The environment and space, not phylogeny, determine trait dispersion in a subtropical forest

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Summary

1. A central aim of forest ecologists is to quantify the relative importance of different community assembly mechanisms in tropical and subtropical tree communities. Recent work in this field has focused on the importance of functional trait similarity and abiotic filtering. While important, none of this work has simultaneously: linked these trait dispersion patterns to the underlying abiotic environment, considered dispersal limitation and quantified the degree to which patterns of trait dispersion may be explained simply by shared ancestry.

2. Here we use data from a subtropical Chinese forest to accomplish this goal. We first examine the trait dispersion (leaf area, specific leaf area, seed mass, wood density, maximum height and five traits together) on local scales by comparing the observed trait dispersion pattern to that expected from a null model. Then we use a variance partitioning approach to examine the degree to which spatial proximity, environmental similarity or the phylogenetic dispersion of the species determine the observed trait dispersion.

3. The results show that, on local scales, trait dispersion is often non-randomly filtered. Further the widespread trait clustering observed is largely explained by the environment and space, while the phylogenetic dispersion of species in a sample explains relatively little. This result further underscores that inferring an assembly mechanism from a pattern of phylogenetic dispersion is tenuous.

4. The work is important in that it is the first to partition the variation in tree trait diversity into its spatial, environmental and phylogenetic components and that it demonstrates that functional trait data often lack enough phylogenetic signal on local scales to confidently link patterns of trait and phylogenetic dispersion. Ultimately, the findings suggest a strong role for abiotic filtering and dispersal limitation during community assembly on local spatial scales and that shared evolutionary history plays a relatively small role.

Key-words: abiotic environment, community assembly, dispersal limitation, evolutionary history, forest dynamics plot, functional trait, null model

Introduction

The assembly of communities is governed by a combination of niche-based partitioning in space and time as well as stochastic processes and dispersal limitation (e.g. Gravel et al. 2006; Adler, HilleRisLambers & Levine 2007). Dissecting the relative contribution of these processes in tropical and subtropical tree communities is particularly challenging (Wright 2002). This is because the majority of species are rare, likely dispersal limited on ecological time scales (Hubbell et al. 1999) and their long life spans make them not amenable to experimental investigations. Further, quantifying aspects of form and function related to fitness across hundreds of species presents a substantial methodological challenge. Plant ecologists are increasingly using quantitative functional traits of trees as a way to meet this challenge (e.g. Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Paine et al. 2011). These easily measured traits are generally only proxies of the actual physiological traits of interest. That said, even measuring these simple traits in diverse assemblages can take months or years in the field to collect and they have been shown to be reliable indicators of plant resource allocation decisions and ecological strategies (e.g. Westoby 1998; Westoby...
et al. 2002; Wright et al. 2004; Chave et al. 2009). They therefore provide the most pragmatic approach for estimating the functional similarity of tens or hundreds of co-occurring species in tropical and subtropical communities. Plant functional traits have been used to infer community assembly mechanisms primarily by measuring the trait diversity in an assemblage and comparing it to that expected from a null model (Weiser, Clarke & Kelby 1998; Kraft, Valencia & Ackerly 2008). When trait diversity is less than that expected (i.e. trait clustering) an abiotic filtering mechanism is generally inferred and when diversity is higher than expected the importance of biotic interactions is inferred. Studies from tropical tree communities to date have generally reported trait clustering in local assemblages leading to an inference of abiotic filtering (Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Swenson 2011). A missing component of this work is that these patterns of trait clustering are never explicitly linked to the abiotic environment that is inferred to filter the traits. Stronger inferences regarding the role of abiotic filtering would come from directly assessing the degree to which the underlying abiotic environment predicts patterns of trait dispersion. Further, previous tests have generally failed to account for dispersal limitation and other spatial processes that are likely important during community assembly. In sum, we know little about how much of the observed spatial variation in trait dispersion can be explained simply by abiotic gradients and/or spatial proximity.

