Trait-mediated assembly processes predict successional changes in community diversity of tropical forests

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Interspecific differences in relative fitness can cause local dominance by a single species. However, stabilizing interspecific niche differences can promote local diversity. Understanding these mechanisms requires that we simultaneously quantify their effects on demography and link these effects to community dynamics. Successional forests are ideal systems for testing assembly theory because they exhibit rapid community assembly. Here, we leverage functional trait and long-term demographic data to build spatially explicit models of successional community dynamics of lowland rainforests in Costa Rica. First, we ask what the effects and relative importance of four trait-mediated community assembly processes are on tree survival, a major component of fitness. We model trait correlations with relative fitness differences that are both density-independent and -dependent in addition to trait correlations with stabilizing niche differences. Second, we ask how the relative importance of these trait-mediated processes relates to successional changes in functional diversity. Tree dynamics were more strongly influenced by trait-related interspecific variation in average survival than trait-related responses to neighbors, with wood specific gravity (WSG) positively correlated with greater survival. Our findings also suggest that competition was mediated by stabilizing niche differences associated with specific leaf area (SLA) and leaf dry matter content (LDMC). These drivers of individual-level survival were reflected in successional shifts to higher SLA and LDMC diversity but lower WSG diversity. Our study makes significant advances to identifying the links between individual tree performance, species functional traits, and mechanisms of tropical forest succession.

community turnover | hierarchical Bayes | individual variation | secondary forest | species interactions

Quantifying the relative importance of mechanisms that drive community assembly remains a central challenge in ecology. Interspecific variation in ecological strategies is considered a major driver of community assembly and has been classified by Chesson (1) into relative fitness (i.e., per capita population growth rate) differences and stabilizing niche differences (2). These processes act concurrently, and their importance may vary over space and time (3). However, the simultaneous effects of different assembly mechanisms on community dynamics have not been well-characterized, particularly in diverse communities such as tropical forests. High dynamism of vegetation composition during tropical forest succession creates an ideal opportunity to investigate the drivers of community assembly.

Interspecific niche and fitness differences can be characterized through the lens of interspecific functional trait variation, an approach that can shed light on drivers of community functional composition and dynamics (2, 4, 5). Traits may mediate niche and fitness differences in at least four ways (Fig. 1). First, interspecific trait variation can be correlated with fitness independent of neighbor density, such that species possessing traits associated with the highest fitness should exclude species with unfavorable traits (1, 2) (*1* in Fig. 1). Second, traits may be associated

with a species' sensitivity to neighbor density (i.e., a trait × crowding interaction effect on fitness). As a result, certain trait values may have relatively low fitness under high crowding (6–9) (*2* in Fig. 1). For example, species with low wood specific gravity (WSG) might have higher fitness at the initiation of succession but be disadvantaged later in succession because of sensitivity to crowding. Third, negative density effects of neighbors may be asymmetric between species and dependent on hierarchies (i.e., species with favorable traits experience weaker negative density effects of neighbors with unfavorable traits, generating relative fitness differences) (10) (*3* in Fig. 1). For example, species with high WSG may have stronger negative density effects on neighbors with low WSG than vice versa (10). Fourth, trait variation may be related to local niche differences between neighbors, such that greater trait differences weaken negative density effects of neighbors and promote stable coexistence of functionally diverse neighbors (11, 12) (*4* in Fig. 1). Overall, traits associated with fitness differences (*1–3* in Fig. 1) are expected to decrease in diversity over time, whereas traits associated with stabilizing niche differences (*4* in Fig. 1) are expected to increase in diversity, assuming no trait bias in immigration. Gaining a more nuanced, complete, and predictive understanding of community assembly requires that we quantify the effects of these assembly processes on species demography and the associated changes at the community level (13, 14).

Successional tropical forests exhibit rapid community assembly and thus, provide an ideal system for testing assembly theory (15). High species richness and elevated tree growth and mortality rates

