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Individual-level trait variation and negative density dependence affect growth in tropical tree seedlings

Maria Natalia Umaña[1,2] | **Elise F. Zipkin**[3] | **Caicai Zhang**[4,5] | **Min Cao**[4] | **Luxiang Lin**[4,6] | **Nathan G. Swenson**[1,4]

[1]Department of Biology, University of Maryland, College Park, Maryland; [2]School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut; [3]Department of Integrative Biology and Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, Michigan; [4]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, China; [5]University of Chinese Academy of Sciences, Beijing, China and [6]Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Mengla, Yunnan, China

Correspondence
Maria Natalia Umaña, Department of Biology, University of Maryland, College Park, 20742 MD.
Email: maumana@gmail.com

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Abstract

1. Individual-level interactions with neighbours and their surrounding environments are key factors influencing performance that ultimately shape and maintain diversity in tropical plant communities. Theory predicts that the strength of these interactions depends on the similarity among neighbours, the turnover in composition caused by individuals that enter as new recruits and individuals that die, and fitting to local conditions. Despite considerable phenotypic variation among individuals and high community dynamics, these three factors have rarely been considered together for understanding growth variation, especially for seedling communities in the tropics.
2. We address this outstanding challenge by quantifying the influence of trait dissimilarity among neighbours, temporal turnover in neighbours, and individual trait variation on seedling growth, based on an unprecedented dataset containing individual-level demographic and functional trait data for tropical tree seedlings.
3. The results showed that trait dissimilarity associated with resource acquisition does not influence growth. However, conspecific negative density-dependent effects on growth were evident through the initial density of conspecifics and the increase in conspecifics during the study period. Also, individuals with relatively larger investments in leaf biomass allocation attained higher growth rates, suggesting that seedlings adjust their resource allocation to tissues related with light capture.
4. *Synthesis*. Together, these findings indicate that tropical seedling communities are structured by local abiotic factors that ultimately result in individual variation in resource acquisition traits and by biotic interactions driven by negative density dependence. These biotic interactions are highly dynamic and depend on conspecifics turnover, even at short temporal scales. Thus, to gain further insights into the forces structuring seedling communities, future studies should account for temporal variability in immediate neighbours and individual-level phenotypic variation that influence individual interactions.

KEYWORDS
China, conspecifics, functional traits, hetero-specifics, plant–plant interactions, relative growth rate, Xishuangbanna

1 | INTRODUCTION

Community structure and composition result from a combination of biotic- and abiotic-based forces that simultaneously influence individual performance. Neighbourhood biotic interactions, such as conspecific negative density dependence, where individual performance and population growth diminishes as the density of conspecific individuals increases, is hypothesized to play a central role in maintaining species diversity and driving species composition in natural communities (Harms, Wright, Calderón, Hernández, & Herre, 2000; Hubbell, Ahumada, Condit, & Foster, 2001; Janzen, 1970; LaManna et al., 2017; Webb & Peart, 1999; Wright, 2002). Beyond negative density dependence, the local abiotic environment and how well individuals fit those local conditions are also important factors influencing performance. Irrespective of neighbourhood biotic composition, individuals vary in the efficiency of resource uptake and this also determines their persistence in the community (Augspurger, 1984; Bagchi et al., 2011; Rüger, Huth, Hubbell, & Condit, 2009). Examining how these different mechanisms interact to determine observed patterns of individual performance is critical for understanding the underlying causes of community assembly.

Species' phenotypes are powerful means to investigate the role that biotic interactions and abiotic environments play in structuring natural communities (McGill, Enquist, Weiher, & Westoby, 2006). Individual-level phenotypic information, in particular, is critical since interactions among individuals scale up to produce emergent community-level patterns (Bolnick et al., 2011; Clark, 2010; Hart, Schreiber, & Levine, 2016). Despite growing interest in understanding individual-level dynamics (Violle et al., 2012), trait-based analyses predicting performance have typically ignored this variation and have applied a species-mean trait value to all individuals within a species (Fortunel, Wright, & Garwood, 2016; Kunstler et al., 2012; Uriarte et al., 2010). Averaging trait values across species might ignore important phenotypic differences useful for characterizing neighbourhoods. This, coupled with the fact that neighbouring conspecifics have a far greater impact on focal tree demography than neighbouring hetero-specific species (Kobe & Vriesendorp, 2011; Kunstler et al., 2016), suggests that incorporating individual-level trait variation is an essential step for understanding how biotic neighbourhoods and local conditions influence demographic patterns.

