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LETTER

A core-transient framework for trait-based community ecology: an example from a tropical tree seedling community

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Abstract

Trait-based studies in community ecology have generally focused on the community as a unit where all species occur due to stochasticity, determinism or some mixture of the two. However, the processes governing population dynamics may vary greatly among species. We propose a core-transient framework for trait-based community studies where a core group of species has a strong link to the local environment while transient species have weaker responses to the environment. Consistent with the expectations of the framework, we found that common species exhibit clear linkages between performance and their environment and traits while rare species tend to have weaker or non-significant relationships. Ultimately, trait-based ecology should move beyond applying a set of processes to a community as a whole and towards quantifying inter-specific variation in the drivers of population dynamics that ultimately scale up to determine community structure.

Keywords

Plant traits, relative growth rate, seedlings, soil nutrient, tropical forest.

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INTRODUCTION

One of the most controversial issues in ecology is the degree to which communities are assembled by stochasticity or a set of deterministic processes (Brown 1984; Chase 2005; Hubbell 2001.). This issue is even more challenging to solve in species-rich ecosystems where communities are characterized by hundreds of species. The majority of the studies that have endeavoured to address the determinism vs. stochasticity problem have considered communities as a *unit* (White & Hurlbert 2010; Hubbell 2001, MacArthur 1957). That is, is the community as a whole structured predominately by deterministic or stochastic processes? However, empirical evidence suggests that these processes might not be generalisable for all the species in the community (White & Hulbert 2010; Coyle et al. 2013). For example, habitat association patterns in diverse tropical tree communities have been shown to be very strong for some species, while being very diluted for other species (Harms *et al*. 2001; John *et al*. 2007; Condit *et al*. 2013). This presumably indicates that some species have a strong link to the local conditions, while others do not. Specifically, some species could be strongly linked to the local environment allowing them to persist at a site, while other species that are less linked to the available environments may take advantage of stochastic environmental fluctuations (e.g. tree fall gaps) (Magurran & Henderson 2003) or they may simply be sink populations where individuals do not persist and successfully reproduce thereby limiting population growth. The former group of species may be called core species while the latter group may be called transient species (White & Hurlbert 2010; Coyle *et al*. 2013).

The core-transient framework is generally described in terms of the temporal dynamics of species. However, the variation in temporal patterns across species should be related to differences in ecological strategies across species, and this should ultimately be reflected in differences in survival, traits, resource use and abundance (Magurran & Henderson 2003; Supp *et al*. 2015). Specifically, core species may be characterized as being well-suited for the local habitat. These species will have strong trait–environment relationships that increase the growth rates and probability of survival that will lead to greater reproductive success, population persistence and abundance (MacArthur 1960; MacArthur 1957). In other words, the deterministic success of individuals from the juvenile-to-adult stages locally will explain the presence of juveniles in the next generation. On the other hand, transient species may be characterized as species that are more dependent on occasional immigration events where arriving individuals are not well-suited to the local habitat and will exhibit weak linkages with the local environment and reduced demographic performance (Magurran & Henderson 2003). In other words, the deterministic lack of demographic success of individuals in these species (i.e. a failure to successfully reproduce and recruit locally) will result in small local populations maintained by the occasional stochastic arrival of propagules from other populations (Holt & Gaines 1992). Thus, rare species will be more associated with transient dynamics characterized by source-sink dynamics or opportunistic colonisation, where stochastic arrival via immigration is the main force that

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governs the occurrence of these species (Pulliam 1988; Holt & Gaines 1992).

Similar to the core-transient framework, the core-satellite framework also distinguishes between two main categories of species (Hanski 1982). However, core and satellite species are described based on their spatial distribution (number of sites occupied) on a regional scale, while core and transient species are described based on their temporal dynamics. Thus, satellite species are not always the same as transient species (Supp *et al.* 2015). For example, spatially restricted species might be persistent components of the community, or broadly distributed species might be transient components. Thus, these two hypotheses are certainly related, but here we focus on a core-transient framework.

Here, we propose that the core-transient framework can be integrated into trait-based community ecology. Plant responses to the environment are mediated by their traits (McGill *et al.* 2006). The match between a trait of an individual and its environment dictates their performance, fitness and overall population growth (Arnold 1983). Individuals and species, by nature of their trait differences, will be differentially linked to a given environment (Grime 1979, 2006). This approach, however, fails to recognize that not all of the present species will have strong trait-environment or demographic rate-environment–trait relationships (Supp *et al.* 2015). Specifically, some species may be transient and not well-suited to the local environment. We argue that trait-based community ecology could benefit from refocusing on trait–performance relationships across local environments, how these relationships vary across species and ultimately producing emergent community properties such as species relative abundance.

