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Habitat heterogeneity explains mosaics of evergreen and deciduous trees at local-scales in a subtropical evergreen broad-leaved forest

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Abstract

Questions: Mosaics of evergreen and deciduous trees that are characteristic of evergreen broad-leaved forests (EBLF) are thought to arise from habitat heterogeneity, but empirical evidence for this is limited. We test this assertion asking: (1) whether environmental heterogeneity explains the distribution of deciduous and evergreen trees; (2) which are the most important environmental variables; and (3) does their importance change with scale?

Location: Tiantong National Forest Park, Ningbo, Zhejiang, China.

Methods: We used data from a 20-ha individual-mapped EBLF in spatial point-pattern analyses testing the scale of aggregation within, and segregation between, the two life forms. We used a heterogeneous Poisson process model to remove the effects of environmental heterogeneity, predicting segregation would disappear if the mosaic was due to habitat heterogeneity alone. Finally, we tested the relative importance of theoretically important environmental variables using multivariate regression trees at three spatial scales (10, 20 and 50 m grid cells).

Results: We found evergreen and deciduous trees were aggregated at scales below 125 m and 60 m, respectively, and mutually exclusive at scales <120 m. Evidence of any spatial segregation between the life forms was removed at all scales after controlling for environmental heterogeneity. Only soil phosphorus concentrations contributed to spatial patterns at all scales, with values >0.27–0.30 $g \cdot kg^{-1}$ favouring deciduous species.

Conclusions: Our study is consistent with habitat heterogeneity creating the observed mosaics of evergreen and deciduous tree species, but micro-habitat heterogeneity contributed even at scales <20 m. Soil phosphorus availability appears to be the major environmental variable maintaining these mosaic patterns at hillslope scales in EBLF.

Introduction

Understanding how species co-exist in diverse communities is critical for predicting the consequences of global change (Gilman et al. 2010; Walther 2010; Adler et al. 2012). Functional traits offer a means to infer processes of community assembly (e.g. Kraft et al. 2008; Cornwell & Ackerly 2009) although recent studies have shown that

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patterns of trait dispersion can change depending on the role of the traits in the community (Mayfield & Levine 2010; Herben & Goldberg 2014; Kraft et al. 2014, 2015b). For example, in the case of growth and architectural traits, determining whether or not they link directly to resource acquisition ability can reveal the relative importance of competition and niche differentiation in constructing communities (Herben & Goldberg 2014). Therefore, there are risks in using single functional traits to infer community assembly processes (Kraft et al. 2015b).

Often more than one process is operating and their relative importance depends on the observed scale (Götzenberger et al. 2012; Adler et al. 2013). Species interactions and niche differences generally take effect at neighbourhood scales (Kraft et al. 2015b) while habitat heterogeneity tends to be more evident at larger scales (Kraft & Ackerly 2010; Shipley et al. 2012; Kraft et al. 2015b). Evergreen and deciduous trees are two plant life forms possessing a collection of distinct functional traits. The mosaic pattern of these life forms found in evergreen broad-leaved forest (Fig. 1; Song 1988, 1995) is generally assumed to be the result of a leaf trait-based habitat filtering process (Song 1995), although empirical validation of this theory is limited (e.g. Goldberg 1982; Murata et al. 2009). Moreover, the environmental factors most responsible for the filtering effect that maintains this pattern, or their scale-dependence, are not well understood (e.g. Lipscomb & Nilsen 1990; Tang & Ohsawa 2002; Song et al. 2014).

