



# Community assembly in a tropical cloud forest related to specific leaf area and maximum species height

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## Keywords

Ecological filtering; Environmental gradient; Limiting similarity; Plot size; Species co-existence

## Nomenclature

Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China 2004)

Received 24 February 2014

Accepted 21 October 2014

Co-ordinating Editor: Sándor Bartha

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## Introduction

Ecologists are increasingly recognizing that variation in functional traits can contribute to community assembly (Weiher & Keddy 1999; McGill et al. 2007; Houseman & Gross 2011; Shipley et al. 2012). Approaches that focus on the role of functional variation among individuals (Paine et al. 2011) and species (Weiher et al. 1998) can contribute to our understanding of the origin of existing trait variation, and quantify the filters that constrain species

## Abstract

**Question:** We tested whether co-existing tree species in tropical dwarf forests were deterministically assembled along gradients of air temperature, relative humidity and light availability, according to two important functional traits, specific leaf area (SLA) and maximum species height ( $H_{\max}$ ).

**Location:** Tropical montane cloud forest, Bawangling Nature Reserve, Hainan Island, south China.

**Methods:** Null model analyses were used in conjunction with trait and species composition data collected to test our hypotheses at four plot sizes (25 m<sup>2</sup>, 100 m<sup>2</sup>, 400 m<sup>2</sup> and 900 m<sup>2</sup>), addressing whether the consistent importance of variation in SLA and  $H_{\max}$  extends to these unique forests, as well as theoretical predictions concerning how patterns change with plot size.

**Results:** Low SLA species were significantly over-represented within forest communities for the two largest plot sizes, and taller-growing tree species were over-represented across all four plot sizes. Plot-level analyses indicated that low SLA species were associated with lower temperatures.

**Conclusions:** Our results show that tropical dwarf forests are deterministically assembled with respect to these two traits, and are consistent with other studies indicating that SLA responds to abiotic filters. Co-existing tree species were not significantly divergent for these two traits, indicating that variation in these two traits among trees does not contribute to niche differences (i.e. limiting similarity) and therefore co-existence within forest plots. Finally, our study demonstrates that patterns of community assembly change with plot size; however, trait convergence did not increase with plot size as previously predicted.

membership and organization within natural communities (Houseman & Gross 2011; de Bello et al. 2012; Götzenberger et al. 2012).

A common approach to understanding the importance of particular traits combines field data and null models to test whether co-existing species possess non-random collections of important traits (Weiher et al. 1998; Franzén 2004; Stubbs & Wilson 2004; Kraft et al. 2008; Schamp & Aarssen 2009; Dante et al. 2013). For example, maximum species height ( $H_{\max}$ ) and specific leaf area (SLA) have

been associated with competitive vigour and relative growth rates (Poorter & Evans 1998; Westoby 1998; Cornelissen et al. 2003; but see Poorter et al. 2008 for a more complex view of variation in SLA), and several studies have found evidence that these traits play significant roles in plant community assembly (Weiher et al. 1998; Kraft et al. 2008; Schamp & Aarssen 2009; Campetella et al. 2011; Cleland et al. 2011; Laliberté et al. 2012; Spasojevic & Suding 2012; Wilson & Stubbs 2012).

Null models have been commonly used to assess whether traits reflect niche differentiation (i.e. limiting similarity; MacArthur & Levins 1967), with divergence (over-dispersion) or regular spacing of traits taken as evidence of niche differentiation. Trait convergence, by contrast, has been generally taken as evidence of environmental filtering that results in increased similarity among co-existing species (Weiher & Keddy 1995; Díaz et al. 1998; Weiher et al. 1998; Grime 2006); however, it has also been noted that competition may result in trait convergence if one end of the trait spectrum (e.g. large maximum height) is competitively superior (Grime 2006; Schamp et al. 2008; Mayfield & Levine 2010). Because of the potential for multiple mechanisms contributing, environmental filtering is more strongly supported when plot-level effect sizes of null model tests are correlated with a particular abiotic gradient (Schamp & Aarssen 2009; Schamp et al. 2010). Finally, while measures of trait spread are commonly explored, a competitive advantage within the trait spectrum may also contribute to non-random differences in the mean trait value among co-existing species, with one end of the trait spectrum tending to be over-represented relative to null expectations (Grime 2006; Schamp & Aarssen 2009).

Null model studies have produced evidence for trait divergence in sand dune communities for some traits (Stubbs & Wilson 2004), and also among wetland communities (Weiher et al. 1998); however, other studies have found no evidence of these patterns for particular sets of traits (Franzén 2004; Schamp et al. 2008) and, in general, evidence of divergence has been rare (Götzenberger et al. 2012). At this point, too few studies have been done to assess the generality of observed patterns or to understand the potential for different traits to contribute to these patterns in different systems.

