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Changes in Patterns of Species Co-occurrence across Two Tropical Cloud Forests Differing in Soil Nutrients and Air Temperature

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ABSTRACT

Patterns of co-occurrence of species are increasingly used to examine the contribution of biotic interactions to community assembly. We assessed patterns of co-occurrence at four scales, in two types of tropical cloud forests in Hainan Island, China (tropical montane evergreen forests, TMEF and tropical dwarf forests, TDF) that varied significantly in soil nutrients and temperature. We tested if the patterns of co-occurrence changed when we sorted species into classes by abundance and diameter at breast height (dbh). Co-occurrence differed by forest type and with plot size, with significant species aggregation observed across larger plots in TDF and patterns of species segregation observed in smaller plots in TMEF. Analyses of differential abundance and dbh classes also showed that smaller plots in TMEF tend to have negative co-occurrence patterns, but larger plots in TDF tend to show patterns of aggregation, suggesting competitive and facilitative interactions. This underscores the scale-dependence of the processes contributing to community assembly. Furthermore, it is consistent with predictions of the stress gradient hypothesis that facilitation will be most important in biological systems subject to abiotic stress, while competition will be more important in less abiotically stressful habitats. Our results clearly demonstrate that these two types of tropical cloud forest exhibit different co-occurrence patterns, and that these patterns are scale-dependent, though independent of plant abundance and size class.

Abstract in Chinese is available with online material.

Key words: community assembly; competition; facilitation; species association; stress gradient hypothesis.

IDENTIFYING AND QUANTIFYING THE MECHANISMS GOVERNING THE ASSEMBLY OF NATURAL communities are of critical importance in ecology (Diamond 1975, Gotelli & Graves 1996). Of particular interest is the focus on biotic interactions as a mechanism for assembly (Chesson 2000). Positive and negative species interactions are often important in structuring natural community (*e.g.*, Brooker *et al.* 2008, Bulleri *et al.* 2014). Negative species interactions usually refer to competition (although they may also refer to predation), whereas positive species interactions refer to facilitation. Studies on species interactions among lichens, mosses and seed plant communities have demonstrated that both competition and facilitation can play crucial roles in community assembly (Gotelli & McCabe 2002, Brooker *et al.* 2008, Bowker *et al.* 2010).

Competition occurs when neighbouring plants require a similar set of resources such as light, soil nutrients, moisture, or space and at least one of these resources is in short supply (Grime 1977). When species' niches overlap, the weaker competitor may be excluded (MacArthur & Levins 1967). With facilitation, by contrast, neighbouring organisms improve the surrounding abiotic and biotic conditions in a way that benefits a species (Callaway 2007). They might increase a species' distribution (Choler *et al.* 2001, Holmgren & Scheffer 2010), survival, growth, reproduction (Bertness & Grosholz 1985) or community diversity in general (Hunter & Aarssen 1988, Pugnaire *et al.* 1996, Chu *et al.* 2008). For example, Choler *et al.* (2001) carried out a neighbour removal experiment in natural alpine plant communities in the Southwestern Alps and found that neighbours enhanced the distribution and abundance of many species. The species continuum commonly observed along environmental stress gradients is influenced both by competition and facilitation, in accord with the stress gradient hypothesis (Callaway *et al.* 2002). This hypothesis predicts that the relative importance of facilitation for community assembly increases with increasing abiotic stress (*e.g.*, low air temperature, drought, strong wind, disturbance and lack of nutrients); likewise, the relative importance of competition decreases along this same gradient (*e.g.*, Callaway

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et al. 2002, Brooker *et al.* 2008, Long *et al.* 2013, but see also Holmgren & Scheffer 2010).

Two complementary empirical methods can be used to examine competition and facilitation. First, we can perform experiments on the effects of competition, studying the strength and universality of species interactions in various communities (Gurevitch *et al.* 2000). Second, we can test if patterns of species co-occurrence indicate that either competition or facilitation organises species within natural systems (Gotelli & Graves 1996, Veech 2014). There have been considerable improvements in statistical null models employing presence–absence matrices (or a species abundance matrix) to detect patterns of non-random species co-occurrence (Gotelli 2000, Zhang *et al.* 2009, Bowker *et al.* 2010). For example, Gotelli and McCabe (2002) comprehensively analysed the published presence–absence matrices from 96 studies and found that non-random species co-occurrence patterns were common in natural communities, with the predominant pattern being negative co-occurrence. After analysing the species co-occurrence patterns of 45 species in 4540 different geographical areas, Adams (2007) found non-random species co-occurrence patterns at both regional and continental scales, indicating that competition is an important process organising species on the landscape.