To co-exist, stabilizing niche differences must compensate for any difference in relative fitness between species (or life forms), causing the superior competitor to limit itself more than it does other species as its abundance increases (Chesson 2000). Stabilizing differences arise from trade-offs in functional traits that affect species' overall performance along different niche axes (Chesson 2000; Amarasekare 2003; Kneitel & Chase 2004; Adler et al. 2013). Spatial heterogeneity could promote co-existence of evergreen and deciduous species by reducing niche overlap if conditions vary in a way that suits different life forms at different locations (Tilman 1982; Chase & Leibold 2003). Current theories for the co-existence of mosaic patches of evergreen and deciduous tree species in evergreen broad-leaved forests (EBLFs) are generally framed around such trade-offs. Even after accounting for phylogeny, broad-leaved deciduous tree species have a more acquisitive leaf strategy than evergreens and have higher leaf water, N and P content (Bai et al. 2015). Evergreen trees often have inferior photosynthetic capacity (Baldocchi et al. 2010; Kamiyama et al. 2010), lower N- and water-use efficiency (Aerts 1990; Sobrado 1991) and lower growth rates (Dhaila et al. 1995; Baldocchi et al. 2010). Relative fitness differences due to the cost–benefit trade-off in leaf lifespan (Kikuzawa 1991; Sobrado 1991) could be expected to result in co-existence from habitat partitioning along resource axes involving nutrients or water availability (Tilman 1982; Chesson 2000; Adler et al. 2013).

Fig. 1. Photograph of the mosaic-like distribution of evergreen and deciduous patches in Tiantong National Forest Park. The photograph was taken after the leaves of deciduous trees fell in the autumn. [Colour figure can be viewed at wileyonlinelibrary.com]

Globally, the distribution of deciduous trees is thought to reflect the competitive advantages of avoiding leaf maintenance costs during unfavourable growth conditions, particularly low temperatures and droughts (Chabot & Hicks 1982; Wolfe 1987; Reich et al. 1992). Topographic controls on temperature and soil moisture variation can however influence deciduous species distributions even at hillslope scales (Song et al. 2014). As an important widely distributed biome (Ovington 1983; Fujiwara & Box 1999; Greller 2003), EBLFs cover large areas of the warm temperate and subtropical zones in East Asia, including one quarter of the total area of China (Kira 1991; Song 1995). The described mosaics are important in maintaining the overall structure and function of EBLF, but are also known to be sensitive to anthropogenic and natural disturbance (Song & Wang 1995), and possibly to climate change (Box et al. 1999). It is important to confirm the role of habitat heterogeneity empirically and to determine which of the possible environmental controls apply at different scales to inform any future conservation interventions that might be required.

We tested support for the importance of habitat heterogeneity in constructing the mosaic pattern of evergreen and deciduous trees using spatial analysis in a stem-mapped 20-ha EBLF plot. Specifically, we tested: (1) whether, and over what scale, there was spatial aggregation within, and segregation between, evergreen and deciduous species; (2) if variations in environmental conditions explained these spatial patterns; and (3) what was the relative importance of the environmental factors on the distribution of both life forms and whether such importance changes with the scale under consideration.

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Methods

Study site

This study was conducted in a 20-ha stem-mapped EBLF dynamic plot located in the Tiantong National Forest Park (TNFP), 28 km south of Ningbo, Zhejiang Province, East China (hereafter, Tiantong plot). The region has a typical subtropical monsoon climate with a hot, humid summer and a drier, cold winter (Song & Wang 1995; Wang et al. 2007). According to the records from a local meteorological station, annual mean air temperature is 16.2 °C and the record low temperature is −8.8 °C. The warmest and coldest months are Jul and Jan, with 28.1 and 4.2 °C monthly mean temperatures, respectively. Mean annual precipitation is 1374.7 mm, falling mostly between May and Aug (Song & Wang 1995).

Vegetation sampling

The 500 m × 400 m Tiantong plot (29°48.817′ N, 121°47.116′ E) was established in the core zone of the Tiantong National Forest Park in the autumn of 2010, following a standard Center for Tropical Forest Science (CTFS) protocol (Condit 1998). The mean elevation of the plot is 447.25 m (range: 304.3–602.9 m) and the slope ranges from 14° to 50°. All free-standing woody stems with DBH $\geq$ 1 cm were measured, tagged, mapped and identified to species. In total, 94 605 living individuals, consisted of 79 deciduous and 73 evergreen tree species, were recorded (Yang et al. 2011). The importance value, IV = (relative dominance + relative abundance)/2, for evergreen species was 79.9, and 20.1 for deciduous species.