In terms of biotic interactions, high trait similarity is expected to lead to strong competitive interactions for similar resources, which ultimately may result in low individual performance (Macarthur & Levins, 1967). However, high similarity in traits could also lead to high performance if neighbourhood interactions are associated to particular trait values that are advantageous in a given environment (Ågren & Fagerström, 1984; Goldberg & Landa, 1991; Kunstler et al., 2012; Mayfield & Levine, 2010). In this case, limiting dissimilarity in a given niche axis would promote higher performance, ultimately favouring high phenotypic similarity among locally co-occurring individuals (Ågren & Fagerström, 1984; Goldberg & Landa, 1991). Thus, examining the role of trait dissimilarity (Td) or similarity among neighbouring individuals on growth could elucidate the main forces influencing individual interactions.

When examining the effects of neighbours on performance, we should consider that neighbourhoods are highly dynamic (Green, Harms, & Connell, 2014). Previous studies have found that the density of neighbours has a significant effect on survival and recruitment (Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Harms et al., 2000; Hubbell et al., 2001; Hubbell, Condit, & Foster, 1990; LaManna et al., 2017; Webb & Peart, 1999), yet these studies have not explicitly accounted for the potential effect that temporal turnover in neighbouring individuals may have on performance. Because the number of neighbours changes through recruitment and mortality as individuals grow, the immediate competitors' composition shifts constantly (Hubbell & Foster, 1986). This generates biotic uncertainty within the neighbourhood of focal trees, and thereby alters the perceived influence of local interactions (Abakumova, Zobel, Lepik, & Semchenko, 2016; Semchenko, Abakumova, Lepik, & Zobel, 2013). For instance, individuals that experience an increase of neighbours should face stronger interactions that impair performance. Considering the effect of this change in neighbourhood composition is also critical for understanding the role of biotic interactions on performance and would expand the dynamic perception of the forest.

Together with neighbourhood biotic interactions, individual variation in resource acquisition strategies should simultaneously generate variation in individual performance (Bagchi et al., 2011; Grime, 1979; Keddy, 1992; Laughlin, Strahan, Adler, & Moore, 2018; Weiher & Keddy, 1995; reviewed by Wright, 2002). Individual fitting to local conditions should be evidenced when considering individual-level traits and performance information across communities. For example, light conditions are particularly limiting for performance during early life stages (Augspurger, 1984; Chazdon, Fetcher, Chazdon, & Fetcher, 1984). Thus, functional traits related to light capture and photosynthetic efficiency should have a predominant role in determining seedling growth rates. Although previous studies have found that species-level traits are related to performance (Iida et al., 2014; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010), additional insights on the trait-performance relationship could be gained by integrating individual-level trait information.

We collected an unprecedented dataset containing individual-level growth and trait data for tree seedlings in a Chinese tropical rainforest to address the key challenges outlined above. Our results provide insights into the role of local biotic and abiotic factors determining seedling performance in tropical tree communities. We focus on the seedling stage because of the important compositional changes that occur at this point, which are likely to impact the community structure of latter ontogenetic stages (Green et al., 2014; Harper, 1977; Poorter, 2007). Specifically, we ask: (a) Does dissimilarity in resource acquisition traits influence patterns of seedling growth? We hypothesized that if seedling interactions are determined by niche differences, then Td will result in increased growth; while if limiting dissimilarity on traits drives individuals' interactions, then trait similarity should lead to higher growth rates. (b) Are there negative density dependence effects reflected on patterns of seedling growth? (c) Do shifts in biotic neighbourhood composition have an effect on seedling growth? We hypothesized that, if conspecific negative density dependence is realized *via* growth, then conspecific density and increases in the number of conspecifics will impair performance. This effect should not be evidenced for hetero-specifics. (d) Are individual-level focal traits influencing seedling growth and therefore represent better predictors of performance than species-level traits? We hypothesized that if individual fitting to the local environment has an impact on performance, variation in focal individual traits should determine growth, but this effect might not necessarily be manifested when using species-level traits.

