



Disentangling the Effects of Biotic and Abiotic Factors on Leaf Functional Traits of Understory Species in a Deciduous Broad-Leaved Forest in China

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ABSTRACT

Plant trait patterns contribute to understanding the process of community assembly. Using a trait-based method, recent studies have found that, both the spatial component and abiotic environment filtering drives community structuring. However, the community abiotic environment may be influenced by overstory community and species composition, and it is not enough to disentangle the environment filters only considering abiotic factors. In this paper, leaf size and SLA of 11 understory species were measured, and variation partitioning was used to explore the explanation power of spatial process, three topographic variables and seven biotic factors describing the overstory community. The results indicated spatial structure, topography and overstory characters contribute to the leaf variation, and biotic environment have significant effects on leaf trait variations. We concluded that community structure and species composition play important roles in community trait patterns, and biotic filtering should be considered in future trait-based studies.

INTRODUCTION

Understanding the relationship between the environment and plant characteristics are central in ecology, and captured ecologists attention more than one century ago (Cowles 1899). Research over past decades indicated some plant traits are dimensions of ecological strategy variation, known as plant functional traits (Violle et al. 2007), and contribute to community assembly at local and regional scales (Weiher et al. 1998, Shipley et al. 2006, Kraft et al. 2008, Kooyman et al. 2010, Kraft et al. 2015).

Plant functional traits change with the shift of environment gradients, such as temperature, moisture, soil nutrients, and light availability (MacGillivray et al. 1995, Cunningham et al. 1999, Rijkers et al. 2000, Lacourse 2009). Among plant functional traits, leaves are most sensitive to environmental variation (Wright et al. 2004, Traiser et al. 2005). For example, leaf size and specific leaf area (projected leaf area per unit leaf dry mass, SLA) declined with increasing light (Ackerly et al. 2002) and decreasing moisture or nutrient availability (Fonseca et al. 2000). Leaf dry-mass investment per unit of light-intercepting leaf area (Leaf mass per area, LMA) increased with decrease in water (Cunningham et al. 1999). In most past work, plant functional traits were averaged at community levels, to test the habitat filtering or random process shaping trait variation (Kraft et al. 2008, Cornwell & Ackerly 2009, Liu et al. 2013, Kraft et al. 2015), response to climate change (Michalet et al. 2014) or to predict species abundance (Shipley et al.

2006). However, environmental variables were usually spatially dependent; spatial process are important during community assembly (Legendre et al. 2009), it is needed to evaluate the abiotic filtering and spatial relationship on the trait variation patterns.

Apart from the abiotic environment, the biotic environment (e.g. species composition and abundance) relates to the spatial distribution of environmental variables, and plays a role in plant trait variation (Weiher et al. 1998, Cornwell & Ackerly 2009, Pescador et al. 2015). However, although much research has measured plant functional traits at community levels, little work has analysed the overstory community structure on trait variation, even studies on succession trait shifts (Garnier et al. 2004, Lebrija-Trejos et al. 2010, Douma et al. 2012, Piqueray et al. 2015). Generally, understory species are influenced by overstory composition and structure (Richards & Williamson 1975, Barbier et al. 2008). Understory vegetation is usually density dependent (Condit et al. 1994), and influenced by overstory composition and structure through modification of resource availability (light, water and soil nutrients), physical characteristics of the litter layer (Barbier et al. 2008) or tree fall (Richards & Williamson 1975). The recent studies showed the main factors explaining variation in shrub species composition were landscape pattern variables; shrub species richness was principally explained by local variables (Campagne et al. 2006), topographic variables have a stronger influence on understory composition than overstory structure in the southern distribution limits of temperate forests in Eu-

rope. Soil based habitat filtering was also found to structure understory palm communities (Andersen et al. 2012). For the inconsistent results above, we argue the biotic environment (community structure and species composition species composition) and space process (dispersal limitation) on trait shifts, which contributes to evaluating the trait-based method of community assembly.