Environmental variables

The Tiantong plot was divided into grid cells at three sizes: 10 m × 10 m, 20 m × 20 m and 50 m × 50 m. For each cell (hereafter quadrat) at each scale, four topographic variables (elevation, slope, aspect and convexity) were measured and three soil variables (pH value, total N concentration and total P concentration) were analysed. The original elevation data were measured by total station on nodes of 20 m × 20 m grids in the 20-ha plot, and then elevations for the 10 m × 10 m and 50 m × 50 m grids were interpolated using kriging. Elevation in each quadrat was defined as the mean value for the four corners of each cell (Harms et al. 2001; Valencia et al. 2004). Convexity of each quadrat was determined as the elevation of the focal quadrat minus the mean elevation of the eight surrounding quadrats. For quadrats on the edge of the mapped area, convexity was obtained as the elevation of the centre point of the quadrat minus the mean of the four corners of the same quadrat (Yamakura et al. 1995). By joining the elevations at three corners of the quadrat, each was divided into four triangular planes and this was used to calculate slope and aspect. For each quadrat these values were calculated as the deviation of the average angle of the four planes from the horizontal plane (slope) and the north direction (aspect) (Harms et al. 2001; Lai et al. 2009). Aspect values were linearized into a north–south range with the formula cosine $(180^{\circ} - x) + 1.1$, where x is the aspect in degrees from north (Wang et al. 2007).

Soil samples were collected in Mar 2011, based on the protocol proposed by John et al. (2007) and CTFS (http://ctfs.si.edu/datasets/bci/soilmaps/BCIsoil.html), but with a modified sampling design and intensity. In our plot, a regular 20 m × 20 m grid was used as a base point for soil sample, with two additional sample points taken at 2, 5 or 8 m along a random compass direction from each base point. This resulted in 1310 sampling points for the whole plot. At each sample point, above-ground litter and humus layers were first removed and roughly 400 g of topsoil was sampled from 0–10-cm depth. Soil samples were air-dried and sieved with 2.0 and 0.2 mm mesh screens, with the latter used for total N and P analysis. Soil pH (soil:water volume ratio of 1:5) was analysed with a Beckman glass electrode. Soil total N concentration (TN) was measured using an elemental analyser (Vario Micro Cube; Elementar, Langenselbold, DE). Soil total P (TP) was estimated using a continuous flow analyser (SAN^{++}; Skalar, Breda, NL).

Univariate spatial point-pattern analysis

We used univariate pair correlation functions ($g_e(r)$ or $g_d(r)$) to represent the spatial distribution patterns of evergreen and/or deciduous trees, respectively (Wiegand & Moloney 2014). We used complete spatial randomness (CSR) to test whether the spatial distribution of either evergreen or deciduous trees is random, aggregated or regular. CSR is a widely used null model for univariate point patterns that assumes no interactions among individuals of each life form (Wiegand & Moloney 2004). The simulation envelopes were computed based on 199 Monte Carlo simulations ($\alpha = 0.01$) from 0 up to 200 m at 5-m intervals.

Spatial association analysis

The cross-pair correlation function ($g_{ed}(r)$) was used to describe the spatial association between evergreen (marked as e) and deciduous (marked as d) species (Wiegand & Moloney 2004). This gives the expected number of deciduous trees at distance r from an arbitrary evergreen tree, divided by the intensity of deciduous trees across the whole plot. Whether the distribution of the two life forms in the Tiantong plot is independent, attractive or repulsive at distance r is determined by comparing the observed $g_{ed}(r)$ with the predicted $g_{ed}(r)_{\_\text{null}}$ under a null community assumption. Null communities were generated using the random labelling null model (Szwagrzyk & Czerwczak 1993; Schurr et al. 2004), where life form tags (evergreen and deciduous) were permuted among all individuals while their spatial distribution was held constant. A 99% point confidence envelope of $g_{ed}(r)_{\_\text{null}}$ at each distance r was determined based on 199 null communities under the random labelling null model. If the observed $g_{ed}(r)$ values fall below the confidence envelope, it suggests that deciduous species are less frequently found within distance r of evergreen species than expected under the independence assumption of the two life forms, and *vice versa* (Wiegand & Moloney 2004). All values of $g_{ed}(r)$ and $g_{de}(r)$ in this study were calculated at 5-m intervals from 0 m up to a distance of 200 m, allowing variations in spatial association between the two life forms to be examined over this scale.