An integration of a core-transient framework in trait-based ecology makes several clear and novel predictions linking traits, performance, the environment and abundance. We begin with the transient species that are poorly linked to the local environment. The traits of these species are mismatched with the given environment, which leads to sub-optimal rates of resource acquisition and ultimately demographic performance and low abundance (Supp *et al.* 2015). A hypothetical example of this could be a shade intolerant species attempting to establish in the shaded understory of a closed canopy forest (Kobe 1999). The leaf traits of these species are poorly matched to a shaded environment and intra-specific variation in traits will not lead to variation in performance. This is because, for these species, the most shade tolerant trait values are still shade intolerant (Rozendaal *et al.* 2006). Thus, we expect these species to have weak or non-existent performance-environment/trait and trait–environment relationships and to have smaller populations controlled via deterministic demographic failure of seedlings, the stochastic arrival of new propagules and not local deterministic demographic success of adults (Magurran & Henderson 2003; Supp *et al.* 2015). On the other hand, there will be species that have an average phenotype that is matched to the given environment, and intra-specific variation in traits will be related to intra-specific variation in demographic performance. A hypothetical example of this would be a shade tolerant species in the same forest understory where variation in traits in response to the light environment will lead to variation in performance. We expect that these species will have stronger performance-environment/trait and trait–environment relationships that are indicative of deterministic processes governing their, on average, larger populations.

Across the life cycle, plants go through several key ontogenetic transitions. In diverse tropical tree communities, the seedling stage is perhaps the most important. Differential demographic rates between seedlings have been shown to leave a lasting and large imprint on adult community structure (Poorter 2007; Green *et al.* 2014). Further, seedlings have been shown to have strong non-random patterns of mortality that are potentially linked to environmental conditions (Augspurger 1984; Holste *et al.* 2011). However, this generally has not been linked back to individual-level performance–trait–environment relationships nor to a core-transient framework. In this study, we sought to apply the core-transient framework we outline above by focusing primarily on trait-environment and performance—environment–trait relationships across species. Specifically, we examined the role that local environmental conditions and individual traits play in influencing tree seedling growth performance for communities in a tropical forest in China. We ask the following questions: (1) How does the influence of environmental local conditions on deviations from expected growth vary across seedling species? (2) How are individual-level seedling traits linked to deviations in growth rates across species with different abundances?

METHODS

Study site

This study was developed in a tropical rainforest at Xishuangbanna, Yunnan province in China (101°340′ E, 21°360′ N). The region comprises a matrix characterized by large areas of preserved forest surrounded by areas of intensive human land use. The region has a typical monsoon climate, with a mean annual precipitation of 1,493 mm, a mean annual temperature of 21.8 °C and two seasons differentiated by precipitation patterns, with a dry season starting in November and ending in April (Cao *et al.* 2008). This study was conducted in a large well-preserved forest just outside of the town of Mengla.

Data collection

A total of 218 seedling plots of 1 × 1 m^2 were established in a regular grid across 2-ha. All of the seedlings with a height lower than 50 cm were identified, tagged and monitored for growth and survival during 1 year from 2013 to 2014. After 1 year, all of the seedlings were collected in order to quantify traits. We estimated the relative growth rate of each individual by computing the change in log-transformed height. Then, we estimated the relative growth rate (RGR) deviation of each individual seedling from the species mean RGR and divided this value for the standard deviation. Using the RGR deviation allowed us to compare the performance of each seedling relative to the expected value for the species and we used this value as the response variable in our models.

Eight traits including organ-level and biomass allocation traits were measured for all individuals present in the seedling plots. For the organ-level traits, we calculated the leaf area, specific leaf area and measured leaf thickness based on one to three leaves for each individual. Fresh leaves were scanned then dried in oven for 72 h at 70 °C to measure the dry leaf mass (g). For the biomass allocation traits, we estimated the leaf mass fraction, stem mass fraction, root mass fraction, stem specific length and leaf area ratio according to Poorter *et al.* (2012). Stems, roots and leaves were separated with pruners manually in the lab and later dried in the oven under the same conditions described above. We used principal component analyses to summarize the eight traits by the first three orthogonal axes (76% of variance explained) (Table S1).