The present study was aimed to test the above inconsistent results using a trait-based method. We hypothesized, both biotic and abiotic factors, related to the variation of trait. Leaf functional traits of 11 understory species were quantified in a deciduous broad-leaved forest plot. Our objectives were to explore the role of space structure (spatial autocorrelation and dispersal limitation), community structure and topographic variables in shaping leaf trait variation. Specifically, we test whether the biotic factors of overstory community and spatial process (or their joint effects) have effect on the trait variation pattern of understory trees. The more details of how biotic variables affect trait distribution is not included in this paper.

MATERIALS AND METHODS

Study Location

One 100 m × 100 m permanent forest plot (Yaoluoping plot) was built in Yaoluoping Nature Reserve (E30.95°-31.01°, N116.03°-116.18°), Dabieshan Mountain, Anhui province, China (Fig. 1). The mean annual precipitation is 1400 mm and the mean annual temperature is 10-14°C, but differed among seasons with the hottest month being July and the coldest month being January.

Data Collection

The plot was divided into 25 20m × 20m quadrates; trees with DBH above 2 cm were mapped, tagged using an aluminium plate with a unique number and identified by species. The plot had 28 families, 42 genera, 62 species and 6133 stems with DBH ≥ 2 cm. The mean DBH was 6.5 cm and the maximum DBH was 101.3 cm. The most abundant tree was *Lindera glauca*, a shrub species of Lauraceae family, accounting for 37% of the total individuals. There were 10 singleton species in the plot. The overstory species of this plot are deciduous broad leaved tress, such as *Castanea seguinii*, *Quercus serrata* and *Platycarya strobilacea*. Eleven of 27 shrub species with the abundance above 10 individuals were selected in the plot.

Leaf size (cm²) and SLA (cm²/g) of the 11 shrub species were measured by the method of Cornelissen et al. (2003). Specifically, 10 to 20 individuals for each species were included, and at least 10 fresh leaf samples per trees for each of the 11 species were taken from the tallest parts of trees,

which were fully expanded and exposed to direct sunlight. The leaf size was measured as mean value of one-sided projected surface area for each species and the SLA was calculated as the mean value of one-sided surface area divided by the dry leaf mass. Leaf size and SLA were arithmetically averaged in each subplot (Fig. 2).

Statistical Analysis

Three topographic variables and 7 community structure variables (Fig. 3) were used as abiotic and biotic environmental variables, respectively. Topographic variables included slope, mean elevation, convexity (the relative elevation of a quadrat with respect to its immediate neighbours, it was the elevation of the centre point minus the mean of the four corners for edge subplot) of each subplot. Community structure variables included maximum and mean tree height of the quadrat, maximum and mean DBH, total base area density, and Shannon-Wiener index (Fig. 3). We relate above biotic variables to understory light shelter, competition and resource acquisition. To explore the nonlinear effects of the abiotic and biotic environmental variables on trait variation, quadratic and cubic of the seven biotic and three abiotic factors were also used as the explanatory variables.

To analyse spatial structure, the 20m × 20m quadrats in the Yaoluoping plot were decomposed to a set of orthogonal principal coordinates of neighbour matrices (PCNM) eigenfunctions (Borcard & Legendre 2002, Legendre et al. 2008) by distance using the function of the ‘vegan’ package in R (Legendre et al. 2009). PCNM eigenfunctions represent a spectral decomposition of the spatial relationships among the grid cells (Legendre et al. 2009). PCNM eigenfunctions with positive eigenvalues obtained by PCoA of a truncated geographic distance matrix among the subplots were generated and used as explanatory variables to analyse the spatial variation of the trait data.

Principal coordinate analysis (PCoA) was used to obtain the principal components of the biotic and abiotic variables. The variation of trait was partitioned using RDA analysis between PCoA axis (biotic and abiotic variables respectively) and PCNMs, forward selection analyses was used to select the significant PCoA axis and PCNMs ($P < 0.05$) by the ‘forward.sel’ function in the ‘pack for’ package using 999 permutations (Legendre et al. 2009). All procedures were carried out in the R statistical language (R Core Team 2013).

