

LETTER

Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest

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Abstract

As distinct community assembly processes can produce similar community patterns, assessing the ecological mechanisms promoting coexistence in hyperdiverse rainforests remains a considerable challenge. We use spatially explicit neighbourhood models of tree growth to quantify how functional trait and phylogenetic similarities predict variation in growth and crowding effects for the 315 most abundant tree species in a 25-ha lowland rainforest plot in Ecuador. We find that functional trait differences reflect variation in (1) species maximum potential growth, (2) the intensity of interspecific interactions for some species, and (3) species sensitivity to neighbours. We find that neighbours influenced tree growth in 28% of the 315 focal tree species. Neighbourhood effects are not detected in the remaining 72%, which may reflect the low statistical power to model rare taxa and/or species insensitivity to neighbours. Our results highlight the spectrum of ways in which functional trait differences can shape community dynamics in highly diverse rainforests.

Keywords

Forest dynamics, growth model, phylogenetic relatedness, spatial interactions, trait hierarchy, trait similarity, tropical forests.

Ecology Letters (2016)

INTRODUCTION

Much of classic ecological literature emphasises how niche differences among competitors promote species diversity (Chesson 2000; Silvertown 2004). However, it can be challenging to reconcile this perspective with the local co-occurrence of hundreds of tree species per hectare in lowland tropical rainforests (e.g. Valencia *et al.* 2004). Some have argued that co-occurring tree species may be largely equivalent in these highly diverse forests and, therefore, that species diversity is maintained by dispersal assembly mechanisms operating at broad spatiotemporal scales (Hubbell 2006; Rosindell *et al.* 2011), while other evidence points to a key role of stabilising mechanisms such as habitat partitioning, density-dependent enemy attack and recruitment limitation in these communities (Wright 2002; Comita *et al.* 2009; Myers *et al.* 2013). Functional traits provide an important tool in assessing community assembly processes, as they reflect key tradeoffs that can drive variation in species performance across environments (Engelbrecht *et al.* 2007; Cornwell & Ackerly 2009). In particular, traits of co-occurring species can be leveraged to make inferences about the role of distinct community assembly processes (Kraft *et al.* 2008; Swenson & Enquist 2009; Paine *et al.* 2012; Fortunel *et al.* 2014), with some important caveats (e.g. Mayfield & Levine 2010; Kraft *et al.* 2015). Despite substantial efforts in this area, consensus on the relative role of these

diverse ecological mechanisms in shaping tropical rainforests is largely lacking.

Many previous studies examining the ecological mechanisms underlying species coexistence in tropical forests focused on analysis of co-occurrence patterns within communities (e.g. Kraft *et al.* 2008; Swenson & Enquist 2009; Fortunel *et al.* 2014). However, as multiple ecological processes can produce similar patterns of community functional composition, it remains difficult to implicate one particular mechanism in producing the community pattern without additional data (reviewed in Adler *et al.* 2013). A promising way forward is to quantify the linkage between individual performance and the functional composition of its local neighbourhood by utilising forest dynamics data that captures variation in performance rather than simple co-occurrence patterns (Canham *et al.* 2006; Uriarte *et al.* 2010; Kunstler *et al.* 2012). Here, we focus on the negative impacts of neighbours on growth that arise through competition for shared resources or potentially through shared natural enemies, as they are widely thought to contribute to tropical forest dynamics (Wright 2002; Comita *et al.* 2009; Myers *et al.* 2013).

If similar species compete more strongly for shared resources or if they are more likely to share specialist natural enemies than dissimilar species, theory predicts that niche differentiation among species can promote local coexistence

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(Chesson 2000; Adler *et al.* 2007). Providing that functional traits are good predictors of shared resource use or defences, functionally similar species are expected to compete more intensely for shared resources (Adler *et al.* 2013) or to share more natural enemies (Paine *et al.* 2012) than functionally dissimilar species. If functional traits are phylogenetically conserved, close relatives are predicted to compete more strongly (Cahill *et al.* 2008) or to share more pests (Paine *et al.* 2012) than distant relatives. Additionally, competition for shared resources may also be driven by hierarchical differences in species competitive abilities, where superior competitors exclude inferior species over time (Mayfield & Levine 2010; Kunstler *et al.* 2012).

Empirical tests of how functional traits influence the strength of neighbourhood interactions in adult trees have been somewhat contradictory. For example, while growth and mortality patterns were consistent with an influence of trait similarity of neighbours in post-disturbance subtropical–tropical forests (Uriarte *et al.* 2010; Lasky *et al.* 2014), in mature temperate alpine forests, growth was best described by trait hierarchies (Kunstler *et al.* 2012). Previous work has found relatively little evidence for the role of phylogenetic similarity between neighbours in predicting variation in performance (Uriarte *et al.* 2010; Kunstler *et al.* 2012). However, as these studies focused on relatively few species (19 and 22 respectively), it is challenging to generalise these results to high-diversity, old-growth tropical forests.

