNC and LPC are positively related to plant nutrient economy and relative growth rates (Niklas

et al., 2005). TWD represents construction costs and the ability to withstand many abiotic and biotic stresses (Chave et al., 2009).

On the field, three branches per individual were taken from the upper, mid, and lower positions on the sunlit side of the tree crown. We collected approximately 20 ~ 30 mature leaves (with full light and without apparent physical damage) from each branch, which were subsequently combined into a composite sample from the same individual. Simultaneously, three twigs from each branch were sampled for each individual. The leaves and twigs were wrapped in a moist paper towel, placed into a sealed plastic bag, and stored in a cooler until they were processed in the laboratory.

The leaf (SLA, LNC, and LPC) and wood (TWD) traits were immediately measured in the laboratory within 12 h on each sampling day. The twig lengths and diameters at the mid-points along the lengths were measured. The twig diameter was measured at two angles perpendicular to each other using an electronic vernier caliper (accurate to 0.1 mm). The twig cross-sectional areas were calculated from the diameter. The twig volume was calculated assuming the twig to be approximately a cylindrical shape, with the mid-point of the twig diameter as the cylinder diameter, and stem length as the cylinder height.

Simultaneously, twenty undamaged leaves were randomly selected from each composite sample and scanned using a leaf area meter (LI-3100, Li-Cor, USA) to determine the leaf area, after which the fresh mass of these leaves was weighed. The samples were then dried in an oven at 75 °C for 48 h for leaves, and over 72 h for twigs to determine the dry masses of the leaf and twig samples, to calculate the SLA (leaf area divided by leaf dry mass), and TWD (twig dry mass divided by twig volume). Finally, the leaf samples were ground to determine the LNC and LPC, using a flow-injection autoanalyzer (SAN++, Skalar, Breda, The Netherlands).

2.3. Microenvironment properties

We quantified microenvironment properties including soil physicochemical and topographic variables. The microclimates were not included as they had a negligible effect on the variations in trait distributions under consideration across quite a limited spatial extent. The original dataset was available from (Zhang et al., 2012) at the quadrat level. Topographic variables included elevation, slope, and convexity, whereas soil physicochemical variables included soil total carbon, nitrogen, and phosphorus contents, soil pH, soil water content per volume, bulk density, and humus depth.

To consider the effects of microenvironment properties on trait distributions, 10 soil physicochemical and topographic variables for each individual location were determined from 75 locations across the plant functional trait plot, using a kriging interpolation approach with the Extract tool in ArcGIS 10.1. We detailed the field and laboratory measurements of microenvironment properties and spatial interpolation for each individual location in the supplementary file (Appendix S1).

2.4. Design of within-community scales

Since our objective was to test whether microenvironment properties and plant competition structure trait distributions at within-community scales, the community was defined at a very fine spatial scale. Because 2500 m^2 is the smallest reasonable area to include the largest proportion of species (80%) according to the species-area relationship for the studied forests (Song et al., 2013), we designed the scale of community as a circle with radii of 30 m (i.e., with area of approximate $900\pi = 2826$ m^2), around each focal plant (see below). By following this protocol, there were 2,700 communities in total, and all individuals within a given community were included and assumed to be interacting locally.

To examine the relative effects of microenvironment properties and plant competition on trait distributions at varied neighbourhood scales within communities, we subsequently set nested radii as 2.5 m, 5 m, and 15 m inner circles. The spatial scale with area of 6.25 π m^2 (r = 2.5 m)

represents the average crown diameter of 1.25 m for the smallest trees and shrubs (with the DBH about 1 cm). The radii of 5 m and 15 m represent the average crown diameter of 2.5 m and 7.5 m for each of the sub-canopy trees and canopy trees.

We employed an extrapolated approach to eliminate potential edge effects of the plant functional trait plot (Colwell et al., 2004). Specifically, we duplicated all individuals from the inside to the outside of four boundaries of the study plot. To guarantee that there were sufficient replicated individuals for each scale, the duplications were established within differently sized rectangles. We kept the long-side of the rectangle as a constant (i.e., 100 m), and shifted the short-side of the rectangle over 2.5 m, 5 m, 15 m, and 30 m scales, respectively. In this case, there were 2,700 focal plants involved in the subsequent analysis.

