LETTER

Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings

María Natalia Umaña,[1]* Caicai Zhang,[2,3] Min Cao,[2] Luxiang Lin[2] and Nathan G. Swenson[1,2]*

Abstract

One of the few rules in ecology is that communities are composed of many rare and few common species. Trait-based investigations of abundance distributions have generally focused on species-mean trait values with mixed success. Here, using large tropical tree seedling datasets in China and Puerto Rico, we take an alternative approach that considers the magnitude of intraspecific variation in traits and growth as it relates to species abundance. We find that common species are less variable in their traits and growth. Common species also occupy core positions within community trait space indicating that they are finely tuned for the available conditions. Rare species are functionally peripheral and are likely transients struggling for success in the given environment. The work highlights the importance of considering intraspecific variation in trait-based ecology and demonstrates asymmetry in the magnitude of intraspecific variation among species is critical for understanding of how traits are related to abundance.

Keywords

Functional traits, relative growth rate, species relative abundance, tropical forest.

Ecology Letters (2015) **18**: 1329–1337

INTRODUCTION

Ecology is a discipline with few universal laws or consistent emergent patterns (Lawton 1999). Among these are the presence of few common and many rare species in communities (e.g. Preston 1948; MacArthur 1957). The relative consistency in this pattern across systems suggests shared foundational principles that determine community structure and dynamics (McGill *et al.* 2007; Morlon *et al.* 2009). Uncovering the mechanisms underlying patterns of species abundance distributions (SADs) therefore represents one of the grand challenges motivating a great deal of research in ecology (Brown 1995; Hubbell 2001).

An outstanding challenge for those studying SADs is that most hypotheses predict a 'hollow curve' shape, where most species are rare and few are dominant (McGill *et al.* 2007). Recent work has approached this problem by employing Maximum Entropy (MaxEnt) principles where multiple emergent ecological patterns (e.g. SADs, species area curves) can simultaneously be predicted using only a few constraints (e.g. Harte *et al.* 2008). For example, the shape of the SAD can be predicted with a high degree of accuracy (> 70% variation explained) by knowing the total number of individuals and species (White *et al.* 2012; Locey & White 2013). While this work impressively predicts the shape of the SAD, it is still unknown what factors control the commonness and rarity of individual species within the SAD. In other words, ecologists are still challenged by the question of: what causes a particular species to be common or rare?

The consideration of organismal function is likely key for understanding why some species are common while others are rare (McGill *et al.* 2006). Indeed, classic models of the SAD consider not just its shape, but also how it should be related to niche or resource axes (e.g. MacArthur 1957; Sugihara 1980). Given that functional traits are expected to be linked to resource use strategies and performance (e.g. Westoby *et al.* 2002), traits should be related to abundance (McGill *et al.* 2006). However, recent meta-analyses have shown that species traits are typically not correlated with relative abundances in communities indicating that linking traits and abundance is not a simple task (Murray *et al.* 2002). Additional investigations that rely on MaxEnt type approaches that include trait information (e.g. Shipley 2006; Shipley *et al.* 2006; Laughlin *et al.* 2012) have been used to predict the relative abundances. Although, some of this work has been criticised (Shipley *et al.* 2006) when the number of constraints imposed is high relative to the number of predicted values (Haegeman & Loreau 2008). In sum, community ecologists and macroecologists are still struggling to clearly link functional traits with abundance and ultimately performance.

A major outstanding question in trait-based community ecology is the relative importance of intraspecific variation and how incorporating such information may help us understand community structure and dynamics (e.g. Bolnick *et al.* 2011). For example, recent work has taken up this challenge by quantifying whether our perception of trait dispersion changes if we consider individual-level trait values (Paine *et al.* 2011) or by testing whether models that consider intraspecific trait distributions provide stronger predictions of

[1]*Department of Biology, University of Maryland, College Park, MD 20742, USA*

[2]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China*

[3]*University of Chinese Academy of Sciences, Beijing 100049, China*

Correspondence: E-mails: maumana@gmail.com; swenson@umd.edu

relative abundance compared to MaxEnt models utilising species level mean trait values (Laughlin *et al.* 2012). However, we have very few studies in the rapidly growing functional trait literature that examine how intraspecific variation itself is related to the abundance of a species. This is, perhaps, surprising given that trait variation among individuals within a population can alter interactions with other species and should therefore be key for understanding community dynamics (Van Valen 1965; Roughgarden 1972; Bolnick *et al.* 2003, 2011).

There are two main predictions for how trait variation within a species could be related to its abundance. First, in a highly heterogeneous environment, common species may be expected to be generalists with broad tolerances. Such species should be more variable or flexible in their traits allowing them to perform well under a variety of abiotic and biotic conditions, whereas rare species may be more phenotypically constrained or specialized on a spatially or temporally rare resource thereby limiting their ability colonize and perform well (Gaston *et al.* 1997). Conversely, in a less heterogeneous environment, we would expect common species to have a superior phenotype across sites that should therefore be under stabilising selection, whereas rare species may have phenotypes ill-suited to most of the available habitats and may be more variable in their struggle to adjust to the available sites (Brown 1984). In both of the above cases, we may expect common species to have lower variation in their performance (e.g. growth) compared to rare species that may fail or succeed depending upon their ability to adjust to local conditions or disperse to a favourable site.