While a number of research groups have now measured functional traits across hundreds of co-occurring tropical tree species, a number of other groups have taken an alternative route to quantifying the ecological similarity of their study species. In particular, researchers have utilized phylogenetic distance as a proxy for ecological similarity (Webb 2000). This approach was traditionally based on the idea that recently diverged species may be more functionally similar to one another compared to species that diverged long ago. Practically, this approach is also appealing because time and financial constraints often make quantifying relatively easily measured traits impossible and informatics tools now exist to estimate phylogenetic trees for communities within minutes (Webb & Donoghue 2005). This approach is, of course, more indirect and will fail if phylogenetic relatedness does not indicate ecological similarity (Webb et al. 2002; Cavender-Bares et al. 2004), but it will likely continue to be used. Further the question of how much does shared evolutionary history matter to community assembly remains interesting.

As stated above, we have argued for the need to explicitly link the abiotic environment and spatial relationships to increasingly measured patterns of functional trait dispersion in diverse tree communities. We have also posed the question of to what degree can patterns of trait dispersion be simply explained by the shared evolutionary history of species. Here we propose that a variance partitioning approach can be applied to address these challenges simultaneously (Pavoine et al. 2011). Specifically, partitioning the variation in trait dispersion into its purely spatial, environmental, and phylogenetic effects and their joint effects should allow one to answer the degree to which the abiotic environment, dispersal limitation and/or shared evolutionary history govern patterns of trait dispersion. It is predicted that dispersal limitation will increase the amount of variation explained by the spatial component, abiotic interactions will increase the amount of variation explained by the environmental component and shared evolutionary history will increase the amount of variation explained by the phylogenetic component (Fig. 1). If little variation is explained by the environmental component we may infer that patterns of trait clustering are not associated with filtering by the measured abiotic variables. If little variation is explained by the phylogenetic component we may infer that shared evolutionary history does not explain the patterns of trait dispersion and importantly that measurements of phylogenetic dispersion may be misleading. If little variation is explained by the spatial component we may infer a diminished role for dispersal limitation.

The present work analyzes the functional trait dispersion of 159 tree species in the 24-ha Gutianshan Forest Dynamics Plot in subtropical China. Specifically, we measured leaf area, specific leaf area (SLA), seed mass (SM), wood density (WD) and maximum height for the species in the plot. Next we quantified the trait dispersion in 600 400 m² subplots using null models with pairwise and nearest neighbor trait dispersion metrics. Using soil nutrient and topography data and a molecular phylogeny we then partitioned the amount of variation in trait dispersion that

Fig. 1. Partitioning the variation of the dependent variable [trait dispersion (T)] by three sets of independent variables [environment (E), phylogeny (P) and space (S)]. The rectangular area represents 100% of the variation in trait dispersion. Joint effects are denoted with ‘+’ signs. ‘U’ is the unexplained fraction. Abiotic filtering is expected to contribute to the purely environmental (E) and the joint environmental effects (E + P, E + S and E + P + S). Dispersal limitation is expected to contribute to the purely spatial (S) and the joint spatial effects (P + S, E + S and E + P + S). The imprint of shared evolutionary history is expected to contribute to the purely phylogenetic (P) and the joint environmental effects (P + S, E + P and E + P + S).
could be explained by abiotic factors, spatial autocorrelation, and the phylogenetic dispersion of the taxa in the subplot or their joint effects. The results are discussed with respect to the general contribution of evolutionary history, the environment and dispersal limitation to observed patterns of trait dispersion in this diverse community.

Materials and methods

Study location

The present study was conducted in the Gutianshan (GTS) 24-ha forest dynamics plot (29°15′-101°-29°15′34″ N, 118°07′01″-118°07′40″ E), which was established in the summer of 2005 in the Gutianshan National Nature Reserve, Kaihua County, southeast China. The plot has not been disturbed in the past 80 years and may be considered to be a middle-to-late successional forest (Legendre et al. 2009). The plot contains approximately 140,000 individual trees (dbh ≥ 1 cm) from 49 families, 103 genera and 159 species (Lai et al. 2009; Legendre et al. 2009). The mean annual temperature in GTS is 15.3 °C, with the hottest month being July and the coldest month being January. The mean annual precipitation is 1963 mm with a prolonged dry period between October and February. The plot topography is very rugged with altitude ranging from 446-3 to 714.9 m and with slopes varying from 13 to 62 °C.