Significance

The assembly of ecological communities results from multiple mechanisms acting concurrently. Disentangling their relative importance represents a major challenge. Our study quantifies the relative importance of four trait-mediated mechanisms and associated changes in functional diversity over succession. We leverage the rapid community assembly in tropical successional forests and the rich information in functional trait data and spatially explicit long-term tree demographic data. Trait correlations with average species survival rates were the most important processes affecting survival and linked to a decrease in wood trait diversity during succession. Simultaneously, evidence for stabilizing niche differences associated with leaf traits was reflected in increasing leaf functional diversity. Our results suggest mechanisms by which individual performance affects successional change in community-wide diversity.
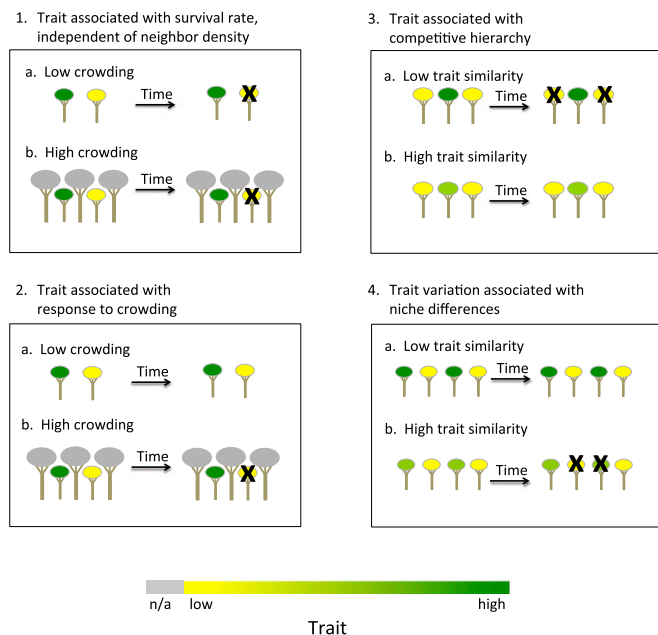
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Fig. 1. Illustration of the four mechanisms of trait-mediated assembly included in our models. Assembly may be driven by species differences in (*1*) survival independent of crowding by neighbors, (*2*) response to increased crowding, (*3*) competitive hierarchies, and (*4*) local niche. All four processes may be revealed through the lens of functional trait variation (the spectrum from yellow to green) and its effects on mortality (black Xs). Note that the color schemes are not meant to be mutually compatible. In *1*, the green color is associated with greater fitness (e.g., because of higher survival) compared with yellow, independent of neighborhood crowding. (*2*) Green traits have lower sensitivity to crowding relative to yellow traits (irrespective of neighbors' traits, which are shown in gray). (*3*) Species have trait hierarchies. Here, green is dominant (i.e., greener species always have greater negative effect on the performance of yellower neighbors than vice versa). (*a*) Because their traits are very different, the green species has a stronger competitive effect on the yellow species compared with (*b*) the competitive effect of the yellow-green species on the yellow species. (*4*) In contrast, when trait variation is associated with stabilizing niche differences between neighbors, negative density effects are experienced similarly by both species. (*a*) Neighbors with greater trait-associated niche difference (green vs. yellow) have a weaker competitive effect relative to (*b*) species with less difference in traits (green vs. yellow-green).

relative to old-growth forests contribute to rapid species turnover and increase the likelihood of detecting assembly processes across succession (16). As succession proceeds, increased crowding alters local resource availability, which may drive species turnover (17–19). Early successional forests are typically dominated by species with acquisitive traits, such as low WSG and high specific leaf area (SLA), which enable rapid growth, resource capture, and high fitness under conditions of high resource availability (17, 20, 21). In contrast, traits that tend to dominate older forests [e.g., dense wood and tough leaves (22, 23)] are thought to promote long-term survival and fitness under high crowding and low resource availability (17, 24). Trait diversity is also expected to change as succession proceeds, although the direction and mechanisms of diversity changes remain unclear (23). Despite considerable previous efforts, few researchers have tested these hypotheses using demographic data in diverse systems.

We use a long-term dataset of tropical forest succession to disentangle how trait-mediated processes drive community dynamics. Spatially explicit longitudinal studies of individual performance offer a powerful approach to reveal drivers of community dynamics (9, 12, 14, 25–27). Empirical studies of functional community assembly have typically compared static community patterns across sites using aggregated trait metrics (28–30). These studies assume that community patterns are the result of prior assembly processes. However, static and aggregated patterns provide limited capability to distinguish between multiple, often opposing assembly processes (14, 31).