It is possible that both competitive and environmental filtering work simultaneously on different traits in the same plant community (Kraft et al. 2008; Bernard-Verdier et al. 2012; Wellstein et al. 2014). Weiher et al. (1998) found that species height, shoot biomass, unit leaf area and stem diameter were significantly divergent, while crown cover, height plasticity and ability to spread were convergent among wetland sites. Furthermore, a trait may be convergent at one end of an abiotic gradient but divergent

at another (Schamp & Aarssen 2009; Kunstler et al. 2012; Spasojevic & Suding 2012). Patterns of trait filtration can also vary with plot size. Stubbs & Wilson (2004) and Schamp et al. (2008, 2011) demonstrated that different patterns may be observed when different plot sizes are examined. It was predicted that trait convergence would be increasingly prominent in larger plot sizes (Weiher & Keddy 1995), where the impact of ecological filtering will be increasingly evident compared to smaller scales, at which competition should play a greater role. This prediction is also in line with suggestions that small-scale abiotic variation may be less important in community assembly as the grain of abiotic variation becomes smaller than the foraging areas of constituent species (Tamme et al. 2010), and as mass effects may obscure abiotic filtering at smaller scales or in heterogeneous communities (Lundholm 2009). At this time, however, the number of studies that have considered patterns across multiple plot sizes is insufficient to address this prediction.

Tropical dwarf forest is an unusual type of montane cloud forest (Aldrich et al. 1997). Trees in these forests are typically deformed, elfin and covered in epiphytes. Environmental conditions are characterized by low air temperature, strong winds, frequent fog and relatively high levels of ultraviolet radiation compared with lower-altitude forests (Bruijnzeel & Hamilton 2000). These are highly diverse communities, including endemic and threatened species (Bubb et al. 2004; Eisermann & Schulz 2005), and may experience unique community assembly processes. The small stature of trees made it possible for us to accurately measure two important traits (SLA and  $H_{\max}$ ) for all co-occurring tree and shrub species. Based on previously published work (Ackerly & Cornwell 2007; Schamp & Aarssen 2009; Paine et al. 2011; Spasojevic & Suding 2012), we predicted that variation in these two important functional traits will play a significant role in assembling plant species within tropical cloud forest communities.

Specific leaf area is an important functional trait that has been related to specific ecophysiological differences (e.g. photosynthetic rate, Cornelissen et al. 2003; relative growth rate, Poorter & Evans 1998), and to the assembly of natural communities (Weiher et al. 1998; Campetella et al. 2011; Wilson & Stubbs 2012). Other research suggests that interspecific differences in SLA are related to variation in abiotic conditions (Ackerly & Cornwell 2007; Campetella et al. 2011; Spasojevic & Suding 2012). Maximum species height, which has been associated with the ability to compete for light resources (Gaudet & Keddy 1988; Falster & Westoby 2003; but see Aarssen et al. 2006; Schamp et al. 2013), is recognized as one of a few key plant species functional traits (Westoby 1998) and can contribute to community assembly in forest systems (Schamp & Aarssen 2009). Because both  $H_{\max}$  and SLA are recog-

nized as playing a consistent role in both competitive assembly and habitat filtering, these are ideal traits for exploring trait-based assembly rules in abiotically stressful, vertically structured tropical montane forests.

In this study, we addressed three questions. First, we tested whether co-existing species in tropical cloud forests, which vary with respect to temperature and water availability, are deterministically assembled with respect to SLA and  $H_{\max}$ . Second, we tested for evidence of environmental filtering by testing whether plot-level assembly patterns were correlated with variation in air temperature, relative humidity and light availability. Finally, we tested the prediction that trait-based assembly patterns are increasingly convergent in larger plot sizes (Weiher & Keddy 1995) by examining how patterns of assembly differ across four plot sizes.

## Methods

### Study sites

This study was conducted in the tropical cloud forest of Bawangfeng Mountain (BWMF), including Songlinding Mountain (19°05'00.2" N, 109°12'41.1" E) and Yajiasong Mountain (19°05'17.4" N, 109°12'42.6" E), in the Bawangfeng Nature Reserve (BNR; 18°50'–19°05' N, 109°05'–109°25' E), Hainan Island, south China. Tropical cloud forest is composed of primary old growth forest (no history of human disturbance) ca. 0.40 km<sup>2</sup> in area, mainly distributed as mountaintop islands starting above altitudes of 1250 m. The mean daily air temperature in the rainy season (May–Oct) ranges from 16.25 to 20.57 °C, and the mean daily relative humidity in the rainy season ranges from 87.88% to 100% (Long et al. 2011a). Soils are montane meadow soils developed from sandstone (Hu & Li 1992). The study forest is located on an eastern slope with inclination ranging from 36 to 45°. It has an average tree height of 4.79 ± 2.80 m, a density of 9633 stems ha<sup>-1</sup>, a basal area of 54 m<sup>2</sup> ha<sup>-1</sup> and total of 139 tree species (trees ≥1 cm DBH). Dominant tree species include *Distylium racemosum* Sieb. & Zucc., *Symplocos poilanei* Guill., *Syzygium buxifolium* Hook. et Arn., *Cinnamomum tsoi* Allen, *Engelhardtia roxburghiana* Wall. and *Rhododendron moullainense* Hook. f.