2 | MATERIALS AND METHODS

2.1 | Study site and data collection

This study evaluated seedling communities across 218 1 × 1 m plots established next to a 20-ha forest dynamics plot in a tropical seasonal rainforest in Xishuangbanna, Yunnan, China (101°34′E, 21°36′N). The Xishuangbanna region has a typical monsoon climate with a dry season between November and April and a rainy season from May to October (Cao et al., 2008). The mean annual temperature is 21.8°C and the mean annual precipitation is 1,493 mm (Cao et al., 2008). In each seedling plot, we tagged, identified and measured all freestanding individuals smaller than 50 cm in height. Only 5% could not be identified and were thus recorded as clearly distinguishable morpho-species.

We collected all seedlings for trait measurements after 1 year of monitoring the change in maximum height of each individual in the field. We measured eight traits related to leaf morphology and biomass allocation that combined represent main strategies for resource acquisition: leaf thickness, leaf area (LA), specific leaf area (SLA), leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF), leaf area ratio (LAR) and specific stem length (SSL) (Poorter et al., 2012; Westoby, 1998; Wright et al., 2004). Specific leaf area is part of the "leaf economic spectrum" where leaves with low structural investment achieve higher photosynthetic rates (Wright et al., 2004). Leaf area is an architectural trait related with mechanical support, light capture, and transport functions on leaves (Poorter & Rozendaal, 2008; Westoby, Falster, Moles, Vesk, & Wright, 2002). Leaf thickness is an indicator of leaf mechanical resistance (Onoda et al., 2011). Stem, leaf, and RMF indicates the biomass that the seedlings allocate to each tissue (Poorter et al., 2012). LAR indicates how much leaf tissue is allocated per unit of plant mass (Poorter et al., 2012). Specific stem length indicates how length increases per unit of stem mass. For leaf traits, we used 1–3 fully expanded and undamaged leaves that were scanned and posteriorly dried in an oven for 72 hr at 70°C. For biomass allocation traits, all leaves, stems, and roots were manually separated and dried for 72 hr at 70°C to measure dry mass. The traits were collected following standardized methodology (Cornelissen et al., 2003; Poorter et al., 2012).

2.2 | Growth rates

We monitored all individuals for changes in total height for 1 year (seedling height was measured in the first census after the establishment of the plots and then 1 year later). To reduce the amount of error associated with growth measurements, all the seedlings were marked at the base with a red marker at the moment of tagging. Posterior measurements were all made from that same point. The relative growth rate (RGR) was computed as $\log(M_{t+\Delta t}) - \log(M_t)/\Delta t$, where M indicates height at successive time steps t (Hoffmann & Poorter, 2002). RGR was estimated in cm/year; all negative values and values that exceed four standard deviations from the mean were discarded (*c*. 7%).

2.3 | Trait dissimilarity

Since the eight traits used in this study (SLA, LA, leaf thickness, LMF, SMF, RMF, LAR and SSL) may covary, we diminished trait redundancy by applying a principal component analysis (PCA; Appendix S1 Table S1.1, Figure S1.1). We selected the three first PC axes (that explained 76% of the variation) and these orthogonal axes were used in further analyses (Appendix S1 Table S1.1, Figure S1.1). The first PC axis was positively associated with SSL and LAR (Appendix S1 Figure S1.1), the second PC axis was associated with leaf investment, where seedlings that invested more in leaf biomass and LA had low PC2 values; and the third PC axis was associated with stem and root biomass allocation, where seedlings that invested more in stem biomass and less in root biomass had high PC3 values. The first two PC axes describe strategies related with the efficiency of light capture, while the third PC axis describes strategies related with soil nutrient and water uptake. We calculated Td as the mean Euclidean pairwise distance in traits (PC axes) between each focal seedling individual and its seedlings neighbours (conspecifics and hetero-specifics separately) within each plot. For ease of interpretation, these variables were centred at their community averages and divided by its standard deviation.

2.4 | Model implementation

We evaluated the effect of Td, neighbourhood seedling density, change in the number of neighbours and focal traits on individuals' RGR. We only used individuals that had at least one conspecific in the plot at the time of sampling: in total we used 1,022 seedlings, from 61 species distributed in 171 plots (note that the number of conspecifics could be different in the first census). The base-level of the hierarchical model describes the RGR of seedling *i*, of a species *j*, as a function of Td among conspecifics and hetero-specifics, density of conspecifics and hetero-specifics, change in the number of conspecifics neighbours and hetero-specific neighbours, three PC-trait axes, initial seedling size, and a plot-level random effect (denoted τ_k for plot k). Mean and range values for all predictor variables are in Appendix S1, Table S1.2. The variation in individual RGR at given Td and plot effect is modelled using a normal distribution:

$$G_{ijk} \sim N(\lambda_{jik}, \sigma_{\lambda}) \quad (1)$$

where λ, the RGR for each seedling *i* from species *j* and plot *k*, is modelled as:

$$\begin{aligned}\lambda_{jik} = {} & \alpha0_j + \alpha1_j \times \text{Td.Co.sp}_{ijk} + \alpha2_j \times \text{Td.Het.sp}_{ijk} \\ & + \alpha3 \times \text{Ch.Co.sp}_{ijk} + \alpha4 \times \text{Ch.Het.sp}_{ijk} \\ & + \alpha5 \times \text{Dens.Co.sp}_{ijk} + \alpha6 \times \text{Dens.Het.sp}_{ijk} \\ & + \alpha7 \times \text{Init.Size}_{ijk} + \alpha8 \times \text{PC1}_{ijk} + \alpha9 \times \text{PC2}_{ijk} \\ & + \alpha10 \times \text{PC3}_{ijk} + \tau_k \end{aligned} \quad (2)$$

The covariate Td.Co.sp represents the Td among conspecifics, Td.Het.sp represents the Td among hetero-specifics, Ch.Co.sp represents the change in the number of conspecific neighbours for the time period evaluated in this study, Ch.Het.sp represents the change in the number of conspecific neighbours for the time period evaluated in this study and Init.Size represents the initial size of the seedlings when the first census started. The covariates PC1, PC2 and PC3 represent the three PC axes for the PCA using all traits (Appendix S1, Table S1.1, Figure S1.1). The parameter $\alpha0_j$ represents the intercept; the parameters $\alpha1_j$ and $\alpha2_j$ represent the conspecific and hetero-specific Td effects respectively and are linked to question 1. For questions 2 and 3, α3 and the parameter α4 represent the effect of the turnover in conspecific and hetero-specific individuals respectively; the parameters α5 and α6 represent the initial conspecific and hetero-specific density respectively; For question 4, the parameters α8, α9 and α10 represent the effect for focal trait values represented by three PC axes respectively. Given that mean growth and the magnitude of trait variation vary across species, the parameters $\alpha0_j$, $\alpha1_j$ and $\alpha2_j$ were modelled assuming that each species *j* was a random effect, drawn from a normal distribution with mean $\mu_{\alpha0}$, $\mu_{\alpha1}$ and $\mu_{\alpha2}$ respectively, and standard deviation $\sigma_{\alpha0}$, $\sigma_{\alpha1}$ and $\sigma_{\alpha2}$.

To examine whether patterns of seedling growth rates were better predicted by one particular dimension of trait variation over others, we developed four separate models for the different Td types: (a) Multivariate model using the first three PC axes (PC1, PC2, PC3) to calculate Td.Co.sp and Td.Het.sp. (b) PCA1 model using only the PC1 values to calculate Td.Co.sp and Td.Het.sp. (c) PCA2 model using only the PC2 values to calculate Td.Co.sp and Td.Het.sp. (d) PCA3 model using only the PC3 values to calculate Td.Co.sp and Td.Het.sp. We used an additional model (Species-PCA) to answer question 4, in which we estimated the PC axes effects (α8, α9 and α10) using species-level information (mean trait values by species). For this last model, Td was based in the PC2 axis, given that the PCA2 model was selected as the best model. We compared these models using the deviance information criteria (DIC).

We fit the models using Markov Chain Monte Carlo sampling techniques in *JAGS 3.4.0* interfaced using the *r2jags* package (Su & Yajima, 2015; Model, Appendix S1). We set diffuse prior distributions for all parameters (Model, Appendix S1). We ran three parallel chains with random initial values. We examined convergence visually with a threshold of 1.1 for the Gelman and Rubin convergence diagnostic for all parameters (Gelman et al., 1995; Spiegelhalter, Best, Carlin, & Van Der Linde, 2002). For the growth models, we used 70,000 iterations, a burn-in period of 10,000 iterations and thinned by 10. We computed the mean and the 95% credible intervals of all model parameters (Gelman & Hill, 2007; Gelman et al., 1995; Spiegelhalter et al., 2002). We assessed the fit of the model by checking the posterior predictive distribution of the fit of the actual dataset with the fit of an "ideal" dataset, and computed the Bayesian *p*-value following (Kéry, 2010).