Our novel approach simultaneously quantifies the relative importance of multiple assembly processes and links these processes to contrasting effects on functional diversity. We use trait data for over 200 tree species, and we develop spatially explicit statistical models of tree survival over 15 y across eight 1-ha forest plots at diverse stages of succession in lowland wet forests of Costa Rica (*SI Appendix*, Table S1). We ask three central questions about trait-mediated effects on tree survival rates, a major component of fitness, and successional community dynamics.

  i) What are the simultaneous effects and relative importance of four trait-mediated assembly processes on tree survival? Specifically, we ask four subquestions about the processes.
   i.i) How are functional traits related to interspecific variation in average survival?
   i.ii) How do trait relationships with survival change with variation in neighborhood crowding?
   i.iii) Do competitive interactions depend on trait hierarchy, indicating that crowding effects are based on dominance?
   i.iv) Do competitive interactions with neighbors depend on absolute trait differences between neighbors, suggesting stabilizing niche differences?
  ii) Is the demographic evidence for trait-mediated fitness and niche differences (*i*) reflected in community-level changes in trait diversity across successional stages? We expect that traits associated with relative fitness (i.e., associated with greater average survival, decreased sensitivity to crowding, and hierarchical dominance) will decrease in diversity over time, whereas traits associated with stabilizing niche differences will increase in diversity during forest succession.
  iii) Is the demographic evidence for trait-mediated fitness differences reflected in functional differences between second-growth specialists and old-growth specialists? We expect that traits associated with greater relative fitness will be more strongly associated with old-growth specialists compared with second-growth specialists.

To answer these questions, we built hierarchical Bayes models of community-wide stem survival, which include parameters for each assembly process in questions *i.i–i.iv* (12, 27) (details in *Methods*). We fit models for each of three functional traits associated with resource use and life history: SLA (defined as leaf area per unit dry mass), leaf dry matter content (LDMC; defined as leaf dry mass over leaf fresh mass), and WSG (defined as the density of wood relative to the density of water). These traits represent leading axes of ecological variation among tropical tree species that have been previously implicated in interspecific variation in resource use efficiency, species interactions, and life history strategies (32–34). SLA represents a major axis of variation between rapid resource acquisition for species with high SLA vs. conservative strategies with low tissue turnover for species with low SLA (32, 35). Species with high LDMC have lower leaf protein and reduced ability to exploit resource-rich environments but better performance under low resources and drought (7, 34, 36, 37). WSG is associated with a tradeoff between rapid growth rates for species with low WSG and high structural support and resistance to natural enemies for species with high WSG (9, 33).

Results

Trait Relationships with Average Survival. Consistent with expectations, average survival rates (independent of neighborhood) were significantly higher for species with high LDMC and WSG compared with species with low LDMC and WSG (*1* in Fig. 2 and *SI Appendix*, Fig. S1). Contrary to expectations, SLA was not significantly associated with survival.
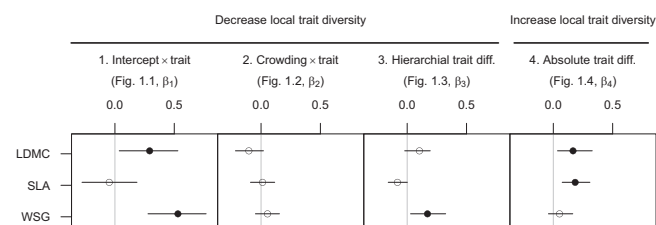
Standardized regression coefficients with greater absolute values are relatively more important in explaining survival. In this regard, our model offers a clear way of comparing the relative importance of the trait-based parameters that we studied. The regression coefficient that determines the relationship between traits and survival of each species independent of neighborhood variation (β_1) had the greatest magnitude of the four types of trait effects considered (corresponding to *1–4* in Figs. 1 and 2).

Neighborhood Crowding and Trait Relationships with Survival. On average, species survival decreased with increased neighborhood crowding, which was measured by the neighborhood crowding index (*NCI*) (*Methods*). However, interspecific variation in sensitivity to crowding was not significantly associated with any of the three traits (*2* in Fig. 2, β_2-parameter and *SI Appendix*).
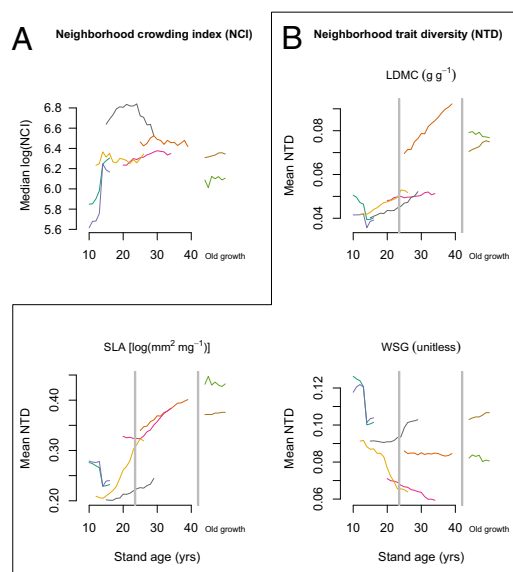
Trait-Mediated Competitive Dominance Hierarchy. The effects of trait-mediated hierarchical dominance interactions, measured by hierarchical trait differences with neighbors [signed trait difference weighted by *NCI* (*NCIH*)] (*Methods*), were only significant for WSG (*3* in Fig. 2, β_3-parameter and *SI Appendix*). We found that negative crowding effects on survival were lower for focal trees when their WSG was higher than that of neighbors. Note that hierarchical effects were dependent on the signed trait difference, size, and proximity of neighbors and thus, are distinct from WSG effects on species average survival rates (β_1).