### Data collection

Vegetation and environmental data were collected from square plots of four sizes (25 m<sup>2</sup> – 120 plots; 100 m<sup>2</sup> – 42 plots; 400 m<sup>2</sup> – 22 plots; 900 m<sup>2</sup> – 19 plots) within the cloud forest of BWMF, where altitude ranged from 1313.24 to 1395.24 m. There were ten 900-m<sup>2</sup> plots distributed in Songlinding Mountain and nine 900-m<sup>2</sup> plots distributed in Yajiasong Mountain; the distance between

each two plots was >50 m. Before the vegetation survey, each 900 m<sup>2</sup> was divided into 36 plots of 5 m × 5 m. This helped us randomly choose the 400-m<sup>2</sup> plots inside these 19 larger plots (Appendix S2, Fig. A2). After the species richness and distance between each 20 m × 20 m plot were measured, the autocorrelation indices for these plots were calculated. This analysis showed that the 22 plots (400-m<sup>2</sup> scale) were not spatially autocorrelated (plots in Songlinding Mountain,  $r = 0.03$ ,  $P = 0.32$ ; plots in Yajiasong Mountain,  $r = -0.08$ ,  $P = 0.67$ ). Similarly, 100-m<sup>2</sup> plots were randomly chosen inside the 400-m<sup>2</sup> plots (Appendix S2, Fig. A3), and the 25-m<sup>2</sup> plots were randomly chosen inside the 100-m<sup>2</sup> plots (Appendix S2, Fig. A4). We measured the height of all individual trees and shrubs (height of the highest sucker/shoot) appearing in the study plots (excluding those clearly suckering from other trees), with DBH ≥1 cm using a clinometer (base to highest point on the tree); species names were recorded in accordance with Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China 2004). Average values per species were calculated using measures from all plants of each species across plots.

Specific leaf area and  $H_{\max}$  for each species were determined as the average calculated across all measures for each individual plant of that species in each of the 900-m<sup>2</sup> plots. Trait measurements therefore spanned the gradients along which each species was found. The number of samples contributing to this mean varied with species abundance; on average, species means were derived from 11 samples. SLA was determined using recently expanded sun leaves (current year's growth) of each species (DBH ≥1 cm); all measurements were taken within the study area. Leaf area was quantified for four to six freshly collected leaves per sampled tree (all adult plants sampled per species per plot) using a leaf area meter (Li-Cor 3100C Area Meter; Li-Cor, Lincoln, NE, US; Cornelissen et al. 2003). Leaves were then dried to a constant weight at 70 °C for at least 3 d and weighed to the nearest 0.01 g. From these measurements, SLA (mm<sup>2</sup> mg<sup>-1</sup>) was calculated.

Relative humidity (%) and air temperature (°C) were measured in 400-m<sup>2</sup> plots during the rainy season (May–Oct 2009). Both were logged hourly from May to October at 1.3 m above the soil and recorded with HOBO Pro Temp/RH dataloggers (U23-001. Onset, Bourne, MA, US; Lebrija-Trejos et al. 2010) placed in the centre of 22 of our 20 × 20 m study plots. We have shown that there is a gradient of relative humidity and air temperature within BWMF (Long et al. 2011b). From these measurements, the mean daily temperature, maximum daily temperature, minimum daily temperature, mean daily relative humidity, maximum daily relative humidity and minimum daily relative humidity were calculated for each plot.

Photosynthetic photon flux density (PPFD) was measured with two Field Scout Quantum Meters (3415FSE; Spectrum Technologies, Schenectady, NY, US) between 10:00 and 12:00 h in 3 d of June 2009, at 1.3 m above soil level, both under the forest canopy and out in the open (i.e. without canopy cover) in each plot. Then PPFD at 1.3 m above soil was calculated as the fraction of that measured under the canopy relative to in the open area without canopy; the percentage reduction of PPFD was calculated as an indicator of percentage light intercepted by the forest canopy layer. Five measurements were randomly taken in each plot each day.

### Data analysis

Plant composition (presence–absence) and trait data were used in conjunction with a null model to assess whether observed trait distributions within the community differed from what would be expected if traits were assigned randomly across study species (Stubbs & Wilson 2004; Schamp et al. 2008). Our null model analyses used several test statistics to test evidence that species are filtered into these communities non-randomly with respect to SLA and  $H_{\max}$ . We investigated four trait distribution measures (test statistics) as community assembly processes may alter trait distributions in several ways (e.g. Weiher et al. 1998; Stubbs & Wilson 2004; Cornwell et al. 2006; Kraft et al. 2008; Schamp & Aarssen 2009; Spasojevic & Suding 2012). (1) Mean: this tests whether the mean value for a particular trait among co-existing species is higher or lower than expected by chance. If mean  $H_{\max}$  among co-existing species is higher than expected under the null model, this suggests a size advantage (Schamp & Aarssen 2009). (2) Skewness: this is a measure of distribution symmetry and inequality. Differences in skewness relative to what is expected under the null model can indicate whether species with higher or lower trait values are over- or under-represented in plots compared to what is expected. For example, if plot-level skewness in mean  $H_{\max}$  is lower than expected under the null model, this would indicate a subtle shift such that in combination with a higher mean  $H_{\max}$  of co-existing species suggests that larger species are favoured (Schamp & Aarssen 2009). (3) Mean nearest trait distance (meanNTD): this is calculated as the mean Euclidean trait distance between each species and its closest neighbour (in trait value) within plots, reflecting how densely packed co-existing species are with respect to a trait of interest (Weiher et al. 1998; Schamp et al. 2008). Higher meanNTD values than expected by chance indicate that co-existing species are divergent with respect to that particular trait, as is predicted under limiting similarity; while lower values indicate convergence (Weiher et al. 1998; Stubbs & Wilson 2004). (4) Variance in nearest trait dis-