Given that density-dependent effects are known to be highly variable across species (Comita et al., 2010; Zhu, Comita, Hubbell, & Ma, 2015), we fitted five additional models (Multivariate, PCA1, PCA2, PCA3 and PCA at species level), in which we specified species-level random-slope parameters for neighbourhood density coefficients (conspecific and hetero-specifics α5 and α6) and a model accounting for predictor correlations. The results for this set of additional models are described in Appendix S2. However, the DIC values were higher than in the models presented in the text.

TABLE 1 Trait dissimilarity (Td) coefficient means (95% credible intervals) of two hierarchical models [(PCA2 and species-principal component analysis (PCA)]. "PCA2" model shows the result for the model that used Td based on the second PC axis, this model was selected as the best model and uses individual-level trait information. "Species-PCA" model shows the result for the model that used species-mean trait values for the PC axes fixed affect, and Td was calculated based on the second PC axis. The $\alpha1_j$ and $\alpha2_j$ represent the conspecific and hetero-specific Td parameters respectively

	Td	
Model	μ[α1]	μ[α2]
PC2	−0.001 (−0.02, 0.018)	0.006 (−0.014, 0.025)
Species-PCA	−0.004 (−0.023, 0.015)	0.004 (−0.015, 0.024)

3 | RESULTS

Our models evaluated the role of Td, density dependence and focal trait values on seedlings growth rates. The best model was the PCA2-model and the worst model was the species-level trait-PCA (Table S1.3). The following results describe the best model (PCA2-model); the results for the other models can be found in Appendix S1 (Figures S1.2 and S1.3, Table S1.4).

For the results on the role of Td among conspecifics and hetero-specifics on seedling growth rates (question 1), we found that seedling growth was not related to neighbourhood Td, either among conspecifics or hetero-specifics (Table 1). For questions 2 and 3 in regards to density-dependent effects on growth, we found evidence for negative density-dependent growth that was based on initial density of conspecifics (Figure 1; Appendix S1, Table S1.4) and the change in the number of conspecific neighbours (Figure 1; Appendix S1, Table S1.4). Our model also evaluated the effects of density and the change in the number of