Species distributions generally change with spatial scale, being aggregated at some scales, but random or uniform at others (Wang *et al.* 2010, Petit & Fried 2012). Understanding how patterns of species co-occurrence change across different spatial scales is critical to understanding how ecological processes drive community assembly in general (Zhang *et al.* 2009, Bowker *et al.* 2010). For example, competition may be important at smaller spatial scales (Weiher & Keddy 1995, Matesanz *et al.* 2011), whereas it is not clear which ecological processes influence species distribution at large spatial scales (Zhang *et al.* 2009). Using species co-occurrence analyses, Maestre *et al.* (2009) found that lichens in semiarid Mediterranean environments coexist through facilitation, depending on which spatial scale was considered. Ecological processes are complex (Horner-Devine *et al.* 2007), and the correlation between co-occurrence patterns and spatial scale may be habitat specific. However, more studies are needed to address the way co-occurrence patterns change with scale in various natural systems.

Compared with low-altitude forests, tropical cloud forests are characterised by low air temperatures, strong winds, frequent clouds and relatively high air humidity (Bruijnzeel & Hamilton 1998, Long *et al.* 2011a). The tropical cloud forest on Hainan Island is mainly distributed on mountaintops more than 1200 m asl: on Bawangling Mt., Wuzhishan Mt., Jianfengling Mt., Diaoluoshan Mt. and Yinggeling Mt. (Hu & Li 1992), which mainly include tropical montane evergreen forest (TMEF) at lower altitudes and tropical dwarf forest (TDF) at high altitude (Bubb *et al.* 2004). Previous research using size-distance regressions indicated that these two types of tropical cloud forest have been assembled by both competition and facilitation (Long *et al.* 2013). The importance of competition increased as soil resources decreased from TMEF to TDF, while the importance of facilitation increased with increasing air temperature stress from TMEF to TDF. In addition, variation in soil phosphorus and air temperature contributed to trait-based assembly rules related to specific leaf area and plant height in these forests (Long *et al.* 2011a,b, 2015).

In this study, we used null models to test for non-random patterns of species co-occurrence in TMEF (1200 m to 1250 m asl) and TDF (over 1350 m asl), two forests that differ strongly in stress due to soil nutrients and air temperature. We hypothesised that: (1) species in these two tropical cloud forests would have non-random patterns of co-occurrence; and (2) the nature of co-occurrence patterns would change with plot size and across different classes of plant species abundance and size.

METHODS

STUDY SITE.—We conducted this study in high-altitude forests of the Bawangling Nature Reserve (BNR) (18°50′–19°05′ N, 109°05′–109°25′ E), Hainan Island, South China (Fig. S1). The BNR covers *ca* 500 km^2, with altitudes ranging from *ca.* 100 m to 1654 m asl. The mean annual temperature at *ca* 100 m asl is 23.6°C and the annual precipitation is 1677.1 mm, with a distinct wet season from May to October and a dry season from November to April (Zang *et al.* 2005). The TDF is mainly distributed around the mountaintops at altitudes exceeding 1350 m asl; while the TMEF is adjacent to TDF, mainly distributed at altitudes from 1200 m to 1250 m asl. Soils in TMEF and TDF are oxisols and ultisols respectively. These two types of forest are primeval old growth forests and are collectively classified as tropical cloud forest because of frequent fog cover (Long *et al.* 2011c).

DATA COLLECTION.—We chose two study sites in the TMEF and TDF, (TMEF: Site1, 19°05′24.5″ N, 109°12′56.2″ E; Site 2, 19°05′33.2″ N, 109°12′53.2″ E; TDF: Site1, 19°05′04.8″ N, 109°12′43.5″ E; Site 2, 19°05′12.4″ N, 109°12′36.4″ E; Fig. S1). In each site, four plots covering 2500 m^2 were randomly established, with more than 50 m between each plot. We selected square plots of four sizes (5 m × 5 m—780 plots; 10 m × 10 m—190 plots; 20 m × 20 m—25 plots; 30 m × 30 m—16 plots) within each 2500 m^2 plot. The four plot sizes were determined using a random number table. We subdivided each plot into 5 m × 5 m subplots for enumerating all free trees, shrubs and lianas with diameter at breast height (dbh) $\geq$1 cm, and identified all individuals to species in accordance with the Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China 2004). We used up to 157 species in the TMEF and 133 species in the TDF for co-occurrence analysis (Supporting Information, Table S1 and S2).