Traits and Stabilizing Niche Differences Among Neighbors. Two of three traits exhibited significant evidence for niche differences in neighbor interactions. Focal trees had significantly greater survival when there were greater absolute differences with neighbors in LDMC and SLA [absolute trait difference weighted by *NCI* (*NCIS*)] (*4* in Fig. 2, β_4-parameter). Our findings suggest that, overall, increased trait difference with neighbors was associated with increased survival of focal trees.

Successional Changes in Trait Diversity. Median neighborhood crowding (*NCI*) among individuals in 10-m radius neighborhoods increased rapidly during early succession (10–14 y after abandonment) (Fig. 3). After 15–20 y, median crowding remained roughly constant but declined in old-growth stands. Neighborhood trait diversity (*NTD*) was measured as the average trait difference between focal trees and their neighbors weighted by neighbor size and proximity. *NTD* showed divergent changes with

Fig. 3. Change in stem neighborhoods with increasing stand age. (*A*) Change in median *NCI* [log(*NCI*)] (*Methods*). (*B*) Change in *NTD*, which is weighted by neighbor proximity and size. Gray lines indicate divisions between stand age categories used to test the effect of stand age on *NTD*. *NTD* represents the average trait difference between focal trees and their neighbors weighted by neighbor size and proximity calculated for each trait (*Methods*). Each of the eight 1-ha forest plots is represented by a differently colored line.

stand age depending on the functional trait (Fig. 3 and *SI Appendix*). *NTD* measured with LDMC (linear mixed effects model; $t = 3.8$, $P = 0.0003$) and SLA ($t = 5.3$, $P < 0.0001$) significantly increased from early-growth to midsuccessional to old-growth stands. In contrast, WSG showed a decreasing trend in *NTD* in older stands, although the trend was not significant ($t = -1.2$, $P = 0.2291$).

Trait Differences of Second-Growth vs. Old-Growth Specialists. We used a recently developed multinomial model to classify 66 species as second-growth specialists and 133 species as old-growth specialists based on relative abundances in each habitat; the remaining 189 species were either generalists or too rare to classify (38). Old-growth specialists had significantly greater WSG (mean = 0.57) compared with second-growth specialists (mean = 0.44, Wilcoxon test: $P < 10^{-7}$). In contrast, old-growth specialists did not have significantly different LDMC (mean = 0.35 g g^{-1}) or log SLA (mean = 2.68 log mm^2 mg^{-1}) compared with second-growth specialists (mean LDMC = 0.34 g g^{-1} and mean log SLA = 2.71 log mm^2 mg^{-1}; $P = 0.60$ and $P = 0.54$, respectively).

Discussion

We coupled a long-term study of tree demography in successional forests with a novel modeling approach to reveal the relative importance of four trait-mediated, spatially explicit mechanisms underlying community assembly during tropical forest succession. Our models included trait-mediated effects associated with relative fitness differences—mean survival, responses to crowding, and dominance hierarchies—and effects associated with stabilizing niche differences within local neighborhoods.