In addition, functional traits can also capture inherent variation in individual performance among species (i.e. fitness differences *sensu* Chesson 2000). For example, tropical tree species with rapid growth and mortality are predicted to exhibit traits indicative of a resource-acquisitive strategy, including high specific leaf area (SLA) and low wood density, maximum size and seed mass (Westoby *et al.* 2002; Poorter *et al.* 2008; Wright *et al.* 2010). Such light-demanding species are expected to be more susceptible to crowding than shade-tolerant species (Baribault & Kobe 2011; Lasky *et al.* 2014). Due to these relationships, we expect intrinsic variation in performance across species (independent of any neighbourhood effects) to be related to trait differences.

Given the ongoing uncertainty about the processes shaping tropical forest dynamics as well as the diversity of ways in which functional traits can influence plant performance in a community context, the goal of our study is to assess how trait differences shape neighbourhood dynamics in a hyperdiverse lowland tropical rainforest. Specifically, our study is designed to test the following (in some cases compatible) hypotheses:

H₁: Intrinsic variation in performance across species is predicted by functional traits (Kraft *et al.* 2015). In particular, species with resource-acquisitive strategies have greater growth rates than species with resource-conservative strategies (Poorter *et al.* 2008).

H₂: Individuals within species perform better when found with functionally dissimilar neighbours because they will compete less for shared resources (Adler *et al.* 2013) or share fewer pests (Paine *et al.* 2012). Moreover, if functional traits are phylogenetically conserved, individuals within species perform better when found with phylogenetically disparate neighbours.

H₃: If competitive hierarchies are important, negative neighbourhood effects on the performance of focal individuals increase with hierarchical distance of functional traits (Kunstler *et al.* 2012).

H₄: Species sensitivity to neighbourhood crowding depends on their functional traits (Lasky *et al.* 2014). Specifically, individual performance is more strongly reduced by neighbourhood crowding in shade-intolerant species than shade-tolerant species.

H₅: Variation in performance across individuals within species is unrelated to variation in functional traits of neighbours.

Given the demographic trade-off between rates of growth and mortality in closed-canopy forests (e.g. Wright *et al.* 2010) and the higher data demands of estimating mortality rates relative to growth rates, our study focuses on tree growth. To test our hypotheses, we use spatially explicit neighbourhood models of tree growth with functional and phylogenetic data for 1100 tree species from a 25-ha plot of lowland rainforest in Amazonian Ecuador. Our work is novel in (1) quantifying neighbourhood interactions for each species separately in a hyperdiverse tropical rainforest (2) evaluating the role of functional similarity, trait hierarchies and shared ancestry together in predicting neighbourhood effects on tree growth and (3) testing if the role of trait differences is consistent in both common and rare species.

MATERIAL AND METHODS

Study site and surveys

The Yasuní Forest Dynamic Plot (FDP) is a 25-ha permanent forest census plot situated in lowland, old-growth and aseasonal rainforest in Yasuní National Park and Biosphere Reserve in Ecuador (Anderson-Teixeira *et al.* 2015). It contains > 150 000 mapped trees ≥ 1 cm in diameter at breast height (DBH) from over 1100 species (Valencia *et al.* 2004). In November 1997, November 2004 and July 2008, the forest was censused and the DBH of every living individual was recorded. While neighbourhood effects can vary over time (Lasky *et al.* 2014), annualised radial growth rates at Yasuní do not substantially differ between the two census intervals ($t = -1.05$, $P = 0.2945$) and preliminary analyses of neighbourhood effects on a subset of species showed similar patterns for both census intervals. Therefore, we focused on growth rates during the most recent (2004–2008) census interval.

Species traits and phylogeny

We focused on eight traits describing the four major axes of plant functional strategies: leaf, wood, height and seed (Westoby *et al.* 2002; Chave *et al.* 2009). Species leaf traits (SLA, size, thickness, nitrogen concentration and C : N ratio) were measured on randomly selected, censused individuals within the Yasuní FDP as part of previous research (Kraft *et al.* 2008; Kraft & Ackerly 2010). Height estimation was

complicated in the plot by a very dense canopy, therefore we used species maximum DBH (following King *et al.* 2006), which is allometrically related to height. Because increment borers are prohibited on the permanent plot, wood specific gravity (WSG) was measured for 670 species on trees located within 5 km of the plot as part of previous work (Hietz *et al.* 2013). Fresh seeds or fruits of 477 species were collected from or underneath fruiting trees in and around the plot; seeds were removed from fruit if necessary and cleaned of any fleshy parts, then dried at 65 °C for a minimum of 48 h to obtain their mass. For rarer species that have yet to be sampled locally, we used published WSG and/or seed mass estimates (Chave *et al.* 2009; Royal Botanic Gardens Kew 2015), and when these were unavailable, genus or family means were substituted (45 and 51% of the species, respectively, Table S1). Recent literature has emphasised the role of intraspecific trait variation in community ecology (Violle *et al.* 2012). However, as the vast majority of trait variation fell among rather than within many of the most common species in our study (81 and 88% of the variation in SLA and WSG, respectively, Kraft *et al.* 2008; Osazuwa-Peters *et al.* 2014; Siefert *et al.* 2015), we used species mean traits, recognising that it may be valuable (but a substantial effort) to quantify individual-level trait variation for all species in the plot in the future. A phylogenetic tree from Kraft & Ackerly (2010) was used for phylogenetic analyses.