2.5. Quantification of plant competition and trait distributions

We employed Hegyi index to quantify plant competition between focal plants and their neighbours (Hegyi, 1974). Competition is largely associated with the spatial distance between competitors and focal plants, as well as the DBH of competitors. We calculated the plant competition for a given scale according to equation (1).

$$H_i = \sum_{n \neq i} \frac{DBH_n}{DBH_i \times ((Distance_{in}) + 1)} \tag{1}$$

where H_i is the competition index of the focal tree i. DBH_n, DBH_i, and $Distance_{in}$ are DBH of the nth neighbouring tree, DBH of the focal tree i, and distance between tree i, and the nth neighbouring tree.

We repeated this calculation 2700 times for each of the four spatial scales, according to the number of the remaining focal individuals following the removal of edge effects. This resulted in corresponding quantities of plant competition indices at each scale.

Five metrics of trait distribution (i.e., mean, range, variance, skewness, and kurtosis) were calculated for four leaf and wood traits at four spatial scales (6.25π, 25π, 225π, and 900π m^2). We detailed the trait distributions calculation in Appendix S2. Consistent with the algorithm of plant competition, five metrics of trait distribution were calculated across 2700 focal plants at four spatial scales for SLA, LNC, LPC, and TWD, respectively.

3. Statistical analysis

We performed principal component analyses to reduce multicollinearity for each of the soil nutrients (soil total carbon, nitrogen, and phosphorus contents), soil moisture and texture (SWCV, soil bulk density, and humus depth), and topography (elevation, slope, and convexity). The first principal component (representing more than 74% of the total inertia) (Table S2) of each microenvironment property was used as a composite variable in subsequent regression models. To determine the spatial heterogeneity of microenvironment properties and variations of plant competition at within-community scales, the variance of each microenvironment group and plant competition was calculated for 2,700 focal plants in the functional trait plot at four spatial scales (6.25π, 25π, 225π, and 900π m^2), respectively. We also used one-way ANOVAs to check the significant shifts in trait distributions across four spatial scales, and the significant differences were tested by the least-squares mean separation with Tukey's correction.

To examine whether trait distributions were affected by microenvironment properties and plant competition, multiple linear regression was carried out separately for each trait distribution of four traits at four spatial scales. In total, we developed 80 models with each trait distribution (5 distributions × 4 traits × 4 scales) as a function of microenvironment properties and plant competition. The significances of all models and each parameter in the model were assessed according to $P <$ 0.05. Subsequently, the relative effect of each predictor on trait distribution was determined using the variance partitioning analysis based on

Z-scores. The relative effect was quantified as the ratio of a parameter estimate to the sum of all parameters (expressed in %). For each model, we grouped five variance fractions: i) soil nutrients, ii) soil pH, iii) soil moisture and texture, iv) topography, and v) plant competition. Moreover, we used parameter estimates to illustrate the directions and effect sizes of five variance fractions on trait distributions. All predictors were Z-score transformed prior to analyses, and the parameter estimates of all predictors were fixed to their mean value. All statistical analyses were conducted using R software, v. 3.6.1 (R Core Team 2019).

4. Results

4.1. Variations in microenvironment properties, plant competition, and trait distributions across spatial scales within communities

Soil physicochemical and topographic variables fluctuated considerably over four spatial scales, reflecting high microenvironment heterogeneity (Fig. 2a-d; Table S1). Variances in soil nutrients, soil moisture and texture, and topography were generally increased, and variances in soil pH declined with increasing spatial scales (Fig. 2a-d). Plant competition was significantly stronger at small scales than at large scales (Fig. 2e).

With respect to trait distributions, range, skewness, and kurtosis of leaf and wood traits increased with an increase in spatial scales ($P <$ 0.001). Ranges of leaf and wood traits, means of specific leaf area, and leaf nitrogen content were slightly higher at large spatial scales than at small spatial scales ($P <$ 0.001). Means of leaf phosphorus content and twig wood density did not significantly change across four spatial scales (P greater than 0.05) (Fig. S2).

4.2. Effects of microenvironment properties and plant competition on trait distributions

The joint effects of microenvironment properties and plant competition for trait distributions increased significantly, while the relative effect of plant competition on trait distributions declined with increasing spatial scales (Fig. 3 and Fig. 4). The highest proportion of total variance accounted for by plant competition (10%) was found at the scale of 6.25π m^2 for kurtosis of twig wood density (Fig. 4). At such smallest neighbourhood scale, despite the low explanatory power, plant competition slightly restricted ranges of leaf phosphorus content and twig wood density, and reduced skewness of leaf phosphorus content and kurtosis of leaf phosphorus and nitrogen contents, as well as twig wood density.