Among these mechanisms, our evidence indicated that the most important were trait-mediated relative fitness differences among species (Fig. 2, β_1). The link between traits and average survival is not surprising given that the traits that we studied are closely associated with resource acquisition, storage, and defense (32, 33, 35, 39–41). Among the traits considered, WSG was the strongest predictor of species average survival, independent of variation in neighborhood crowding. In accordance with other studies, we found that higher WSG was associated with higher survival

Fig. 2. Standardized regression coefficients modeling the effects of trait-mediated assembly processes on survival. Numbered β-subscripts 1–4 correspond to research questions *i.i–i.iv* and similarly numbered processes *1–4* in Fig. 1, respectively. The first three modeled processes (*1–3*) promote lower trait diversity among neighbors, whereas the last process (*4*) promotes greater trait diversity. Circles show posterior medians of β-coefficients, and lines indicate 95% confidence intervals (filled circles indicate significant effects). Positive β indicates greater survival with increasing values of the covariate. For example, positive β_1 for WSG for survival indicates that species with greater WSG had greater survival, independent of crowding effects. Negative β_2 for LDMC for survival indicates that species with greater LDMC were more sensitive to crowding effects (*NCI*), although the finding was not significant. Positive β_3 for WSG for survival indicates that trees with higher WSG had a greater negative impact on neighbors with relatively lower WSG than vice versa (*NCIH*). Positive β_4 for LDMC and SLA indicates greater survival for focal trees with high absolute trait differences with neighbors (*NCIS*).

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(9, 40, 42, 43). WSG is closely related to resistance to physical damage but also correlates with other traits that may reduce mortality, such as resource conservation and high leaf toughness (44). Additionally, we found that average species survival was greater for species with high LDMC values. Like WSG, high LDMC is associated with conservative resource use strategies and drought resistance (34, 36, 37). Our study sites are closed canopy midsuccessional and old-growth stands with low light availability, which may favor persistence of species with high LDMC and WSG that can avoid mortality by withstanding low resource availability.

We did not find significant effects of species traits on sensitivity to crowding (Fig. 2, β_2). The lack of crowding response effects may seem surprising given findings that traits associated with late-successional species typically confer higher relative fitness under low resource conditions (17, 24). Successional niche theory predicts a tradeoff between species having high fitness under low crowding and species with high fitness under high crowding (21). This tradeoff is thought to be a major empirical driver of community turnover (45). Our findings may be partly due to the fact that the youngest stands in our dataset were 10 y in age, and we had fewer young stands with low crowding compared with mid-successional stands with high crowding. Additionally, high fitness of early-successional specialists may be caused by rapid growth and fecundity, vital rates that we did not include here (8). Thus, we may have been limited in our ability to characterize traits associated with fitness during initial stages of succession. Because our study was observational, we were unable to observe all species under a full range of crowding conditions, potentially limiting our power to detect interspecific variation in crowding responses. Nevertheless, our observations reflect the conditions that species encounter in natural stands and thus, reflect the importance of assembly mechanisms at work under realistic crowding variation.

Our study provides evidence for the importance of trait-associated stabilizing niche differences in succession. We found significant effects of trait similarity between focal trees and neighbors (β_4), consistent with the hypothesis that species niche differences associated with functional traits mediate species interactions. SLA, a key indicator of ecological strategy (35), showed the strongest demographic evidence for stabilizing niche differences among neighbors (Fig. 2, β_4). SLA is closely linked to a tradeoff between photosynthetic rate and cost of leaf construction or leaf lifespan (32). Species that differ in SLA may compete less strongly and be more likely to stably coexist compared with species with similar SLA. Additional studies from mature tropical forests have implicated SLA in environmental filtering and niche differentiation (27–29), although SLA-mediated interactions were less important in hurricane-prone forests in Puerto Rico (12). Differences in LDMC among neighbors also were associated with higher survival, although previous studies did not find an importance of LDMC for neighborhood niche differences among tropical trees (12, 28, 29). Additionally, effects of trait similarity between focal trees and neighbors (β_4) were significant, whereas focal tree trait effects on crowding response (β_2) were not, indicating that crowding effects are more dependent on the composition of neighborhoods than the traits of focal trees.

Our models showed weaker evidence for fitness differences associated with trait-mediated hierarchical interactions than trait-mediated stabilizing niche differences. However, hierarchical effects of high WSG species were evident in that species with greater WSG had stronger impacts on neighbors with lower WSG (Fig. 2, β_3). This pattern may be the result of greater resource conservation in species with high WSG values (10). This result supports the findings by Kunstler et al. (10) in French forests, where neighborhood interactions were better modeled by hierarchical trait effects than effects of absolute trait differences. Although we found hierarchical effects only for WSG, the difference in our findings might be attributed to the fact that Kunstler et al. (10) did not incorporate trait associations with species average demography, which were the most important trait-mediated drivers in our study. Our results suggest that the most

important differences among species in community assembly may be fitness differences independent of variation in neighbor density.