Neighbourhood models of tree growth

We employ a neighbourhood modelling approach (Canham *et al.* 2006; Uriarte *et al.* 2010) to assess the role of phenotypic differences among species in shaping local forest dynamics. Species have inherent differences in growth, and as such, our model assumes that each species has a specific maximum potential growth rate. Individual growth is then predicted by adjusting the species-specific maximum potential growth rates to account for the size of the focal individual and the spatial structure of the neighbourhood: $g = g_m \times \delta \times v$, where g is the predicted growth, g_m is an estimated species-specific maximum potential growth rate in the absence of neighbours, δ is the size effect and v is the neighbourhood effect.

Size effects (δ) reflect the assumption that species have an optimal size at which maximal growth occurs. The size effect is modelled as a lognormal distribution (Uriarte *et al.* 2004):

$\delta = \exp\left(-\frac{1}{2} \left[\frac{\ln(DBH/X_0)}{X_b}\right]^2\right)$, where X_0 and X_b describe the peak and breadth of the lognormal function and DBH is the diameter at breast height of the focal individual.

The effect of a neighbouring tree on the growth of a focal individual is expected to increase with neighbour size (DBH) and decrease with neighbour distance to the focal individual (Canham *et al.* 2006). This effect is also assumed to depend on differences among species in their effects on the focal individual, captured by an interaction coefficient (λ_{ik}) describing the effect of neighbour of species i on focal species k . The net effect of the neighbours on a focal individual of species k is given by the neighbourhood crowding index (NCI):

$NCI_{focal,k} = \sum_{i=1}^S \sum_{j=1}^{n_i} \frac{DBH_j^k}{Distance_{ij}^{\alpha_k}} \times \lambda_{ik}$. Effects are summed over

all n_i individuals of S neighbouring species within a given radius of the focal individual. The parameters α_k and β_k permit non-linear scaling of the effects of neighbour size and distance, respectively, and they are assumed to be properties of species k , thus capturing the sensitivity of the focal species k to neighbourhood effects.

Neighbourhood effects (v) on the focal individual growth are calculated using a negative exponential function of NCI: $v = \exp(-C \times NCI_{focal}^D)$, where C and D are species-specific estimated parameters and NCI_{focal} is the NCI for a focal individual.

Although the relevant neighbourhood radius can vary with the focal tree size (Stoll & Newbery 2005; Uriarte *et al.* 2010), preliminary sensitivity analyses using both 10 and 20 m radii suggested that our estimates of the shape of the distance decay were robust to this choice. We therefore used a fixed 10 m radius because of computing time constraints, which is comparable with previous studies (Kunstler *et al.* 2012; Lasky *et al.* 2014). To avoid edge effects, focal trees located within 10 m of the edge of the plot were excluded from the modelling.

Testing alternate neighbourhood models

To address our hypotheses about how trait and phylogenetic similarities shape neighbourhood dynamics ($H_{2,3,5}$), we compare 21 models that make different assumptions about the nature of the interaction coefficients λ_{ik} (Table 1, see λ_{ik} equations in Table S2). The control model (M_1) assumes that tree growth depends solely on the focal tree size (δ), with no neighbourhood effects (v). The neighbour-equivalence model (M_2) assumes that all neighbours have equivalent effects on the focal tree growth (H_5 , all λ_{ik} fixed to 1). The phylogeny-based model (M_3) assigns a fixed λ_{ik} to each competitor based on the cophenetic similarity scaled between 0 and 1 to the focal species (H_2). Similarly, a set of 16 trait-based models (M_{4-19}) were evaluated by assigning a fixed λ_{ik} to each competitor based on (1) absolute trait similarities scaled between 0 and 1 (H_2 , Uriarte *et al.* 2004) and (2) hierarchical trait similarities scaled between 0 and 2 (H_3 , Kunstler *et al.* 2012) to the focal species. To account for correlations among traits, two additional trait-based models (M_{20-21}) were evaluated by assigning a fixed λ_{ik} based on species absolute similarity scaled between 0 and 1 (H_2) in a multi-dimensional space defined by (1) the first (centred and standardised) trait axis determined by a principal component analysis (PCA) on the eight studied traits, which accounted for 32.6% of the trait variation and approximates the leaf economics spectrum, and (2) the four-first (centred and standardised) trait axes determined by the same PCA, which together accounted for 75.8% of the trait variation (see Table S3 for details).