Importantly, the above two predictions can be unified into a general framework relating intraspecific trait variation and abundance across scales. We expect the link between intraspecific variation and abundance to critically rely upon the environmental heterogeneity of the system and therefore spatial scale. Specifically, on local scales where environmental heterogeneity is reduced, common species will be those with phenotypes that best fit the environment and individuals within those species with large deviations from the optimal phenotype will disadvantaged thereby reducing phenotypic variation in common species. However, on larger spatial scales where there is more environmental heterogeneity, common species in the system will most likely be those species that can colonize and increase their population sizes in a variety of different environments where the optimum phenotype will differ thereby increasing phenotypic variation in common species. Thus, we expect the link between intraspecific variation and abundance to be intimately tied to the degree of environmental heterogeneity and therefore changing from negative relationship locally to a positive relationship regionally, but these predictions remain largely untested on any spatial scale in the functional trait literature.

Perhaps nowhere are patterns of relative abundance more striking and fascinating than in diverse communities (Dobzhansky 1950; Lynch & Neufeld 2015). For example, upwards of 50% of the species in tropical tree communities may be considered 'rare' (e.g. Hubbell & Foster 1986). Locally rare tropical tree species may simply be explained by ecological equivalence and probabilistic birth-death given the relative abundance distribution in a meta-community (Hubbell 2001). However, rare species may be functionally divergent and simply ill-suited to most of the available habitats and/or more susceptible to pests and pathogens or specialized on rare habitats. Ill-suited rare species may be expected to be more variable in their phenotypes, whereas specialized rare species may be less variable. Despite the large interest in the relative abundances of tropical trees we have no clear tests of these fundamental predictions.

In diverse tropical tree communities, the seedling stage is critical for determining the relative abundance and species composition of the entire forest. Specifically, the transition from seedling to sapling represents a major demographic bottleneck that severely reduces population sizes differentially across species thereby greatly influencing the structure of tree communities in later ontogenetic stages (Green *et al.* 2014). This demographic bottleneck makes the study of seedling dynamics essential for our understanding of the processes that determine the relative abundance distributions and species composition of diverse tropical tree assemblages.

Here, we tested the above predictions by quantifying the relationship between species relative abundance and the variance in growth rates and traits, by using data from 1974 seedling individuals of 142 species in a tropical rain forest in China and 1771 seedling individuals of 53 species in a tropical rain forest in Puerto Rico. These seedlings were monitored during 1 year for growth in 218 and 200 plots, respectively, and then harvested for trait measurements. Using this data we specifically asked: (1) What is the relationship between intraspecific trait variation and relative abundance? (2) What is the relationship between intraspecific growth rate variation and relative abundance? (3) Do common species have higher growth rates compared to rare species? and (4) Are rare species occupying extreme positions of the community trait distribution, while dominant species occupy a core position?

METHODS

Study sites

This study was conducted in two tropical rain forests. The first study site was located in Xishuangbanna, Yunnan, China (101°34′ E, 21°36′ N). This region is characterized by monsoon climate with a strongly seasonal variation between dry (November–April) and wet season (May–October). The annual mean temperature is 21.8 °C and mean annual rainfall is 1493 mm (Cao *et al.* 2008). The second study site is located in the El Yunque National Forest, in Puerto Rico (65°47′ W, 18°19′ N). El Yunque also has a seasonal climate with heaviest rains falling during the Atlantic Ocean hurricane season (June–December) with a mean annual rainfall of 3548 mm and an average temperature of 23 °C.

Seedling plots

In Xishuangbanna, we established 218 1 × 1 m seedling plots arrayed in a regular grid to monitor seedling dynamics during

12 months (2013–2014). The sampling grid was located in an area forest that is relatively homogeneous with respect to elevation and light levels as compared to the heterogeneity found in the entire forest. All free-standing seedlings smaller than 50 cm in height were tagged, identified and measured. Not all species could be identified to the species level, 5% were determined to the genus level and were ultimately recorded as clearly distinguishable morphospecies. The seedlings were monitored every 2 months to assess growth and survival. New recruits were also tagged, measured, identified and incorporated into the census. Relative growth rates (RGR) were calculated for each seedling using basal diameter and height measurements.

In El Yunque, Puerto Rico, we established 200 1 × 1 m plots that were also arrayed in a regular grid and seedling dynamics were monitored for the same year as in China. The seedling measurements followed the same procedure as the one described for China and 3% of the species were determined to the morphospecies level. Because part of this study sought to investigate intraspecific variation in traits and growth, we only used those individuals that were present from the first to the last census.

Trait measurement and abundance

Recent work has highlighted the importance of trait variation across ontogenetic stages and its influence on inferences regarding community assembly (e.g. Spasojevic *et al.* 2014). In this study, all trait data were measured from the individuals in our seedling plots and all of the abundance values in our analyses represent the seedling abundance of the species in our seedling plots. Thus, trait and abundance data from other ontogenetic stages or outside of our seedling plots was not used in this study.