tance (varNTD): this is a measure of the variance in Euclidean distances between each species and its nearest neighbour in trait space within a plot (standardized to the trait range for that plot), and a measure of the evenness of species packing. Values of varNTD that are lower than expected under the null model are generally interpreted as evidence of limiting similarity (Schamp et al. 2008; Schamp & Aarssen 2009). These values were used for each plot to assess plot-level assembly, while mean values across plots were used to assess community-level assembly rules (Weiher et al. 1998; Stubbs & Wilson 2004; Schamp et al. 2008; Dante et al. 2013).

When selecting a null model with which to test a hypothesis, it is essential to keep every feature of the randomized data as it is in the observed data except the feature that the study aims to test (Tokeshi 1986). In the chosen null model, species richness per plot and species occurrences within 25 m<sup>2</sup>, 100 m<sup>2</sup>, 400 m<sup>2</sup> and 900 m<sup>2</sup> plot sizes remain fixed; only trait values were randomized among species such that within-species relationships between these two traits were conserved (Stubbs & Wilson 2004; Schamp et al. 2008). That is, the actual trait values measured for species within these communities were retained, but the traits were assigned to species at random without replacement within the null model (Cornwell et al. 2006; Schamp et al. 2008; Schamp & Aarssen 2009; Spasojevic & Suding 2012). This null model is recognized as having good type I and type II error rates compared to some others (Hardy 2008). Approaches that conserve trait abundance relationships imply that we know that these traits contribute to patterns of abundance in the community, while the approach we use allows that traits are independent of abundance within the community (e.g. Dante et al. 2013).  $H_{\max}$  or SLA are not related to species abundance in this study community (Spearman correlation test; 25 m<sup>2</sup>: SLA,  $P = 0.52$ ;  $H_{\max}$ ,  $P = 0.40$ ; 100 m<sup>2</sup>: SLA,  $P = 0.90$ ,  $H_{\max}$ ,  $P = 0.24$ ; 400 m<sup>2</sup>: SLA,  $P = 0.33$ ,  $H_{\max}$ ,  $P = 0.44$ ; 900 m<sup>2</sup>: SLA,  $P = 0.87$ ;  $H_{\max}$ ,  $P = 0.36$ ). We generated distributions of each test statistic with 9999 random permutations of the trait matrix (10 000 when actual test statistics are included in the distribution), and determined the probability test statistics for each trait differed from that expected under the null model. Because test statistics can be either greater or less than expected, two-tailed  $P$ -values were calculated for each test statistic/trait combination. All  $P$ -values were calculated as:  $P = \text{MIN} [2S/(10\ 000), 2L/(10\ 000)]$ , where  $S$  and  $L$  refer to the number of null test statistics greater than or equal to, or less than or equal to, the measured test statistic (Bersier & Sugihara 1997).

We also examined standardized effects ( $z$ -scores) for each plot relative to the null expectation for that plot.

Standardized effects for each forest plot and each test statistic were calculated as  $(O - M)/S$ , where  $O$  is the observed value for each test statistic and forest plot,  $M$  and  $S$  are the mean and SD, respectively, for each test statistic across 9999 randomizations of the trait distribution for that plot. As used here, the standardized effects can be either positive or negative, indicating the magnitude and direction of difference in trait distributions compared to null model expectations. The use of standardized effect sizes served two functions; first, it revealed how many plots showed significant patterns of trait-based assembly, and second, plot-level scores were correlated with plot-level abiotic conditions for the 400-m<sup>2</sup> plot size to assess the influence of gradients on trait-based assembly. Correlations between plot-level z-scores also indicate whether both competitive and ecological filtering are acting on a given trait simultaneously but at different ends of an abiotic gradient (Schamp & Aarssen 2009; Bernard-Verdier et al. 2012; Spasojevic & Suding 2012). Tests were completed with R 2.9.2 software (R Foundation for Statistical Computing, Vienna, AT).

## Results

### Variation in species richness and traits

The mean species richness per plot at 25 m<sup>2</sup>, 100 m<sup>2</sup>, 400 m<sup>2</sup> and 900 m<sup>2</sup> was  $12.56 \pm 3.01$ ,  $26.67 \pm 3.89$ ,  $44.36 \pm 5.10$  and  $55.00 \pm 6.12$ , respectively. Specific leaf area and  $H_{\max}$  both varied considerably among the 110 species examined, with SLA spanning one order of magnitude and variation in  $H_{\max}$  spanning two orders of magni-

tude; both trait distributions were positively skewed (Fig. 1).