Species selection for modelling

The 21 models have from three (M_1) to seven parameters (M_{2-21}). To ensure that we could obtain robust parameter estimates, we followed the ‘one in ten’ rule that states that one predictive variable can be studied for every 10 events (Harrell *et al.* 1996). We therefore focus on 315 species that

Table 1 Percentage of species best predicted by each alternate neighbourhood model for the 315 focal tropical tree species (detailed results for each species are available in Table S1)

Model	Similarity index	11-model comparison			21-model comparison		
		Total	Absolute distance	Hierarchical distance	Total	Absolute distance	Hierarchical distance
Control	None	71.7	NA	NA	71.1	NA	NA
Neighbour equivalence	All neighbours equivalent	1.3	NA	NA	0.0	NA	NA
Phylogeny-based	Phylogeny	7.0	7.0	NA	3.5	3.5	NA
Trait-based	SLA	3.2	1.0	2.2	1.3	0.3	1.0
	WSG	7.3	4.8	2.5	3.8	2.5	1.3
	Maximum DBH	3.5	1.6	1.9	1.6	0.6	1.0
	Seed Mass	6.0	2.5	3.5	2.5	1.3	1.3
	Leaf Size	–	–	–	3.8	2.2	1.6
	Leaf Thickness	–	–	–	2.2	1.3	1.0
	Leaf Nitrogen Concentration	–	–	–	2.2	1.3	1.0
	Leaf C:N Ratio	–	–	–	2.9	0.6	2.2
	PCA axis 1	–	–	NA	1.9	1.9	NA
	PCA axes 1–4	–	–	NA	3.2	3.2	NA

*Dashes denote models that were not used in the 11-model comparison. NA indicates parameters not included in the model.

SLA, specific leaf area, WSG, wood specific gravity, DBH, diameter at breast height, C : N, Carbon to Nitrogen, PCA, principal component analysis.

have more than 80 individuals between the 2004 and 2008 censuses at Yasuní (Table S1). Together, these 315 species represent 130 815 individuals, accounting for ~66% of the stems in the plot, and display wide variation in life-history characteristics. For each of these species, model parameters were estimated using maximum likelihood. We compared the 21 models using the Akaike Information Criterion corrected for small sample size (AICc) to identify the best model for each species (Burnham & Anderson 2004).

Hereafter, we focus on a subset of 11 of the 21 models corresponding to the control model (M_1), the neighbour-equivalence model (M_2), the phylogeny-based model (M_3) and a subset of the trait-based models corresponding to four traits describing the major axes of plant functional strategies (SLA, WSG, maximum DBH and seed mass), using absolute and hierarchical distances (Table 1). Additional trait-based models run with leaf size, leaf thickness, leaf nitrogen concentration, leaf C : N ratio, and multivariate trait similarity measures are presented, along with detailed results from the complete 21-models comparison in the supplementary information (Table S1).

Linking functional traits and sensitivity to crowding

To test if there were trait correlates to species sensitivity to neighbours (H_4), we conducted *t*-tests of mean trait values between the group of species showing a crowding effect and the group of species not showing any neighbours influence. We also used a *t*-test to examine whether the two groups differed in species abundances in the plot at the last census (2008).

Linking functional traits and maximum potential growth

To explore whether species mean traits were good proxies for maximum growth (i.e. growth in the absence of neighbours) (H_1), we used species maximum potential growth estimates (g_m) from the best model and ran Spearman correlation tests

with species traits. An alternative analysis using estimates of g_m from the control model yielded qualitatively identical conclusions.

All analyses were conducted in the R 3.2.1 statistical platform (R Development Core Team 2016) using package *ade4* (Dray & Dufour 2007), *ape* (Paradis *et al.* 2004) and *lme4* (Bates 2005). Neighbourhood models were fitted using the function *optim* in R on the Deepthought2 High-Performance Computing cluster at the University of Maryland, College Park.

RESULTS

As predicted (H_1), estimates of species-specific maximum potential growth rate (g_m) across the 315 focal tree species at Yasuní from the best model were correlated with three of four key traits (Fig. 1, Table S4). Specifically, g_m increased with increasing SLA and maximum DBH and decreased with increasing WSG (Fig. 1a,b,c), while it showed no relationship with seed mass (Fig. 1d).

Comparing the control model to the neighbour-equivalence model, the phylogeny-based model and the four trait-based models describing the major functional axes (SLA, WSG, maximum DBH and seed mass) to test the importance of crowding effects on tree growth ($H_{2,3,5}$), we found that the six models including neighbourhood effects (v) best predicted the growth of 89 species, whereas the control model best predicted the growth of the remaining 226 species (Table 1, see Table S1 for details). Comparing all 21 alternate models yielded similar results (Tables 1 and S1). Across all 315 species, the model with the smallest AICc value had on average an 85% chance of being the best among those considered (mean Akaike weights = 0.85, Table S1). Models including neighbourhood effects were unequivocally supported for 98.9% of the 89 species sensitive to crowding as there was considerably less support for the second-best model, be it another model including neighbourhood effects (82 species, mean $\Delta AICc = 4.8$) or the control model (7 species, mean