Another goal of our study was to link trait-mediated effects on survival rates to long-term changes in trait diversity at the community level. We expected that traits associated with stabilizing niche differences among neighbors would display increased trait diversity as stands age. Consistent with this expectation, absolute difference in neighbor SLA and LDMC was associated with significantly higher survival, suggesting niche differences among neighbors, and these same traits also showed greater neighborhood trait diversity in older stands. We previously observed increasing phylogenetic diversity with stand age in our plots (46), which assuming that traits are conserved, is likely influenced by trait-mediated niche differences. However, the demographic effects of trait-mediated niche differences were countered by strong trait correlations with average demography, suggesting that assembly simultaneously changed community trait means and variance. The only trait that exhibited decreased diversity over time was WSG. This result is consistent with the strong correlation between WSG and average survival rates and competitive hierarchies suggesting relative fitness differences, which are expected to reduce neighborhood trait diversity. Although other assembly processes can contribute to changes in neighborhood trait diversity, we did not observe a significant trend in neighborhood trait diversity caused by recruits replacing dead stems (*SI Appendix*).

We expected that traits associated with higher relative fitness would be more prevalent among old- vs. second-growth specialists. The trait–demographic relationships that we modeled were largely consistent with differences that we observed between second- and old-growth specialists and findings from previous studies. WSG is related to physical sturdiness and was significantly higher among old- vs. second-growth specialists, and it was also associated with higher species survival (Fig. 2 and *SI Appendix*, Fig. S1). Thus, higher survival of better defended and structurally sound species is likely a major driver of successional habitat specialization, consistent with previous observations of successional trait changes of other forests (10, 19, 22). Our results suggest that communities shift to functional types with the highest survival during succession. Additionally, it is possible that trait differences between second- and old-growth specialists were associated with competition colonization tradeoffs (21), although we did not quantify colonization ability.

Our results offer important insights into the mechanisms of successional community dynamics. Researchers have hypothesized that increased crowding drives community succession, because species with acquisitive functional traits that colonize and grow rapidly early in succession compete poorly under crowded conditions later in succession (18, 21, 45). We did not find evidence to support this hypothesis, because no trait was significantly associated with species response to crowding. However, additional traits that we did not study may be associated with crowding responses and other fitness and niche differences. Also, note that a given trait may be associated with variation in both fitness and niche (5). Our results suggest that second-growth specialists with low WSG have lower fitness than old-growth specialists, leading to declining populations during forest succession (22). The presence of second-growth specialists in successional habitats may be promoted by colonization abilities and rapid generation time, possibly trading off with competitive ability and long-term persistence (21). Finally, our results are consistent with other studies that show trait-dependent changes in functional diversity over succession (23, 30). Our results suggest that differences in successional trajectories among traits are partly caused by the degree to which traits are associated with fitness vs. niche differences.

Conclusions

We used the large amount of information contained in individual tree neighborhoods and long-term performance to elucidate multiple functional and demographic drivers of tropical forest community assembly. Our analysis revealed evidence of major assembly roles for (*i*) trait-based demographic differences that

contribute to interspecific fitness differences and (*ii*) trait-based stabilizing niche differences that reduce interspecific competition and contribute to successional increases in functional diversity (1, 2). Specifically, we showed that traits likely linked with niche differences (SLA and LDMC) increased in diversity with succession, whereas a trait likely linked with only fitness differences (WSG) decreased in diversity with succession. Our long-term study indicates that higher WSG likely enhances species survival and fitness, supporting hypothesized links between functional traits, demography, and successional change (47). Our study makes significant advances to the goal of quantifying the mechanisms underlying community assembly and dynamics in natural communities. Future studies should include vital rates not modeled here to definitively link neighborhood interactions, per capita population growth rates, and species and functional diversity with community assembly.

Methods

Study Sites and Data. We annually monitored woody stems ≥5 cm in diameter at breast height (DBH) in six successional and two mature forest 1-ha plots in the Caribbean lowlands (50–220 m above sea level) of Costa Rica (19, 46, 48, 49) (*SI Appendix*, Table S1). Four successional plots were monitored beginning in 1997, and the remaining plots were monitored beginning in 2005. Here, we include data through the 2011 census. All plots had been cleared and grazed lightly for several years before abandonment and had closed canopies from the initiation of vegetation monitoring (50). Each stem was identified to species, tagged, mapped, and annually measured for DBH. After excluding stems within 10 m of plot edges (4,870 stems), we modeled the survival of 5,265 unique stems across the 1997–2011 study period. Survival was not modeled for 440 stems belonging to species with unknown trait data.