The effect of habitat heterogeneity on the association of the two life forms was investigated using a heterogeneous Poisson process (HPP) null model. The HPP was used to generate a series of null communities, in which spatial distributions of the two life forms were independent, given the effect of environmental variation. We held the pattern for one life form (e.g. deciduous species) unchanged, and then used HPP to simulate the pattern of the other (e.g. evergreen species) with the density function estimated via a moving window, and then did the same for the other life form (Wiegand & Moloney 2004). For both evergreen and deciduous trees we used a moving window with radius of 20 m to estimate their corresponding density functions. This is analogous to the density when habitat heterogeneity was controlled. The bivariate pair-correlation function was then applied to interpret the local neighbourhood density (Wiegand & Moloney 2004). To estimate the significance of summary statistics using the null model, we calculated simulation envelopes based on 199 Monte Carlo simulations ($\alpha = 0.01$; Appendix S1) from 0 up to 200 m at 5-m intervals.

Habitat preference analysis

Habitat preference analysis indicates whether evergreen and deciduous species have different habitat requirements. We used multivariate regression trees (MRT; De'ath 2002; Larsen & Speckman 2004) to analyse habitat preference, where the importance values of each life form in each quadrat was the response variables and seven environmental variables described above (see 'Environmental variables') as predictor variables. Cross-validation was used to prune tree size and avoid over-fitting. As cross-validation relative error (CVRE) commonly indicates an optimal tree size (De'ath 2002; Legendre & Legendre 2012), we followed the '1se' rule suggested by Breiman et al. (1984) to achieve the most parsimonious tree structure. Additionally, we applied the group-equalized association index (De Caceres & Legendre 2009) to measure the correlation between deciduous and/or evergreen trees and the site groups generated by MRT. We used a permutation test procedure (= 999 times) to assess the significance of the life form–site clusters associations (De Caceres & Legendre 2009), randomly reassigning the importance values of each life form to the target sites and comparing the observed value with this distribution.

Habitat preference analyses were implemented in R 3.0.0 (R Foundation for Statistical Computing, Vienna, AT), and spatial pattern analyses were performed using the grid-based software Programita (Wiegand & Moloney 2004).

Results

Univariate spatial point pattern of the two life forms

Deciduous and evergreen trees were clumped at scales <60 and 125 m, respectively, while each of their distributions became regular at scales exceeding 100 and 150 m, respectively (Fig. 2).

Spatial association between the two life forms

Deciduous trees were segregated from evergreen trees at scales <120 m, but they became positively associated at 150–200 m (Fig. 3a). In contrast, evergreen trees were always segregated from the deciduous trees (Fig. 3b). However, the spatial segregation between the two life forms disappeared after the influence of habitat heterogeneity on each life form was removed using the HPP null model (Fig. 4).

Habitat preference of the two life forms

Divergence in habitat preference for the two life forms was evident at all examined scales, although the hierarchical structures of the regression trees changed with increasing scale (Fig. 5). The first split in trees of all three spatial scales was associated with soil total P, with threshold concentrations close to 0.3 g·kg^{-1}. This was the only environmental variable selected in regression trees at all three scales (Fig. 5). The variation in importance value explained for the two life forms was similar at all scales, ranging from 25% to 36%.