To estimate the local environmental conditions for each plot, we measured soil and light availability (Table S2). We sampled the soil from each seedling plot after the trait data collection was finished. At each point, we collected 50 g of topsoil (0–10 cm in depth) avoiding leaves, flowers and stones from each of the corners of the plot. This material was air-dried and sifted. We determined the cation availability, using Mehlich III extraction method and atomic emission inductively coupled plasma spectrometry (AE-ICP). Total nitrogen (N) and carbon (C) were determined by total combustion using auto-analyser. In addition, we measured pH with an acidity detector and soil texture. All the soil analyses were conducted at the Biogeochemical Laboratory at Xishuangbanna Tropical Botanical Garden. These soil variables were summarized by a principal component analysis (PCA). For further analyses, we used the first three orthogonal axes, which explained 70% of the total soil variation (Table S3). PC1 scores were associated K, Mg and Zn, PC2 scores were associated with Ca and pH and PC3 scores were associated with C and N.

Light availability in the understory was assessed using hemispherical photographs for each seedling plot. The pictures were taken systematically with a Nikon FC-E8 lens and a Nikon Coolpix 4500 camera at 1 m above the ground before sunrise and with cloudy conditions between March and April 2014. To analyse the images, we used Gap Light Analyser software (http://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla) (Table S2).

Data analyses

To quantify whether more abundant species have more predictable relationships with their environment than the less abundant species, we first grouped species into abundance classes. To avoid spurious results due to potentially arbitrary binning decisions and differences in sample size per bin, we repeated the analyses, using five different binning methods:

(1) Two groups of species with nearly the same number of species (bin-2): a first group with 26 species and 152 individuals (6–11 individuals per species); and a second group with 27 species and 1354 individuals (14–455 individuals per species.
(2) Three groups of species with nearly the same number of species (bin-3): a first group with 18 species and 94 individuals (6–8 individuals per species); a second group with 18 species and 162 individuals (9–23 individuals per species); and a third group with 17 species and 1250 individuals (24–455 individuals per species).
(3) Four groups of species with nearly the same number of species (bin-4): a first group with 14 species and 68 individuals (6–7 individuals per species); a second group with 13 species and 84 individuals (8–11 individuals per species); a third group with 13 species and 208 individuals (12–39 individuals per species); and a fourth group with 13 species and 1146 individuals (41–455 individuals per species).
(4) Two groups binned by abundance (bin-abundance-2): a group for species with > 100 individuals (3 species, 700 individuals); and a group for species with 5–100 individuals (50 species, 806 individuals).
(5) Three groups binned by abundance (bin-abundance-3): a group for species with > 100 individuals (3 species, 700 individuals); a group for species with 20–100 individuals (16 species, 581 individuals); and a group for species with 5–20 individuals (33 species, 210 individuals). We used the threshold of 20 individuals by extrapolating the criteria used by Hubbell & Foster (1986) to define rare tree species (1 individual per hectare) into the seedling community. Thus, we defined 10 the seedlings by hectare as rare species as the total area of the study is roughly 2 ha.

We restricted our analyses to species with more than five individuals in the entire study system in order to have enough power to model each of the species.

Given that rare species may not always be transient species, we performed an additional analysis by comparing species abundance from our seedling plots with the seedling abundance from a set of 500 permanent seedling plots located in a forest close to our study site. By comparing species abundances at these two sites, we classified rare species in two categories: rare transient species that were locally rare at our site, but abundant at the network of 500 plots. The remaining species were considered rare non-transient species the rest. We then generated growth-environment/trait and trait-environment models for each group. The rare-transient species had weaker relationships between growth– and trait–environment relationships than the rare-non transient species (see Appendix S1).

We also explored a rarefaction approach that was designed to control for large plot random effect in our models where all plots were equally represented in the resampled datasets. Additionally, a simulation experiment was performed to assess whether our rarefaction approach had sufficient power to detect a known signal. The power analysis demonstrated that the rarefaction approaches could not detect a known signal for a dataset similar to our observed dataset. Thus, we do not provide the rarefaction results in the main text, but these results can be found in Appendix S2.

Next, for each of the abundance classes, we quantified the relationship between the growth deviations of the species and their surrounding environment or traits. Specifically, we modelled individual RGR deviations as a function of local abiotic conditions or traits, using linear mixed-effects models (Gelman & Hill 2007). In the first set of models (one per abundance class), the RGR deviation was modelled as a function of the three edaphic PC's and light (fixed effects), and the plot-specific intercept (random effect). A second set of models (one per abundance class) included trait data. Here, we modelled RGR deviation as a function of the trait-PCs (fixed effects), and plot-specific intercepts (random effect). A second set of models was generated, but included species-specific intercepts as random effects. The results were similar, but the variance explained was lower. We show only the results using plots as random effects, but provide the results from the second set of models in the Appendix S3. In addition to the models evaluating the relationship between RGR deviations and traits, or abiotic variables, we also explored the relationship between traits and environment (see Appendix S4). We used a Wald Z-statistic to test for significance of each fixed effect in the models and used parametric bootstrapping with 10 000 simulations to estimate the 95% confidence intervals. We evaluated the homogeneity and normality in the distribution of the residuals by plotting the fitted values against residual values (Fig. S1). We evaluated the goodness-of-fit for the models by calculating the marginal and conditional R^2 for linear mixed models (Nakagawa & Schielzeth 2013). These coefficients of determination provided information on the variance in growth rates explained by the different models. In the following, we compare both the effect sizes with their corresponding confidence intervals as well as their *P*-values to compare model parameters. In other words, our discussion regarding the relationships between a species and the environment considers both the strength of the fixed effect means and *P*-values. Given that coefficients of variation represent the variance explained by the overall model and not the individual fixed effects, the R^2 values were not used to compare bins. All the analyses were performed in *R* statistical software version 3.2.1 (R Development Core Team 2015), using the *lmer* function of the 'lmer4' package (Bates *et al.* 2015).