We randomly chose twenty-nine and thirty-two 10 m × 10 m plots within the 30 m × 30 m plot sizes of TMEF and TDF respectively, to measure soil concentrations of total and available N and P, air temperature and photosynthetically active radiation. We collected five soil cores (diameter 4 cm and depth 20 cm) in each plot. We air-dried soil samples, ground them to a fine powder with a mill, and hand-sieved them for analysis.

We ground soil for total nitrogen (g/kg) analysis to *ca* 0.15 mm. We digested each 1 g soil sample in 98% H_2SO_4 with K_2SO_4—$CuSO_4 \cdot 5H_2O$—Se. For ammonium measures, we obtained N from the digest by steam distillation, using excess 0.1 mol/l NaOH to raise the pH. We collected the distillate in 2% H_3BO_3, and then titrated it with 0.05 mol/l H_2SO_4 to pH 5.0. We calculated total nitrogen concentration for the sample according to changes in the volume of 0.05 mol/l H_2SO_4.

For determining available nitrogen (mg/kg), we ground soil to *ca* 1 mm. We added 2.0 g samples to Devards's Alloy and digested them with 20 g/l boric acid solution and 1.8 mol/l NaOH. Finally, we diluted the digest with 0.01 mol/l HCl to pH 5.0. We calculated available nitrogen concentration for the sample according to changes in the volume of 0.01 mol/l HCl.

We also ground soil for total phosphorus (g/kg) analysis to *ca* 0.15 mm. We digested each 0.25 g soil sample with 60% $HClO_4$ and diluted the digested sample with an ammonium-vanadomolybdate reagent. We prepared a standard curve by reading the absorbances at 700-nm wavelength. We estimated total phosphorus concentration of the samples using the calibration curve.

To determine available phosphorus (mg/kg), we ground soil to *ca* 1 mm and digested 3.0 g samples with 0.03 N NH_4F—0.025 N HCl solution. Next, we diluted the digested sample with 0.06 mol/l boric acid solution, deionised water and an ammonium-vanadomolybdate reagent, and added 0.25% p-nitrophenol indicator, and read the absorbances to prepare a standard curve at 700–nm wavelength. We determined available phosphorus concentration of the samples using the calibration curve (Anderson & Ingram 1989).

We logged air temperature (°C) hourly from May to October at 1.3 m above soil level, using HOBO Pro Temp/RH dataloggers (Onset, U23-001, USA) placed at the centre of each study plot, and calculated mean daily temperature for each plot. We measured photosynthetically active radiation (PAR, μmol/m/sec) 1.3 m above soil level, between 1000 h and 1200 h, using a Field Scout Quantum Meter (3415FSE, Spectrum Technologies, Inc., USA). PAR at this level differed from above-canopy radiation, but does indicate the light climate of the understory in the two forests (Chazdon 1988).

DATA ANALYSIS.—We assessed differences in soil nutrients, air temperature, and PAR between TMEF and TDF using Wilcoxon's Rank-Sum tests.

We transformed survey data into three types of presence–absence matrices. The first contained all the trees, shrubs and lianas with dbh ≥1 cm. The second contained four restricted tree species abundance classes (abundance ≥50, abundance ≥100, abundance ≥200 and abundance ≥400). We chose tree species with high abundance to avoid the 'dilution effect' (Gilpin & Diamond 1982, Gotelli & Graves 1996), in which a null model test may inappropriately give neutral results because it contains several non-interacting species. The third type of matrix contained three tree species diameter classes (1 cm ≤dbh <5 cm, 5 cm ≤dbh <10 cm and dbh ≥10 cm). We classified tree species into abundance and diameter classes to test if tree species co-occurrence patterns changed with abundance or size. Each abundance and size class included all four plot sizes; thus, 20 presence–absence matrices were analysed for each of the two forest types.