Soil and topography data collection

Four topographic variables were quantified for each 20 × 20 m subplot for our analyses: mean elevation, slope, convexity and aspect. Slope and aspect were measured in the field; mean elevation and convexity were calculated from the measured elevation data. Detailed information regarding the collection of this data is provided in Legendre et al. (2009). A total of 13 soil nutrients (Fe, Mn, Zn, Cu, K, P, Ca, Mg, B, Al, N, pH, Nmin) were obtained from soil samples taken from the GTS plot. Soil cores were taken to a depth of 10 cm from 893 points using both regular and random sampling methods. In particular the GTS plot was divided into 30 × 30 m grids, with grid intersections as basal points and two points along 2, 5 and 15 m in a random compass direction from the grid basal point as two additional points (Zhang et al. 2011). In total, the four topographic and 13 soil nutrient variables were utilized to characterize the abiotic environment in the GTS plot.

Functional trait data collection

Four functional traits for each species were measured from the field: leaf area (LA), SLA, SM and WD. An additional trait, maximum height (Hmax), was compiled from the Flora of China (Wu & Raven 1994–2009) and the Flora Reipublicae Popularis Sinicae (Editorial Committee for Flora Reipublicae Popularis Sinicae 1961–2004).

Measurement protocols for LA, SLA and SM followed Cornelissen et al. (Cornelissen et al. 2003) and WD measurements followed Wright et al. (Wright et al. 2010). Specifically, at least 10 fresh leaf samples for each of the 159 species were taken from the tallest parts of trees, which were fully expanded and exposed to direct sunlight. The LA 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. The SM was an average value of oven-dry mass (under 80 °C for 48 h) from 30 to 200 collected mature seeds for each species without any appendages. We collected wood samples from 5 to 15 individuals for each species. The WD was estimated as a mean ratio of oven-dry mass to fresh volume.

DNA sequencing and phylogenetic inference

Plant leaf material was collected during the summer of 2009 and 2010 from three individuals for each of the 159 species occurring in the GTS plot. Three common barcoding genes rbcLa, matK and trnH-psbA were amplified using polymerase chain reaction (PCR) and sequenced following the methods described in (Kress et al. 2009, 2010). DNA contigs were further assembled using ContigExpress in VectorNTI11 (InVitrogen Corp., Carlsbad, CA, USA). Sequences were aligned using MUSCLE 3.8 (Edgar 2004). We used RAxML via CIPRES to reconstruct a maximum likelihood (ML) tree (Stamatakis 2006). The ML tree was further calibrated using nonparametric rate smoothing in the software r8s (Sanderson 2003). A figure of the phylogenetic tree is available in the supplemental information (see Fig. S1, Supporting information). After inferring the molecular phylogeny, the inferred basal topology was compared to the basal topology of the APG III phylogenetic backbone to determine whether a constraint tree was needed. The basal topologies were congruent except for two species that are located in ‘unplaced’ families in the APG III phylogeny and therefore this lack of congruence is not surprising. Rather than constrain our inferred tree by unplaced or dubious lineages we kept our original basal topology.

Variation partitioning analyses

Trait dispersion analyses

The community trait dispersion was calculated using two indices. First we calculated a mean pairwise trait distance (PW) between all individuals in a forest subplot. Second we calculated a mean nearest neighbor trait distance (NN) between all individuals in a forest subplot. The distances between individuals were calculated from a trait dendrogram. The trait dendrogram was generated by first generating a trait Euclidean distance matrix. Hierarchical clustering was then applied to this matrix to generate the dendrogram. A dendrogram was used as it is analogous to
a phylogenetic tree, which we used for the phylogenetic analyses explained below. We generated six trait dendrograms, including five for each trait and one for all the traits (AT) combined. The community trait dispersion was quantified using the observed PW and NN values and comparing them to a null distribution of PW and NN values. This allowed us to calculate a standardized effect size for the PW and NN metric (S.E.S. PW and S.E.S. NN respectively). To generate the null distribution we randomized species names on the trait dendrograms 9999 times and recalculated the PW and NN metrics for subplots. This randomization procedure retains observed trait combinations and correlations and only changes the identity of the species with that trait combination. The 9999 random values were used to calculate S.E.S. PW and S.E.S. NN as follows:

\[
\text{S.E.S.PW}_{\text{sample}} = \frac{-1 \times (\text{PW}_{\text{sample}} - \text{mean} \left( \text{PW}_{\text{random}} \right))}{\text{sd} \left( \text{PW}_{\text{random}} \right)}
\]

\[
\text{eqn 1}
\]

\[
\text{S.E.S.NN}_{\text{sample}} = \frac{-1 \times (\text{NN}_{\text{sample}} - \text{mean} \left( \text{NN}_{\text{random}} \right))}{\text{sd} \left( \text{NN}_{\text{random}} \right)}
\]

\[
\text{eqn 2}
\]

Where PW

subscript sample and NN

subscript sample are the observed PW and NN for the community and PW

subscript random and NN

subscript random are the 9999 random PW and NN values. Thus S.E.S. PW

subscript indicates the basal or overall trait dispersion of a community, while S.E.S. NN is calculated from the nearest neighbors, therefore indicates the terminal trait dispersion of a community. The high S.E.S values indicate lower than expected trait diversity and low S.E.S. values indicate higher than expected trait diversity.

As the present study was interested in quantifying the amount of variation in S.E.S. PW and S.E.S. NN that could be explained by the phylogenetic dispersion of the assemblage, we calculated two widely used phylogenetic metrics that are mathematically analogous to S.E.S. PW and S.E.S. NN. The first was the net relatedness index (NRI; Webb et al. 2002), which is a phylogenetic analog of the S.E.S. PW. The second was the nearest taxon index (NTI; Webb et al. 2002), which is a phylogenetic analog of S.E.S. NN. The NRI and NTI are calculated using the same set of equations as S.E.S. PW and S.E.S. NN respectively except they utilize phylogenetic branch lengths instead of trait dendrogram branch lengths. As with the functional trait analyses, the phylogenetic analyses randomized species names on the phylogeny. It therefore retained the observed phylogenetic topology. In total, we calculated S.E.S. PW, S.E.S. NN, NRI and NTI for 600 subplots in the GTS each of which was 20 × 20 m in area.

**PCNMs for the spatial variation information**

The spatial relationships among the 20 × 20 m subplots was obtained via principal coordinate analysis (PCoA) of a truncated distance matrix, which was composed of Euclidean distance between subplots. We used the function ‘PCNM’ from the R package ‘vegan’ to obtain the spatial information across the 600 subplots in the GTS plot. The spatial relationships among the subplots were then decomposed to a set of orthogonal PCNM eigenfunctions (Borcard & Legendre 2002; Legendre, Borcard & Peres-Neto 2008). The PCNM variables were then used to analyze the spatial variation.

**Partitioning the variation into three sets of explanatory variables**

We partitioned the variation in the trait dispersion pattern into an environmental component, a phylogenetic dispersion component, a spatial component and their joint effects by using sequential linear regressions followed by subtractions (Desvoides et al. 2003; Cubo et al. 2008) (Fig. 1). Here we briefly explain this procedure. First, for environmental variables (E), a forward variable selection procedure was used to extract those variables, which were significantly related to the dependent variables (T) (i.e. trait dispersion values). Second, for the spatial PCNM variables (S), the same method was applied to reduce the number of explanatory eigenvectors, retaining only those that were significantly related to the dependent variables (T). Last, a sequential regression of the dependent variables (T) was computed on E, S and phylogenetic dispersion (P) and their joint variables E + S, E + P, P + S and E + P + S (Fig. 1). The coefficient of determination adjusted \( R^2 (R^2_{adj}) \) from each part indicated the proportion of the variance in T that could be explained exclusively from the individual independent variable or the interaction of multiple independent variables. All the procedures were carried out in the R statistical language (R Development Core Team 2012). The forward selection analyses used the function ‘forward.sel’ in the ‘packfor’ package using 9999 permutations and the variation partitioning and significance tests used the functions ‘varpart’ and ‘anova.cca’ in the ‘vegan’ package using 9999 permutations.