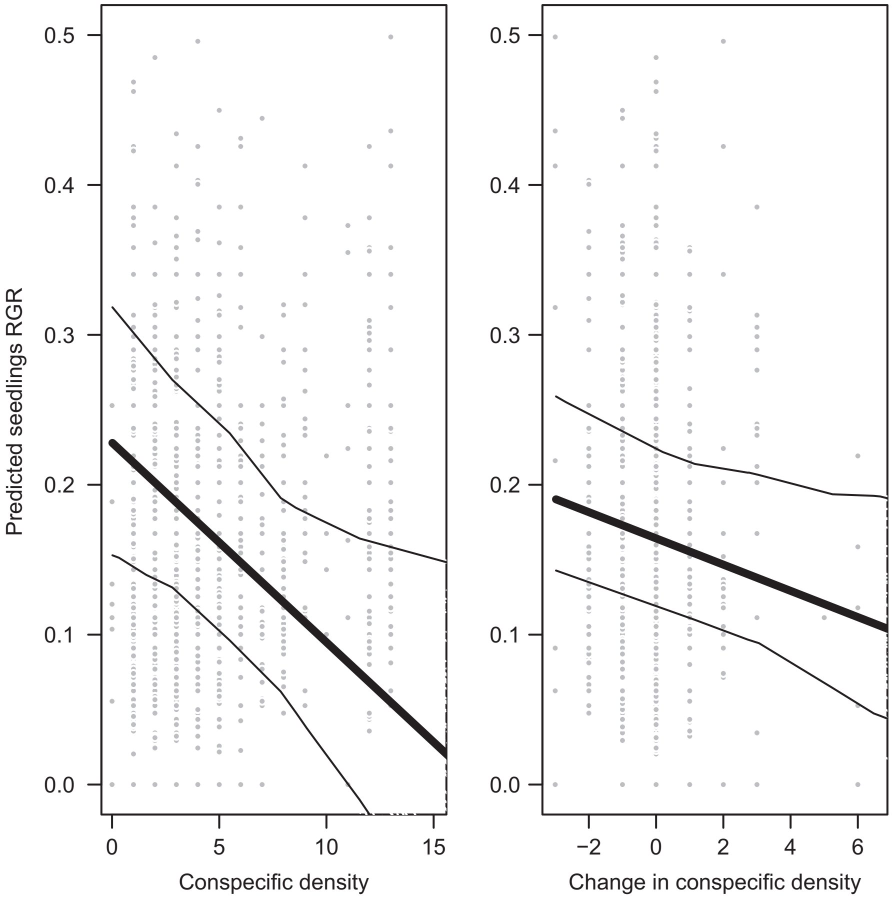

FIGURE 1 Conspecific neighbourhood density effects on seedling relative growth rate from the best model (PCA2). Left plot shows the effect of initial conspecific density on seedling growth. Right plot shows the effect of change in conspecific density on seedling growth. The black lines represent the main effects and the thin black lines represent the 95% credible interval

hetero-specifics on seedling growth rates, but we found that hetero-specific effects were not significant in driving seedling growth rates (Appendix S1, Table S1.4).

Next, we evaluated the role of focal traits, measured either at the individual-level or at the species-level (species-mean trait values), on seedling growth rates (question 4). We found that the trait values of the focal individuals were strong predictors of seedling growth rates (Figure 2), suggesting that the local abiotic context exerts an important influence on individual performance. In particular, PC2, which was negatively related with LMF and LA, showed a significant negative correlation with individual RGR. This indicates that seedlings allocating higher biomass to leaf tissues exhibit enhanced growth. In addition, PC3, positively related with stem biomass allocation and negatively with root mass allocation, had a significant positive effect on individual RGR. These results were only significant when using individual-level trait values and not when examining species-mean values (Species-PCA model; Figure 2). Additional results for intercept, plot variance and goodness-of-fit are reported in Appendix S1 (Figure S1.2 and S1.4, Table S1.4).

4 | DISCUSSION

We evaluated the role of individual-level trait variation and density-dependent forces on seedling growth in a tropical forest. Our results indicated that seedling growth rates are influenced by high conspecific density in the neighbourhood and by individual traits associated with allocation on leaf and stem biomass. Our approach accounted for the effects on growth of gains and losses of seedlings through recruitment and mortality, respectively, on growth, and indicated that turnover of conspecifics has a significant influence on seedling growth and may alter the local interactions. Combined, these results suggest that both resource-based strategies related to light capture and conspecific negative density dependence drive local plant community structure.

4.1 | The role of Td on seedlings growth

We examined different models in which Td was calculated based on different functional dimensions. Our results showed that the model that calculated trait dissimilarities based on the PC axis related to leaf biomass allocation strategies performed best predicting differences in growth among individuals, yet its effect was not significant. In other words, Td at the local scale did not have strong effects on seedling growth. These findings are in agreement with previous studies suggesting that competition for limiting resources is weak in tropical seedling communities (Moles, Westoby, Moles, Westoby, & Westoby, 2004; Paine et al., 2008; Svenning, Fabbro, & Wright, 2008). Other studies examining the role of Td among species on tree performance have also shown no benefit from being dissimilar from neighbours (Kunstler et al., 2012, 2016). Here, we further show that even when