The effects of microenvironment properties on trait distributions strongly increased with increasing spatial scales, and associated effect size depended on the microenvironment types (Fig. 3 and Fig. 4). The highest proportion of total variance accounted for by microenvironment properties (88.9%) was found at the scale of 900π m^2 for mean values of twig wood density. At this largest spatial scale, soil nutrients exerted considerable effects on mean, range, and variance of twig wood density. Increased soil nutrients resulted in a positive shift in mean leaf phosphorus content and specific leaf area, but a negative shift in mean leaf nitrogen content and twig wood density, a reduction in variance of twig wood density, an increase in skewness and kurtosis of specific leaf area and twig wood density. Similarly, soil nutrients increased ranges of leaf and wood traits and variances of leaf traits, and decreased skewness of leaf nitrogen content.

Topography explained more variations in most trait distributions than soil nutrients did at the 225π m^2 and 900π m^2 scales. Mean specific leaf area increased, whereas means of leaf nitrogen content and twig wood density decreased with topographic convexity and slope steepness. Topography restricted the variability of twig wood density, and increased skewness and kurtosis of leaf and wood traits (except for skewness of leaf nitrogen content). Meanwhile, ranges of leaf and wood traits and variances of leaf traits increased, and skewness of leaf nitrogen
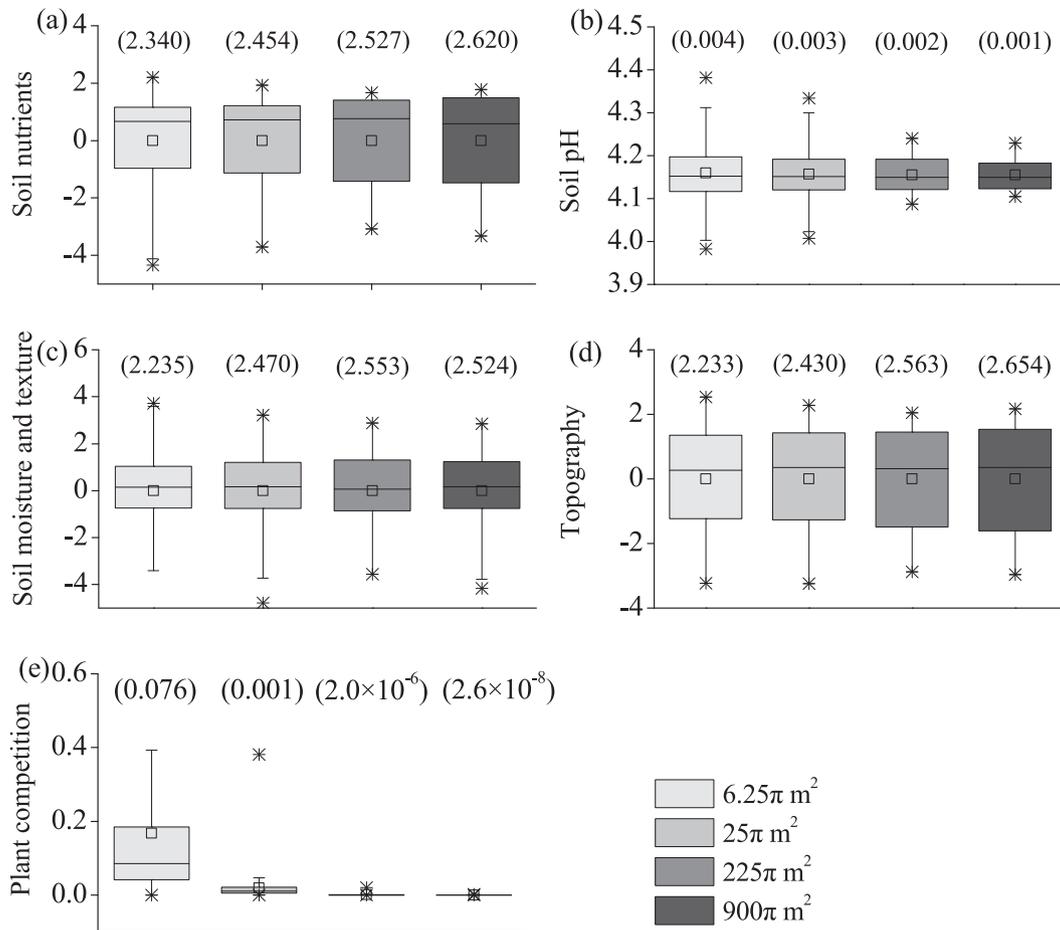
Fig. 2. Variations in microenvironment properties and plant competition across four spatial scales within communities. The first principal component (PC1) was used for the statistical description of soil nutrients (soil total carbon, nitrogen, and phosphorus contents), soil moisture and texture (soil water content per volume, bulk density, and humus depth), and topography (elevation, slope, and convexity) at each scale. Mean values are displayed by small boxes, and variances are shown in brackets.

content decreased with convexity and slope steepness (Fig. 3 and Fig. 4).