At the two finer scales (10 m and 20 m cell size; Fig. 5a, b), deciduous trees tended to dominate in regions with rich P (TP > 0.27 g·kg^{-1}), high elevation (>480 m), gentle slope (<29°) and low N (TN < 3.9 g·kg^{-1}). However, total

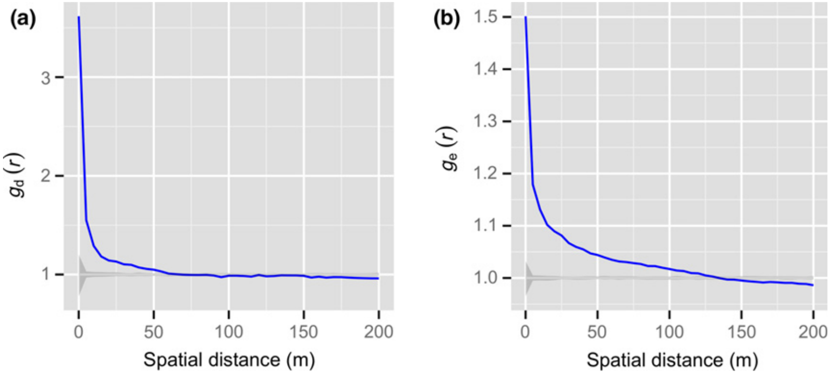

Fig. 2. Univariate spatial point-pattern analysis of evergreen and deciduous species within the 20-ha Tiantong plot across spatial scales. (**a**) and (**b**) represent the spatial pattern of deciduous and evergreen species ($g_d(r)$ and $g_e(r)$), respectively. The pair correlation functions are shown as lines (blue). The grey ribbons indicate the 99% simulation envelopes under the complete spatial random (CSR) null model. [Colour figure can be viewed at wileyonlinelibrary.com]

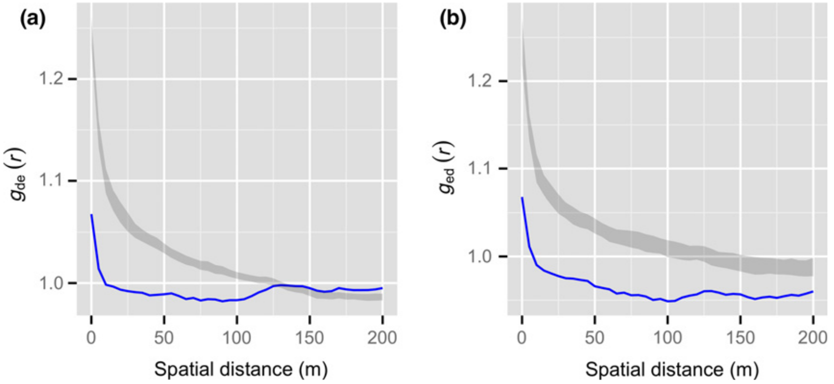

Fig. 3. Spatial associations between evergreen and deciduous species across spatial scales within the 20-ha Tiantong plot. (**a**) and (**b**) show the spatial association between the two life forms ($g_{de}(r)$ and $g_{ed}(r)$), respectively. The g-functions ($g_{de}(r)$, $g_{ed}(r)$) are shown with lines (blue). The grey areas represent the 99% confidence envelopes under the random labelling null models. [Colour figure can be viewed at wileyonlinelibrary.com]