RESULTS

The averaged leaf size and SLA are rather changeable in the plot (Fig. 2). Topographic variables are relatively homoge-

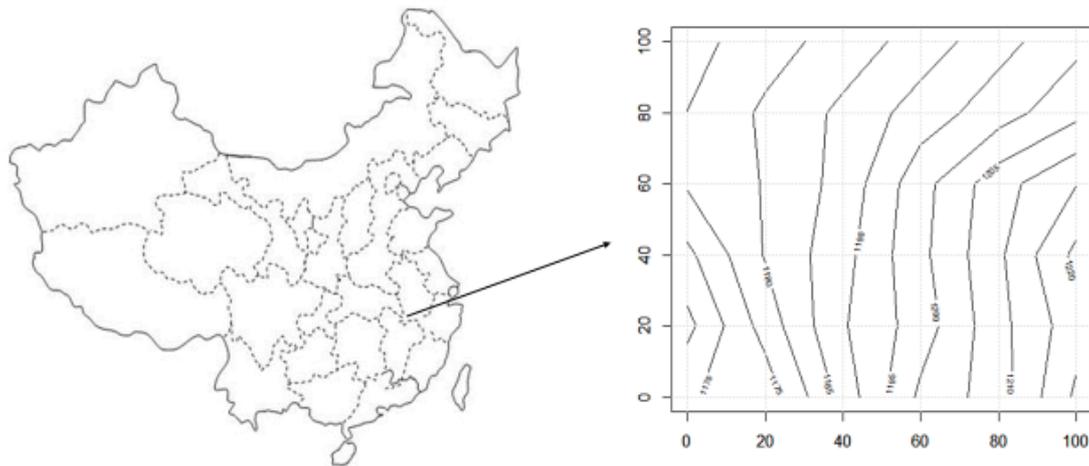


Fig. 1: Location and topography of Yaoluoping plot. Note: The lines in the right part are elevation contour lines, the X-axis and Y-axis represent the length of the plot at 20-m intervals.

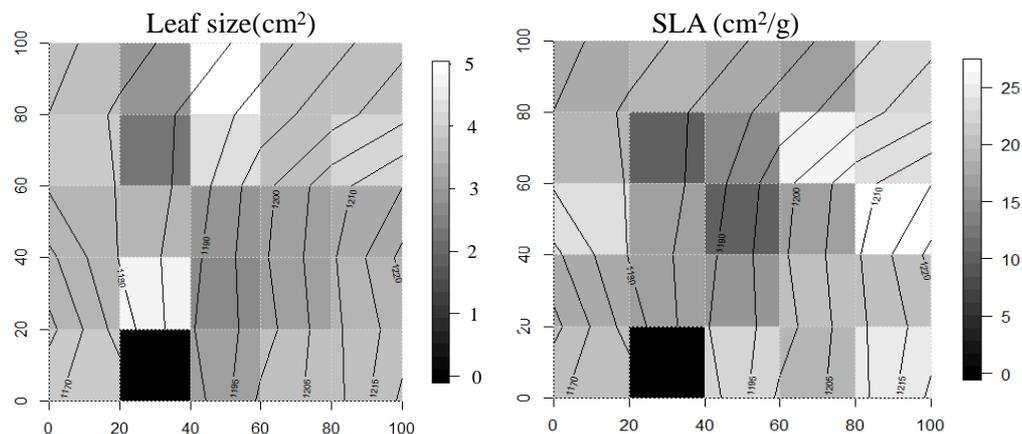


Fig. 2: Spatial distribution of SLA (left) and leaf size (right) in Yaoluoping plot. Note: The grid means the 20m \times 20m quadrates subplot. The black area (zero) indicated no leaf trait were available.

neous, especially the mean elevation only dropped from 1180 m to 1210 m. However, the biotic variables except for mean tree height and Shannon-Weiner index, have drastic variation among the subplots.

Variance partitioning results indicated that a significant amount of variation in leaf traits of 11 understory species could be explained by the spatial environment (Fig. 4). For leaf size, 12%, 15% and 5% of the variation could be explained by pure spatial component, community structure and topographic variables, respectively. Spatial structure and topography jointly account for 10% of the leaf size variation, with only 1% of the variation explained by spatial component and community structure interactions. For SLA, pure space and community structure account for 6% and 3% of the variation. Space and topography interactions

account for 4% of the variation. For both traits, 16% and 6% of the variation could be explained by pure spatial structure, and topographic variables, respectively. Spatial component and topography jointly account for 2% of the variation. The explanation power of space and community structure was better than topographic variables, and more of the leaf size variation was explained than SLA.