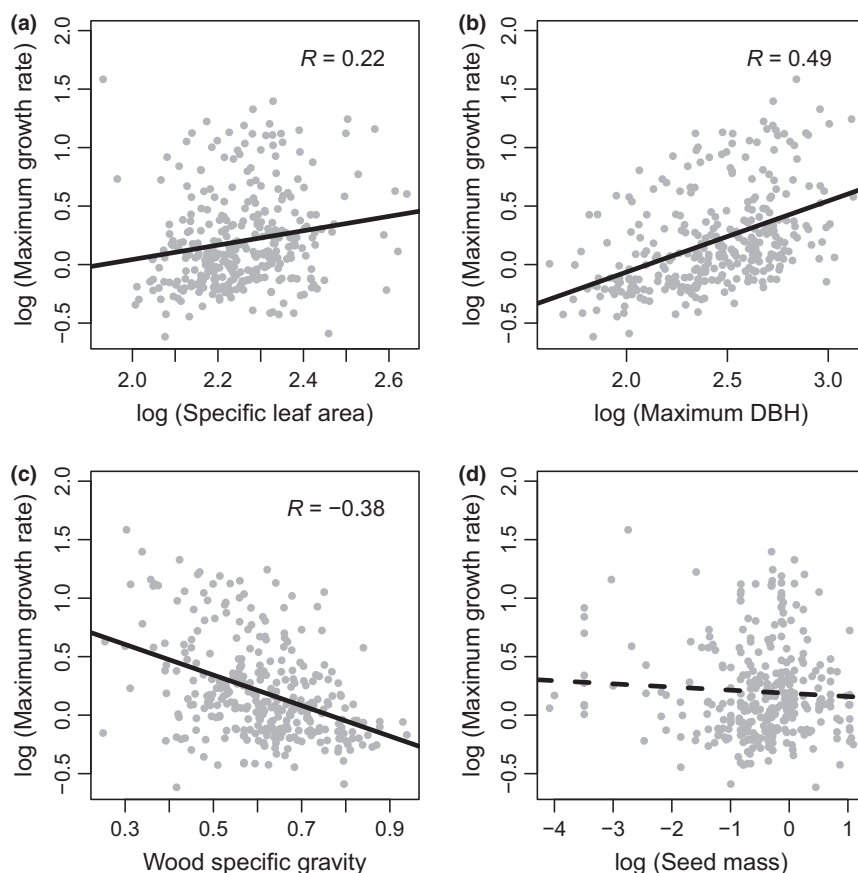


Figure 1 Relationships between maximum potential growth rate, estimated from the best model, and (a) specific leaf area, (b) maximum diameter at breast height (DBH), (c) wood specific gravity and (d) seed mass in 315 tropical tree species. When correlations are significant, Spearman correlation coefficients (R) are indicated and ordinary least-squares regression lines are drawn with solid lines (and with dashed lines otherwise).

$\Delta\text{AICc} = 3.1$). Only one of the latter seven species (*Unonopsis veneficiorum*) had modest differences ($\Delta\text{AICc} < 2$) with the control model. The control model was strongly supported for 95.6% of the 226 species not showing crowding effects since it was on average the best-supported model by a reasonable margin (mean $\Delta\text{AICc} = 7.1$) and had modest differences ($\Delta\text{AICc} < 2$) with models including neighbourhood effects for only 10 of those 226 species.

For the 89 species best described by models including neighbourhood effects (v), we found that the vast majority of these best fit models (85 of 89, Table 1) included an effect of functional or phylogenetic distance (H_{2-3} ; distinct λ_{ik} in M_{3-21}), while only four best fit models treated neighbours as equivalent (H_5 ; all $\lambda_{ik} = 1$ in M_2). Among these 85 species, the phylogeny-based model best described growth in 22 species, whereas a trait-based model best described growth in 63 species. Among the 63 species best described by trait-based models, half of the models (31) included trait similarities (H_2), while the other half (32) included trait hierarchies (H_3). Similar results were seen in the 21-model comparisons (Table S1).

Comparing traits of species that were sensitive to crowding vs. those that were not (H_4), we found that species sensitive to neighbours had higher maximum DBH and lower WSG (Fig. 2b,c), but they showed no difference in terms of SLA and seed mass (Fig. 2a,d). Moreover, those species sensitive to crowding tended to be more abundant in the plot overall (Fig. 3).

DISCUSSION

Combining spatially explicit demographic censuses with functional traits and phylogenetic relationships for 315 tropical tree species, our study captures the diversity of ways that functional trait variation can influence tree growth and species interactions in a hyperdiverse, old-growth tropical forest.

Functional traits capture species differences in maximum potential growth

We found that traits capture inherent demographic differences among tree species (H_1). Among the 315 studied species at Yasuní, SLA, maximum DBH and WSG were correlated with maximum potential growth rates (independent of any neighbourhood effects). These correlations make sense from a physiological perspective: trees with higher SLA can optimise light interception and achieve greater photosynthesis, while taller trees can reach higher canopy levels and are better competitors for light (Westoby *et al.* 2002), with both strategies potentially leading to higher growth (Wright *et al.* 2010). Conversely, denser wood requires greater construction costs, but provides higher resistance to mechanical damage (Chave *et al.* 2009), resulting in slower diameter growth (Poorter *et al.* 2008). Our study highlights that trait differences between tropical trees may drive competitive dominance via density-independent