Increased soil moisture and texture led to positive shifts in means of leaf nitrogen content and twig wood density, a negative shift of mean leaf phosphorus content, reduction in trait ranges, variances in specific leaf area and leaf nitrogen content, and increases in skewness of leaf nitrogen content. In contrast, variances of twig wood density increased, whereas skewness of specific leaf area and twig wood density, kurtosis of leaf and wood traits decreased with higher soil moisture and texture. Soil pH negatively shifted means of traits (except for positively shifted mean of specific leaf area), and increased skewness of specific leaf area, and kurtosis of specific leaf area, leaf phosphorus content, and twig wood density. In contrast, soil pH increased trait ranges, and variances in leaf phosphorus content (Fig. 3 and Fig. 4)

5. Discussion

Using a novel dataset encompassing individual-based plant traits and high-resolution environmental data from a subtropical forest in eastern China, we tested the relative effects of microenvironment properties and plant competition on trait distributions across four spatial scales within communities. The effects of microenvironment properties were remarkably stronger than plant competition on trait distributions at larger spatial scales, while plant competition was only effective at the very smaller spatial scale (i.e., 6.25π m^2). Our results provide strong evidence that environmental filtering still stands out within communities (Adler et al., 2013). This is partially consistent with the null model

simulated results that environmental filtering occurs at local scales (Kraft and Ackerly, 2010; Zhang et al., 2018). However, our results do not support the traditional notion that environmental filtering plays no role in the competitively driven niche partitioning process within communities (Gomez et al., 2010; Gross et al., 2013). Indeed, fine-scale microenvironment variations drive species assembly at within-community scales (Conti et al., 2017; Kang et al., 2017; Segoli et al., 2012). Below we discuss how microenvironment filtering and plant competition simultaneously shape the functional structures of locally coexisting individuals.