After 1 year of monitoring, all surviving individual seedlings were extracted from the soil and collected permitting the quantification of leaf functional traits as well as plant allocation traits for each individual. For each individual we measured the fresh leaf area (LA in cm^2) of 1–3 fully expanded leaves. These leaves were then weighed and leaf thickness was measured using the middle section of leaf lamina avoiding primary and secondary veins. Roots were cleaned and separated from the main stem and the length of the main stem was measured (cm). All the leaves and leaflets, stems and roots were then dried in an oven for 72 h at 70 °C and measured for dry mass (g). Specific leaf area (SLA) was calculated as: SLA = LA/dry mass. Leaf mass fraction (LMF) was calculated as: LMF = leaf dry mass/total plant dry mass. Stem mass fraction (SMF) as: SMF = stem dry mass/total plant dry mass. Root mass fraction (RMF) as: RMF = root dry mass/total plant dry mass. Leaf area ratio (LAR) was calculated as: LAR = leaf area/total plant dry mass. Stem specific length (SSL) was calculated as: SSL = stem length/stem dry mass (Poorter *et al.* 2012). LMF, SMF, RMF, SSL and LAR are traits that provide information about the allocation strategies of plants, while SLA, leaf thickness and LA are considered non-integrative traits specific to resource acquisition by leaves.

Growth rate

The relative growth rate of seedlings was calculated as the change in log-transformed basal diameter and total height from the first to last census. All seedlings were marked on their stem at the initial point of measurement and subsequent measurements were made at the same location. The total height of each seedling was measured from the mark to the most distant part of the main stem. The RGR was estimated in cm per year and all negative values were discarded.

Data analyses

Because of the substantial variation in sample size (i.e. abundance) between species in our study, we utilized rarefaction to generate comparable estimates of variation in traits and RGR across species. Specifically, for those species with four or more individuals, we randomly sampled without replacement four individuals and calculated the variation in the trait and RGR values for those individuals. This procedure was repeated 999 times to generate 95% confidence intervals and a mean variance value. All trait data were transformed for normality and scaled prior to analyses. For the trait variation analyses we considered all traits individually, but because many of our traits may co-vary we also performed a principal components analysis (PCA) to mitigate trait redundancy using all individuals across species at a single site (i.e. China or Puerto Rico). A PCA was used over other ordination techniques as we utilize continuous trait data and we were interested in the Euclidean distance separating individuals in multivariate space. The first three resulting PC axes explained 70.7 and 72.9% of the total trait variation in China and Puerto Rico, respectively (Table S1). The position of individuals along these three axes was also used in the rarefaction analyses. For each species, the estimated mean variance for each trait, each PC axis and both RGR, was then correlated with the log-transformed total abundances of the species in the study site using a Pearson's correlation coefficient.

Next, we were asked whether mean RGR using the height and basal diameter data was significantly related to abundance. This calculation included all species in the study even if they had fewer than four individuals. A Pearson's correlation coefficient was then calculated to relate the mean RGR values to the log-transformed total abundances of the species in the study site.

In order to evaluate the relative position of species along the total breadth of functional trait space, we performed analyses with the individual trait data positions of individuals on the PC axes. Specifically, we wanted to address whether rare species occupy peripheral positions along single trait axis while common species occupy core positions. To do this, we subtracted the mean trait value for the entire community from the median trait value computed for each species. Thus, the displacement of a species from the overall community trait distribution was calculated. We also quantified the deviation of the median trait value of species from the median community trait value and found similar results and therefore only provide the deviation of the median trait value for a species from the mean of the community distribution. Smaller devia-

tion values indicate that a species is close to the mean trait value of the community, whereas a large value indicates a species occupies an extreme position in the community-wide trait distribution. To evaluate if there was a significant correlation between the relative position of a species in functional trait space and its abundance, we calculated Pearson's correlation coefficients between the absolute values of the deviations against the log-transformed abundance. Negative coefficient correlation values indicated that abundant species had mean trait values closer to the median of the community, while rare species tended to have mean trait values more distant from the median of the community.

RESULTS

In total 1974 seedling individuals from 142 species were harvested and measured for traits in China and a total of 1771 from 53 species in Puerto Rico. For the aspect of the study focusing on intraspecific variation, we used only species with four or more individuals. Thus, for the intraspecific variation results described below, we analysed 1614 individuals from 62 species in China and 617 seedlings from 28 species in Puerto Rico.

This study quantified intraspecific variation in traits and RGR for seedling communities and related this variation to relative abundance. The results from China and Puerto Rico were generally consistent. Specifically, we found a negative correlation between intraspecific variation in traits and relative abundance, indicating that common species tend to exhibit lower variance in traits when compared to relatively rare species (Table 1, Figs S1 and S2). However, intraspecific variation in some individual traits was not related to abundance. For example, in China we found that leaf thickness, RMF and specific stem length (SSL) were not significantly correlated with species abundance and in Puerto Rico leaf area (LA) and leaf thickness were not significantly related to abundance, while LAR and SLA had marginal *P*-values (Table 1, Figs S3 and S4). The correlation between species relative abundance and intraspecific variation in RGR was only significant for growth based on height measurements in the seedlings from China and growth based in basal diameter for seedlings from Puerto Rico (Table 2, Figs S5 and S6). Thus, the results provide mixed support for common species having lower variation in RGR.

Mean RGR was variable among species and not consistently related to relative abundance, where some common species had higher mean RGR while other exhibited lower RGR than expected by chance. Similar patterns were found irrespective of whether we measured RGR using basal diameter or total height data for China and Puerto Rico (Table 3, Figs S7 and S8).