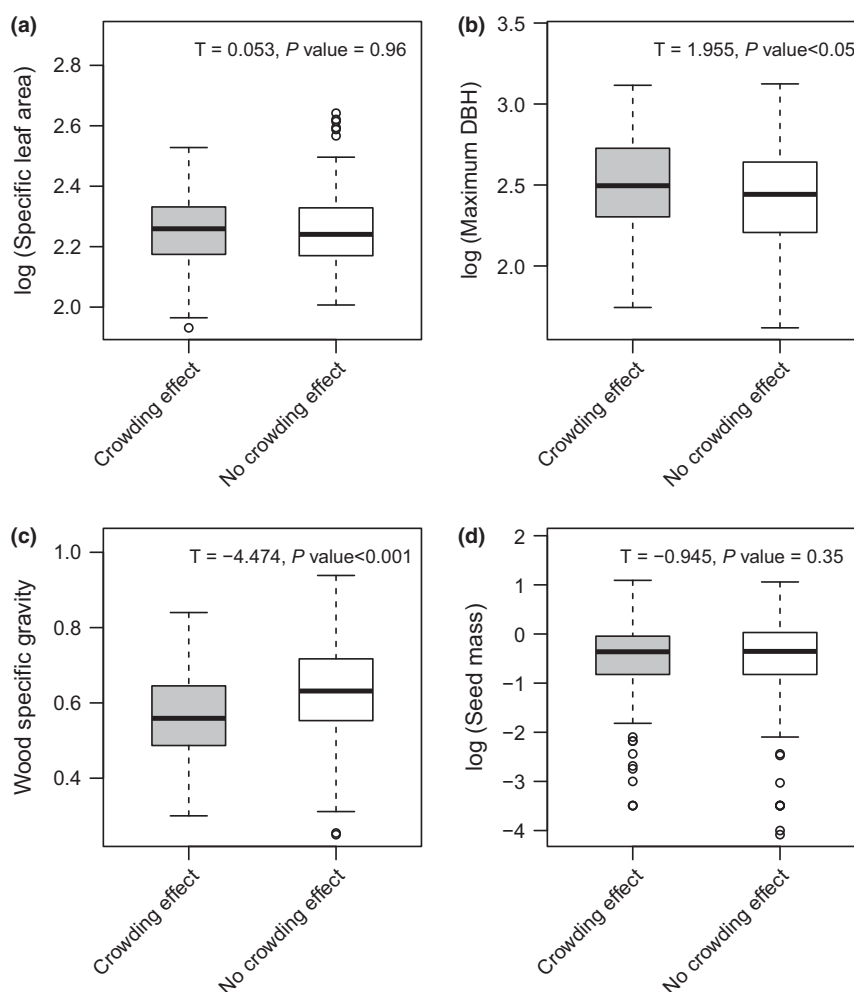


Figure 2 Boxplots of (a) specific leaf area, (b) maximum diameter at breast height (DBH), (c) wood specific gravity and (d) seed mass by response groups to crowding: species showing evidence of crowding in grey, species showing no evidence of crowding in white. The line in the box indicates the median; the whiskers above and below the box indicate the 90th and 10th percentiles. The *t*-tests between the two groups are indicated.

performance differences (here species growth in the absence of neighbours, a component of fitness *sensu* Chesson 2000).

Functional traits differences predict neighbourhood interactions

Among species exhibiting neighbourhood effects at Yasuní, the best-supported model of tree growth included an effect of functional or phylogenetic distances. This result suggests that crowding effects were shaped by the neighbour identity relative to the focal species at Yasuní (H_{2-3}), adding to a recent body of work showing that species niche similarities associated with traits influence neighbourhood interactions in forests in a variety of settings (Uriarte *et al.* 2010; Kunstler *et al.* 2012; Lasky *et al.* 2014).

In our modelling approach, traits can predict neighbourhood effects on tree growth in two ways: hypothesis H_2 states that neighbours decrease focal tree growth because they are functionally similar to the focal individual, thus competing for shared resources (Uriarte *et al.* 2010) or sharing the same pests (Paine *et al.* 2012), whereas hypothesis H_3 proposes that neighbours are competitively superior to the focal individual, therefore pre-empting shared resources (Kunstler *et al.* 2012).

Among the species whose growth was best predicted by a trait-based model at Yasuní, we showed roughly similar support for both absolute and hierarchical trait distances in capturing focal species dynamics, in contrast to previous work in alpine forests showing strong support for trait hierarchies (Kunstler *et al.* 2012). This result suggests that competitive interactions can produce divergent patterns of community functional composition within tropical forests (depending on whether trait similarities matter in an absolute or hierarchical way for a given focal species), as has been previously proposed (Mayfield & Levine 2010; Kraft *et al.* 2015).