5.1. Strong role of microenvironment filtering in local community assembly

We found strong trait convergence with respect to changes in topography, soil nutrients, soil moisture and texture, and soil pH at within-community scales, as trait mean shifted, trait range and variance decreased, and trait skewness and kurtosis increased, with increase in soil nutrients, topographic convexity and slope steepness, soil moisture, and soil pH. Positive shifts in means of SLA and LPC, and negative shifts in means of LNC and TWD suggest that fertile soils filter plants toward having large leaf size and significant phosphorous content, but low nitrogen and wood density (Fig. 5a). This pattern can be further evidenced by reductions of variance in TWD and evenness in TWD (high skewness and kurtosis) as the result of increased soil nutrients. These results are consistent with the whole-plant economics spectrum theory: plants
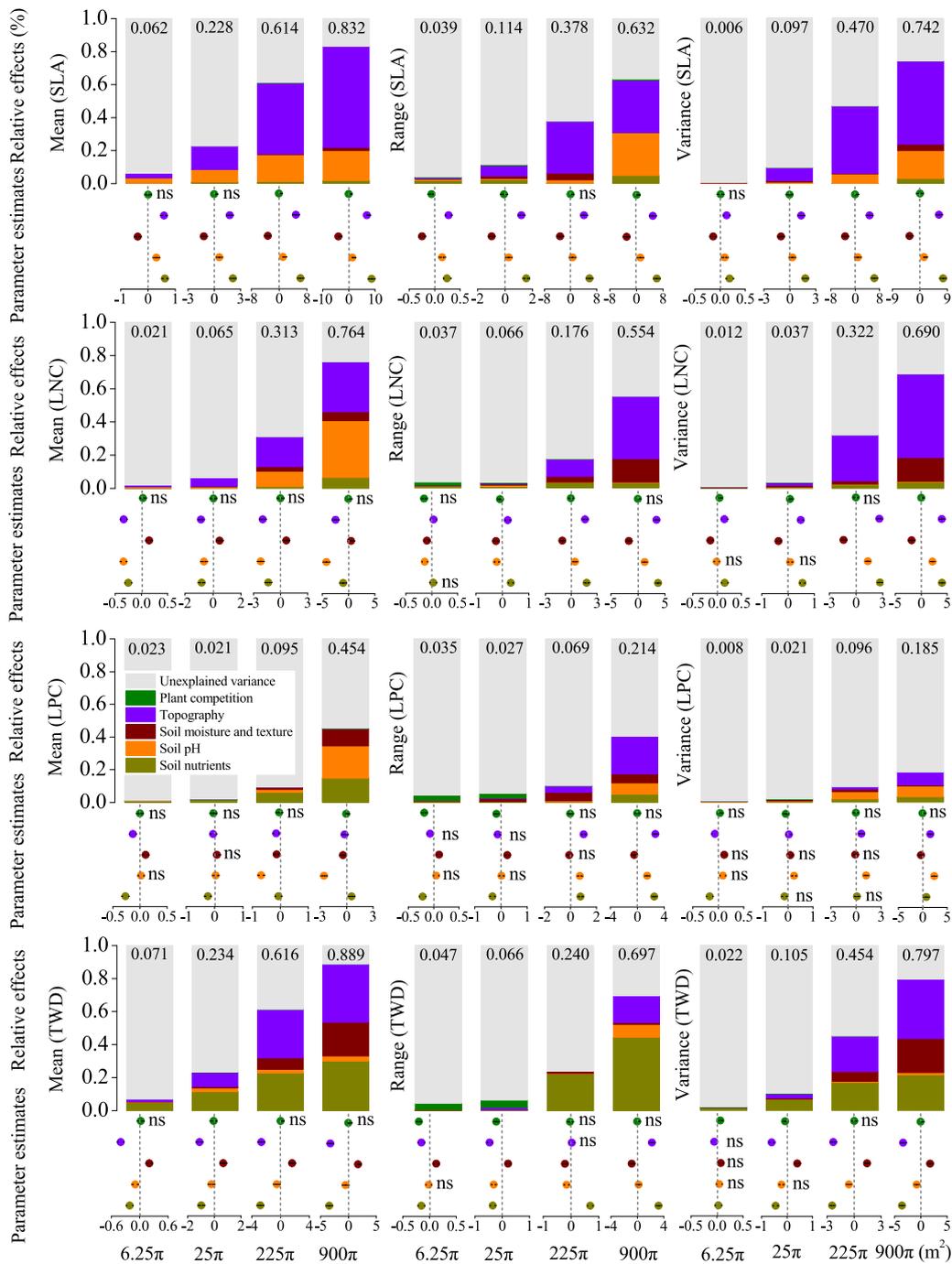
Fig. 3. Relative effects of soil nutrients, soil pH, soil moisture and texture, topography, and plant competition on the mean, range, and variance of leaf and wood traits across four spatial scales within communities. The parameter estimate (standardized regression coefficients) and its associated 95% confidence intervals, as well as the percentages of explained variances of each variable are shown. All models are significant ($p < 0.05$), and adj. r^2 are shown at the upper end of the histogram. The non-significant variables are expressed by ns. Abbreviation: SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; TWD, twig woody density.

growing in nutrient-rich soils are generally acquisitive by deploying large leaves with a high concentration of growth-limited nutrients, but low quality tissue matter (Reich, 2014). Since plant growth and litter decomposition in the studied forests are more phosphorus than nitrogen-limited (Yan et al., 2010), the mean value shifted positively for LPC but negatively for LNC as soil nutrients increased.

Topography is an additional potent driver of trait distributions within communities. We found that high convexity and slope steepness negatively shifted the mean values of leaf and twig traits (except for

