

Tree seedling trait optimization and growth in response to local-scale soil and light variability

MARIA NATALIA UMAÑA ^{1,4}, GABRIEL ARELLANO ¹, NATHAN G. SWENSON,² AND JENNY ZAMBRANO³

¹Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109 USA

²Department of Biology, University of Maryland, College Park, Maryland 20742 USA

³The School of Biological Sciences, Washington State University, Pullman, Washington 99164 USA

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Abstract. At local scales, it has been suggested that high levels of resources lead to increased tree growth via trait optimization (highly peaked trait distribution). However, this contrasts with (1) theories that suggest that trait optimization and high growth occur in the most common resource level and (2) empirical evidence showing that high trait optimization can be also found at low resource levels. This raises the question of how are traits and growth optimized in highly diverse plant communities. Here, we propose a series of hypotheses about how traits and growth are expected to be maximized under different resource levels (low, the most common, and high) in tree seedling communities from a subtropical forest in Puerto Rico, USA. We studied the variation in the distribution of biomass allocation and leaf traits and seedlings growth rate along four resource gradients: light availability (canopy openness) and soil K, Mg, and N content. Our analyses consisted of comparing trait kurtosis (a measurement of trait optimization), community trait means, and relative growth rates at three resource levels (low, common, and high). Trait optimization varied across the three resource levels depending on the type of resource and trait, with leaf traits being optimized under high N and in the most common K and Mg conditions, but not at any of the light levels. Also, seedling growth increased at high-light conditions and high N and K but was not related to trait kurtosis. Our results indicate that local-scale variability of soil fertility and understory light conditions result in shifts in species ecological strategies that increase growth despite a weak trait optimization, suggesting the existence of alternative phenotypes that achieve similar high performance. Uncovering the links between abiotic factors, functional trait diversity and performance is necessary to better predict tree responses to future changes in abiotic conditions.

Key words: biomass allocation traits; canopy openness; kurtosis; leaf area; specific leaf area; Puerto Rico; soil nutrients.

INTRODUCTION

Understanding how abiotic factors drive functional trait distributions and growth of local communities is important for determining community responses to future changes in environmental conditions (Violle et al. 2007, Estrada et al. 2016, Sakschewski et al. 2016). Trait distributions of plant communities are assumed to be the outcome, to some degree, of environmental conditions exerting selective forces and favoring species that make a good fit for given conditions. In other words, traits are assumed to reflect optimal or, at least, optimized ecological strategies for any given environment (although this set of optimal traits may change due to temporal changes in conditions; Southwood 1977, Grime 1979, Keddy 1992, McGill et al. 2006). As a

result, local species composition should cover a relatively narrow range of trait values that fit the requirements of the environment there. However, this expectation contradicts the often-observed pattern of a wide diversity of forms and functions in tropical plant communities and suggests the existence of alternative phenotypes with equivalent performance (Marks and Lechowicz 2006, Worthy et al. 2020).

At local scales, the distribution of a given resource is typically unimodal, with some resource values being more frequent than values located at the tails of the distribution (Fig. 1, Appendix S1: Fig. S1; Abrams 1995, Brigatti et al. 2007). For example, levels of canopy openness (used as a proxy for understory light availability) are often around 10% in tropical forests. However, light availability values, even in a closed forest, can range between <1% and 35%, with these extreme values being less frequent than mean values (Chazdon and Fetcher 1984). Similarly, soil resources may exhibit a similar peaked hump-shaped distribution, with soils showing

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⁴E-mail: maumana@gmail.com

low and high levels of fertility toward the tails of the distribution (Appendix S1: Fig. S1). As traits reflect the interaction between the organisms and their environment, local variation in abiotic factors is expected to have an impact on trait distributions in plant communities and on growth. There are at least three potential scenarios describing trait distributions at the community level, and plant growth in response to resource gradients:

Scenario 1: Peaked trait distributions toward common conditions

In the first scenario, uncommon conditions are too rare to lead to peaked trait distributions, trait optimization, given that resources are not suitable and abundant enough to maintain stable populations that represent a

good fit for those conditions, while common conditions represent suitable areas and allow trait optimization (Fig. 1A; McGill et al. 2006, Violle et al. 2007). These two different levels of trait optimization would imply better performance (e.g., growth) for individuals present in the most common conditions and lower performance of those individuals in places with uncommon resource levels.

Scenario 2: Peaked trait distributions toward rare conditions

Uncommon conditions that represent extremes of the resource distribution (characterized by either low or high resource levels) could lead to trait optimization due to strong selective forces that operate under these conditions (Fig. 1B). For example, in high-light conditions