Traits associated with neighbourhood effects on tree growth included all four widely considered axes of plant functional variation (Westoby *et al.* 2002). Specifically, neighbourhood effects on tree growth was best explained by models including WSG for 23 species, seed mass for 19 species, maximum DBH for 11 species and SLA for the remaining 10 species. Greater WSG relates to stronger mechanical support and potentially lower sap transport (Chave *et al.* 2009), suggesting that competitive outcome is influenced by differences in construction cost and hydraulic conductance among tropical trees (Uriarte *et al.* 2010; Silvertown *et al.* 2015). Bigger seeds typically

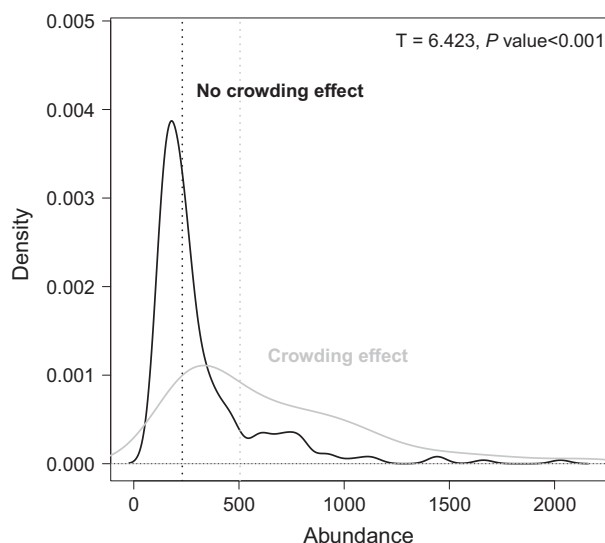


Figure 3 Abundances of (1) species showing evidence of crowding effects on tree growth (in grey) and (2) species showing no effect of crowding on tree growth (in black). Median values are indicated in dotted lines. The t -test between the two groups is indicated.

disperse over shorter distances but provide a higher chance of recruitment in closed canopies (Westoby *et al.* 2002), implying that species interactions are affected by a tolerance-fecundity trade-off via differences in tolerance to stresses such as shade or drought (Muller-Landau 2010). Greater SLA can be linked to higher light capture, lower shade tolerance and lower defence against herbivores, whereas maximum DBH is a key determinant in the asymmetric competition for light (Westoby *et al.* 2002). Our findings thus emphasise that resource partitioning and competition for light are likely important drivers of tropical forest dynamics.

Phylogenetic similarity between neighbours and focal individuals best predicted neighbourhood effects on tree growth for 22 species, which together represent 25% of the species displaying sensitivity to neighbours in our site. Phylogenetic similarity, as an integrated measure of functional similarity in both measured and unmeasured traits related to resource partitioning and defence against natural enemies, provided in this case further support for the role of functional similarity in shaping forest dynamics (H_2) as these traits are known to be conserved (Kraft & Ackerly 2010). This result is consistent with previous studies focusing on recruitment stages (Webb *et al.* 2006; Paine *et al.* 2012), but diverges from previous studies of adult trees (Uriarte *et al.* 2010; Kunstler *et al.* 2012). Neighbourhood effects were linked to phylogenetic similarity at Yasuní FDP but not at Luquillo FDP, which may be related to the high number of species and hence of congeneric and confamilial neighbours in Ecuador, in contrast with the relatively low number of closely related species in Puerto Rico (Uriarte *et al.* 2010).

Functional traits indicate species sensitivity to crowding

We found that traits revealed differential responses of tree growth to neighbours among tropical tree species (H_4). Species showing evidence of crowding effects on tree growth at Yasuní exhibited greater maximum DBH and lower WSG than the

other species. Lower WSG can be related to the functional strategy of pioneer species that grow fast by producing light wood (Poorter *et al.* 2008). Our results stand in line with previous studies in temperate forests where shade-intolerant species responded more strongly to neighbours than did shade-tolerant species (Baribault & Kobe 2011), and in subtropical forests where the growth of pioneer species decreased with increasing neighbour crowding (Uriarte *et al.* 2004). Shade-tolerant, late-successional species can reach greater size and thus overgrow pioneer neighbours, but grow slowly because of the high construction costs of dense wood (Chave *et al.* 2009) and might be affected by crowding as long as they remain in the understory. Our study further emphasises that asymmetric competition for light is an important driver of community assembly in tropical forests.

Importance of neighbourhood effects in tropical forests

The role of plant–plant interactions, from competition to facilitation, in structuring hyperdiverse tropical forests is an active topic of discussion (Wright 2002; Hubbell 2006; Adler *et al.* 2007; Rosindell *et al.* 2011). Here, we quantified the negative influence of neighbours on tree growth in an old-growth tropical forest from both a functional and a phylogenetic perspective.

Consistent with hypotheses H_2 and H_3 , we found clear evidence that neighbours influenced tree growth in 28% of the 315 studied species at Yasuní, with models including neighbourhood effects being unequivocally supported for 98.9% of these 89 species. These species, which together represent 46% of the stems in the plot, appear to support the role of local interactions in shaping forest dynamics (Chesson 2000; Wright 2002; Adler *et al.* 2007). However, in line with hypothesis H_5 , tree growth was apparently independent of neighbourhood interactions in 72% of the studied species, with the control model being strongly supported for 95.6% of these 226 species. The majority of tropical tree species in our study thus showed no evidence of crowding effects reducing their growth. These are decidedly mixed results in comparison to earlier studies that found considerably stronger support for neighbourhood interactions in lower diversity temperate (Canham *et al.* 2006), alpine (Kunstler *et al.* 2012), subtropical (Uriarte *et al.* 2010) and tropical (Stoll & Newbery 2005) forests, underlying current challenges in evaluating the strength of species interactions in the dynamics of high-diversity systems.