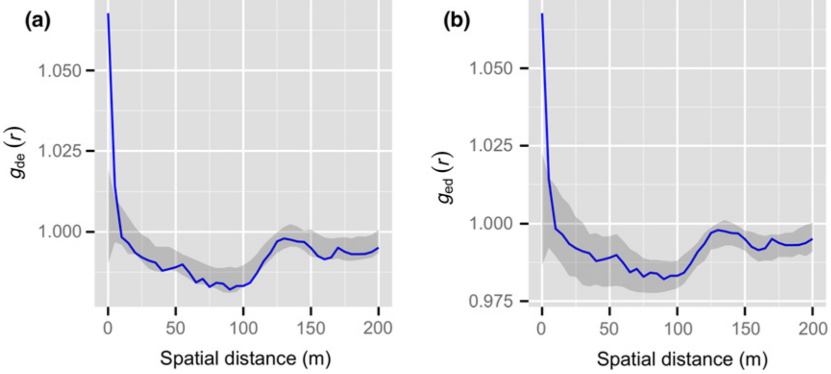

Fig. 4. Inter-type spatial association analysis between evergreen and deciduous species within the 20-ha Tiantong plot with controlled environmental heterogeneity at 20-m scales. (**a**) and (**b**) show the spatial association between evergreen and deciduous woody plants ($g_{de}(r)$ and $g_{ed}(r)$), respectively, when environmental heterogeneity at 20-m scale was controlled for. Lines (blue) represent $g_{de}(r)$ and $g_{ed}(r)$ and grey shading indicates the 99% confidence envelopes under the heterogeneous Poisson process (HPP) null model. [Colour figure can be viewed at wileyonlinelibrary.com]

N merely controlled the dominance of deciduous trees at the 10-m scale, and evergreen trees were not significantly associated with those high N habitats ($P = 0.833$).

At the largest scale (50 m) the two-leaf MRT (Fig. 5c) showed that total P entirely split deciduous and evergreen species, explaining 31% of the importance value variance.