DISCUSSION

Contrasting results showed topographic variables, not overstorey structure, have a strong influence on understory composition (Gracia et al. 2007). In the present study, variation partitioning showed the appropriate amount of leaf trait variation of 11 shrub species was explained by space and biotic variables (Fig. 3). Although the explanation power

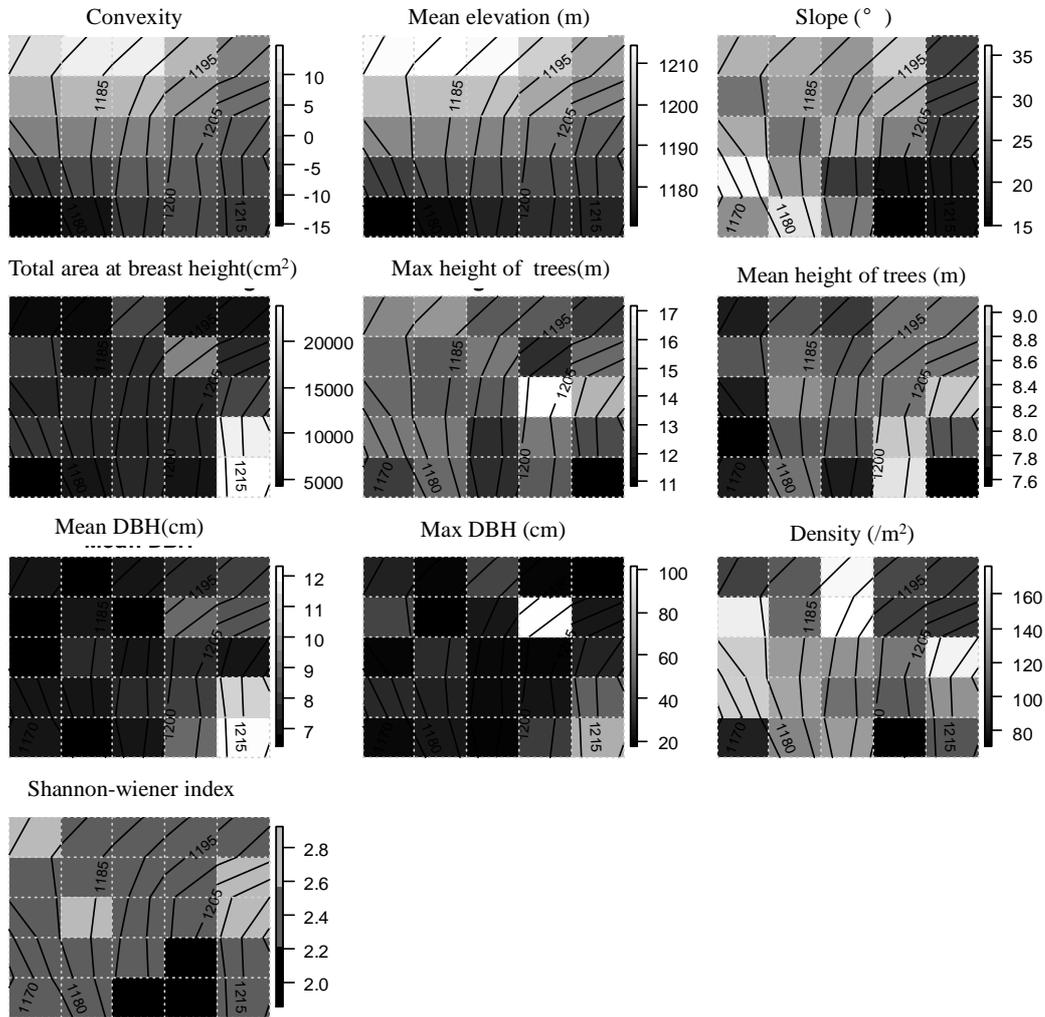


Fig. 3: Spatial distribution of environmental variables in Yaoluoping plot.