We report a higher detection of neighbourhood effects for the most abundant species at Yasuní (Fig. 3), which may arise for several reasons. First, as the density of individual species decreases with increasing species richness from temperate to tropical systems, the probability that individuals of two species meet in small-scale neighbourhoods decreases and, as a consequence, deterministic effects of niche differences can become less common over time (Hubbell 2006) or simply harder to detect even if important (the stochastic dilution hypothesis, Wiegand *et al.* 2007). Second, high diversity leads to low relative abundance for many species, and neighbourhood dynamics are more challenging to assess for rarer species since they have a lower chance of having conspecific (except if species are locally clumped because of strong dispersal-limitation, Condit *et al.* 2000) or functionally similar neighbours than more abundant species (Comita *et al.* 2010; Paine *et al.*

2012). Our study integrates 315 species including many less abundant species, and this may contribute to differences in strength of the neighbourhood interactions relative to earlier studies that focused on the 20 most abundant species with more than 300–400 stems (Uriarte *et al.* 2010; Kunstler *et al.* 2012). Finally, our analysis used a robust version of neighbourhood dynamics models that permits direct comparisons with foundational papers on neighbourhood interactions in temperate and subtropical forests (Canham *et al.* 2006; Uriarte *et al.* 2010; Kunstler *et al.* 2012). The model complexity (relative to the rarity of many taxa in the study) may contribute to the low detection of crowding effects we report. However, alternative analyses using a simplified version of neighbourhood models, where alpha and beta parameters were set to their mean values over all species from the neighbourhood equivalence model, still resulted in the majority of species (60% of the 315 studied species) showing no crowding effects (data not shown), suggesting that statistical power alone is not the main driver of this result. Further study is needed to clarify how the strength of species interactions varies with abundance in high-diversity systems.

Our study focused on the role of phenotypic differences in crowding interactions at the neighbourhood scale (Kunstler *et al.* 2012; Lasky *et al.* 2014), yet other trait-based community assembly processes acting at different spatiotemporal scales likely also contribute to shaping tropical forests dynamics (Kraft *et al.* 2008; Comita *et al.* 2009; Myers *et al.* 2013). Future studies would require additional data to evaluate their contribution to species dynamics, such as for instance spatiotemporal data of abiotic factors to analyse variation in neighbourhood interactions across environmental gradients (Baribault & Kobe 2011; Lasky *et al.* 2014).

CONCLUSIONS

Examining variation in tree growth as a function of neighbourhood structure, we highlight ongoing challenges inherent in assessing species dynamics in hyperdiverse systems where most species are invariably rare. For many of the most abundant species at our site, we find that functional traits can matter in a diversity of ways in shaping tree dynamics and neighbourhood interactions. Species traits describing major axes of plant functional strategies are strongly correlated with maximum potential growth rates, highlighting the potential for trait differences to capture growth differences among tropical tree species. Traits similarities and hierarchies predict neighbourhood effects on tree growth, emphasising a role of resource partitioning in driving species interactions. Finally, species traits relate to sensitivity to crowding, suggesting that shade-intolerant species suffer more from neighbourhood effects than shade-tolerant species. Taken together, these results show the spectrum of ways in which functional differences between species contribute to the neighbourhood dynamics of one of the most diverse terrestrial plant communities on the planet.

ACKNOWLEDGEMENTS

We are grateful to everyone who has contributed to the Yasuní FDP project, in particular M. Zambrano, P. Alvía,

W. Loor, A. Loor, J. Suárez, G. Grefa and J. Suárez. We thank C. Hernández for data management and Á. Pérez for helping with species identification. We thank V. Persson and M. Zambrano for help weighing seeds. We thank the Pontifical Catholic University of Ecuador, the Mellon Family Foundation, NSF, Smithsonian Tropical Research Institute and The Government of Ecuador (through *Donaciones del Impuesto a la Renta*) for funding the forest census efforts. Collection of seed mass was supported by NSF grants DEB-0614525 and DEB-1122634. We thank the Division of Information Technology at the University of Maryland, College Park, for access and support to the Deepthought2 HPC cluster. N. Kraft was partially supported by NSF DEB-1456246. This manuscript was improved by suggestions from M. Uriarte, J. Lasky, L. Chen, G. Kandlikar, I. MacFadden, M. Vaz, and three anonymous reviewers.

AUTHORSHIP

CF and NK designed the study, formatted data and analysed output data. RV collected demographic data; NK, JW and NG collected trait data. CF performed modelling work and wrote the first draft of the manuscript. All authors contributed to revisions.

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SUPPORTING INFORMATION

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Editor, Maria Uriarte

Manuscript received 7 October 2015

First decision made 15 November 2015

Second decision made 13 February 2016

Third decision made 28 April 2016

Manuscript accepted 15 May 2016