We used standardized, published protocols for all functional trait measurements (more details in *SI Appendix*) (39, 51). We measured functional traits for 215 species of a total of 389 species, including 200 of 226 tree species that had four or more individuals in any of the annual censuses. Measurements were made on 1–62 individuals per sampled species. In addition to SLA, LDMC, and WSG, we measured leaf size (centimeters^2), leaf thickness (millimeters), leaf toughness (N millimeter^{-1}), and leaf density (milligrams millimeter^{-3}). Results for leaf size, thickness, toughness, and density can be found in *SI Appendix*.

Demographic Models. We separately fit survival models for each trait to manage model complexity and correlations among traits (SLA vs. WSG, $r = -0.07$; WSG vs. LDMC, $r = 0.30$; LDMC vs. SLA, $r = 0.63$). Each model included the species sampled for that trait. We excluded species with missing traits from analysis of survival, although their effects on focal stems were included as an additional term.

The model takes the form

$$\mu_{ptsim} = \beta_{1s} + \beta_{2s} \log(NCI_{ptsim}) + \beta_{3s} NCIH_{ptsim} + \beta_{4s} \log(NCIS_{ptsim})$$
$$+ \beta_{5s} \log(DBH_{ptsim}) + \beta_{6s} \log(NCIU_{ptsim}) \quad [1]$$
$$+ \iota_i + \varphi_p + \gamma_t + \upsilon_{pt},$$

where $e^{-\mu_{ptsim}}$ gives the scale parameter for a Weibull distribution, determining expected survival time. The subscripts refer to stem *m* of individual *i* (potentially multistemmed) of species *s* in plot *p* measured in census years *t* and *t* + 1. The first four terms in the regression are associated with the four studied ways in which functional trait variation affects community assembly (corresponding to *1–4* in Fig. 1). The first term of the regression, β_{1s}, is a species-specific intercept, whereas the next three terms determine the effects of crowding by neighbors (*NCI*), crowding by neighbors dependent on trait hierarchy (*NCIH*), and crowding dependent on absolute trait differences between focal trees and neighbors (*NCIS*). Additional coefficients describe effects of size (*DBH*) and crowding by neighbors with unknown traits (*NCIU*). All coefficients in a given trait model were fit simultaneously, including second-level regressions (Eqs. 2 and 4). Expected survival time $b(\mu_{ptsim})$ was modeled with Weibull-distributed process error, where survival time was left- and right-censored from the recensus date (52). Covariate effects (e.g., *DBH* and *NCI*) are included as their state in year *t*. Normally distributed random effects for individual, plot, year, and year × plot are ι_i, φ_p, γ_t, and υ_{pt}, respectively.

Trait relationships with average survival. To address question *i.i* above, we modeled how species traits affect species average survival, β_{1s}, in a second-level (i.e., species-level) regression:

$$\beta_{1s} = \beta_{1.0} + F_s \beta_1 + \varepsilon_{1s}, \quad [2]$$

where β_1 gives the effect of functional trait F_s, ε_{1s} is the normally distributed random effect of species *s*, and $\beta_{1.0}$ is the intercept for all species. High values of $|\beta_1|$ indicate a close link between a trait and average survival.
Neighborhood crowding and trait relationships with survival. To address question *i.ii*, we modeled how the traits of a focal tree mediate its response to crowding (β_{2s}). First, we calculated *NCI* for each stem *m* based on the size and distance of its neighbors,

$$NCI_{ptsim} = \sum_{j=1,\, m \neq j}^{J} \frac{DBH_j^2}{d_{mj}^2}, \quad [3]$$

where d_{mj} is the distance between stem *m* and neighbor *j*, of which there are *J* total neighbors within a specified radius. We used a radius of 10 m, which is sufficient to capture the great majority of neighborhood effects (25, 53). As noted above, to avoid edge effects, we excluded stems within 10 m of plot boundaries in our analysis.