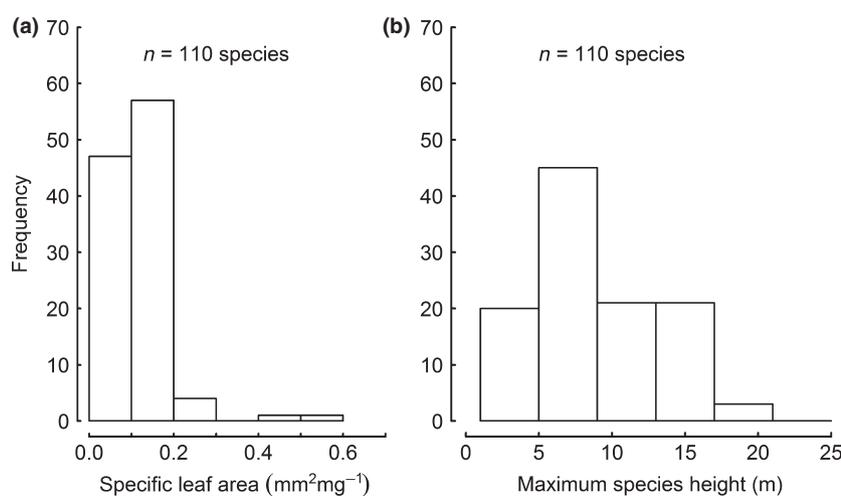
### Community assembly and plot size

Co-existing tree and shrub species had significantly lower mean SLA than expected at 400 m<sup>2</sup> and 900 m<sup>2</sup> plot sizes (Table 1), evidence of deterministic assembly based on this trait. The mean  $H_{\max}$  of co-existing tree and shrub species was significantly higher than expected by chance across all four plot sizes (Table 1), and distributions of  $H_{\max}$  among co-existing species were significantly less skewed than expected by chance at the three smallest plot sizes (Table 1). Both findings support the influence of  $H_{\max}$  on the assembly of species within tropical cloud forests. Our results indicate that trait distributions among co-existing species are more scale-dependent for SLA than for  $H_{\max}$ , although the influence of  $H_{\max}$  may be changing subtly with increasing plot size.

Coexisting species were neither significantly divergent nor convergent for either trait, providing no evidence that these traits independently reflect niche differences among species in these habitats (Table 1).

### Plot-level assembly patterns and abiotic conditions

In 400-m<sup>2</sup> plots, the plot-level standardized effect of null model tests for the mean SLA among co-existing species was positively correlated with plot-level measures of mean daily air temperature and maximum daily air temperature (Fig. 2a,b), but not significantly correlated with PPFD ( $\rho = -0.30$ ,  $P = 0.17$ ) or relative humidity ( $\rho = -0.03$ ,



**Fig. 1.** Frequency histograms highlighting the within-community variation in species traits with respect to: (a) species specific leaf area; and (b) maximum species height, within the target tropical cloud forest. Within-species variance in SLA ranged from 0.001 mm<sup>2</sup> mg<sup>-1</sup> to 0.531 mm<sup>2</sup> mg<sup>-1</sup> (CV%: 54.19%), and for  $H_{\max}$  between 1.60 and 35.0 m (CV%: 50.96%).

**Table 1.** Results of null model tests. The results of null model tests exploring whether observed trait distributions for specific leaf area (SLA) and species maximum height ( $H_{\max}$ ) are convergent/divergent (MeanNTD, VarNTD) or more or less skewed than expected by chance (Mean, Skewness) in montane tropical forests, across four plot sizes (25 m<sup>2</sup> (120 plots), 100 m<sup>2</sup> (42 plots), 400 m<sup>2</sup> (22 plots) and 900 m<sup>2</sup> (19 plots)). Community-level significant tests ( $\alpha \leq 0.05$ ) are presented in bold. The number of plots for which the observed test statistic is significantly larger or less than expected is presented in brackets.

Plot Size	Test Statistic	Specific Leaf Area			Maximum Species Height		
		<i>P</i>	Direction	Plots	<i>P</i>	Direction	Plots
25 m <sup>2</sup>	Skewness	0.94	–	(3,2)	<b>0.01</b>	<b>obs &lt; exp</b>	(0,9)
	Mean	0.66	–	(1,3)	<b>0.01</b>	<b>obs &gt; exp</b>	(40,0)
	MeanNTD	0.23	–	(5,0)	0.51	–	(0,0)
	VarNTD	0.68	–	(0,0)	0.78	–	(0,0)
100 m <sup>2</sup>	Skewness	0.78	–	(0,0)	<b>0.01</b>	<b>obs &lt; exp</b>	(0,10)
	Mean	0.076	–	(0,4)	<b>0.0008</b>	<b>obs &gt; exp</b>	(34,0)
	MeanNTD	0.25	–	(0,0)	0.88	–	(0,0)
	VarNTD	0.91	–	(0,0)	0.86	–	(0,0)
400 m <sup>2</sup>	Skewness	0.36	–	(0,0)	<b>0.01</b>	<b>obs &lt; exp</b>	(0,0)
	Mean	<b>0.005</b>	<b>obs &lt; exp</b>	(0,9)	<b>0.0007</b>	<b>obs &gt; exp</b>	(19,0)
	MeanNTD	0.25	–	(0,2)	0.29	–	(0,0)
	VarNTD	0.56	–	(1,0)	0.60	–	(0,0)
900 m <sup>2</sup>	Skewness	0.45	–	(0,5)	0.20	–	(0,0)
	Mean	<b>0.032</b>	<b>obs &lt; exp</b>	(0,5)	<b>0.002</b>	<b>obs &gt; exp</b>	(18,0)
	MeanNTD	0.49	–	(0,6)	0.47	–	(0,0)
	VarNTD	0.62	–	(0,0)	0.75	–	(0,0)