RESULTS

In total, we analysed 1506 seedlings distributed in 214 plots. Although we originally had 218 plots, we analysed 214 plots (53 species) because trait information was incomplete for individuals present in four plots and some of the seedling communities in these plots contained only very rare species (< 5 individuals) that could not be used in the analyses.

The models relating RGR deviations to the environment were consistent across abundance binning protocols (Figs 1 and 2, Table 1). However, we will present the results from each binning method for completeness. When using the bin-2 binning protocol, models that predicted growth deviations as a function of environmental variables were not significant for the rare group. However, we found a significant relationship between RGR deviations and the environment (light % and soil PC1) for the common species group (Table 1). The conditional coefficients of determination for these models were 0.04 and 0.14 for the rare and the common species groups respectively (Table 2). Higher PC1 scores were associated with higher K, Mg and Zn. The other two orthogonal axes describing soil composition did not show strong relationships with RGR deviations.

When using the bin-3 binning protocol, models that predicted growth deviations as a function of environmental variables were not significant for the moderately rare and rarest groups. However, we found a significant relationship between RGR deviations and the environment (light % and soil PC1) for the common species group (Table 1). The conditional

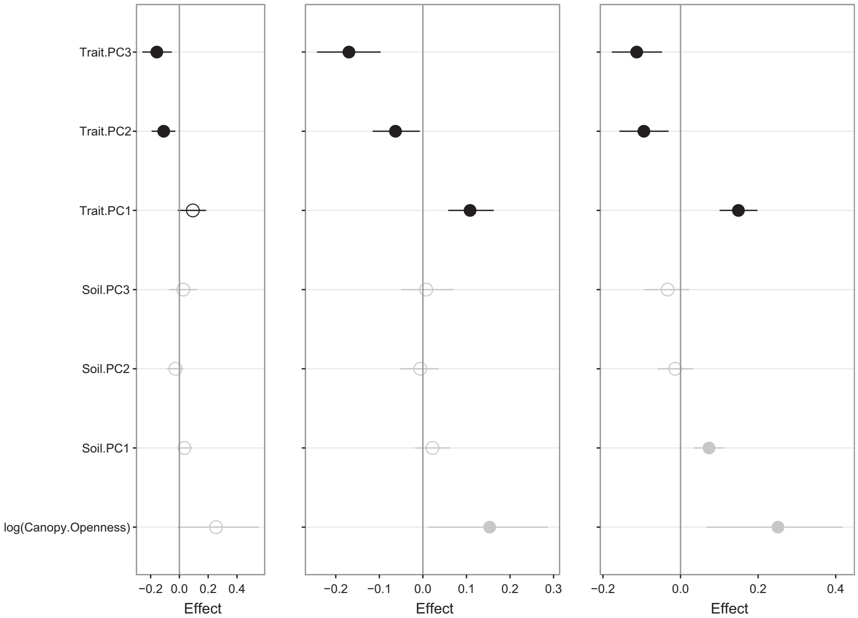

Figure 1 Coefficient estimates (mean and 95% confidence intervals) for models using bin-abundance-3 groups (rare, medium, common). Black dots represent models predicting deviations in growth rates from seedling traits. Gray dots represent models predicting deviations in growth rates from environmental variables. Right: group of species with more than 100 individuals; center: group of species with more than 20 individuals and less than 100; left: group of species with less than 20 individuals. Filled circles represent significant results (95% credible intervals excluded zero).