Next, we quantified the relative position of rare and common species within the entire range of trait values for the entire community. For seedlings in China, we found that for LAR, SSL, LMF, SMF and RMF, common species tended to occupy core positions within the functional trait space for the total community (Fig. 1, Figs S9–S12), while rare species tended to occupy extreme positions. In other words, for most traits, rare species occupied the periphery of community trait

Table 1 Pearson's correlations between species relative abundance and variance in individual traits and PC axes

Variable	Site	r	P-value	d.f.	t
PCA1	XTBG, China	−0.25	0.04 *	60	−1.9
PCA2	XTBG, China	−0.32	0.008**	60	−2.66
PCA3	XTBG, China	−0.29	0.02*	60	−2.34
Leaf area	XTBG, China	−0.31	0.01**	60	−2.57
Specific leaf area	XTBG, China	−0.28	0.03*	60	−2.19
Leaf area ratio	XTBG, China	−0.25	0.04*	60	−2.01
Leaf mass fraction	XTBG, China	−0.31	0.01**	60	−2.54
Stem mass fraction	XTBG, China	−0.29	0.02*	60	−2.41
Root mass fraction	XTBG, China	−0.18	0.15	60	−1.42
Leaf thickness	XTBG, China	−0.14	0.25	60	−1.15
Specific stem length	XTBG, China	−0.19	0.13	60	−1.51
PCA1	El Yunque, Puerto Rico	−0.43	0.02*	26	−1.85
PCA2	El Yunque, Puerto Rico	−0.41	0.04*	26	−2.15
PCA3	El Yunque, Puerto Rico	−0.46	0.01**	26	−2.55
Leaf area	El Yunque, Puerto Rico	−0.33	0.1	26	−1.7
Specific leaf area	El Yunque, Puerto Rico	−0.36	0.05	26	−1.86
Leaf area ratio	El Yunque, Puerto Rico	−0.37	0.05	26	−1.95
Leaf mass fraction	El Yunque, Puerto Rico	−0.46	0.01**	26	−2.54
Stem mass fraction	El Yunque, Puerto Rico	−0.53	0.006**	26	−2.99
Root mass fraction	El Yunque, Puerto Rico	−0.45	0.02*	26	−2.45
Leaf thickness	El Yunque, Puerto Rico	−0.31	0.11	26	1.318
Specific stem length	El Yunque, Puerto Rico	−0.44	0.02*	26	−2.35

Asterisks represent the level of significance: **$P \leq 0.01$; *$P < 0.05$.

Table 2 Pearson's correlations between species relative abundance and variance in relative growth rates (RGR)

Variables	Site	r	P-value	d.f.	t
Variance RGR-b	XTBG, China	−0.16	0.24	60	−1.13
Variance RGR-h	XTBG, China	−0.27	0.02*	60	−2.26
Variance RGR-b	El Yunque, Puerto Rico	−0.41	0.04*	26	−2.16
Variance RGR-h	El Yunque, Puerto Rico	−0.042	0.83	26	−0.2

RGR was based on measurements of basal diameter (-b) and height (-h). Asterisk represent the level of significance: *$P < 0.05$.

space. For LA, SLA and leaf thickness, the results did not show a consistent pattern since dominant species were found across the total trait range, as were rare species (Figs S13–S15). In Puerto Rico, we found that LAR was the only trait that showed common species occupying central position within the community (Fig. 2, Figs S16–S22).

DISCUSSION

A major goal in ecology is to uncover the main forces that generate emergent patterns across ecosystems. The hollow

Table 3 Pearson's correlations between species relative abundance and mean relative growth rates (RGR)

Variable	Site	r	P-value	d.f.	t
Mean RGR-b	XTBG, China	0.18	0.16	60	1.42
Mean RGR-h	XTBG, China	−0.11	0.39	60	−0.85
Mean RGR-b	El Yunque, Puerto Rico	0.14	0.47	26	0.72
Mean RGR-h	El Yunque, Puerto Rico	−0.38	0.06	26	−2

RGR was based on measurements of basal diameter (-b) and height (-h).