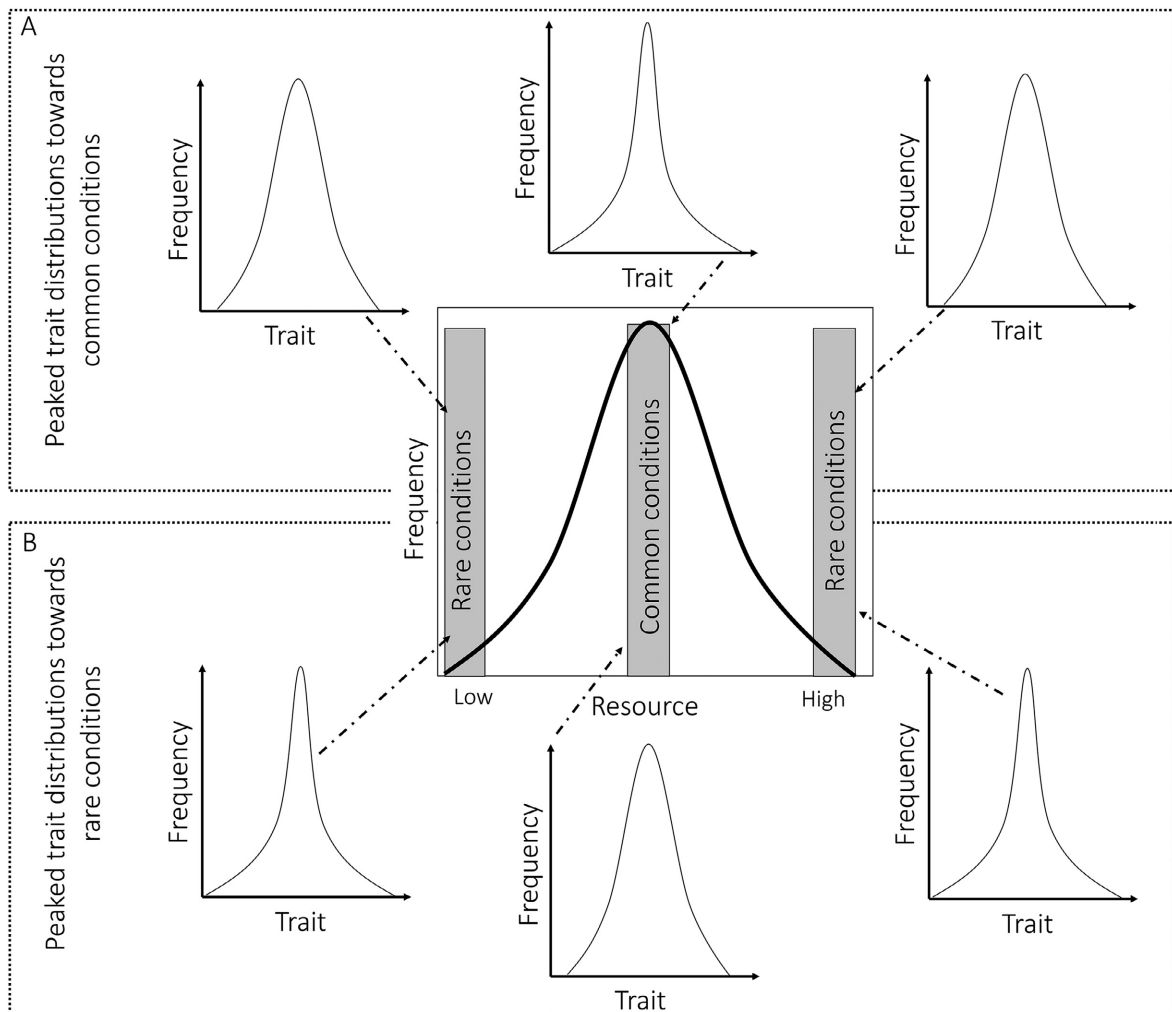


FIG. 1. Conceptual diagram depicting changes in trait distributions (kurtosis) between rare and the most common resource levels. In the center, the plot depicts the variation in a given resource that describes a unimodal distribution with values at the two extremes being less frequent than the values in the central section. Based on these three resource levels, we show two scenarios (A and B) of how trait distribution is expected to vary between rare and common resource levels.

species that acquire resources fast and efficiently out-compete other species leading to optimization in leaf traits. Similarly, in nutrient-poor soils only a handful of specialized species may persist, representing a (relatively) narrow range of traits. Empirical evidence has shown that trait values are more strongly selected at the extremes of the resource distribution characterized by either low or high resource levels, with trait optimization occurring at these extremes rather than at most common ones (Weiher et al. 1998, Cornwell and Ackerly 2009, de Bello et al. 2009, Kraft and Ackerly 2010, Swenson et al. 2011, Bernard-Verdier et al. 2012, Bruelheide et al. 2018). For instance, a previous study found that open sites (i.e., treefall gaps) exert strong selective forces on tree communities allowing only light-demanding species to successfully colonize these forest gaps (trait optimization), while intermediate and low light level sites exhibit greater diversity of life forms (lower trait optimization; Hubbell 2005). Other studies have also shown that across environmental gradients, low soil nutrient levels tend to favor stress-tolerant species, resulting in trait optimization toward lower extremes of the resource distribution (Pinho et al. 2018). These patterns in trait distributions have been well documented at the landscape and regional scales (Cornwell and Ackerly 2009, Enquist et al. 2015, Šimová et al. 2015). At local scales, similar trends are expected if extreme abiotic conditions select for particular traits that maximize organisms' performance (e.g., high growth; Fig. 1B).

Scenario 3: Low peaked trait distributions occur in both common and rare resource levels

Alternatively to these two scenarios, traits might not be strongly optimized toward a single or a narrow range of values. Instead, plants may display contrasting phenotypes that constitute alternative solutions for the given local conditions (Marks and Lechowicz 2006, Muscarella and Uriarte 2016, Worthy et al. 2020). For example, Hirose and Werger (1995) found that in a tropical forest different species of trees exhibit contrasting strategies for capturing light that result in similar performance. In this case, we should observe a lack of trait optimization across different resource levels, yet species may still achieve high performance anywhere along the local gradient of conditions.