Second, we modeled trait effects on species response to crowding, β_{2s} (Eq. **1**), in an additional second-level regression:

$$\beta_{2s} = \beta_{2.0} + F_s \beta_2 + \varepsilon_{2s}, \quad [4]$$

where β_2 determines the influence of functional trait F_s on species response to *NCI*. High values of $|\beta_2|$ indicate a close association between interspecific variation in traits and sensitivity to crowding.
Traits and competitive dominance hierarchies. To address question *i.iii*, we modeled crowding effects dependent on trait hierarchy between neighbors, where the competitive effects of a species pair are asymmetric (e.g., low trait value more negatively affected by crowding of neighbor with high trait value). These effects, *NCIH*, are calculated as

$$NCIH_{ptsim} = \sum_{k=1}^{S} \left[\lambda_{sk} \sum_{j=1,\, m \neq j}^{J_k} \frac{DBH_j^2}{d_{mj}^2} \right], \quad [5]$$

where *s* is the focal species and *S* is the total number of neighbor species *k*. The effect of crowding is mediated by the trait differences between neighbors, λ_{sk}, which are calculated as $\lambda_{sk} = F_s - F_k$, where F_s and F_k are the traits of focal species *s* and neighboring species *k*, respectively (10). The effect of *NCIH* is determined by the β_3-coefficient (Eq. **1**), which when positive, indicates that neighborhood crowding effects are relatively weaker when focal tree trait value F_s is greater than the neighbors' trait value F_k. When β_3 is negative, crowding effects are relatively weaker when focal tree trait value F_s is less than the neighbors' trait value F_k. *NCIH* = 0 for conspecific neighbors (i.e., *s* = *k*).
Traits and niche variation among neighbors. To address question *i.iv*, we assumed that crowding effects could depend on absolute symmetric trait differences between focal stem *m* and neighbors *j* (of J_k neighbors of species *k*) as follows:

$$NCIS_{ptsim} = \sum_{k=1}^{S} \left[|\lambda_{sk}| \sum_{j=1,\, m \neq j}^{J_k} \frac{DBH_j^2}{d_{mj}^2} \right]. \quad [6]$$

As opposed to *NCIH*, *NCIS* is based on the absolute value of trait differences, λ_{sk} (12). The sign of the β_4-coefficient determines the effect of *NCIS* (Eq. **1**), with positive values indicating that greater trait differences with neighbors lead to amelioration of crowding effects. *NCIS* = 0 for conspecific neighbors (i.e., *s* = *k*).
Trait-independent effects. Ontogenetic changes in survival are modeled by the *DBH* parameter (β_{5s}), which is species-specific and drawn from a normal distribution with mean β_5. We lacked trait data for some rare species. To account for potential bias in their crowding effects, we calculated an additional term, *NCIU*, with coefficient β_{6s} (Eq. **1**). *NCIU* was not weighted by traits and was equal to *NCI* summed only for neighbors *j* belonging to species with missing trait data.

Interspecific variation in trait-mediated crowding responses was modeled such that species-specific parameters β_{3s}, β_{4s}, and β_{6s} were drawn from normal hyperdistributions with means β_3, β_4, and β_6, respectively (9, 27). For regression purposes, *NCI* and *NCIS* were transformed by adding one and taking the log, because metrics were highly right-skewed. Trait, *NCI*, *NCIS*, *NCIH*, and *NCIU* metrics were all standardized to mean zero and unit SD to facilitate interpretation and comparisons among parameters (54).

We fit separate survival models for each trait. All parameters were given proper diffuse priors, and posterior sampling was conducted by Markov Chain Monte Carlo using JAGS software (http://mcmc-jags.sourceforge.net/). β-Parameters were considered significant when 95% confidence intervals did not overlap with zero. We conducted predictive checks by simulating

survival for each stem based on the underlying parameter posterior samples and calculating accuracy of predictions (54).

Successional differences in neighborhood trait diversity. We also studied successional changes in *NTD* of each stem, which were the weighted average trait differences between a focal stem and its neighbors. We calculated *NTD = NCIS/NCI* to weight pairwise trait differences by the proximity and size of neighbors (i.e., the components of *NCI*). For each plot in each year, we calculated the mean *NTD* for each trait. We classified stand age as a categorical ordinal covariate [1 = early successional (<24 y old), 2 = midsuccessional (24–39 y old), 3 = old growth (unknown age)]. We then tested whether *NTD* for each trait changed linearly across the three stand age categories using a linear mixed effects model with plot as a random effect (implemented using the R package nlme) (55).

Trait differences between second- and old-growth specialists. We tested for trait differences among species classified as second- vs. old-growth specialists. Classifications were taken from a multinomial analysis of species relative abundances in second- vs. old-growth stands (38). We tested for differences in species traits between the two categories using Wilcoxon rank sum tests.

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