$r = -0.18$, P−value = 0.02
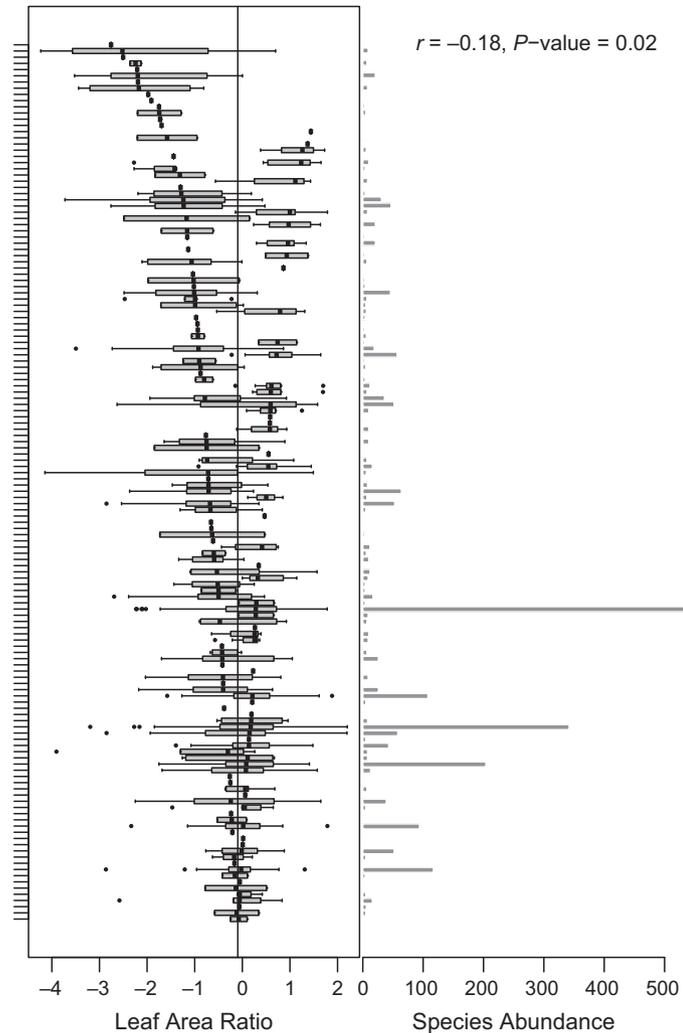
Figure 1 The relative position of species in the leaf area ratio (LAR) distribution in Xishuangbanna, China. Left Panel: the *x*-axis represent the difference between median LAR species trait and mean LAR for the entire community. The *y*-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LAR by species. Right Panel: species relative abundance. The coefficient of correlation and the p-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and mean of the community against the log-transformed abundance of the species.

$r = -0.29$, P−value = 0.04

Figure 2 The relative position of species in the leaf area ratio (LAR) distribution in El Yunque, Puerto Rico. Left Panel: the *x*-axis represent the difference between median LAR species trait and mean LAR for the entire community. The *y*-axis arrays species from bottom to top based upon how close they are to the mean community trait value. Each boxplot represents the distribution of LAR by species. Right Panel: species relative abundance. The coefficient of correlation and the *P*-value result are provided in the upper right from the Pearson correlation analysis between the absolute values from the differences among median of the species and mean of the community against the log-transformed abundance of the species.

curve of SADs in communities, where most species are rare and relatively few are dominant, is one such emergent pattern. Despite the progress made in predicting this pattern based on
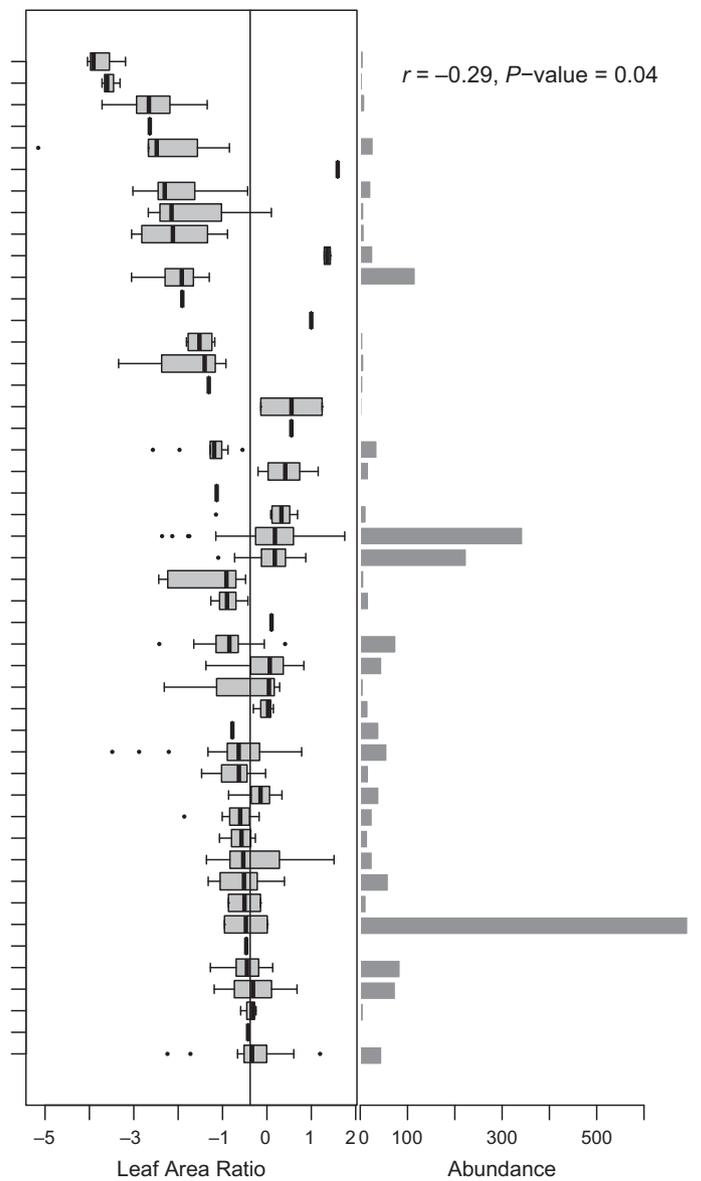
a few parameters (Hubbell 2001; Harte *et al.* 2008), determining the mechanisms that cause particular species to be common or rare in a given SAD is a major open avenue of research. Our results advance research on SADs by moving beyond determining the shape of the curve and providing a framework for understanding what species make up the rare and common species within any given curve by including information regarding intraspecific variation in organismal

traits and performance. Here, we have provided the results from tropical tree seedlings demonstrating that variance in traits and RGR are often negatively related to species abundance. Additional analyses indicate that common species are not necessarily faster growing and in many cases, particularly in one study site, rare species tend to occupy the periphery of trait space. In the following we discuss these results in greater detail.