We used two indices to analyse co-occurrence patterns. The C-score is a commonly used metric of species co-occurrence (Stone & Roberts 1990) that has good general statistical properties (Gotelli 2000). We calculated the C-score as $\sum (S_i - Q)(S_k - Q)/(R(R-1)/2)$, where S_i represents the total occurrence frequency of species *i*, *R* represents the number of species and *Q* represents the number of quadrats simultaneously occupied by two individuals of the same species. The C score is significantly higher or lower than expected by random if competition or facilitation influences the species assemblage (Gotelli & McCabe 2002). We also used the Variance ratio (V ratio), which refers to the species variance in each quadrat. We calculated the V ratio as σ^2(*column sums*) / $\sum$row σ^2. The V ratio has acceptable statistical properties when used with some randomisation schemes (see below) and reflects the influence of competition on marginal sums. If competition or facilitation affects the system under consideration, the observed V ratio would be significantly lower or higher, respectively, than that expected at random.

We adopted a well-studied randomisation algorithm, SIM2, with good type I and II error rates for the two metrics described above (Gotelli 2000). SIM2 fixes the row sums (species occurrence totals) and allows those species to be shuffled equiprobably among sites (Gotelli 2000, Gotelli & Entsminger 2006). This algorithm is appropriate for analysing 'sample lists', particularly when comparing standardised samples collected from areas of homogenous habitat conditions (Gotelli 2000), and TMEF and TDF habitats have little within-site abiotic variation.

To facilitate the comparison of species co-occurrence patterns, we calculated the standard effect size (SES), essentially a z-score, for each presence–absence matrix of each species (Gurevitch *et al.* 2000). The SES was calculated as follows: $(I_{\mathrm{obs}} - I_{\mathrm{sim}}) / \delta_{\mathrm{sim}}$, where I_{obs} is the observed co-occurrence index, I_{sim} is the mean simulated index, and δ_{sim} is the standard deviation of the simulated index after 5000 null randomisations. Assuming the null distributions are normal, SES values represent significantly non-random co-occurrence for C-values and V ratios either less than -1.96 or greater than 1.96. For C-score, values higher than 1.96 indicate non-random species segregation, whereas values lower than -1.96 indicate aggregation. By contrast, V ratios higher than 1.96 indicate non-random species aggregation, whereas values lower than -1.96 indicate significant species segregation.

We calculated the observed and simulated species co-occurrence indices using the Ecosim 7.72 software (Gotelli & Entsminger 2006) and made the figures using R 2.9.2 (R Development Core Team 2009). Co-occurrence patterns for shrub species and liana species in TMEF and TDF are described in Figures S2 and S3.

RESULTS

COMMUNITY CHARACTERISTICS BY FOREST TYPE.—Dominant species in TMEF include *Cryptocarya chinensis* (Hance) Hemsl., *Cyclobalanopsis championii* (Benth.) Oerst., *Ternstroemia gymnanthera* (Wright et Arn.)

Sprague, *Exbucklandia tonkinensis* (Lec.) Steen., *Cinnamomum tsoi* Allen. and *Syzygium araiocladum* Merr. et Perry. In TDF, dominant species include *Distylium racemosum* Sieb. & Zucc., *Syzygium buxifolium* Hook. et Arn., *Engelhardtia roxburghiana* Wall., *Symplocos poilanei* Guill., *Rhododendron moulmainense* Hook. F and *Cinnamomum tsoi* Allen. The Sørensen similarity coefficient between these two forest types was 0.73. The mean plant density in TMEF was significantly lower than TDF (Wilcoxcon's rank test, $W = 79$, $P < 0.001$) and the mean plant height and diameter at breast height in TMEF were significantly higher than in TDF (Wilcoxcon's rank test, $W = 1.46 \times 10^6$, $P < 0.001$; $W = 1.84 \times 10^8$, $P < 0.001$).

The total nitrogen, total phosphorus, available nitrogen and mean daily air temperature were significantly higher in TMEF than TDF; while available phosphorus and PAR were significantly lower in TMEF than TDF (Table 1).

CO-OCCURRENCE PATTERNS FOR OVERALL SPECIES.—At 5 m and 10 m plot scales, overall species in TMEF had significantly low V ratios (Fig. 1B). This result indicates significant segregation at this scale. Moreover, the V ratio indicates that most competitive sorting occurs at the 5 m scale. By contrast, at the 20 m and 30 m plot scales, overall species showed no significant co-occurrence patterns (Fig. 1B).