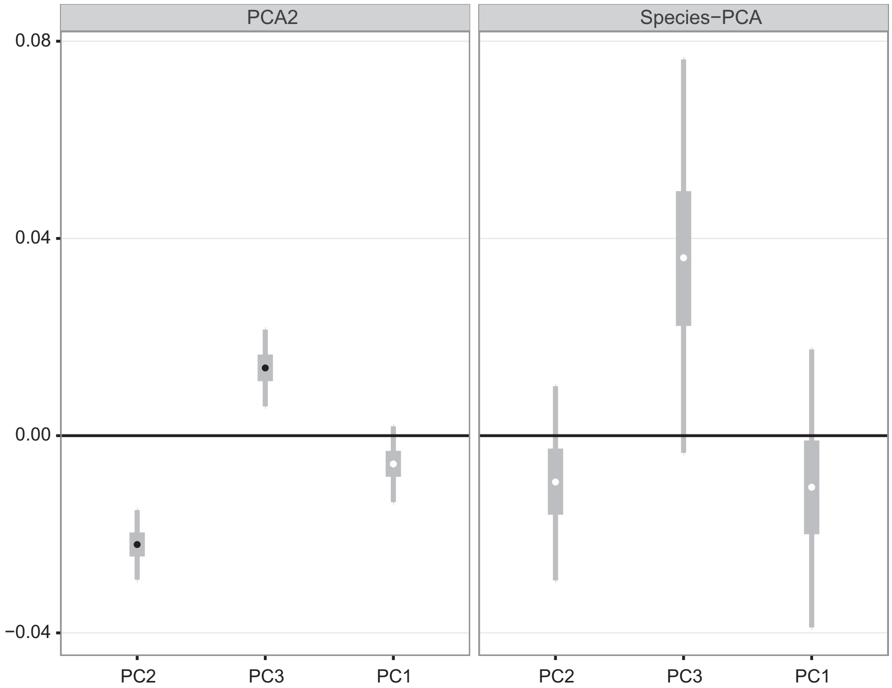

FIGURE 2 Trait PC axes effects (α8, α9 and α10) on seedling relative growth rate (best model PCA2 and species-PCA). Dots represent the mean value, and the segments represent the 50% (thick) and 95% (thin) credible intervals for each species. The three PC axes explain 76% of the total variation of traits. "PCA2" panel shows the result for the model that used individual-level trait information and trait dissimilarity based on the second PC-trait axis. "Species-PCA" panel shows the result for the model that used species-mean trait values for the PC axes fixed effect. Filled circles represent significant results and empty circles represent no-significant results (95% CI)

considering differences among conspecifics, Td does not enhance seedling growth. Instead, our results indicate that seedling communities have overall relatively low Td (Table S1.2), and suggest a potential benefit of being more similar (at neighbourhood scales) for traits related to resource acquisition. The lack of effect of Td on growth may be explained by the fact that traits related to resource acquisition and not to (species-specific) defence from pathogens may fail to infer key demographic processes such as conspecific negative density dependence driven by natural enemies (Bagchi et al., 2014; Coley & Kursar, 2014; Terborgh, 2012). We therefore, hypothesize that negative conspecific effects should be rather related with below- and above-ground chemical defences (Coley & Kursar, 2014; De Coninck, Timmermans, Vos, Cammue, & Kazan, 2015).

4.2 | Negative density dependence realized via conspecific density and temporal conspecific turnover

We found significantly negative effects conspecific density on seedling growth, in agreement with several studies showing that conspecific negative density dependence affects mortality and recruitment in early ontogenetic stages (Chen et al., 2010; Comita et al., 2010; Packer & Clay, 2003; Zhu, Woodall, Monteiro, & Clark, 2015b) especially in tropical regions (Bagchi et al., 2014; Harms et al., 2000; Kobe & Vriesendorp, 2011; Umaña et al., 2016). Our findings not only demonstrate that negative density dependence also affects growth rates but also that its effect is related to the initial density of conspecifics and to the change in conspecifics in the immediate neighbourhood. We therefore emphasize that negative density dependence operates across different demographic variables.

Our approach was novel in that the analyses accounted for the effect of temporal shifts in neighbourhood composition. Immediate neighbours are not static, and this temporal variability may affect local interactions. Negative density-dependent effects on growth might be hidden by the fact that the observed density of conspecifics at one particular moment can change rapidly (Bachelot, Kobe, & Vriesendorp, 2015; Hubbell, 2006; Wright, Muller-Landau, Calderon, & Hernandéz, 2005). If so, one may not be able to capture negative density-dependent dynamics when changes in local conspecific density are not taken into consideration. We found that seedling growth was negatively affected by changes in the number of conspecifics through time (Figure 1), but this effect was not observed when only hetero-specifics were considered. These results highlight the diffuse effects from other species on focal seedling growth (Hubbell & Foster, 1986). As dynamics are particularly fast during early life stages, our results highlight that including more explicitly the dynamic dimension of communities is critical to gain a holistic understanding of negative density dependence forces. The effect of variable numbers of neighbours on seedling growth also highlights the fact that biotic interactions are highly unpredictable across time and space. Under such a scenario, differences among species only driven by niche-based processes, and as a result of character displacement by direct interspecific competition, might be diluted (Hubbell & Foster, 1986). In species-rich systems the unpredictability in the identity of neighbouring species is particularly higher than in less diverse forest, and, because this uncertainty occurs on short temporal scales, it is not always considered in studies of negative density dependence (Hubbell, 1980; Hubbell & Foster, 1986).