SLA), narrowed the variance of TWD, and increased the skewness and kurtosis of LPC and TWD. These results suggest that steep and convex locations select plants with low leaf nutrients and wood density (Fig. 5b). Topography was very heterogeneous and slopes varied from 23.2 to 36.8° in the studied plot (Table S1). Steep slopes were environmentally harsh, i.e., unstable topography (e.g., landslides) and nutrient-poor soils (coefficient between topography (PC1 of elevation, slope, and convex) and soil nutrients (PC1 of soil total carbon, nitrogen, and phosphorous contents) is – 0.73, $P < 0.001$). In general, dominant
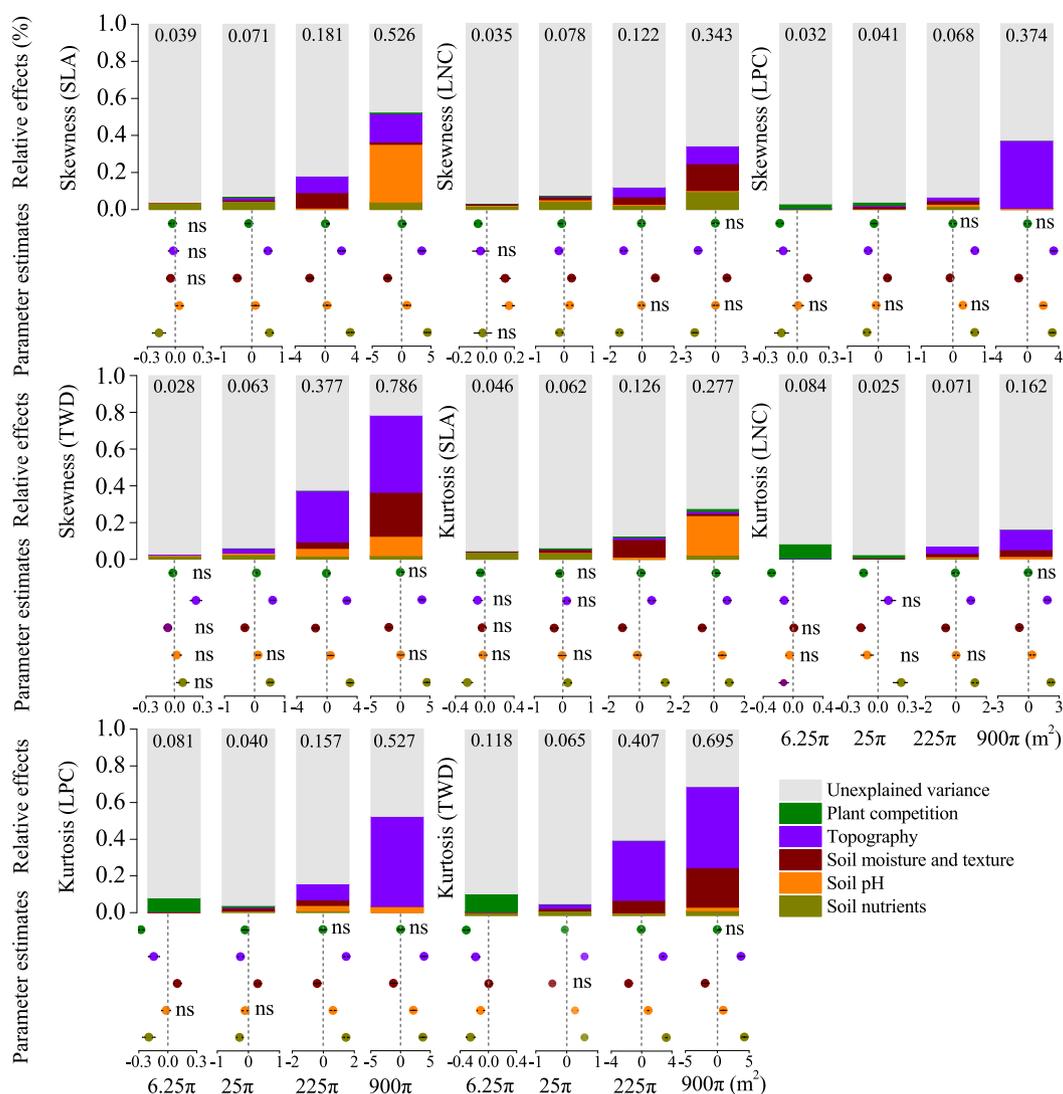
Fig. 4. Relative effects of soil nutrients, soil pH, soil moisture and texture, topography, and plant competition on the skewness and kurtosis of leaf and wood traits across four spatial scales within communities. The parameter estimate (standardized regression coefficients) and its associated 95% confidence intervals, as well as the percentages of explained variances of each variable are shown. All models are significant ($p < 0.05$), and adj. r^2 are shown at the upper end of the histogram. The non-significant variables are expressed by ns. Abbreviation: SLA, specific leaf area; LNC, leaf nitrogen content; LPC, leaf phosphorus content; TWD, twig woody density.

plants occupying very steep slopes are fast-growing deciduous species (e.g., *Litsea elongate*). Plausibly, plants with poor leaf nutrients and low wood density are beneficial for enduring difficult conditions (Aerts and Chapin III, 1999; Reich, 2014).

Soil water regimes are also a crucial filter of local community assembly. Along with a range of soil moisture, strong convergences of SLA, LNC, LPC, and TWD suggest that plants with a high leaf nitrogen content and wood density, and low leaf phosphorus content tend to be dominant in wet soils (Fig. 5c). Plants with high leaf nitrogen contents are considered to be beneficial for enhancing water use efficiency (Wright et al., 2002). Contrasting patterns of leaf nitrogen and phosphorus contents in wet soils might associate with the availability of these two elements in the studied forests. Subtropical forest soils are inherently low in available phosphorus, which can be quickly lost through leaching in wet soils (Yan et al., 2010). It is not surprising that plants in wet soils have high wood density due to local hydraulics. High wood density associates with great hydraulic safety but low conductive efficiency (Chave et al., 2009). This hydraulic trade-off thus informs that, in the studied forests, plants were particularly adapted to wet soils through improving hydraulic safety but reduced conductive efficiency. This

strategy may serve well for enduring waterlogging since the water supply was very abundant in the study region.