At all plot scales, the C score values in TDF were significantly lower than expected by chance (Fig. 1A), whereas the V ratio values were significantly higher (Fig. 1B). These results show that overall species in TDF are significantly aggregated. Based on its lowest C-score and highest V ratio, the strongest and most significant, aggregation patterns were found at the 20 m scale.

CO-OCCURRENCE PATTERNS FOR SPECIES WITH DIFFERENT ABUNDANCE CLASSES.—In the TMEF at 5 m and 10 m plot scales, species with abundances exceeding 50, 100, 200 and 400 had significantly higher C score values and significantly lower V ratio values than expected at random (Fig. 2B and D) indicating significant species segregation at this scale. However, we observed no significant co-occurrence patterns for the four abundance classes at 20 m and 30 m plot scales.

TABLE 1. *Comparison of soil and climate factors between tropical montane evergreen forest (TMEF, mean ± SD) and tropical dwarf forest (TDF, mean ± SD).*

Items	TMEF	TDF	*W*	*P*
TN (g/kg)	2.73 ± 1.20	1.81 ± 0.84	241	0.001
TP (g/kg)	1.14 ± 0.60	0.30 ± 0.10	12	<0.001
AN (mg/kg)	246.50 ± 198.71	80.23 ± 23.62	78	<0.001
AP (mg/kg)	14.80 ± 11.32	18.62 ± 6.92	691.5	0.001
Air temperature (°C)	20.90 ± 2.50	18.02 ± 3.13	0	<0.001
PAR(μmol/m^2/sec)	2.54 ± 0.80	29.50 ± 15.61	928	<0.001

Differences in environmental conditions were compared with Wilcoxon's rank tests. TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; OM, organic matter; Tem, mean daily air temperature; PAR, photosynthetically active radiation; CV, coefficient of variation.

For the TDF, C score and V ratio values for the species with the four abundance classes were lowest and highest, respectively, at the 20 m or 30 m plot scale (Fig. 2A and C), indicating that these species have the strongest, most significant aggregation patterns at this scale.

CO-OCCURRENCE PATTERN FOR SPECIES WITH DIFFERENT DIAMETER CLASSES.—At 5 m plot scales, species with the three diameter classes in TMEF had significantly higher C score values and lower V ratio values than expected by chance (Fig. 3B and D), which indicates significant segregation at these scales. However, at 20 m and 30 m plot scales, species in the three diameter classes in TMEF had no obvious co-occurrence patterns at these two scales (Fig. 3B and D).

In the TDF, species with the three diameter classes had significantly lower C score values and higher V ratio values than expected by chance at the 30 m plot scale (Fig. 3A and C), which indicates that these species are significantly aggregated at these two scales.

DISCUSSION

OVERALL CO-OCCURRENCE PATTERNS.—In TMEF, tests examining all species (*i.e.*, trees, shrubs and lianas) (Figs. 1, S2, and S3), as well as those examining different tree species abundance and dbh classes, produced evidence of significant species segregation at the two smaller plot sizes (Figs. 2B, D, 3B, and D). In TDF, the three types of tree species, shrub species and liana species were significantly aggregated at 20 m and 30 m scales (Figs. 1, 2A, C, 3A, C, S2 and S3). This supports our hypotheses that species in two tropical cloud forests differing in abiotic stress would exhibit different patterns of plant species co-occurrence and that patterns would be scale-dependent. However, contrary to our expectation, analysis by different abundance and diameter classes produced similar patterns, indicating that co-occurrence in these tropical cloud forests is independent of plant abundance and size.

SEGREGATED PATTERNS IN TMEF.—The fact that tree species, shrub species and liana species in TMEF are all significantly segregated suggests that competition is an important driver of community assembly (Figs. 1, 2B, D, 3B and D, S2 and S3). They may be competing for soil resources, since TMEF soil was rich in both N and P (Table 1), and for space, as suggested by the larger tree height and lower tree density in TMEF (Long *et al.* 2011b). Competition is often important in resource-rich conditions (Carlyle *et al.* 2010). Co-occurrence patterns observed here are consistent with previous work examining size-distance regressions to assess the importance and intensity of competition in this forest (Long *et al.* 2013). Species segregation was strongest at smaller scales, consistent with the view that competition occurs at small scales (*e.g.*, Weiher & Keddy 1995, Zhang *et al.* 2009, Matesanz *et al.* 2011). At larger plot sizes in TMEF, we observed no significant patterns of co-occurrence, suggesting no effect of species interactions on species distribution at large scales (Zhang