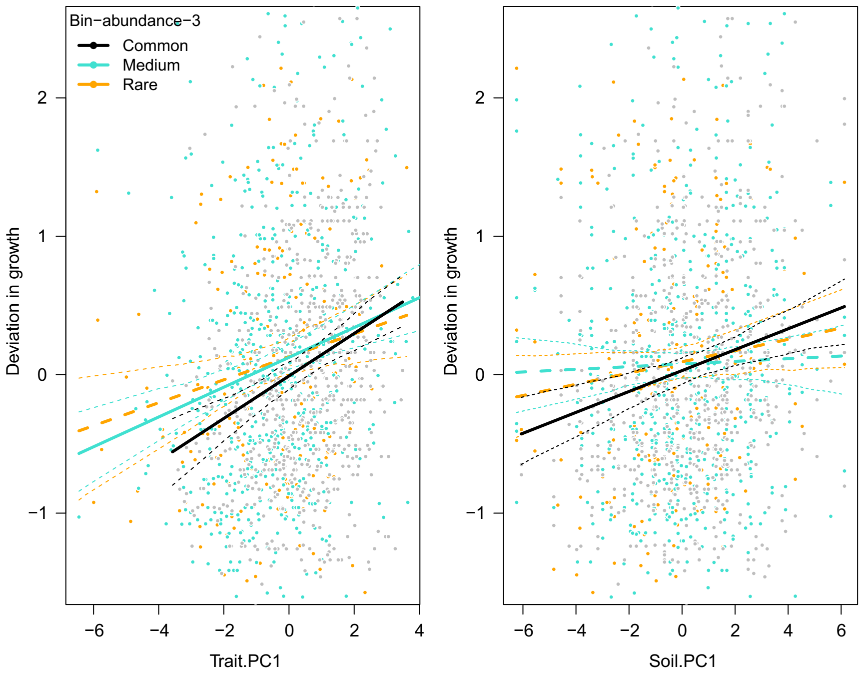

Figure 2 Regression lines of RGR deviations plotted against the predictor variables that showed the strongest response changes across the different binning methods (trait axis PC1 and soil axis PC1). The three colours represent the different abundance groups according to the bin-abundance-3 method (rare, medium and common). Dashed lines represent non-significant effects (95% credible intervals cross zero), continuous lines represent significant effects. Notice that the magnitude of the slope decreases gradually from common to rare species.

coefficients of determination for these three models ranged from 0.002 to 0.15 (Table 2).

When using the bin-4 binning protocol, the first three groups (i.e. all but the most common species group) generally had non-significant relationships between RGR deviations and environmental variables. The one exception was for the group with 81 individuals, which had a significant relationship between soil PC3 and RGR deviations. The last group, which contained the most common species, had significant relationships with light % and soil PC1 (Table 1). The conditional coefficients of determination ranged from 0.04 to 0.17 (Table 2).

When using the bin-abundance-2 binning protocol, we found that the rare group had significant relationship only between RGR deviations and light %, but the common species group had a significant relationship between RGR deviations and PC1 and light % (Table 1). The conditional coefficient of determination was 0.15 for the rare species group and 0.07 for the common species group (Table 2).

When using the bin-abundance-3 binning protocol, we found no significant relationships with any of the variables and growth for the group containing the rarest species. For the group in the middle bin, we found significant relationship with light %, but only the group containing the most abundant species also had significant correlations with soil PC1 (Figs 1 and 2). The conditional coefficients of determination ranged from 0.01 to 0.12 (Table 2).

The results for the models relating RGR deviations to individual trait information were generally similar to those relating RGR deviations to environmental variables. Specifically, higher proportion of fixed effects predicting deviations on RGR and higher estimated fixed effects means were usually found for models including the more abundant species (Figs 1 and 2, Table 3). Individuals with higher growth compared to the average growth of their respective species showed higher SLA, SSL and LAR. Each of these traits is linked to photosynthetic capacity and acquisitive trait strategies. In the following, we present the results for each binning protocol.

When using the bin-2 binning protocol, the group with the rarest species had a significant relationship between RGR deviations and the PC2 and PC3 axes. The models for the most common species group showed that RGR deviations were related to all three PC axes (Table 3). The conditional coefficients of determination were 0.10 and 0.22 for the rare species group and the common species group respectively (Table 2).

When using the bin-3 binning protocol, the group with the rarest species had a significant relationship between RGR deviations and the PC3 axis. The models for the moderately rare group showed significant relationships with trait-PC2 and -PC3 while the models for the most common species group showed that performance was predicted by all three trait-PC axes (Table 3). The conditional coefficients of determination ranged from 0.11 to 0.23 (Table 2).