Abundance and intraspecific variation

The low intraspecific trait variation found for common species (Table 1), indicates a convergent strategy that emphasizes a core physiological association with the habitat allowing high efficiency in exploiting available resources (Grime 2006). We posit that common species have traits optimized for resource use in the given environment and deviations from these optimal values have negative consequences thereby reducing intraspecific variation. Trait convergence has been discussed in previous trait-based community ecology studies, but generally on the interspecific scale (Weiher *et al.* 1998; Swenson & Enquist 2009). Here, we show that trait convergence is also evident at intraspecific level for common species. Contrary with the pattern found for common species, rare species tended to exhibit higher trait variation (Table 1).

When these results are considered in their ecological context, where both sites are located in tropical forests with little topographic complexity, we infer that common species, that have low variation around optimal trait values, are able to easily dominate; whereas, high intraspecific trait variation for rare species may be indicative of their struggle to adjust to the given environment. However, on larger spatial scales with larger environmental heterogeneity or in other local scale sites exhibiting more environmental heterogeneity we might expect the opposite result. For example, high intraspecific trait variation is expected to facilitate the colonisation of new or suboptimal habitats across a region (Gonzáles-Suárez *et al.* 2015). Indeed, some studies have reported that invasive species vary greatly in shoot-root ratios in order to maximize water uptake under variable levels of drought (Brock & Galen 2005). Thus, future research investigating whether regionally common species have higher intraspecific trait variation to ensure success across multiple habitats and whether species have similar levels of intraspecific variation across their range are needed. Furthermore, our predicted relationships between intraspecific variation and abundance across scales should not only apply to tropical tree assemblages, but to other ecosystems and taxa. Therefore, future work is also needed to test whether our predictions are supported more generally.

When considering individual traits, we found that most traits followed the same pattern observed with the multivariate trait analyses. However, intraspecific variation in leaf thickness from seedlings in Puerto Rico and China was not related to abundance. This result is not totally surprising given that previous studies have shown that leaf thickness is highly variable across all species (Onoda *et al.* 2011). In addition to leaf thickness, SSL and RMF did not show the expected pattern for seedlings in China nor did leaf area (LA) for seedlings in Puerto Rico. These results may arise from the

fact that species may not be able to be equally variable across all trait axes and that variation, particularly as it relates to relative allocation to leaves, is likely more important.

Although variation may be beneficial, it is not necessarily linked to increased growth, establishment success or persistence (Robinson *et al.* 2013). Our results show that rare species tend to have higher intraspecific variation in RGR compared to common species (Table 2). In sum, common species are less variable in traits and RGR when compared to rare species. The observed differences in the magnitude of intraspecific variation in traits and RGR between common and rare species suggests not only differences in their ecological requirements, but also likely their permanence of these species in the community (Hanski 1982; Magurran & Henderson 2003). Species that are better adjusted to the present conditions are expected to have superior permanence. Species that are more variable in their traits and performance could arrive occasionally to the community, disappear, and re-colonize later thereby being effectively transient species with sink populations ill-suited to the presently available habitats. Although our results do not demonstrate the transient nature of rare species due to a lack of multi-year census data, it emerges as one potential explanation of the high variability in traits (Magurran & Henderson 2003). Common species, on the other hand, would represent core components of the community strongly associated with environmental conditions that will allow them persist for long periods and attain large population sizes.

Abundance and relative growth rates

The RGR of species may be positively related to abundance given that faster growing species may achieve maturity more rapidly. However, we found no support for this expectation (Table 3). These results are not necessarily surprising given that fast growing species also have higher mortality rates (e.g. Wright *et al.* 2010) thereby regulating the number of individuals that achieve reproductive maturity. For example, species from the genera *Cecropia* (Urticaceae) and *Macaranga* (Euphorbiaceae) are broadly known as pioneer fast growing species in the Neo- and Paleo-tropics, respectively; however, they exhibit high mortality rates as well (e.g. Condit *et al.* 2006; Wright *et al.* 2010) and are not dominant species in relatively undisturbed forests. Furthermore, a recent study that measured the correlation between abundance and growth rates in eastern North American trees found that where trees are most abundant they are rarely growing well (McGill 2012).

Do rare species occupy the periphery of trait space?

The final goal of the present work was to quantify whether rare species tended to occupy the periphery of community trait space. Our individual trait-based analyses results show that, for most traits (i.e., LAR, SSL, LMF, SSL, SMF and RMF) for seedlings growing in China, abundant species tend to exhibit median trait values closer to the mean trait values for the entire community. This indicates that common species tended occupy core positions within the entire community trait distribution, while less abundant species tended to

occupy marginal positions in the community trait distribution. Similar results have been reported in a previous study arguing that rare species disproportionately contribute to ecosystem function (Mouillot *et al.* 2013). Our findings, however, highlight that while rare species do often occupy the periphery of community trait distributions, they are also highly variable in their trait values.