Here, we examine both biomass allocation and non-biomass allocation traits. Biomass allocation traits represent a group of traits that have shown great variation within species and reflect the amount of biomass that plants allocate to a particular organ depending on the resources that are the most limiting for plant growth (Bloom et al. 1985, Poorter et al. 2012, Umaña et al. 2018). For example, according to optimal allocation theory, strong limitation in soil nutrient content should result in increased biomass allocation to roots at the expense of lower biomass allocation to leaves and stems (Bloom et al. 1985). Another group includes non-

biomass allocation traits, such as specific leaf area or leaf area, which have shown strong responses to shifts in a variety of abiotic factors (Chapin 1980, Oksanen et al. 1981, Reich et al. 1997, Craine et al. 2001, Wright et al. 2004). For example, environments with low resource levels tend to be dominated by species with conservative traits such as low specific leaf area and low leaf area (Le Bagousse-Pinguet et al. 2017). Combined, biomass allocation and non-biomass allocation traits capture a wide range of species responses to local-scale resource variation.

We study trait optimization in response to local-scale resource variation and how that results in differences in seedling growth in a subtropical forest. We use growth and trait information collected from all individuals present in 200 seedling plots (~1,800 individuals) in combination with local-scale abiotic information on soil nutrient content (K, Mg, and N) and canopy openness (a proxy for light availability in the forest understory; Appendix S1: Fig. S1). While most trait-based studies have used species' mean traits values, which assumes that all individuals within a species are identical in their traits, here, we have trait and seedling growth information for all individuals. With this information, we can accurately study trait and growth distributions across local-scale resource gradients. Specifically, we ask the following questions:

1. How does trait optimization differ in extreme vs. common resource levels? We propose to examine the three alternative scenarios described above by quantifying trait optimization under different resource levels.
2. How do community mean trait values change across resource levels? We expect changes in trait means across different resource levels depending on the type of trait. Specifically, we expect biomass allocation traits to vary according to the optimal allocation theory (i.e., higher allocation toward most limiting resources), while non-biomass allocation traits will be more conservative (e.g., low SLA and LA) toward the most limiting extremes of resource levels.
3. How does seedling growth vary between extreme vs. common resource levels? Does trait optimization lead to high seedling growth? We predict variation in seedling growth across common and extreme levels of soil nutrient and light conditions, with at least two potential and non-exclusive outcomes: (a) at high resource levels, seedling growth rates are high; (b) seedling growth rates are high in resource levels that show high trait optimization.

METHODS

Field surveys and trait data collection

The study was conducted in El Yunque National Forest, in Puerto Rico, USA (65°47' W, 18°19' N). This

forest, classified as a subtropical wet forest, has a mean annual rainfall of 3548 mm and an average temperature of 23°C (Ewel and Whitmore 1973). The vegetation is dominated by the tree species *Dacryodes excelsa* (Burseraceae) and the palm *Prestoea acuminata* (Arecaceae). In 2013, 200 1 × 1 m seedling plots were established to monitor seedling growth for one year. Seedling plots were arranged in a regular grid separated by 10 m. All tree seedlings ≤ 50 cm in height ($n = 1771$) were measured, tagged, and identified to species (Umaña et al. 2015). Between June and July 2014, all surviving individual seedlings were collected for trait measurements. We measured fresh leaf area (LA; cm²) for one to three fully expanded leaves. The leaves were then dried and weighed to calculate specific leaf area (SLA = LA/dry mass; cm²/g). Roots were cleaned and separated from the main stem. Leaves and roots were dried in an oven for 72 h at 70°C and measured for dry mass (g) to calculate traits related to biomass allocation. Leaf mass fraction (LMF) was calculated as LMF = leaf dry mass/total plant dry mass. Root mass fraction (RMF) as root dry mass/total plant dry mass. Leaf area ratio (LAR) was calculated as LAR = leaf area/total plant dry mass (Poorter et al. 2012). Leaf traits included leaf area (LA) and specific leaf area (SLA). LA reflects the area displayed to capture light (Rozendaal et al. 2006), while SLA describes a range of strategies (conservative to acquisitive) for carbon assimilation (Reich et al. 1997, Wright et al. 2004).

Relative growth rate

We defined seedling relative growth rate (RGR) as the change in log-transformed total height (cm) from 2013 to 2014. The total height of each seedling was measured from the base to the most distant part of the main stem. We standardized relative growth values by subtracting the mean of each species and dividing by the standard deviation per species. This allows comparisons across species with different inherent growth rates, as those involved in the survival-growth trade-off (Arellano et al. 2019).

Soil nutrient content and canopy openness

Soil samples were extracted below the organic litter layer (0–10 cm depth) in July 2014. Each soil sample consisted of mixed soil from each of the plot corners and from the center of the seedling plots, and we collected a total of 200 soil samples. Soil samples were sent to Brookside Laboratories (New Bremen, Ohio, USA) for chemical analyses. Magnesium and potassium (Mg, mg/kg; and K, mg/kg) were extracted using the Mehlich-III solution. Magnesium is an essential macronutrient found in the chlorophyll of green plants and potassium is essential for photosynthesis and protein synthesis as well as carbohydrate transport and storage (Maathuis 2009). Potassium has been found to limit seedling growth in tropical and temperate forests (Tripler et al.