**Results**

**Trait dispersion patterns**

In the GTS plot, the S.E.S. PW of the 600 20 × 20 m subplots primarily showed less trait diversity than expected given the null distribution. Specifically the majority of subplots had lower than expected trait diversity: LA (99.8%), SLA (100%), WD (97.3%) and AT (98.3%) and 17-5%, 50-7%, 25-5% and 9-5% of the subplots had significantly low trait diversity (Table 1; Fig. 2). On the contrary, SM (62.7%) and \( H_{\text{max}} \) (75-7%) were mostly over-dispersed with 0.2% and 5.8% of each being significantly over-dispersed. Similar to the S.E.S. PW results, the S.E.S. NN results generally show low trait dispersion in subplots: LA
Table 1. The proportion of subplots with trait clustering (overdispersion) and the proportion of subplots that are significantly clustered (overdispersed). S.E.S. PW is the standardized effect size of the mean pairwise trait distance. S.E.S. NN is the standardized effect size of the mean nearest neighbour trait distance.

<table>
<thead>
<tr>
<th>Trait</th>
<th>S.E.S. PW</th>
<th></th>
<th>S.E.S. NN</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clustered</td>
<td>Sig-clustered</td>
<td>Clustered</td>
<td>Sig-clustered</td>
</tr>
<tr>
<td></td>
<td>(Overdisp)</td>
<td>(%)</td>
<td>(Overdisp)</td>
<td>(%)</td>
</tr>
<tr>
<td>Leaf area</td>
<td>99.8 (0.2)</td>
<td>17.5 (0.0)</td>
<td>96.0 (4.0)</td>
<td>0.0 (0.33)</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>100.0 (0.0)</td>
<td>50.7 (0.0)</td>
<td>99.3 (0.7)</td>
<td>0.0 (0.0)</td>
</tr>
<tr>
<td>Seed mass</td>
<td>37.3 (62.7)</td>
<td>0.0 (0.2)</td>
<td>60.0 (40.0)</td>
<td>0.0 (0.2)</td>
</tr>
<tr>
<td>Wood density</td>
<td>97.3 (2.7)</td>
<td>25.5 (0.0)</td>
<td>98.2 (1.8)</td>
<td>0.0 (0.2)</td>
</tr>
<tr>
<td>Maximum height</td>
<td>24.3 (75.7)</td>
<td>0.0 (5.8)</td>
<td>69.0 (31.0)</td>
<td>0.0 (2.5)</td>
</tr>
<tr>
<td>All traits</td>
<td>98.3 (1.7)</td>
<td>9.5 (0.0)</td>
<td>90.8 (9.2)</td>
<td>11.7 (0.0)</td>
</tr>
</tbody>
</table>

Fig. 2. The spatial distribution of S.E.S. PW (the standardized effect size of the mean pairwise trait distance) based on five functional traits and all trait combined of Gutianshan plot. The color scale on the right of each map indicates the S.E.S. PW values. “S.E.S. PW > 0” indicates trait dispersion is clustered; “S.E.S. PW < 0” indicates trait is overdispersed. The lines are elevation contour lines at 10-m intervals.

(96.0%), SLA (99.3%), SM (60%), WD (98.2%), \(H_{\text{max}}\) (69.0%) and AT (90.8%) (Table 1; Fig. 3), while only AT had any subplots (11.7%) with significantly low levels of trait diversity (Table 1; Fig. 3).

VARIANCE PARTITIONING RESULTS

The amount of variation in S.E.S. PW and S.E.S. NN for the traits in the GTS plot explained by E, P and S and by their interaction (E + P, E + S, P + S and E + P + S) is provided in Fig. 4 and Table S1 (Supporting information).