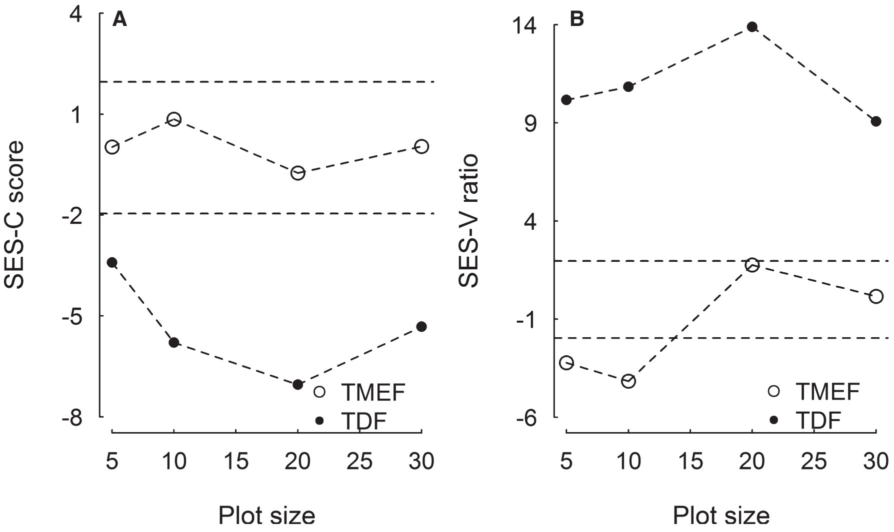

FIGURE 1. Changes in co-occurrence patterns across plot sizes (in m wide for square plots) in tropical dwarf forests (TDF) and tropical montane evergreen forests (TMEF) when all species are included in analysis. SES indicates the standard effect size of the null model test (*z*-score). The SES values at the 95% confidence interval fall between −1.96 and 1.96. C score indicates the checkerboard score of the presence–absence matrix. V ratio indicates the variance ratio. The SES values for C score greater than 1.96 (observed > expected) and less than −1.96 (observed < expected) indicates a significant species segregation and aggregation respectively; while the SES values for V ratio greater than 1.96 (observed > expected) and less than −1.96 (observed < expected) indicates a significant species aggregation and segregation respectively.