$P = 0.91$ ). Similarly, the plot-level standardized effects of null model tests of mean  $H_{\max}$  among co-existing species was positively correlated with percentage reduction of PPFD (Fig. 2c), such that plots with taller species were associated with high PPFD. These same plot-level effect sizes were not significantly correlated with plot-level variation in air temperature ( $\rho = -0.33$ ,  $P = 0.32$ ) and relative humidity ( $\rho = -0.08$ ,  $P = 0.73$ ). No other test statistics were significantly correlated with measures of plot-level abiotic conditions (Appendix S1).

## Discussion

### Community assembly and SLA and $H_{\max}$

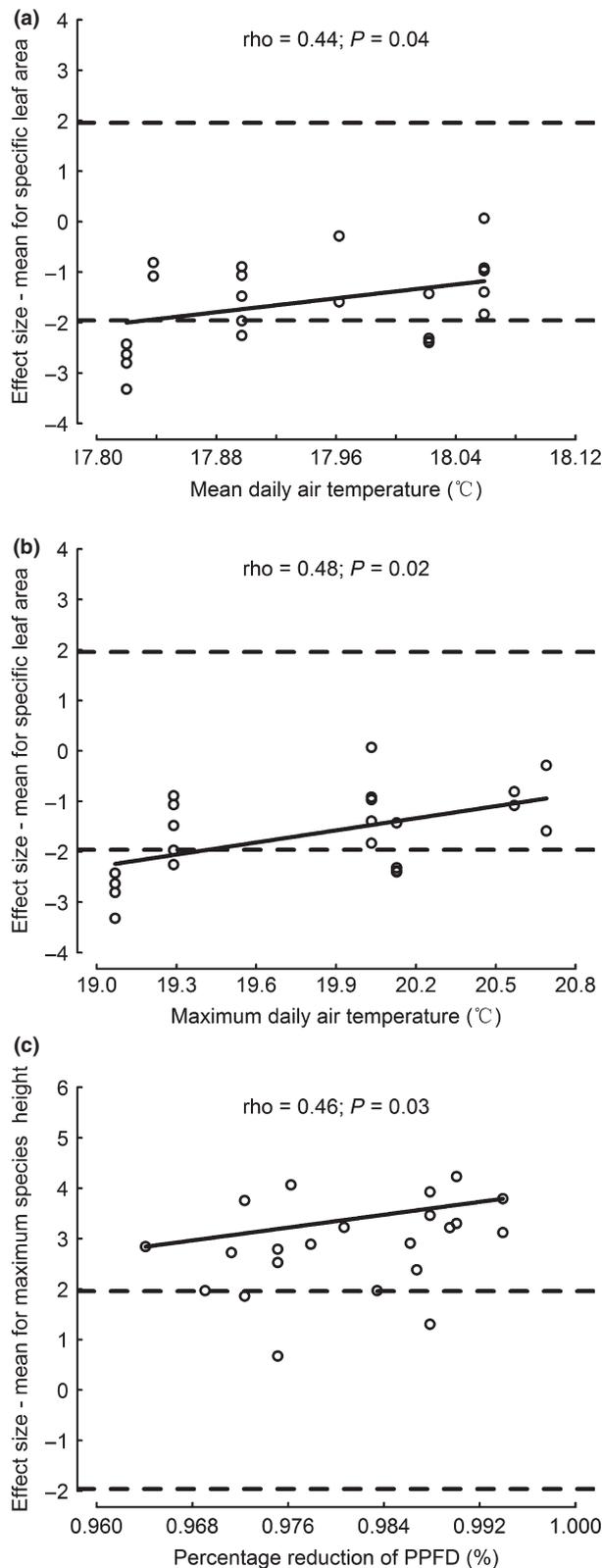
At the community scale, tree and shrub species in tropical cloud forest plots were deterministically assembled with respect to both species SLA (two largest plot sizes) and  $H_{\max}$  (Table 1), supporting predictions that functional traits play a role in determining the organization of species within natural communities (Weiher & Keddy 1995; McGill et al. 2007). Our results also support the growing body of literature indicating that SLA and  $H_{\max}$  are important traits driving assembly in many habitats, including wetlands (Weiher et al. 1998), sand dunes (Stubbs & Wilson 2004), temperate forests (Schamp & Aarssen 2009; Campetella et al. 2011), across broad swaths of chaparral and forest in California (Cornwell & Ackerly 2009), Ecuadorean rain forest (Kraft et al. 2008), tropical rain forests (Paine et al. 2011), alpine tundra (Spasojevic & Suding 2012),

and now montane tropical cloud forest. These two traits clearly contribute to ecologically meaningful species-level trait variation of plant species in general.

### Assembly rules for SLA

For the two largest plot sizes, co-existing species had a lower mean SLA than expected under our null model, indicating that in these communities, low SLA was significantly over-represented, and as may therefore be advantageous (Table 1). Intriguingly, while low SLA species appear to be favoured in general for these larger plots, high SLA species were still present within plots. Future work should focus on understanding the persistence of species with traits that appear to be disadvantageous; these species may represent transient or ‘satellite’ species (Hanski 1982; Gibson et al. 1999), perhaps supported by nearby environments to which they are more suited, and maintained via mass effects.