S.E.S. PW and S.E.S. NN and the WD dispersion for S.E. S. PW, and the whole phylogenetic component (with joint effects of environmental and/or spatial components) of WD dispersion for S.E.S. PW (Fig. 4). See Table S1 (Supporting information) for the detailed P-values of each portion in trait variation partitioning.

Discussion

Community ecologists have sought to link patterns of functional trait dispersion to local-scale environments in order to infer assembly mechanisms. Much of this work has inferred that the abiotic environment plays an important role in determining community assembly (Cornwell, Schwilk & Ackerly 2006; Swenson et al. 2007; Kraft, Valencia & Ackerly 2008; Swenson & Enquist 2009; Uriarte et al. 2010), but this linkage is not always explicitly quantified. Making this linkage is further complicated by the fact that abiotic environments generally display strong spatial autocorrelation. Combine this with the fact that many species may be dispersal limited and inferences regarding abiotic filtering during assembly become difficult without explicitly partitioning the variance in trait dispersion due to space, the abiotic environment or their interactions. Concurrent with the rapid increase in interest in functional trait analyses of plant communities has been an increasing interest in the phylogenetic dispersion of co-occurring species (Webb 2000; Webb et al. 2002; Swenson et al. 2007; Cavender-Bares et al. 2009). Much of the early phylogenetic work in community ecology assumed that ecologically important traits have significant phylogenetic similarity (sensu Swenson, Anglada-Cordero & Barone 2011) where closely related species are likely to have more similar trait values than distantly related species (Webb 2000; Kembel & Hubbell 2006; Swenson et al. 2006). If this assumption is met, then it is predicted that a large fraction of the spatial variability in trait dispersion may be explained by the spatial variability in phylogenetic dispersion. The present study aimed to disentangle these three possible drivers of spatial patterns in trait dispersion by partitioning the variance in trait dispersion explained by space, the abiotic environment or phylogenetic dispersion or their interactions.

We first quantified the dispersion of trait values inside a 24-ha forest dynamics plot in China called GTS. When using a pairwise trait dispersion metric (S.E.S. PW) we found that the majority of traits had less than expected diversity inside 20 x 20 m subplots. This result is consistent with a filtering of phenotypes into local assemblages, which is often considered evidence of abiotic filtering. Two traits, SM and \( H_{\text{max}} \), had the opposite pattern of higher than expected diversity. This result is consistent with work from temperate and tropical plant community studies (Grime 2006; Kraft, Valencia & Ackerly 2008; Swenson &
Enquist 2009) that have shown overdispersion in these two traits believed to be linked to regeneration and light niches, respectively. Thus one may infer that most traits are abiotically filtered into communities while local scale competition along light and regeneration niche axes also significantly contributes to the assembly of these tree communities.

We next quantified the trait dispersion using a nearest neighbor metric (S.E.S. NN). While most values tended to show low trait diversity within subplots, few subplots had observed values significantly different than that randomly expected. Thus we cannot infer any deterministic mechanisms, such as limiting trait similarity, underlying the patterns of trait diversity and the assembly of the GTS tree community. In sum, the trait results, particularly the S.E. S. PW results, are consistent with an abiotic filtering mechanism governing community assembly in the forest plot studied. That said, these analyses were not linked to any abiotic variables that presumably underlie the filtering of species nor were we able to determine how much of this filtering could be understood by shared evolutionary history or dispersal limitation. Therefore we wanted to determine how much of the trait dispersion in the GTS plot could be explained by space, the abiotic environment, and/or phylogenetic dispersion using variance partitioning.

The variance partitioning results showed that a significant amount of the variation in trait dispersion in subplots was explained by the abiotic environment (Fig. 4). Across all traits, at least 20% of the spatial variation in S.E.S. PW could be accounted for by the purely environmental or environment, space, and/or phylogeny interaction. In one case, SLA, over 50% of the variation in S.E.S. PW values could be linked to a pure or joint environmental component (Fig. 4). This is taken as stronger evidence that the patterns of trait clustering are indeed linked to the abiotic environment thereby strengthening our support for an abiotic filtering model of community assembly in this forest. Much less of the spatial variation in the S.E.S. NN values could be explained by environmental variation (Fig. 4) suggesting that trait spacing within local assemblages had little to do with the underlying abiotic environment and may have a large stochastic component. In most cases there was also a strong spatial component to the results suggesting that dispersal limitation and/or spatial autocorrelation in the environment also explain some of the trait dispersion in the forest. Thus an abiotic filtering mechanism certainly does not explain all assembly in this forest and purely spatial processes also contribute significantly to the observed patterns of co-occurrence.