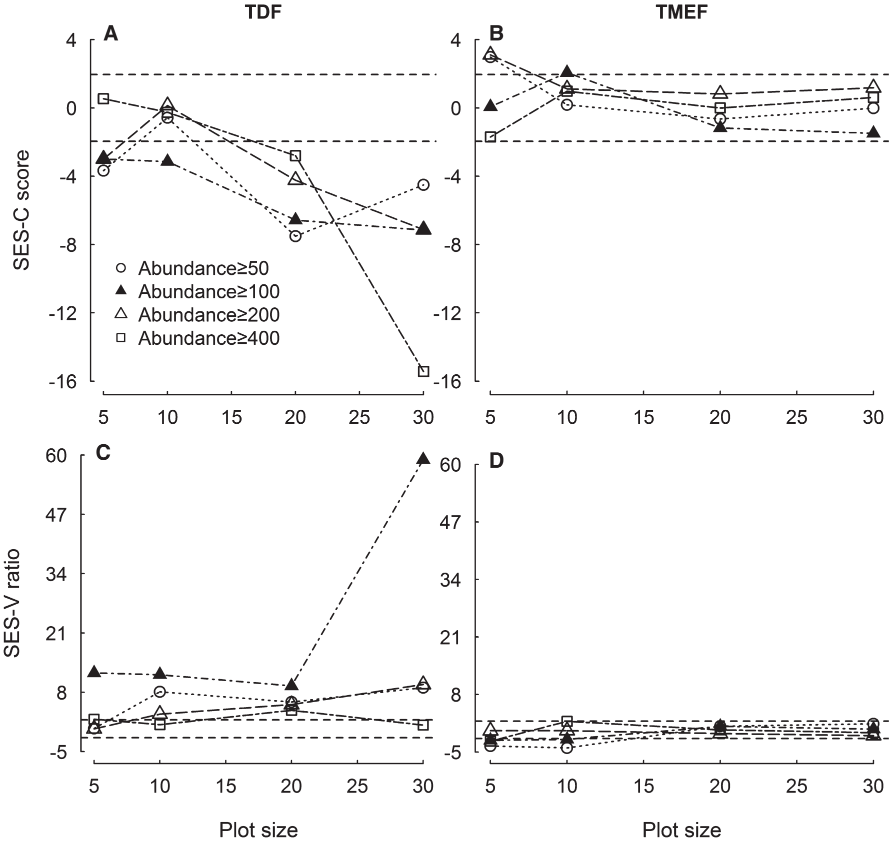

FIGURE 2. Changes in species co-occurrence patterns for different abundance classes in relation to plot size (in m wide for square plots) in tropical dwarf forests (TDF) and tropical montane evergreen forests (TMEF). SES values, C-scores and V ratio as in Fig. 1.

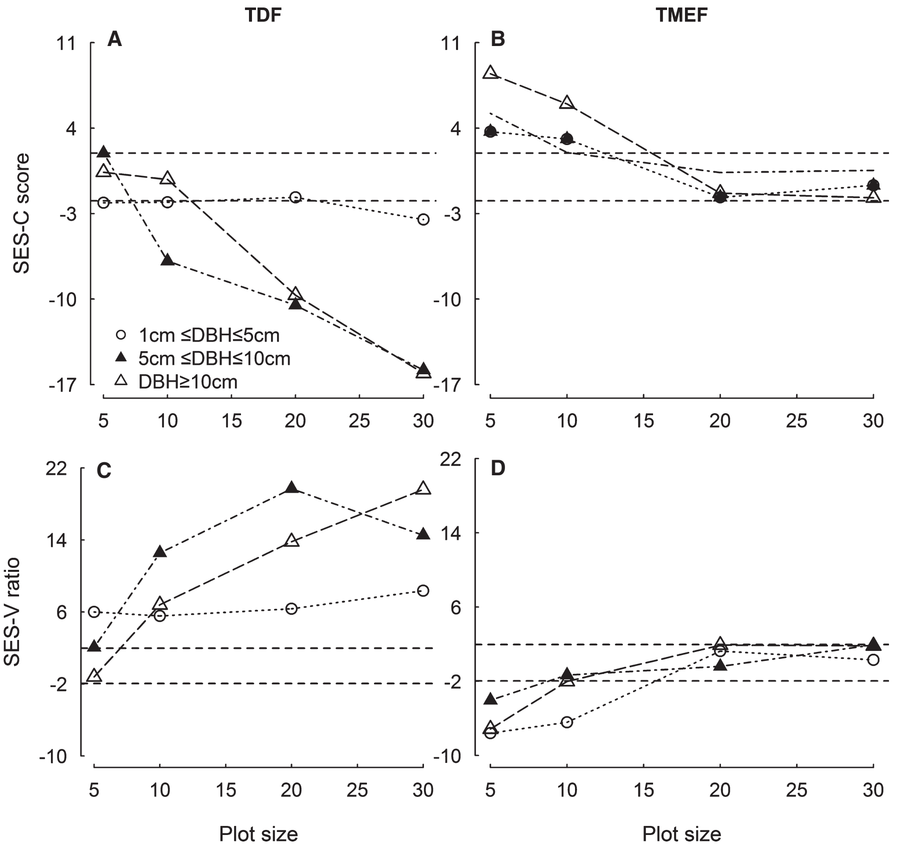

FIGURE 3. Changes in species co-occurrence pattern at different dbh classes in relation to plot size (in m wide for square plots) in tropical dwarf forests (TDF) and tropical montane evergreen forests (TMEF). SES values, C-scores and V ratio as in Fig. 1.

et al. 2009) and supporting the idea that species co-occurrence patterns vary with plot size (Weiher & Keddy 1995, Petit & Fried 2012). These results, in combination with previous work (Grime 1973, Adams 2007), make it clear that competition plays a critical role in determining forest community structure in TMEF.