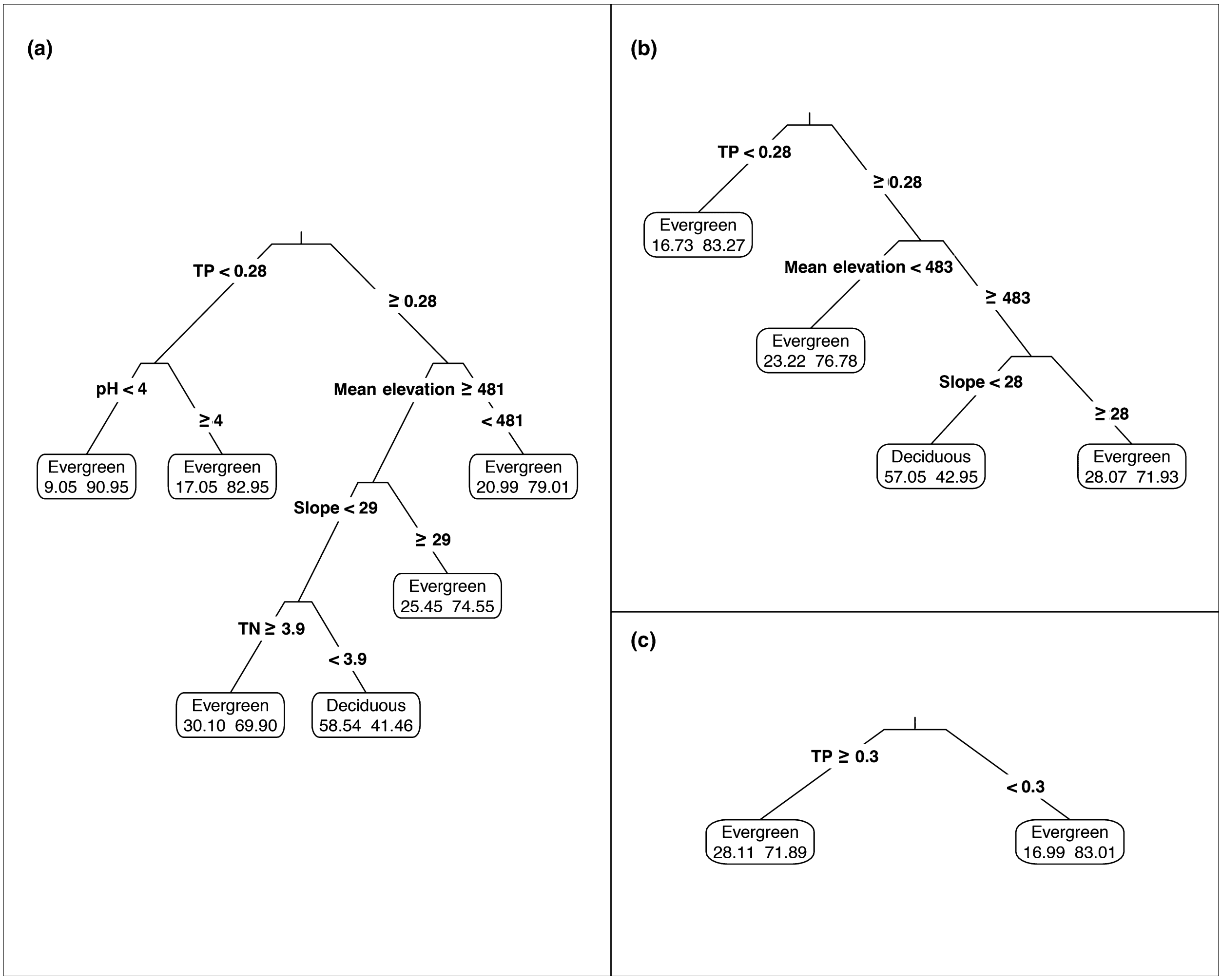

Fig. 5. Results of multivariate regression tree analyses at three spatial scales. (**a**), (**b**) and (**c**) demonstrated the habitat classifications at 10 m × 10 m, 20 m × 20 m and 50 m × 50 m scales. Labels (i.e. Evergreen and/or Deciduous) in the boxes indicate the dominant life form in the classified habitats. Numerals (from left to right) below the labels are the average importance values of deciduous and evergreen trees in the habitat groups and can be compared with the values for the whole plot of 20.1 and 79.9 for deciduous and evergreen species, respectively. Characters and digits on the branches represent the classification thresholds of the environmental factors. Soil total P concentration (TP), soil total N concentration (TN) and soil pH (pH).

Deciduous trees notably preferred sites with higher total P according to permutation tests ($P = 0.001$).

Discussion

Deciduous trees were more dominant in areas where soil total P exceeded concentrations of ~0.3 $g{\cdot}kg^{-1}$, and this differential P preference between the life forms explained around one-third of the variation in importance values across the forest plot. This result is consistent with the observation that P influenced the species co-existence in mature EBLF, because soil P limited the distribution of species with distinct nutrient consumption strategies (Yan 2006). Ecologists typically consider differences in leaf traits between the two life forms are behind this pattern, particularly texture, lifespan and specific leaf area, which provide adaptive advantages for evergreens in nutrient-poor habitats (Loveless 1961, 1962; Poorter & Remkes 1990; Reich et al. 1991, 1992; Sobrado 1991; Eamus 1999; Antunez et al. 2001). Deciduous trees require relatively high soil phosphate availability in the growing season to maximize the benefit of their high photosynthetic rates, while evergreen trees can exploit environments at lower soil phosphate levels and still reach a high photosynthetic rate (Poorter & Remkes 1990; Antunez et al. 2001). The high N-use efficiency of deciduous trees (Sobrado 1991) allows them to prevail in habitats with high total P, but low total N concentrations (TN < 3.9 $g{\cdot}kg^{-1}$ in our study).

Interestingly, Song et al. (2014) found both thermal tolerance and water availability more important than soil

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factors in driving the abundance of deciduous and evergreen trees in EBLF, but their importance changed with elevation. Temperature-related variables controlled community structure on upper slopes, water availability on lower slopes, while edaphic factors were unimportant (Song et al. 2014). This likely reflects scale differences between our study and that of Song et al. (2014), who sampled a latitudinal gradient and much larger spatial extent, using only a single sampling grain. Our two studies thus provide complementary understanding of the evergreen–deciduous spatial mosaic in EBLF and the scale dependence of environmental controls. Plant communities are structured hierarchically via abiotic filters that differentially constrain specific species and/or traits to occupy a given habitat (Weiher & Keddy 1995; Lavorel & Garnier 2002; de Bello et al. 2013). At coarse spatial scales temperature or elevation can structure community-weighted mean trait values (de Bello et al. 2013), consistent with Song et al.'s (2014) findings. In contrast, topographic and edaphic characteristics determine which species dominates at intermediate and fine scales (de Bello et al. 2013), as we found.