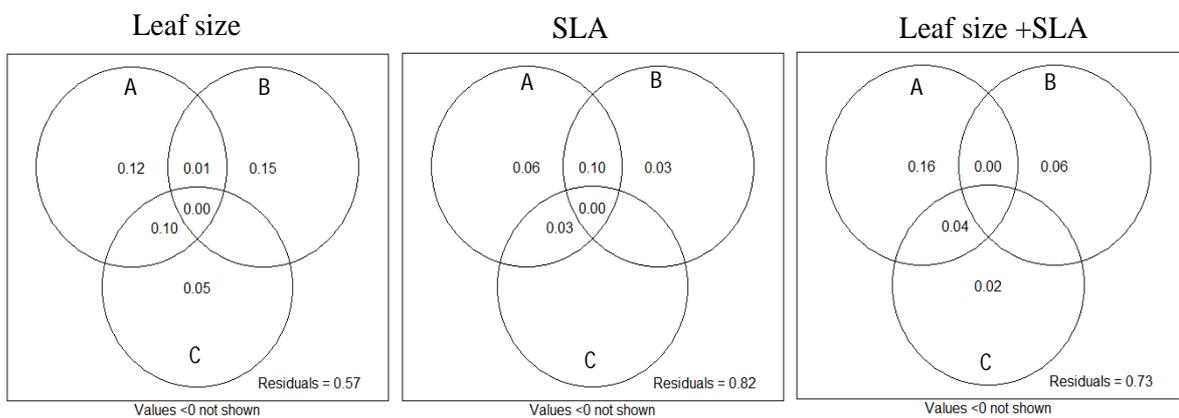


Fig. 4: Variation partitioning of spatial structure (A), community structure (B) and topographic variables (C); *P<0.05.

is relatively lower (not exceeding 30%), our results showed that the biotic variables and spatial process contributed to leaf trait variation.

Many trait-based methods have found that the abiotic environment plays a larger role in community assembly (MacGillivray et al. 1995, Cunningham et al. 1999, Rijkers et al. 2000, Wright et al. 2004, Traiser et al. 2005, Lacourse 2009). Our results showed that purely spatial process or space interactions with topographic variables accounting for at least 6% of SLA, over 10% of leaf size and variation of 2 traits, providing evidence that spatial process such as dispersal and spatial autocorrelation contribute to assembly of the understory species. But, relatively lower variation was explained by topographic variables in this paper, which may be because of the homogeneous topography in this plot. Stochastic components play roles underlying this assembly, similar to less explanation power of the abiotic environment in a 24-ha forest plot (Liu et al. 2013).

Environmental filtering mechanisms cannot account for the entire assembly of a community, as both dispersal limitation and habitat filtering play important roles in the assembly processes (Shen et al. 2013). Using a trait-based method at the community level, our results also indicated that among habitat filtering, biotic filtering (overstory species composition and structure) may play a greater role than abiotic filtering (topographic variables). Overstory composition and structure modified resource availability and abiotic environmental variables may be influenced by overstory characteristics (Barbier et al. 2008). Typical overstory shifts in communities along a successional gradient, as trait variation of most species are influenced by community structure and shape the local environment (Lebrija-Trejos et al. 2010). Forest tending measures can also affect the functional role of understory species in the rain forest (Lu et al. 2015). Leaf size was linked to leaf energy and water balance; SLA positively correlated with potential growth rate and mass-based maximum photosynthetic rate (Cornelissen et al. 2003). The ecological strategy of understory species is shade tolerance and slow-growth (Grubb 1998). The understory species may be more easier to be affected by overstory community structure.

Although our results were from understory species, and lower explanation power of topographic variables may be due to the few variables selected and relatively homogeneous topography in this paper, the mechanisms of how biotic variables affect plant functional trait distributions were also not explored. But, we still strongly suggest biotic filtering should be considered in future trait-based studies. The indirect effects of biotic variables in further studies about the biotic environment effects on trait variation patterns should also be

explored in more complex habitat and larger scale areas.

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