AGGREGATED PATTERNS IN TDF.—In TDF, tree species, whether analysed alone, in abundance or diameter classes, or in combination with shrub and liana species positively co-occurred more than expected by chance at 20 m and 30 m scales (Figs. 1, 2A, C, 3A and C, S2 and S3), indicating that these species are significantly aggregated in this forest system. Species aggregation can be caused by microhabitat heterogeneity, such as the variability in forest-floor micro-relief (Armas *et al.* 2012), light (Holz *et al.* 2002) and soil properties (Roiloa & Retuerto 2006). In this study, however, species in TDF are under long-term air temperature stress (Table 1, Long *et al.* 2011a and b, Long *et al.* 2015). Species living under abiotic stress in TDF may survive and stably coexist by facilitative interactions that improve the abiotic and biotic conditions of neighbours (Choler *et al.* 2001, Callaway 2007, Holmgren & Scheffer 2010, Long *et al.* 2013). Such amelioration of the non-resource environment by neighbouring organisms might be more conducive to plant growth than competition for resources (Callaway *et al.* 2002). Non-resource stresses, such as low temperatures, strong winds and disturbance, may potentially result in species facilitation in TDF for three reasons: first, some neighbouring plant species in TDF may ameliorate the temperature and general microclimate for other surrounding plants/species, improving growth and reproduction. This has been demonstrated by Choler *et al.* (2001), who measured both the inside and outside temperatures of moderately bare subalpine graminaceous plant communities, and found significant differences in temperatures inside and outside local communities during the growing periods. Second, the ‘safety island’ or ‘forest belt’ a given species creates can buffer neighbours from harsh winds, helping seedling regeneration (Billings 1969, Minnich 1984). Third, a large range of surrounding vegetation layers (*e.g.*, tree or shrub layers) usually forms. These layers can improve the environmental conditions for plants by ameliorating soil conditions, enhancing soil stability and blocking harmful disturbances (Wilson & Agnew 1992, Callaway 1995, Jones *et al.* 1997). This study, therefore, supports our previous research findings that species assembly in this community proceeds via facilitation under environmental stress (Long *et al.* 2013).

We observed species aggregation in TDF mainly at large plot sizes, but not at small scales (Figs. 1, 2A, C, 3A, C, S2 and S3), further demonstrating that the species co-occurrence patterns are scale-dependent (Petit & Fried 2012). However, our results contrast with those of Zhang *et al.* (2009), who found that temperate forest species were neither significantly aggregated nor segregated at large plot sizes (*e.g.*, 20 m × 20 m). Species aggregation observed at larger scales may be driven by abiotic patchiness that reflects differential adaptation by various groups of species. Alternatively, facilitation may manifest at this scale as trees ameliorate the stressful environment only when larger in size, meaning this may only be apparent when plot sizes are sufficiently large to span the scale of environmental amelioration.

In this study, the Sørensen similarity coefficient between TMEF and TDF was 0.73, indicating that the two forest types share most forest species. Thus, different species co-occurrence patterns between TMEF and TDF probably resulted from differences in biotic interactions mediated by divergent abiotic conditions (Table 1). For example, low air temperature in TDF may lead to the facilitative interactions among species, whereas high soil resources in TMEF may lead to a greater importance of competitive sorting. The species continuum along soil resource and temperature gradients in these two tropical cloud forests appears to result from both competition and facilitation, consistent with the stress gradient hypothesis (Callaway *et al.* 2002).

In conclusion, we find that species in two tropical cloud forests exhibit different co-occurrence patterns. These patterns were scale-dependent, but were not dependent on specific abundance or size classes of species. Specifically, species in TMEF were significantly segregated at the two smallest plot sizes; in combination with previous research, this segregation appears to be linked to competitive assembly. By contrast, species in TDF were significantly aggregated at the two largest plot sizes, most likely the result of facilitative interactions that ameliorate temperature and soil nutrient stress.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Location of the studied tropical montane evergreen forests (TMEF; the solid triangle) and tropical dwarf forests (TDF; the solid point) in Bawangling Nature Reserve (BNR) in Hainan Island, China.

FIGURE S2. Changes in co-occurrence pattern for shrub species in relation to plot size in tropical dwarf forests (TDF) and tropical montane evergreen forests (TMEF).

FIGURE S3. Changes in co-occurrence pattern for liana species in relation to plot size in tropical dwarf forests (TDF) and tropical montane evergreen forests (TMEF).

TABLE S1. *Surveyed plant species in tropical dwarf forest.*

TABLE S2. *Surveyed plant species in tropical montane evergreen forest.*

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