Observed habitat preferences across all scales tend to support Monk's (1966) view that evergreen vegetation prevails in more acidic, relatively xeric and low-fertility soils, while deciduous vegetation occurs on less acid, moderate moisture and fertile soils (Monk 1966; Goldberg 1982; Aerts 1999). However, with the exception of soil P, these preferences were only evident at scales of 20 m or less. These associations represent the effect of microhabitat heterogeneity rather than niche differentiation because both life forms – and their associated leaf traits – were aggregated at larger scales than that at which the filtering was detected (Fig. 2). Environmental heterogeneity can occur at a range of scales (Kraft et al. 2015a) and fine-scale habitat heterogeneity has been previously shown to regulate community assembly processes (Palmer & Dixon 1990; McAlpine & Drake 2003; Masaki et al. 2007; Firth & Crowe 2010).

Such microhabitat heterogeneity can arise from various combinations of topographic or light gradients, soil properties and even disturbance regimes (McAlpine & Drake 2003; Masaki et al. 2007). For example, microtopographic variation contributes to the co-existence of evergreen and deciduous trees in a mid-montane mixed forest in southwest China (Tang & Ohsawa 2002). At scales below 20 m we found deciduous species preferred low-slope sites, probably due to higher soil moisture availability, which tends to increase with decreasing slope (Upreti et al. 1985; Tamai 2010). Deciduous trees are generally considered to perform poorly in drought conditions (Eamus 1999), while evergreen species are more tolerant of xeric environments, such as sites of steeper slope with relatively dry soil. The Tiantong forest plot has only a small elevation difference (~300 m) and the fine-scale influence of elevation we found might be related to the light environment rather than thermal tolerance (Song et al. 2014) or other topographic effects. Zhang et al. (2013) found gap fraction (or gap density) increased with elevation in the Tiantong plot, suggesting increased light penetration to the forest floor along the elevation gradient. The improved light conditions at high elevations should facilitate the regeneration of deciduous species and promote their growth (Sakai & Ohsawa 1993, 1994; Kamiyama et al. 2010).

The ultimate goal of ecological research is to infer the underlying processes from the observed patterns (Wiegand & Moloney 2014). For sessile organisms (e.g. trees) their location in space probably conserves the fingerprint of several ecological processes, e.g. intra-/interspecific interaction, dispersal limitation and/or environmental heterogeneity (Wiegand et al. 2007; Wang et al. 2010). Such tight relationships between spatial point patterns and ecological theory have stimulated the study of point-pattern analyses in ecology during the last two decades (Wiegand & Moloney 2014; Velázquez et al. 2016). On the other hand, these relationships usually present a significant scale dependence, making their investigation difficult using traditional methods (Wang et al. 2010). Spatial point-pattern analysis can help in assessing the characteristics of point patterns over a range of scales (Wiegand et al. 2007; Wang et al. 2010; Wiegand & Moloney 2014). However, although point-pattern analysis methods possess numerous merits in deducing potential mechanisms, it is hard to tease apart the effects of biotic interactions and habitat heterogeneity in pattern formation using this technique alone (Wiegand & Moloney 2014). While we have used spatial point-pattern analysis to show that habitat heterogeneity explains the mosaic of evergreen and deciduous trees, it is nonetheless a correlative relationship. Detailed understanding of how habitat heterogeneity affects the relative importance of abiotic tolerance vs stabilizing niche effects on relative fitness differences in promoting co-existence requires an experimental approach.

Conclusions

We show that habitat heterogeneity can explain the mosaic co-existence of evergreen and deciduous woody plants in a subtropical evergreen broad-leaved forest in China. Variation in soil total P concentration was the main environmental factor operating at the intermediate spatial extent over which the mosaic is evident (i.e. several hectares). We also found that environmental factors operated hierarchically, and microhabitat heterogeneity is important for structuring the plant community at fine scales. In general, deciduous trees prevailed at sites with higher soil P, higher elevation, lower slope and lower soil N, while evergreen plants prefer the opposite conditions. Our study complements existing understanding of the co-existence of deciduous and evergreen trees at biogeographic scales.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. A brief introduction to spatial point-pattern analysis procedure.

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