2006, Wright et al. 2011). Total soil N concentration was obtained using the total combustion method. Nitrogen is an essential constituent of proteins found in chlorophyll and is needed in substantial amounts (Maathuis 2009). While soil P is an important limiting resource for tropical forests, most of the P concentrations in our samples fell below the detection threshold for the method and we could not use it for the present study.

To assess light conditions, we took hemispherical photographs using a camera Nikon Coolpix5000 with an FC-E8 Nikon fisheye lens (Nikon Inc., Tokyo, Japan). The photographs were taken at 1 m height in the center of each seedling plot at uniform light conditions at dawn with homogeneous light conditions (Glatthorn and Beckschäfer 2014). The photographs were analyzed using the Gap Light Analyzer software (GLA; Frazer et al. 2000; *software available online*).⁵ Appendix S1: Table S1 reports ranges and mean values for all the studied abiotic variables.

Plot selection at different resource levels

Our approach consisted of classifying plots into three resource levels (low, common, and high) and then calculating trait kurtosis per each resource level. This approach allows us to use seedling communities large enough at each resource level in order to have robust measurements of kurtosis, otherwise, our plots are too small to have a high number of trait values (seedling abundance range: [1, 39]; mean = 9). Prior to the analyses, we examined correlations between abiotic variables across the 200 plots (Appendix S1: Table S2) and their distribution. All abiotic variables showed unimodal distribution with the most common resource level around the average resource value (Appendix S1: Fig. S1).

Next, we calculated the relative frequency of each resource level using a kernel density estimation for each abiotic variable using the R function density from package stats (R Development Core Team 2017). Given that the density estimation is affected by the bandwidth, we used two methods to select the appropriate bandwidth. The first method is based on a linear diffusion process (Botev et al. 2010), a nonparametric density estimator independent of a normal model and less sensitive to outliers (Botev et al. 2010). This method was implemented by using the function botev from the package proveance in R (Vermeesch 2020). The second method uses the asymptotic mean integrated squared method error (AMISE) and consists of evaluating the mean integrated squared error of a density estimate based on a normal distribution (see Appendix S2).

We classified subsets of plots into “low-resource” plots, “high-resource” plots, and “the most common resource level” plots, for each environmental variable (hereafter referred to as low, high, and common,

⁵ <https://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla>

respectively). The low-resource plots corresponded to the 10% with the lowest level of the resource. The high-resource plots corresponded to the 10% with the highest level of the resource. The most common resource level plots corresponded to the 10% closest to the most frequent conditions, inferred from the location of the peak in the unimodal estimation of density. Since we have some plots with repeated values for the different resources studied, the number of plots selected per resource level varied between 10–16% of the total number of plots; Appendix S1: Table S3 contains the specific number of plots selected per resource level, and Appendix S1: Fig. S1 indicates the plots that were selected in each resource level (of the 200 plots established, some were excluded from the analyses to focus on the most extreme and common values). To determine whether our results were sensitive to the number of selected plots for each resource level, we repeated all the analyses using the plots with the lowest, highest, or the most common levels of the resource, p in $\{5, 6, \dots, 14, 15\}$. The results (Appendix S3) were not sensitive to the value of p , except in low ranges (likely due to the low sample size, the inherent variability in the tails and/or the skewed distribution of some of the resources studied).

Measurement of trait optimization at each resource level

To examine how trait distribution varied with different resource levels (question 1), we compared trait kurtosis values using information from seedlings located in the low, high, and the most common resource plots. Very peaked distributions (high kurtosis) indicate strong trait optimization, while very flat distributions (low kurtosis) indicate weak trait optimization (Enquist et al. 2015, Le Bagousse-Pinguet et al. 2017). We calculated kurtosis for individual traits per resource level. We choose kurtosis over variance because we are interested in detecting a pointed peak (or lack of it) in trait distributions beyond the information about how spread the data is (Fig. S2 in Appendix S1 shows that the degree to which a given distribution is peaked is independent of the spread of the data; (Enquist et al. 2015).

Given that kurtosis values are difficult to compare with each other, at least in terms of how much they differ from the expected by chance, we used a more interpretable metric than raw kurtosis, by calculating the standardized effect sizes (SES) for the kurtosis values obtained in all resource level classes, for all environmental variables and traits. To calculate the SES for kurtosis, we created null models where each trait value per individual within a community matrix (including all 200 plots) was randomized 999 times and we recalculated kurtosis for each resource level for each randomized dataset. We then obtained a mean null value and standard deviation from the null distribution that were used to calculate the kurtosis SES.

$$\text{SES Kurtosis} = \frac{\text{Observed kurtosis} - \text{meannull kurtosis}}{\text{SDnull kurtosis}}$$

SES kurtosis values >1.96 indicate higher than expected kurtosis in a certain trait given the number of seedlings present in plots at each resource level and SES kurtosis values <-1.96 values indicate a lower than expected kurtosis for a certain trait given the number of seedlings present in plots at each resource level.

Change in mean trait values in each resource level

To determine how community mean trait values change across resource levels (question 2), we calculated and compared mean community trait values at each resource level. When calculating mean trait values, we used all individual seedlings present at each resource level. To allow comparisons between traits measured in different units, we used standardized trait values at the community level (mean = 0, standard deviation = 1). Next, to determine whether trait means at each resource level differ from zero, we performed a bootstrap sampling with replacement. To do this, we randomly selected seedlings (with different trait values) for each resource level 999 times and calculated the mean per trait. If 95% of the values of the bootstrap distribution overlapped zero, then it was considered not significant. In other words, this test examines whether the trait mean at a given resource level differs from the expected for the species.