A number of studies have observed that variation in SLA is related to abiotic conditions such as water availability and temperature (Popma et al. 1992; Cornwell & Ackerly 2009; Poorter 2009), although evidence from tundra suggests that variation in SLA in low productivity systems may contribute to competitive filtering (Spasojevic & Suding 2012). The observed correlation between plot-level standardized effects of our null model tests for SLA and temperature for 400-m<sup>2</sup> plots (Fig. 2a,b) support this link between SLA and abiotic conditions. The fact



**Fig. 2.** Rank correlations between effect sizes for test statistic (i.e. mean value), and air temperature and percentage reduction of photosynthetic photon flux density (PPFD) with respect to **(a, b)** specific leaf area and **(c)** maximum species height in 400-m<sup>2</sup> plots. y-axes represented effect size (z-scores), a standardized measure of the degree to which the mean test statistic differed from that expected at random. Significant effect sizes ( $\alpha = 0.05$ ) for each mean test statistic are indicated when values for the plots (each data point is a forest plot) were more than 1.96 (observed > expected) or less than -1.96 (observed < expected). Significant boundaries are indicated with dashed horizontal lines at these values.

that plot-level standardized effects were correlated with both mean and maximum daily temperature in plots suggests that low temperature exerts a constraint on many trees and shrubs, allowing species with low SLA values to grow more successfully in cooler parts of this system (Callaway et al. 2002; Körner 2002; Long et al. 2011c). Thus, low SLA values appear to contribute to a stress tolerance strategy, organizing species across habitats that vary in temperature (Weiher & Keddy 1995; Kraft et al. 2008). Co-existing species may also be convergent for other traits related to temperature (e.g. leaf longevity, rate of leaf litter decomposition and mineral nutrient content of leaves; Körner 1989) such that lower SLA is associated with a suite of traits that contribute to greater fitness in cooler parts of these forests.

Community assembly related to SLA does not appear to be related to daily relative humidity and irradiance (transmission through canopy), at least for 400-m<sup>2</sup> plots. It is likely that the influence of water availability and solar irradiance are negated by the high mean daily relative humidity (>95%; Holder 2004), and abundant solar irradiance in tropical dwarf forest (Bubb et al. 2004), which is higher than those at lower-altitude tropical forests (Hu & Li 1992). Additionally, variation in light transmission through the canopy may also vary predictably with topography, which was not accounted for in the current study.

#### Assembly rules for $H_{\max}$

The mean  $H_{\max}$  of co-existing tree and shrub species was higher than expected by chance for all plot sizes, while skewness in  $H_{\max}$  was lower than expected for all but the largest plot size (i.e. the right tail of the distribution was not as pronounced); together, these results indicate that taller species were over-represented within plots (Table 1). This result implies that taller species have an advantage within these forests. However, as with SLA, species with small  $H_{\max}$  remain present (i.e. shifts in mean are not coincident with trait convergence). Future work will investi-

gate how shorter-stature species persist in this system, given the apparent advantage of being tall (e.g. Schamp et al. 2013; Schamp & Aarssen 2014).

The observed over-representation of tall species is consistent with research indicating that taller species may have an advantage in competition for light (e.g. Iwasa et al. 1985) and with findings for plant species within North American temperate forests (Schamp & Aarssen 2009). Because tree and shrub species with smaller  $H_{\max}$  values still grew in plots, any size advantage that may exist is necessarily weak or incomplete (Schamp & Aarssen 2009). Moreover, the fact that shorter species of tree and shrub are more common in our study system (Fig. 1) highlights the fact that small species are successful in these communities, a fact that is in conflict with the notion of a size advantage (Schamp et al. 2013). Thus, it is not clear that the explanation for the over-representation of tall tree and shrub species is strictly competitive. Alternative explanations include the possibility that species with smaller  $H_{\max}$  values have narrower niches than taller growing species (Schamp & Aarssen 2009), or that species with small  $H_{\max}$  values may specialize on small packages of light resources not captured by the canopy (i.e. physical space niches; Aarssen et al. 2006; Keating & Aarssen 2009).

Our understanding of these results for  $H_{\max}$  is improved by the fact that plot-level effect sizes for mean  $H_{\max}$  are positively correlated with percentage reduction of PPFD (Fig. 2c). This suggests that tall species are over-represented in plots in which there is a larger reduction in light through the canopy, and that opposing assembly processes operate along this gradient of PPFD. The fact that this over-representation of tall species is in plots with higher reductions in PPFD suggests that perhaps the presence of tall-growing trees and shrubs contributes to improved probability of canopy closure, either through dominance by tall species, or perhaps more likely, through the improved potential for vertical layering of vegetation when the top-most canopy is higher. Which explanation is more correct will depend on whether a more layered vegetation or a collection of species differing in mature size are more likely to contribute to more complete canopy closure. While our results are consistent with the findings of Schamp & Aarssen (2009) for temperate forests, they contrast with other findings that the mean  $H_{\max}$  of co-existing herbaceous plant species is no different from expected by chance in other non-forest systems (Schamp et al. 2008, 2011). Plot-level standardized effects for mean  $H_{\max}$  were not significantly correlated with mean daily temperature or humidity. However,  $H_{\max}$  is thought to be related to temperature when spatial resolution is broader (Moles et al. 2009); consequently, temperature may be relevant to the dispersion of species with respect to  $H_{\max}$  at larger plot sizes.