When using the bin-4 protocol, the group containing the rarest had no significant relationship between RGR deviations and any of the trait-PC axes. The moderately rare species group showed significant relationships with trait-PC3, but the moderately common species groups showed significant relationships with trait-PC3 and -PC1. The grouping with the

Table 1 Fixed effects means [95% CI estimated by bootstrap] estimated by models of environmental effects on performance using different binning thresholds: 2, 4 and 3 of equal number of species and bin-abundance-2. The last two lines show the number of individuals and number of species by category. Bold numbers represent significant coefficient values. Letter 'A' corresponds to the rarest category while letters 'B', 'C', and 'D' correspond to subsequently more common categories of species

	Bin 4				Bin3			Bin 2		Bin-abundance-2	
Parameter	D	C	B	A	C	B	A	B	A	Common	Rare
Log(%light)	**0.24** **[0.1, 0.41]****	0.11 [−0.23, 0.42]	0.33 [−0.3, 0.89]	0.24 [−0.27, 0.8]	**0.22** **[0.07, 0.378]****	−0.03 [−0.44, 0.39]	0.42 [−0.06, 0.92]	**0.22** **[0.07, 0.352]****	0.32 [−0.06, 0.68]	**0.26** **[0.06, 0.43]****	**0.18** **[0.028, 0.40]***
Soil.pc1	**0.05** **[0.01, 0.08]***	0.04 [−0.04, 0.1]	0.055 [−0.05, 0.17]	0.06 [−0.04, 0.2]	**0.04** **[0.01, 0.079]***	0.01 [−0.07, 0.09]	0.042 [−0.04, 0.12]	**0.04** **[0.01, 0.07]***	0.06 [−0.01, 0.13]	**0.08** **[0.03, 0.12]*****	0.02 [−0.021, 0.051]
Soil.pc2	−0.001 [−0.05, 0.04]	0.02 [−0.07, 0.11]	−0.03 [−0.1, 0.07]	−0.04 [−0.18, 0.1]	−0.01 [−0.04, 0.041]	−0.01 [−0.09, 0.08]	−0.06 [−0.18, 0.05]	0.0001 [−0.04, 0.04]	−0.03 [−0.12, 0.05]	−0.01 [−0.06, 0.04]	−0.01 [−0.05, 0.04]
Soil.pc3	−0.02 [−0.08, 0.03]	−0.01 [−0.11, 0.09]	**0.19** **[0.001, 0.39]***	−0.03 [−0.23, 0.2]	−0.01 [−0.06, 0.035]	−0.01 [−0.12, 0.11]	0.02 [−0.16, 0.19]	−0.02 [−0.07, 0.03]	0.09 [−0.04, 0.23]	−0.03 [−0.08, 0.03]	0.01 [−0.04, 0.07]
No. individuals	1146	208	84	68	1250	162	94	1354	152	700	806
No. species	13	13	13	14	17	18	18	27	26	3	50

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2 Marginal and conditional R^2 for all models. Letter 'A' corresponds to the rarest category while letters 'B', 'C', and 'D' correspond to subsequently more common categories of species

Type of model	Bin-type	Marginal	Conditional
Soil & light	Bin2-B	0.02	0.14
	Bin2-A	0.04	0.04
Traits	Bin2-B	0.07	0.22
	Bin2-A	0.10	0.10
Soil & light	Bin3-C	0.02	0.15
	Bin3-B	0.002	0.002
	Bin3-A	0.04	0.04
Traits	Bin3-C	0.06	0.23
	Bin3-B	0.11	0.11
	Bin3-A	0.12	0.12
Soil & light	Bin4-D	0.02	0.17
	Bin4-C	0.01	0.11
	Bin4-B	0.04	0.04
	Bin4-A	0.08	0.08
Traits	Bin4-D	0.07	0.24
	Bin4-C	0.09	0.21
	Bin4-B	0.15	0.15
	Bin4-A	0.06	0.06
Soil & light	Bin-abundance-3 Common	0.04	0.07
	Bin-abundance-3 Medium	0.01	0.01
	Bin-abundance-3 Rare	0.01	0.12
Traits	Bin-abundance-3 Common	0.08	0.10
	Bin-abundance-3 Medium	0.06	0.20
	Bin-abundance-3 Rare	0.10	0.20
Soil & light	Bin-abundance-2 Common	0.04	0.07
	Bin-abundance-2 Rare	0.01	0.15
Trait	Bin-abundance-2 Common	0.08	0.10
	Bin-abundance-2 Rare	0.07	0.27

most common species showed that performance was predicted by all three trait-PC axes (Table 3). The conditional coefficients of determination ranged from 0.24 to 0.06 (Table 2).

The results for the bin-abundance-2 binning protocol showed that the models for both groups had significant relationships with the three trait-PC axes. However, the level of significance for the group containing the rarest species was lower for the PC2 axis (Table 3). The conditional coefficients of determination were 0.27 for the rare species group and 0.1 for the common species group (Table 2).