Variation in seedling growth rates at each resource level

To address how seedling growth varies across resource levels (question 3), we performed a similar analysis from the one used for mean traits, but instead of using functional traits, we used RGR (see raw RGR distributions at each resource level in Appendix S1: Fig. S3). We also performed a bootstrap sampling with replacement to assess the significance of changes in RGR at each resource level (*i.e.*, deviations in RGR from the expected for the species). Furthermore, we evaluated if kurtosis was related to mean RGR at each resource level (question 4) using a linear mixed-effects model (function `lmer`, package `lme4` in R; Bates et al. 2015, R Development Core Team 2017). In these models, the response variable was mean RGR at each resource level. The independent variable was trait kurtosis per resource level; abiotic factors (canopy openness, soil N, Mg, and K) and resource levels (high, low and the most common) were included as intercept-specific random effects, to account for the effects of variation of both variables on growth. The sample size for this model was $n = 60$. To calculate the marginal and conditional coefficients of determination described by Nakagawa and Schielzeth (2013), we used

the function *r2* in the package *performance* (Lüdecke 2020).

RESULTS

Variation in trait distributions with different resource levels (question 1)

Observed kurtosis patterns based on different traits showed a variation across the different studied resource levels (low, common, and high), but the patterns were resource and trait specific (Appendix S1: Fig. S2). For canopy openness, observed kurtosis values for all traits did not differ from a random expectation, but there was a generalized trend for higher SES kurtosis in the most common light conditions, except for RMF (Fig. 2). For soil K content, SLA had higher than expected kurtosis at high resource values while LAR had higher than expected kurtosis at the most common level, the rest of the traits had kurtosis that was not significantly different than expected by the null model. For soil Mg content, LAR had higher than expected kurtosis at the most common resource level, indicating trait optimization and RMF had higher than expected kurtosis at the low resource level. The rest of the traits had kurtosis levels that were not significantly different from the null expectation for soil Mg. For soil N content, SLA, LAR, and LMF had a higher than expected kurtosis at the high resource level indicating trait optimization at high N levels. The rest of the traits had kurtosis that was not significantly different than expected by the null model for soil N. Results obtained using the AMISE method were largely consistent with the results described above, especially for results based on canopy openness and soil N (Appendix S2). For Mg and K, kurtosis values of LAR, LMF, and SLA were less consistent (Appendix S2).

Variation in mean trait values with different resource levels (question 2)

In addition to the kurtosis analyses, we also examined shifts in mean trait values across the three resource levels. For canopy openness, LA and LAR were significantly higher at high-light levels, and LAR, RMF, and SLA were significantly lower at the most common resource level. The means of the rest of the traits were not significantly different from their community-wide means at any level of canopy openness (Fig. 3). For soil K content, LA was significantly higher at low and high resource levels but it was significantly lower at the most common resource level. Also, LAR was significantly higher when soil K was high. The rest of the traits showed means that were not significantly different from the mean community value for soil K (Fig. 3). For soil Mg content, RMF and LA were significantly higher, while SLA was significantly lower at the most common resource level. The rest of the traits showed means that were not significantly different from the mean

community value for soil Mg (Fig. 3). For soil N content, LAR and LMF were significantly higher at the low resource level, while LMF and LAR were significantly lower and RMF was significantly high at the most common resource level, and LA, RMF, and LAR were significantly higher at the high resource level. The rest of the traits showed means that were not significantly different from the mean community value for soil N (Fig. 3).

Community growth rates in three resource levels (question 3)

Mean seedling relative growth rate (RGR) was significantly higher at high levels of canopy openness, soil N, and K content (Fig. 4). For the rest of the resource levels, standardized RGR showed no significant differences. In addition, in the linear mixed-effects model relating trait kurtosis and growth, the kurtosis had virtually no effect on RGR (coefficient = 0.01, 95% CI [-0.01, 0.03]); the model had a low fit (marginal $R^2 = 0.02$ and conditional $R^2 = 0.53$).

DISCUSSION

Understanding how resource variation at local scales determines trait distributions and plant performance remains a major question in ecology. To examine this question, we combined individual trait and growth information collected from tropical seedling communities along local-scale light and soil fertility gradients. We found that trends in trait optimization are not generalizable across soil and light gradients. Specifically, trait optimization was observed for the most common levels of K and Mg as well as in high soil N sites, while traits were not particularly optimized at any level of canopy openness. Variation in growth rates was also resource specific, with seedling growth being the highest when canopy openness and soil K and N content were high but was not related to trait optimization. Overall, these findings suggest that peaked trait distributions do not necessarily match the most common resource levels nor lead to an increase in growth as it is commonly assumed for local-scale studies. Further, we show that seedling growth can increase despite a lack of trait optimization. Below, we discuss in more detail our findings.