Although, in general, trait values from abundant species in China were close to the median values for the entire community, leaf thickness, LA and SLA were exceptions. One explanation for these results may be allocation traits such as LMF or SMF are more likely to be adjusted in order to fit the environment while organ level traits like leaf thickness, LA and SLA are less well-understood without contextual information regarding whole plant allocation (Marks 2007). In particular, traits linked to light availability appear to be important for the ontogenetic stage analysed in this study. For example, LAR reflects how much leaf area is present for unit of plant mass; LMF corresponds to the fraction that the plant allocated to leaves relative to roots and stem, these traits are all related to photosynthetic and respiration rates and therefore are expected to be related to growth (Poorter *et al.* 2012). Therefore, these results suggest that gas exchange rates are likely of key importance during the early ontogenetic stages studied as seedlings are actively adjusting their allocational strategies to exploit available light resources.

Our results from Puerto Rico were not totally consistent with our findings from China. Specifically, rare species were only peripheral with respect to LARs. Although these results contrast somewhat with our China results, we argue that the Puerto Rico findings are mainly the result of past disturbance in the forest. Puerto Rico has been severely affected by two hurricanes (Thompson *et al.* 2002) and has long history of human disturbance that altered the species and functional composition of the plant community (Swenson *et al.* 2012) such that species that are typically rare in older growth forests are now more common due to a still recovering canopy.

Caveats

Although our results are generally consistent for both of the sites evaluated, it remains to be seen if they are totally applicable to other sites. We expect that additional local scale studies in similarly homogeneous environments will find that common species exhibit less intraspecific trait variation. However, we expect that future studies conducted on larger spatial scales or on local scales with more environmental heterogeneity should generally find the opposite result where common species must be variable enough to persist in a large variety of habitats and rare species will be specialized on a spatially or temporally rare habitat. In sum, the future development of a framework relating traits to abundance will require information regarding individual-level trait measurements and measures of environmental heterogeneity across scales.

A second caveat to our study is that the traits considered do not represent the entire spectrum of strategies for tree seedlings (Swenson 2013). Traits related to defense likely also have an important role in structuring seedling communities.

Thus, we recognize that although the traits considered in this study represent the main axis for resource acquisition, there are additional traits that might reflect other important axes of plant function.

CONCLUSIONS

Given the generality of SADs, ecologists have frequently focused their research on the shape of SADs and where species fall in the SAD. In this regard, trait-based analyses of abundance distributions have had mixed success. Such work typically focuses on correlating species mean trait values with abundance. Here, we have taken an alternative approach that considers how intraspecific variation in traits and growth rates are linked to abundance in order to provide novel insights into the mechanisms underlying patterns of commonness and rarity in tropical tree communities. We show that the degree of intraspecific variation in traits and growth is itself variable across species and negatively related to abundance. Common species tend to occupy core positions within the total range of traits relevant for acquiring limiting resources and the variance in these traits is usually less than that found in rarer species. Given these results we propose that common species are well-suited for the available environmental conditions where deviations from their optimal trait values are detrimental whereas rare species are likely to be transient species ill-suited to available conditions and exhibiting high phenotypic variation in their struggle for success. Despite these insights, future studies will be needed to determine whether rare species are actually transient and inherently more phenotypically plastic or have greater genetic diversity, whether common species are phenotypically divergent on very local scales as may be an expected result from competition and whether low trait and growth variation in locally common species is potentially linked to the hyperdominance of a few species in a large and relatively homogeneous environments in regions like the Amazon Basin (Ter Steege *et al.* 2013; Fauset *et al.* 2015).

AUTHOR CONTRIBUTIONS

MNU designed the study; MNU, CZ, MC, LL and NGS conducted the study; MNU performed all data analyses; MNU and NGS wrote the manuscript; CZ, MC and LL commented on and edited the manuscript.

REFERENCES

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. *et al.* (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161, 1–28.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trend Ecol. Evol.*, 24, 183–192.

Brock, M.T. & Galen, G. (2005). Drought tolerance in the alpine dandelion, *Taraxacum ceratophorum* (Asteraceae), its exotic congenr *T. officinale*, and interspecific hybrids under natural experimental conditions. *Am. J. Bot.*, 92, 1311–1321.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *The Am. Nat.*, 24, 225–229.

Brown, J.H. (1995). *Macroeclogy*. University of Chicago Press, Chicago, USA.

Cao, M., Zhu, H., Wang, H., Lan, G., Hu, Y., Zhou, S. *et al.* (2008). *Xishuangbanna Tropical Seasonal Rainforest Dynamics Plot: Tree Distribution Maps, Diameter Tables and Species Documentation.* Yunnan Science and Technology Press, Kunming, China.

Condit, R., Ashton, P., Bunyavejchewin, S., Dattaraja, H.S., Davies, S., Esufali, S. *et al.* (2006). The importance of demographic niches. *Science*, 313, 98–101.

Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.*, 38, 209–221.

Fauset, S., Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A., Brienen, R.J.W. *et al.* (2015). Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.*, 6:6857. doi: 10.1038/ncomms7857.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997). Interspecific abundance-range size relationships: an appraisal of mechanisms. *J. Anim. Ecol.*, 66, 579–601.

Gonzáles-Suárez, M., Bacher, S. & Jescnke, J.M. (2015). Intraspecific trait variation is correlated with establishment success of alien mammals. *Am. Nat.*, 185, 737–746.