Finally, the results for the bin-abundance-3 binning protocol showed that the model considering the group with the rarest species had significant relationships with trait-PC1. The models for the moderately rare and most common species groups showed that performance was significantly predicted by the three trait-PC axes (Figs 1 and 2). The conditional coefficients of determination ranged from 0.2 to 0.1 (Table 2). Additional information on estimates for the intercept and random effects from all the models is available in Table S4.

The results obtained for the conditional R^2, that allow comparisons in the proportion of variance explained by random effects (plots), were higher than the marginal R^2 indicating an important amount of variance relative to the specific sites (Table 2). The models considering trait information had higher values than the models considering environmental variables (Table 2). Overall the coefficients of determination were low to moderate for all the models (Table 2). However, we note that in most cases our coefficients of determination are

Table 3 Fixed effects means [95% CI estimated by bootstrap] estimated by models of trait effects on performance, using different binning thresholds: 2, 4 and 3 of equal number of species and bin-abundance-2. The last two lines show the number of individuals and number of species by category. Bold numbers represent significant coefficient values

	Bin 4				Bin3			Bin 2		Bin-abundance-2	
Parameter	D	C	B	A	C	B	A	B	A	Common	Rare
Trait.pc1	**0.14** **[0.11, 0.179]** ***	**0.10** **[0.02, 0.19]** *	0.05 [−0.09, 0.17]	0.05 [−0.05, 0.21]	**0.14** **[0.11, 0.17]** ***	0.06 [−0.03, 0.16]	0.08 [−0.03, 0.18]	**0.13** **[0.10, 0.17]** ***	0.07 [−0.01, 0.16]	**0.15** **[0.106, 0.205]** ***	**0.11** **[0.12, 0.21]** ***
Trait.pc2	**−0.08** **[−0.12, −0.04]** ***	−0.07 [−0.16, 0.02]	−0.08 [−0.21, 0.03]	−0.08 [−0.26, 0.02]	**−0.07** **[−0.11, −0.03]** ***	**−0.10** **[−0.20, −0.01]** *	−0.11 [−0.24, 0.01]	**−0.07** **[−0.11, −0.04]** ***	**−0.09** **[−0.19, 0.002]** *	**−0.11** **[−0.17, −0.042]** ***	**−0.07** **[−0.16, −0.04]** **
Trait.pc3	**−0.12** **[−0.18, −0.07]** ***	**−0.20** **[−0.34, −0.07]** **	**−0.23** **[−0.4, −0.07]** *	−0.23 [−0.24, 0.07]	**−0.11** **[−0.16, −0.06]** ***	**−0.26** **[−0.42, −0.12]** ***	**−0.16** **[−0.3, −0.01]** *	**−0.13** **[−0.18, −0.08]** ***	**−0.16** **[−0.26, −0.04]** **	**−0.12** **[−0.181, −0.056]** ***	**−0.16** **[−0.18, −0.06]** ***
No. individuals	1146	208	84	68	1250	162	94	1354	152	700	806
No. species	13	13	13	14	17	18	18	27	26	3	50

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

higher than those reported in other models predicting growth from traits (Poorter *et al.* 2008; Iida *et al.* 2014; Paine *et al.* 2015).

DISCUSSION

The main results of our study show that the strength of demography-environment/trait and trait–environment relationships is not consistent across species in a community and the strength of these effects is related to abundance. The results generally support a trait-based core-transient framework for community structure and dynamics. Common species tended to show growth responses to higher light and soil nutrient levels, while rare species, in general, do not have strong responses in growth to gradations in the local environment. Similarly, we found that traits linked to resource acquisition were related to seedling growth for common species, but the relationship was frequently weak for rare species. As predicted by the core-transient dynamics, core species, usually described as common species, tend to be clearly linked to local abiotic conditions and potentially more affected by deterministic forces while transient species, usually described as rare species, tend to be an occasional component of the community not well-suited to the environmental conditions (Magurran & Henderson 2003). We, therefore, have provided trait-based results supporting the core-transient framework that also caution researchers against considering communities as a unit where are all species are similarly influenced by stochastic or deterministic processes.

In the shaded understory of tropical rain forests, resource availability has an important effect on seedling growth (Augspurger 1984; Chazdon & Fetcher 1984; Poorter 1999; Holste *et al.* 2011). Our results show that light and soil nutrients are linked to the traits measured and growth performance. Specifically, we found that the first edaphic principle component (PC) (strongly associated with K, Mg and Zn) played a major role influencing seedling performance. These elements are critical for the photosynthesis (K, Mg: Terry & Ulrich 1974; Leigh & Jones 1984), growth (Mg: Holste *et al.* 2011) and for seed and stem maturation (Zn: Broadley *et al.* 2007). Overall, these elements play critical roles for plant metabolism, but especially in photosynthesis.