Traits are optimized under low, high, and common resource levels

We observed a strong variation of trait optimization across three resource levels. However, these shifts in trait optimization were highly dependent on the type of resource and studied trait. For instance, LA, LMF, and LAR showed peaked distributions when soil N content was high supporting the scenario showed in Fig. 1B. Similar results have been reported in studies including broader environmental gradients than the one included in

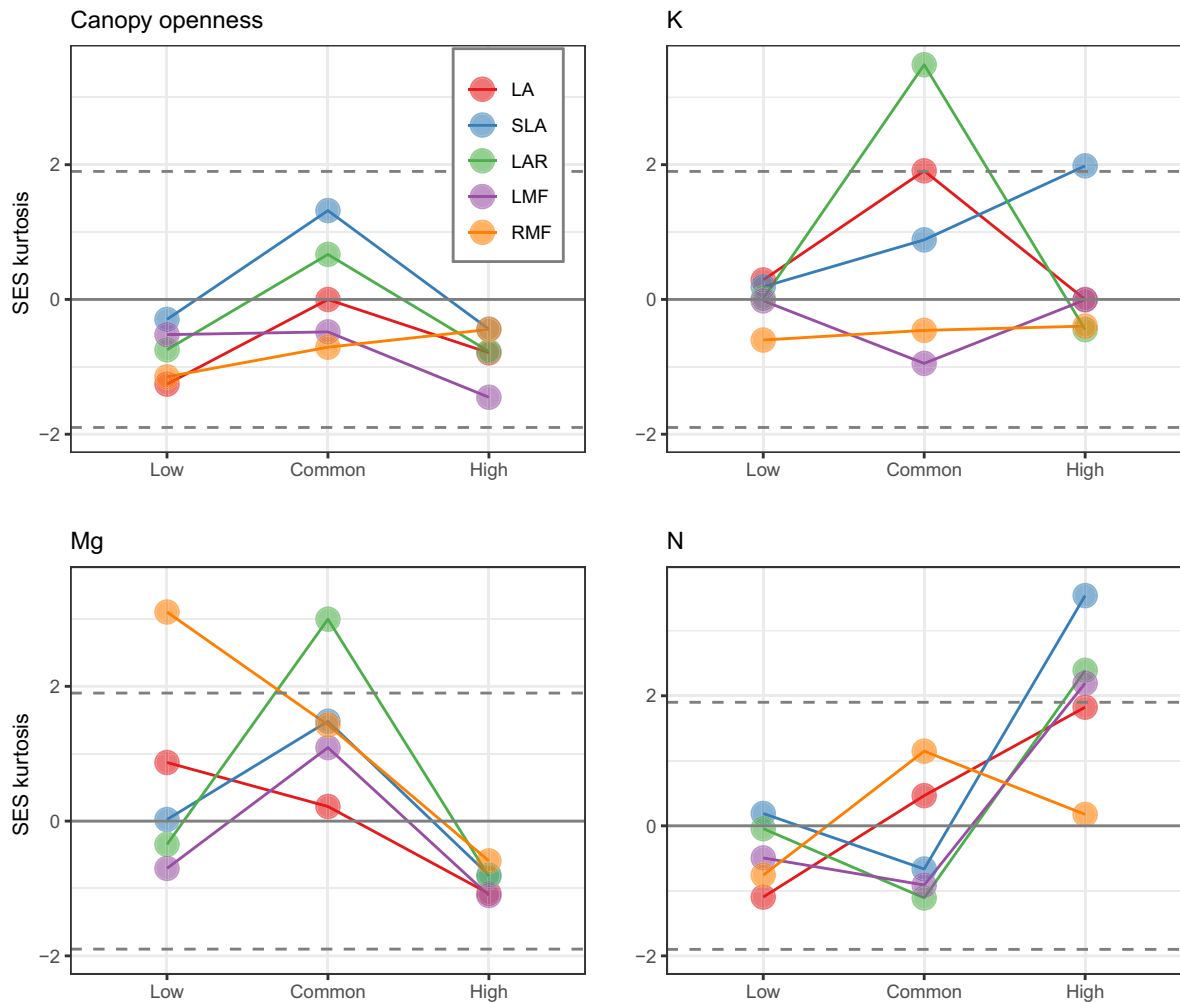


FIG. 2. Standard effect size (SES) kurtosis of trait values for three resource levels (low, common, and high). Positive SES values above indicate kurtosis values higher than expected by chance. Negative SES values below indicate significantly lower than the expected kurtosis in a given community. Dashed horizontal lines represent ± 1.96 , indicating significantly higher/lower kurtosis than expected by chance. Color codes represent individual traits. LA, leaf area; SLA, specific leaf area; LAR, leaf area ratio; LMF, leaf mass fraction; RMF, root mass fraction.

this study, in which high soil fertility leads to high trait kurtosis (Enquist et al. 2015, Le Bagousse-Pinguet et al. 2017). However, when considering soil Mg or K content, peaks in trait distributions (for LAR) were found at sites with the most common resource level, supporting the scenario showed in Fig. 1A and suggesting strong selecting forces on trait distributions under the most common conditions. These results are concordant with previous theoretical studies predicting a high frequency of trait values under the most common conditions (Austin 1986, McGill et al. 2006, Enquist et al. 2015), yet empirical evidence has remained scarce. Surprisingly, we also found a lack of trait optimization for any of the studied traits when considering canopy openness that can be related to high temporal variability in light conditions. Overall, the discrepancies in trait distributions across different resource levels suggest that selective forces operate with

variable intensity at different resource availabilities and may even result in a prevalence of low peaked trait distributions. These results are consistent with another study of tree communities across the entire island of Puerto Rico that examined the variation in community weighed mean trait values with shifts in species occurrence to test for trait optimization (Muscarella and Uriarte 2016). Their results showed that while some traits support the optimization hypothesis (LMA, wood density, and maximum height), there were many other cases where trait optimization was not found.