Soil pH ranged from 4.0 to 4.5 (Table S1) and resulted in a remarkable trait convergence in the studied plot. In neutral acidic soils, there were strongly negative shifts in mean of LNC and LPC and increase in skewness and kurtosis of SLA. This pattern suggests that strongly acidic soils tend to select plants with large-nutrient-rich leaves (Fig. 5d). Soil pH might influence plant traits by affecting soil chemistry and the availability of required nutrients (Le Bagousse-Pinguet et al., 2017; Rothstein, 2010). Acidic soils possess high proton concentrations, and nitrogen and phosphorus can be quickly released to increase the availability of nutrients (Brady and Weil, 2004). In subtropical regions, this may occur when forests age to mature, i.e., soil acidity and nutrients increase in parallel as the result of soil organic matter decomposition (Song et al., 2013). Eventually, this favours acquisitive plant species (i. e., large-nutrient-rich leaves).
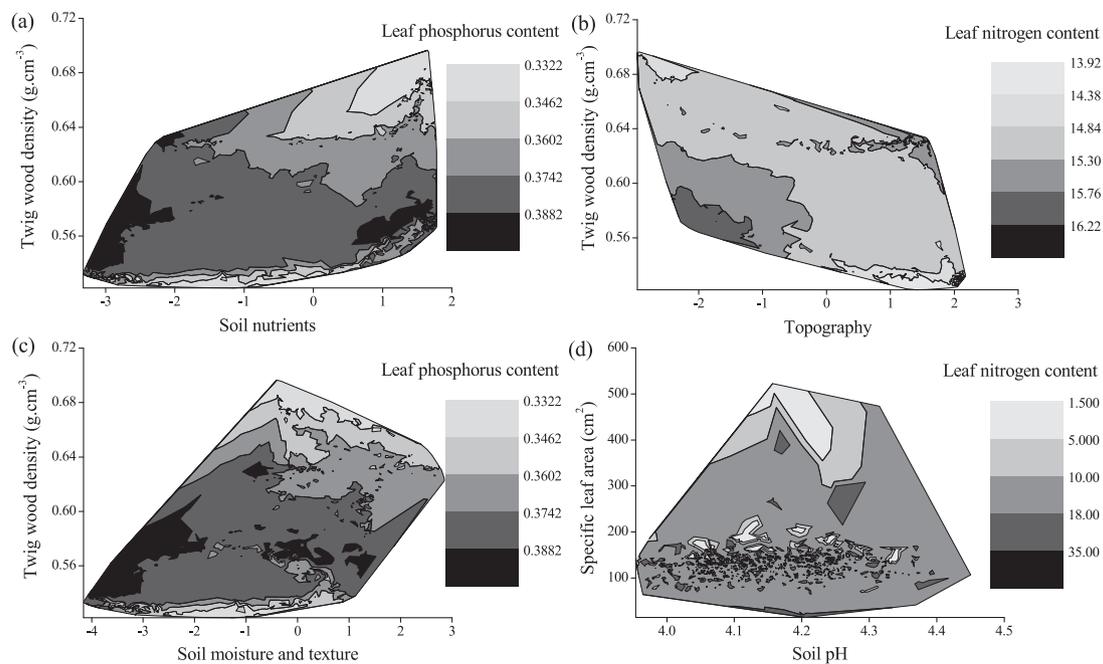
Fig. 5. Spatial distributions of trait values in twig wood density, specific leaf area, leaf phosphorus and nitrogen contents as matched by soil nutrients (a), topography (b), soil moisture and texture (c), and soil pH (d).

5.2. Effects of microenvironment filtering on trait divergence at within-community scales

Our results revealed that microenvironment properties also caused a strong divergence of plant traits, as the range and variances of trait values also increased and the skewness and kurtosis of trait distribution deceased with a range of environmental properties at within-community scales. Large ranges and variances of most traits associating with nutrient-rich soils suggest that fertile soils favoured the local co-occurrence of functionally contrasting plants (Le Bagousse-Pinguet et al., 2017). In contrast, the low skewness and kurtosis of SLA relevant to nutrient-poor soils indicate a great functional evenness of resource acquisition strategies among coexisting plants. The underlying mechanisms might be related to the idea that within-community soil chemical evenness may represent niche differences among coexisting plant species (Pescador et al., 2020; Prado-Junior et al., 2016).