Green, P.T., Harms, K.E. & Connell, J.H. (2014). Nonrandom, diversifying processes are disproportionally strong in the smallest size classes of a tropical forest. *Proc. Natl Acad. Sci. USA*, 111, 18649–186545.

Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *J. Veg. Sci.*, 17, 255–260.

Haegeman, B. & Loreau, M. (2008). Limitations of entropy maximization in ecology. *Oikos*, 117, 1700–1710.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38, 210–221.

Harte, J., Zillio, T., Conlisk, E. & Smith, A.B. (2008). Maximum entropy and the state-variable approach to macroecology. *Ecology*, 89, 2700–2711.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey, USA.

Hubbell, S.P. & Foster, R. (1986). Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé, M.E.). Sinauer Associates, Sunderlands, MA, pp. 205–231.

Laughlin, D., Joshi, C., Bodegom, P.M., Bastow, Z.A. & Fulé, P.Z. (2012). A predictive model of community assembly that incorporates intraspecific trait variation. *Ecol. Lett.*, 15, 1291–1299.

Lawton, J.H. (1999). Are there general laws in ecology? *Oikos*, 84, 177–192.

Locey, K.J. & White, E.P. (2013). How species richness and total abundance constrain the distribution of abundance. *Ecol. Lett.*, 16, 1177–1185.

Lynch, M.D.L. & Neufeld, J.D. (2015). Ecology and exploration of the rare biosphere. *Nature Rev. Microbio.*, 13, 217–229.

MacArthur, R.H. (1957). On the relative abundance of bird species. *Proc. Natl Acad. Sci. USA*, 43, 293–295.

Magurran, A.E. & Henderson, P.A. (2003). Explaining the excess of rare species in natural species abundance distribution. *Nature*, 422, 714–716.

Marks, C.O. (2007). The causes of variation in tree seedling traits: the roles of environmental selection versus chance. *Am. Nat.*, 61, 455–469.

McGill, B.J. (2012). Trees are rarely most abundant were they grow best. *J. Plant Ecol.*, 5, 46–51.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J. & Benecha, H.K., *et al.* (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995–1015.

Morlon, H., White, E.P., Etienne, R.S., Green, J.L., Ostling, A. & Alonso, D., *et al.* (2009). Taking species abundance distribution beyond individuals. *Ecol. Lett.*, 12, 488–501.

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M. *et al.* (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol.*, 11. doi: 10.1371/journal.pbio.1001569.

Murray, B.R., Thrall, P.H., Gill, A.M. & Nicotra, A. (2002). How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecol.*, 27, 291–310.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C. *et al.* (2011). Global patterns of leaf mechanical properties. *Ecol. Lett.*, 14, 301–312.

Paine, C.E.T., Baraloto, C., Chave, J. & Hérault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos*, 120, 720–727.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.*, 193, 30–50.

Preston, F.W. (1948). The commonness, and rarity, of species. *Ecology*, 29, 254–283.

Robinson, J.D., Wares, J.P. & Drake, J.M. (2013). Extinction hazards in experimental *Daphnia magna* populations: effects of genotype diversity and environmental variation. *Ecol. Evol.*, 3, 233–243.

Roughgarden, J. (1972). Evolution of niche width. *Am. Nat.*, 106, 683–718.

Shipley, B. (2006). *From Plant Traits to Vegetation Structure*. Cambridge University Press, Cambridge, UK.

Shipley, B., Vile, D. & Garnier, É. (2006). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science*, 314, 812–817.

Spasojevic, M.J., Yablon, Y.E., Oberle, B. & Myers, J.A. (2014). Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere*, 5, 125.

Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *Am Nat.*, 116, 770–787.

Swenson, N.G. (2013). The assembly of tropical tree communities - the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography*, 36, 264–276.

Swenson, N.G. & Enquist, B.J. (2009). Opposing assembly mechanisms in a neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90, 2161–2170.

Swenson, N.G., Stegen, J.C., Davies, S.J., Erickson, D.L., Forero-Montaña, J., Hulbert, A.H. *et al.* (2012). Temporal turnover in the composition of tropical tree communities: functional determinism and phylogenetic stochasticity. *Ecology*, 93, 490–499.

Ter Steege, H., Pitman, N.C., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E. *et al.* (2013). Hyperdominance in the Amazonian tree flora. *Science*, 342, doi: 10.1126/science.1243092.

Thompson, J., Brokaw, N., Zimmerman, J., Waide, R.B., Everham, E.M., Lodge, D.J. *et al.* (2002). Land use history, environment and tree composition in a tropical forest. *Ecol. Appl.*, 12, 1344–1363.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *Am. Nat.*, 99, 337–390.

Weiher, E., Clarke, G.D.P. & Keddy, P.A. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos*, 81, 309–322.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Weight, I.J. (2002). Plant Ecological strategies: some leading dimensions of variation between species. *Ann. Rev. Ecol. Syst.*, 33, 125–159.

White, E.P., Thibault, K.M. & Xiao, X. (2012). Characterizing species abundance distributions across taxa and ecosystems using a simple maximum entropy model. *Ecology*, 93, 1772–1778.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E. *et al.* (2010). Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology*, 91, 3664–3674.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).