Mean trait values are more acquisitive under high resource levels

We expected a variation in mean trait values in response to different resource levels (Fig. 3). Specifically,

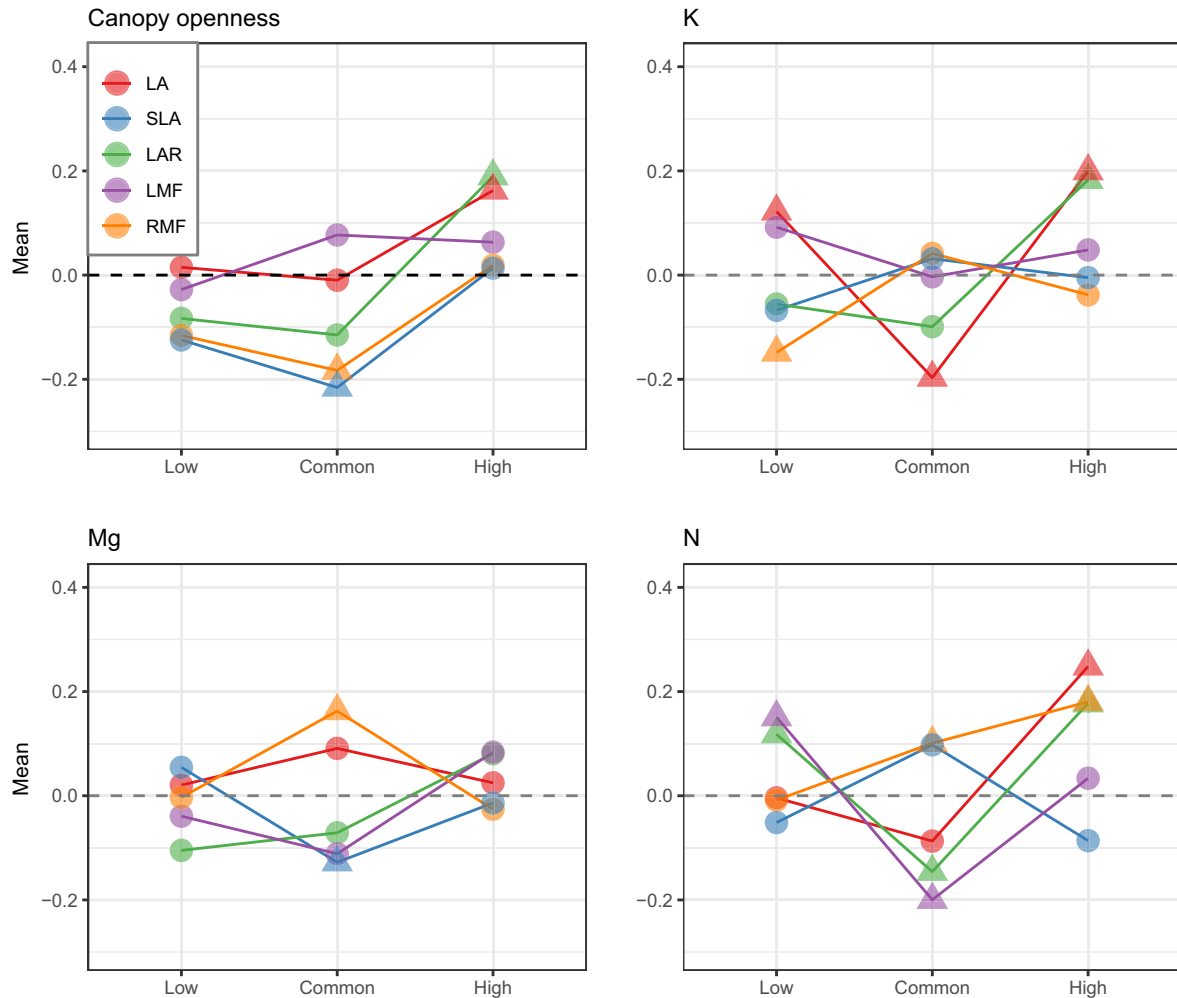


FIG. 3. Differences in mean trait values for three resource levels (low, common, and high). All traits were standardized at the community level (mean = 0, standard deviation = 1) to make them comparable. Positive values indicate that for a given resource level, mean traits are higher than the whole-community mean. Negative values indicate that for a given resource level, mean traits are lower than the whole-community mean. Triangles indicate 95% confidence intervals not overlapping zero when estimating the distribution of the mean after 999 bootstrap resampling, while circles represent 95% confidence intervals that overlap zero. Color codes represent individual traits. Acronyms for traits are the same as in Fig. 2.

we predicted acquisitive strategies (i.e., high SLA and LA) to be predominant at high resource levels and increased biomass allocation to organs involved in the acquisition of limited resources (low resource levels). For leaf allocation traits, our results did not follow the expected trend and instead, showed that seedlings tend to allocate a greater area to leaves (LAR) rather than allocating biomass to roots in habitats experiencing high light levels. These findings contradict the optimal allocation theory in which plants are expected to allocate greater leaf biomass in low light conditions than at higher light availability (Mooney 1972, Bloom et al. 1985). However, for non-biomass allocation leaf traits, our results were consistent with our expectations with LA increasing with high understory light availability and indicating that seedling communities located in more

open environments are characterized by acquisitive traits. These findings are concordant with previous studies conducted at a Neotropical forest where species displayed high leaf sizes values at high light levels contributing to their carbon gain (Lambers and Poorter 1992, Poorter and Rozendaal 2008). It is important to note that similar trends observed for LAR and LA can be also explained by the correlation between both traits (Fig. S4: Appendix S1).