With respect to topography, our results suggest that plants occupying convex locations and steep slopes are characterized by a wider range of leaf and wood economics strategies. For example, the ranges of leaf and twig traits were positively associated with an increased degree of topographic convexity and slope steepness (Fig. 3 and Fig. 4). This pattern aligns with the theory that multiple sets of trait values can allow functionally contrasting species to traverse the filtering of harsh environments (Dwyer and Laughlin, 2017; Lasky et al., 2013). We also observed the increased evenness of LNC (i.e., reduced kurtosis) on topographically benign locations (gentle slopes), where water and soil nutrients are more available. This pattern may associate with strong plant competition when site conditions tend to be superior (Pugnaire and Luque, 2001).

We found that moist soils tend to support plants with a large mean and great variance of TWD (Fig. 3). The great breadth of these water-storing traits indicate a high diversity of hydraulic strategies for plants in wet soils (Cornwell and Ackerly, 2009). Concurrently, we found a more even distribution of LNC and TWD in wet soils than dry soils. Together, these results indicate that, being conditional on diverse hydraulic strategies, plants growing in wet soils also tend to have even space of trait values along with the leaf and wood economics spectra (Fortunel et al., 2014; Kraft et al., 2008).

We found that SLA, LPC, and TWD diverged in neutral acidic soils (increased trait ranges with soil pH). This pattern might reflect the co-occurrence of distinct ecological strategies of plants under the appropriate conditions of acidic soil values (Fig. 3). Soil pH has been demonstrated to shape species and functional diversity (Le Bagousse-Pinguet et al., 2017). In neutral acidic soils, stress-avoidant and stress-tolerant species can coexist within communities through opposing functional strategies under a given level of stress (Poorter et al., 2009; Yan et al., 2013).

5.3. Importance of plant competition in trait-based community assembly

We observed the great explanatory power of plant competition on trait divergence at the smallest spatial scale (6.25π m^2), according to the reductions of trait range, skewness, and kurtosis (Fig. 3 and Fig. 4). Large trait divergence between focal and neighbour plants reflect large degree of niche differentiation (Le Bagousse-Pinguet et al., 2015). Our results indicate that plant competition can regulate more even distribution of trait space, i.e., lower kurtosis (more platykurtic) and less skewness (symmetry), across interactive individuals at neighbourhood scale or fine spatial scale (Le Bagousse-Pinguet et al., 2017; Wiegand et al., 2007). This aligns with the theory that resource competition prevents coexisting plants from being too ecologically similar (Weiher and Keddy, 1995), thus partitioning the space of trait values more regularly within a given restricted trait range (Cornwell and Ackerly, 2009).

We found that plant competition also restricted the ranges of trait values (Fig. 3). This result suggests that strong resource competition can lead to neighbourhood plants with less diverse trait distribution. In contrast, weak resource competition allows coexistence among neighbourhood plants through great leaf area per unit biomass investment (broad range of SLA). This is consistent with the global scale findings that a high specific leaf area correlates with a low competitive effect (Kunstler et al., 2016).

6. Conclusion

Using a dataset of individual-based plant traits and high-resolution

environmental properties in a natural forest, we revealed that within-community microenvironment filtering caused both trait convergence and divergence. On the one hand, the remarkable trait convergence within communities indicates that microenvironment filtering is responsible for structuring species coexistence and maintaining species diversity by selecting a set of functional similar individuals that are shared similar ecological tolerances at levels of across and within species. On the other hand, the pronounced trait divergence under microenvironment filtering suggests that, like the role of plant competition, the fine spatial-scale variation in habitat properties also serves to filter coexisting individuals with distinct plant strategies. Overall, this study provides strong evidence that microenvironment filtering is a predominant driver of species assemblages at within-community scales. From the forest management perspective, our study highlights that, if maintaining high level of functional and species diversity at within-community scales, it is necessary to not solely account for plant-plant interaction, but also need to pay much attention to structuring heterogeneous micro-environmental conditions.

CRediT authorship contribution statement

Mingshan Xu: Conceptualization, Investigation, Methodology, Software, Validation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Li-Ting Zheng:** Investigation, Writing - review & editing. **Dong He:** Investigation, Writing - review & editing. **Han Y.H. Chen:** Supervision. **En-Rong Yan:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data accessibility

Should the manuscript be accepted, the supporting data set will be archived in an appropriate public repository and the data DOI will be included at the end of the article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107893.

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