4.3 | Individual-level focal traits influence seedling growth

Together with conspecific negative density dependence, other local processes also influence seedling growth rates. In particular, how well individuals fit the local abiotic conditions have a determinant role in driving seedling performance (Augspurger, 1984; Chazdon, 1988). Our results showed that individual-level demographic performance in tropical tree seedlings is strongly related to resource acquisition traits linked to the light environment. Specifically, seedlings that invest more in leaf tissue, exhibiting leaves with high LAR (PC2) and high biomass allocation in stems (PC3), showed enhanced growth rates. As light is one of the most important limiting resources in the understory of tropical rainforests (Augspurger, 1984; Chazdon et al., 1984), high biomass allocation in leaves and stem suggest that seedlings prioritize resource allocation in tissues related with light capture (Lambers & Poorter, 1992; Poorter et al., 2012).

When using data based on species-mean trait information, instead of individual-level traits, our model showed poor predictive power of seedling growth rates. This suggests that species-mean trait values average out or obscure important variation on how individuals adjust and respond to their local environment, thereby blurring our perception of individual-level dynamics. Although previous studies have found a significant role of species-level trait information on performance (Iida et al., 2014; Poorter et al., 2008; Wright et al., 2010), most have focused on adult stages and on traits such as wood density and seed mass, which were not considered in this study. In brief, our results demonstrate that individual-level trait information is useful for explaining demographic differences when using traits that often have poor predictive power at species-level and that show remarkable intraspecific variation, as is the case for leaf traits (Siefert et al., 2015). The often-ignored information on trait adjustments occurring across conspecifics is relevant for explaining variation in seedling performance at small spatial scales. We show that variation across individuals in strategies based on light-use regulates seedlings growth and responds to small-scale resource variability. This could be particularly important in the understory of tropical forests, where light is very heterogeneous across space due to treefall gaps (Barik, Pandey, Tripathi, & Rao, 1992; Brokaw, 1985; Connell, 1978; Denslow, 1987). Overall, our findings highlight the necessity of including individual-level information for a further understating of the processes underlying community structure (Violle et al., 2012).

We infer from our results that although there is generally weak intra- and interspecific competition for resources, there is an important role for the fit of an individual's phenotype to the local abiotic context. Thus, even if tropical seedlings are strongly limited by light (Augspurger, 1984; Chazdon & Fetcher, 1984), they are not necessarily intensely competing for this resource in a pairwise manner, probably because overlapping canopies or root systems are not common. Rather, seedlings are mainly tolerating low level of resources (Augspurger, 1984; Chazdon et al., 1984), which makes competition more diffuse among neighbours, especially at early life stages. We suggest that resource levels *per se* and not pairwise competition for resources driving niche differentiation, govern seedling growth. Future studies evaluating the role of competitive interactions experimentally and additional plant traits will provide further insights into the role of competitive interactions. Together, our results reflect the slow growth of individuals responding to a resource-limited environment that survive due to a low density of neighbouring conspecific individuals.

5 | CONCLUSIONS

Based upon the evidence, we argue that a combination of different ecological forces drive demographic patterns of tropical communities in their early life stages. On the one hand, conspecific negative density dependence is key for regulating populations through differential growth. This regulation is dependent on temporal turnover of individuals. Additionally, functional traits of neighbouring conspecific and hetero-specific seedlings had no impact on focal seedling survival or growth. From here we infer a lesser role of niche differentiation among seedlings with respect to resource acquisition. Lastly, we have shown that individual trait values are significant predictors of individual demographic rates irrespective of neighbourhood composition. Growth is driven by the phenotypic fit of an individual to a resource-limited environment where increased investment in traits related to photosynthesis rather than to below-ground resources. This study highlights the importance of spatial and temporal heterogeneity at small scales for understanding the drivers of seedling performance.

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AUTHORS' CONTRIBUTIONS

M.N.U. and N.G.S. developed and framed the research question; M.N.U., C.Z., M.C., L.L. and N.G.S. conducted the study and contributed to the project design; M.N.U. conducted data analyses; E.Z. oversaw data analyses; M.N.U. and N.G.S. wrote the first draft of the manuscript. All authors contributed substantially to the discussion, writing and revisions of the manuscript.

DATA ACCESSIBILITY

Seedling census and trait data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6d1qm1j (Umaña et al., 2018).

ORCID

Maria Natalia Umaña http://orcid.org/0000-0001-5876-7720

Luxiang Lin http://orcid.org/0000-0003-2727-0871

Nathan G. Swenson http://orcid.org/0000-0003-3819-9767

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SUPPORTING INFORMATION

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