By taking together results of mean and kurtosis trait values for variable light conditions, we infer that trait distributions across the three light levels show to some degree shifts in mean functional strategies, yet under each light level, there is no evidence of trait optimization. This indicates that trait selection operates differently across low, most common, and highlight levels but

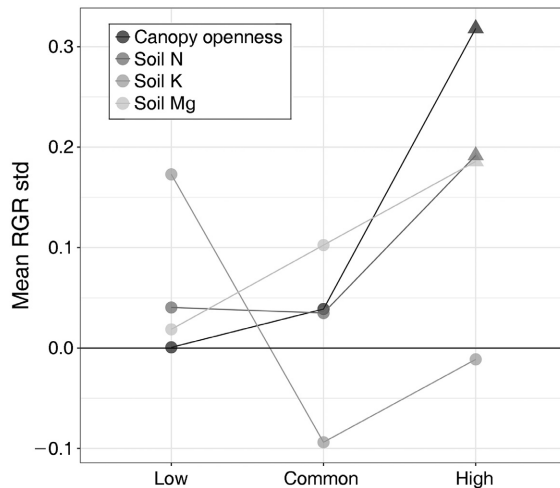


FIG. 4. Differences in mean seedling relative growth rates (RGR standardized at the species level) for three resource levels (low, common, and high). Color codes represent resources (canopy openness and three soil nutrients). Positive values indicate that mean RGR at a given resource level is higher than the whole-community mean. Negative values indicate that mean RGR at a given resource level is lower than the whole-community mean. Triangles indicate that 95% confidence intervals of bootstrap sampling do not overlap zero, circles indicate that the 95% confidence intervals overlap zero.

within each resource level there is a substantial variation in phenotypes that result in platykurtic trait distributions. This agrees with results from a previous study from the El Yunque forest that showed that during the seed-to seedling transition, functional divergence tends to be higher than expected by chance (Umaña et al. 2016).

Mean trait values also varied in response to soil resource levels. We expected greater biomass allocation to roots in poor soil conditions as suggested by the optimal allocation theory (Bloom et al. 1985, Garnier 1991, Marschner et al. 1996, Wright et al. 2011, Santiago et al. 2012) and an increase in SLA as soils become more fertile (Ordoñez et al. 2009). However, these expectations were not supported in this study as we found no general trends for patterns of biomass allocation or distribution of leaf-related acquisitive strategies. One potential explanation is that patterns of biomass allocation and trait variation depend on the interaction of multiple abiotic factors (Blonder et al. 2018). For example, root biomass responds to both soil fertility and water availability that does not always covary at the local scales included here and may result in conflicting trait responses. Another potential explanation is that trait–trait correlations may potentially mask plant responses to variation in resource availability. For example, the significant correlation between leaf and root mass fractions may limit the ability to identify and separate the responses of below-ground and above-ground traits (Fig. S4).

Seedling growth increases under high light and high soil N and K content but is not related to trait optimization

We expected that seedling growth would increase in areas of high resource levels and/or in areas of high trait optimization (high trait kurtosis). Our results show that high light availability and soil N and K content resulted in high seedling growth rates (Fig. 4); however, growth was not related to trait optimization. Our findings related to light suggest that understory light conditions are a key limiting factor in this forest and that at high understory light availability, plants might enhance their growth in the absence of a trait optimization. Our results are concordant with results from other plant community studies that have shown species exhibiting contrasting phenotypes that increase plant performance and conform alternative phenotypes under particular resource conditions (Hirose and Werger 1995, Pistón et al. 2019, Worthly et al. 2020). Our results also agree with previous studies conducted in the studied forest showing light as a key factor influencing performance at early ontogenetic stages (Comita et al. 2009, Uriarte et al. 2018).

For soil nutrients, the direct effects of soil N and K should be carefully interpreted as both variables were significantly correlated making it difficult to determine the independent contribution of each factor to seedling growth ($r = 0.56$, $P < 0.001$, Table S2 in Appendix S1). Although it has been suggested that soil N should not be considered as a limiting factor for tropical forests (Hedin et al. 2009), previous studies in tropical regions have found that soil N may have positive significant effects on plant biomass accumulation and productivity (Vitousek and Sanford 1986, Mirmanto et al. 1999, LeBauer and Treseder 2008, Graefe et al. 2010, Santiago et al. 2012). Similarly, soil K has shown significant effects on seedling growth, as found in our study (Santiago et al. 2012, Wright 2019).

Conclusion

Our findings suggest that high plant growth does not necessarily result from trait optimization. Furthermore, we did not find support for the expectation that the most common resource level translates into highly peaked trait distributions and high seedling growth. Instead, we found that seedling growth at the Luquillo forest is limited by light, soil K, and N content and that increase in growth can be the outcome from co-occurring contrasting phenotypes. Overall, our study suggests that the high functional diversity found in tropical forests partially results from a variety of phenotypic designs that perform well under given resource levels. Also, an important portion of the trait variation observed in our study comes from within species and highlights the need to incorporate this level of information in future studies to gain a better understanding of community responses to local-scale resource gradients.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3252/supinfo>

DATA AVAILABILITY

Data is available from the Dryad Digital Repository (Umaña et al. 2021); <https://doi.org/10.5061/dryad.sqv9s4n29>