Along with space and the abiotic environment we quantified the amount of variance in trait dispersion explained by phylogenetic dispersion. It was expected that if local patterns of trait dispersion can be predicted based upon shared evolutionary history, then a large amount of spatial variation in trait dispersion should be linked to pure or joint phylogenetic effects. In most cases a significant amount of variation in trait dispersion could be explained by the phylogenetic dispersion of the assemblage, but the
amount of variation was typically low particularly for S.E. S.NN (Fig. 4). From this we can infer that examinations of phylogenetic dispersion in this forest would likely not reliably indicate the dispersion of the traits studied and that shared evolutionary history may not be invoked to explain the assembly of trait values. In other words, phylogenetic dispersion may provide faulty inferences regarding trait-based assembly in the present study system. Recent work has highlighted similar difficulties in recovering trait dispersion patterns from patterns of phylogenetic dispersion (Swenson & Enquist 2009) suggesting that great care should be used in future studies that only utilize phylogenetic information. We do, though, point out a notable exception to this general pattern. The spatial distribution of $H_{\text{max}}$ dispersion in the GTS plot was predominantly explained by the spatial variation in phylogenetic dispersion (Fig. 4). This result is important for a couple of reasons. First it shows that the dispersion of this trait has little to do with the environmental variables measured which may be expected given this trait is expected to be related more to the light niche than the soil niche. Second, it shows that the dispersion of this trait can largely be explained by shared evolutionary history between species. This shows that analyses of phylogenetic dispersion may predict the dispersion of $H_{\text{max}}$ values in this forest suggesting that phylogenetic dispersion analyses may be useful in some cases. Lastly, we point out that a large amount of the variation in trait dispersion in the GTS forest plot could not be explained by space, the abiotic variables measured, phylogenetic dispersion or their interactions. This suggests that stochastic processes not linked to spatial distance may play an important role in the assembly of the forest. An alternative, and perhaps more likely, reason for this unexplained variation is that the present study failed to measure key abiotic variables and/or species traits that contribute greatly to the assembly of this forest.

In summary, the present study has shown that local scale tree assemblages in a species rich subtropical Chinese forest plot are often non-randomly filtered sets of the species pool. This was demonstrated by examining the dispersion of several traits on local scales and showing that trait diversity within assemblages was typically lower than that expected given the species pool and a null model. The results are consistent with other studies that have argued for the importance of abiotic filtering during tropical and subtropical tree community assembly (Lai et al. 2009; Legendre et al. 2009). Unlike previous functional trait analyses of tropical tree communities we next examined whether the underlying abiotic environment does indeed predict the trait dispersion in communities. Our variance partitioning analyses show that indeed the abiotic environment in this forest does predict the levels of trait clustering demonstrated providing direct support for an abiotic filtering mechanism. The results also show a strong spatial component underscoring the importance of dispersal limitation as well. Lastly, we have shown that spatial variation in phylogenetic dispersion in this forest often fails to predict the spatial variation in trait dispersion thereby casting doubt on the ability of phylogenetic relatedness to predict the mechanisms underlying trait assembly in this subtropical tree community. Ultimately, by employing a variance partitioning approach we were able to more directly link patterns of trait dispersion to the underlying environment and dispersal limitation while also examining the ability of shared evolutionary history to predict spatial variation in trait dispersion.

Acknowledgements

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References


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**Supporting Information**

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

**Fig. S1.** The phylogenetic tree for the GTS plot constructed using DNA barcodes with each clade colored by order.

**Table S1.** Results of variation partitioning of trait dispersion among environmental, phylogenetic and spatial components. All the significance tests were based on 9999 permutations.