### Trait divergence and convergence

For all plot sizes, community-level tests produced no evidence that co-existing species were significantly divergent or convergent with respect to the two traits considered, and few plots at any plot-size showed significant divergence or convergence for these traits (Table 1). This pattern held when we further investigated similar patterns using RaoQ, an index of functional diversity that has proven powerful in some circumstances (Mason & de Bello 2013; Appendix S3). Trait divergence has been used to identify traits that contribute to niche differentiation among species and therefore co-existence. Consequently, species-level variation in SLA and  $H_{\max}$  alone do not clearly reflect niche differences among species within plots in this study system. Of course, co-existing species in this system may be divergent with respect to other traits that contribute to niche differences and limiting similarity.  $H_{\max}$  has previously been found to be neither convergent nor divergent in temperate forests (Schamp & Aarssen 2009), but has been found to be divergent for tree species in Neotropical forests (Swenson & Enquist 2009). In non-forest communities, there is some evidence that co-existing species may differ in  $H_{\max}$  more than expected by chance (Weiher et al. 1998; Spasojevic & Suding 2012). However, there is also evidence that co-existing species are neither significantly convergent nor divergent in  $H_{\max}$  than expected by chance in old-field communities (Schamp et al. 2008) and grassland communities (Schamp et al. 2011). While it is increasingly clear that species  $H_{\max}$  is an important plant functional trait (Westoby 1998), it is increasingly clear that its role varies with scale and community type. While convergence has been widely considered evidence of ecological filtering, our work demonstrates that such filtering can be revealed by non-random changes to other aspects of trait distributions (i.e. mean and skew) even in the absence of significant convergence (e.g. Schamp & Aarssen 2009).

### Community assembly and plot size

Ecological filtering of species with respect to SLA was confined to the two largest plot sizes considered, consistent with previous findings that plot size can influence the detection of trait-based assembly (Stubbs & Wilson 2004; Schamp et al. 2008, 2011; Table 1), and with predictions that ecological filtering will be more prominent at larger plot sizes (Weiher & Keddy 1995). Patterns for  $H_{\max}$  did not show the same clear dependency on plot size. This is consistent with predictions that only traits related to abiotically driven ecological filtering will be increasingly evident at larger plot sizes where abiotic variation generally plays a larger role in defining composition. While no specific

prediction has been set out, we predict that if deterministic assembly related to  $H_{\max}$  is driven by competition, the impact of this trait may decline at larger scales. This may be occurring in this study site, given that at smaller scales, both mean and skewness of  $H_{\max}$  are non-random, while only mean  $H_{\max}$  remains so at the largest plot size (Table 1). Clarification of the mechanism for non-random community assembly based on  $H_{\max}$  will clearly require more work.

## Conclusions

We found evidence of non-random trait-based assembly rules for tree and shrub species within tropical cloud forest. Species with high  $H_{\max}$  and low SLA values were significantly over-represented (Table 1) overall, suggesting that in these communities these traits are advantageous. Low SLA species were more over-represented in plots with lower temperature at the 400-m<sup>2</sup> scale (Fig. 2a,b), consistent with findings that SLA plays a role in adaptation to abiotic conditions. The role of  $H_{\max}$  is not driven by variation in temperature or relative humidity, but may play a role in competition among tree and shrub species. Finally, the role of SLA in community assembly was confined to the two largest plot sizes considered, a finding that conforms to theoretical predictions for traits related to abiotic stress (Weiher & Keddy 1995).

## Acknowledgements

We thank Xiusen Yang, Jinqiang Wang for help with fieldwork. This work was supported by the National Natural Science Foundation of China (31260109, 31270474 and 30430570), Hainan University Science Foundation for Youth (qnjj1161), Scientific Research Foundation of Hainan University (kyqd1201), Natural Science Foundation of Hainan Province (312064), Educational Commission of Hainan Province of China (key project Hjkj2012-03), Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05050206), and a National Sciences and Engineering Council of Canada grant to B. Schamp.

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## Supporting Information

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

**Appendix S1.** Frequency histograms highlighting the variation in air temperature, relative humidity and percentage reduction of PPFD, as well as rank correlations between standardized effects for test statistics and the above abiotic conditions with respect to specific leaf area (SLA) and maximum species height ( $H_{\max}$ ) in 400 m<sup>2</sup> plots.

**Appendix S2.** Plot design for the 5 m × 5 m, 10 m × 10 m, 20 m × 20 m and 30 m × 30 m plot size, as well as autocorrelation analysis for 20 m × 20 m plot size.

**Appendix S3.** A test of the trait-based community assembly using Rao's quadratic entropy, with respect to specific leaf area and maximum species height at the 5 m × 5 m, 10 m × 10 m, 20 m × 20 m and 30 m × 30 m plot size.