Together with soil nutrients, light showed a significant positive effect on seedling performance. Previous studies have recognized the critical role of light for determining individual performance in early ontogenetic stages in the tropics (Augspurger 1984; Chazdon & Fetcher 1984; Chazdon 1988; Nicotra *et al.* 1999). This is supported by the correlations that we found between traits linked with photosynthetic capacity and growth rates. For example, individuals with high leaf area ratios, high specific leaf areas and high specific stem lengths showed enhanced growth.

The observed differences on the effect of the local environment and traits on individual growth rates across species suggest that there are important ecological differences between species regarding how these species interact with the local environment. The use of available resources is strongly linked with an organism's ability to exploit those resources, but species vary in their traits (Ackerly & Reich 1999; Wright *et al.*

2004; Onoda *et al.* 2011). This variation differentiates their ability to be equally effective responding to gradations in the local resources environment. In shaded tropical understories where the light and soil nutrients are often highly limited and seedling growth is generally slow overall (Augspurger 1984), species with ecological strategies adapted for rapid resource acquisition are expected to have weak responses to the local environment. Intra-specific variation in the traits of these transient species is not expected to be strongly linked to the local gradations in light or soil nutrients experienced. We propose that the populations of these species are governed by the stochastic arrival of seeds from other populations and that the arriving individuals have poor performance given the local environment (i.e. a deterministic outcome) resulting in little-to-no local recruitment. Conversely, core species with conservative resource use strategies are expected to have strong trait-environment and performance-environment/trait relationships (Magurran & Henderson 2003). This is because individuals, on average, for these species are well-suited to the average local environment and intra-specific trait variation can track local scale environmental variability. We, therefore, propose that these core species have a strong deterministic relationship with the local environment where the arrival of new seeds into the population is largely driven by the reproductive success of local adult individuals. This ultimately results in large and persistent populations.

Distinguishing species into core or transient species ultimately requires long-term data that provide evidence of population persistence and measures of growth, survival and recruitment throughout the lives of individuals (Magurran & Henderson 2003). Such data is not available for the species in this study or other tropical tree studies given the long life spans of trees. In order to provide further insights into this possibility, we examined all different models proposed for species that were rare in our data set and abundant in a forest close to our study site (rare-transient) compared with species that were rare for both sites (rare-non-transient) (Appendix S1). We found that overall rare-transient species had weaker relationships between growth deviations and traits as well as for traits and the environment. Thus, rare-transient species are potentially more influenced by factors occurring at larger spatial scales (Magurran & Henderson 2003) and are not strongly linked to the local habitat. This analysis also highlights that not all rare species are necessarily transient species. Thus, despite the fact that the distinction between core and transient has been linked with species abundance (Magurran & Henderson 2003) we do acknowledge that our classification of rare species as transient is imperfect and further studies are needed to better understand the core-transient dynamics.

A further caveat of our study is that the local environment is not characterized solely upon the basis of the abiotic conditions. There are additional factors such as pathogens and herbivores that impact the seedlings performance (Bagchi *et al.* 2010; Mangan *et al.* 2010). These biotic contexts are not explicitly included in our analyses, but they could have potentially influenced the observed variation in seedling growth rate. We attribute the low variation in deviations in growth explained by our models to these effects in addition to unmeasured variables.

Natural communities are composed of species representing a broad range of strategies linked to heterogeneous levels of resource availability. In this study, we have shown that communities can be characterized in two groups of species that differ in the strength of their ecological interactions with the environment and the role of stochastic vs. deterministic forces. Specifically, not all the species in a community exhibit strategies that are strongly linked to set of locally available environmental conditions and this variability affects their ability to respond to increases in resources. Core, generally common, species tend to exhibit clearer responses to local resource availability variation and their traits play an important role in mediating the resource acquisition promoting seedling growth. On the other hand, transient, usually rare, species are more limited in their responses. Our results highlight the importance of moving trait-based community ecology beyond the consideration of a community as a unit where species are equally influenced by stochastic or deterministic factors. Here, we propose a framework that incorporates variation in the response of species to the local environmental conditions where some species are present due to their strong link to local conditions and therefore present due to determinism while other species are less linked to local conditions and are only present due to stochastic events.

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AUTHOR CONTRIBUTIONS

MNU and NGS designed the study; MNU, CZ, MC, LL and NGS conducted the study and contributed to the project design; MNU performed all data analyses; CZ, MC and LL coordinated the soil analyses; MNU and NGS wrote the manuscript; CZ, MC and LL contributed to editing the manuscript.

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