

Small disturbances and subsequent competition for light can maintain a diversity of demographic strategies in a neotropical forest: Results from model–data integration

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Funding information
National Science Foundation, Grant/
Award Number: DEB 1939559

Handling Editor: Susan Schwinnig

Abstract

1. Niche differentiation with respect to light availability as it varies across succession has often been thought to explain tree species coexistence. Demographic light-related niches represented by growth-survival and stature-recruitment trade-offs and captured by demographic groups (slow, fast, long-lived pioneers, short-lived breeders and intermediate) have been shown to accurately represent the biomass dynamics of secondary and old-growth forests in central Panama in a model. However, whether the simple mechanisms of that well-parameterized and accurate model are enough to support the long-term coexistence of demographic groups across these trade-offs has yet to be tested.
2. Here, we develop a model to test whether stochastic, small-scale gap disturbances and subsequent competition for light can support the long-term coexistence of the observed demographic groups in the Barro Colorado Island forest dynamics plot. Specifically, to test whether the demographic differences among species promote coexistence, we compare niche simulation models, parameterized by the different demographic groups, to a variety of neutral models, where the species have the same demographic parameters.
3. Upon exploring the estimated range of possible parameterizations of recruitment (a difficult-to-measure parameter), we identify several parameterizations where differences among groups along the growth-survival and stature-recruitment trade-off axes facilitate long-term coexistence. We find that gap disturbances are essential for these results, indicating that it is the differences in the subsequent competition for light through time that provide the opportunity for stabilizing niche differentiation. Additionally, the parameterizations that generate stable coexistence display successional negative density dependence and realistic within-patch post-disturbance forest dynamics.
4. **Synthesis.** This model–data integration exercise indicates that small-scale disturbances and subsequent competition for light may be significant forces for stable diversity maintenance of demographic groups along the growth–survival and

stature–recruitment trade-off axes in a neotropical forest. This result, however, holds only for a subset of the empirically reasonable recruitment parameters, indicating the importance of improving the understanding of recruitment and its demographic trade-offs for understanding demographic strategy coexistence.

KEY WORDS

determinants of plant community diversity and structure, forest dynamics, metacommunities, plant development and life-history traits, plant population and community dynamics, successional dynamics, tropical forests

1 | INTRODUCTION

Tropical forests are characterized by high tree species diversity, with many forests well exceeding two hundred species in a 50-ha forest plot (Anderson-Teixeira et al., 2015). This high diversity found in tropical forests is puzzling as theory indicates that the number of species that can coexist indefinitely cannot outnumber limiting resources (Gause, 1934; Tilman, 1982). On the other hand, if we have accurate estimates of immigration and speciation rates, we can explain large amounts of species diversity persisting for long periods, assuming we ignore how tree species differ (Hubbell, 2001). However, there are consistent functional differences among tree species, implying that consistent niches may exist and support the functional diversity of coexisting species (D'Andrea et al., 2020; Kraft et al., 2008).

In hyper-diverse Neotropical forests, there has been a notable emphasis on gap disturbances as a mechanism for the maintenance of tree diversity, among several hypotheses of stabilizing coexistence mechanisms (Augspurger, 1984; Givnish, 1999; Levi et al., 2019). A mature forest is a mosaic, composed of forest patches with varying times since disturbance, light availability and canopy heights (Hubbell et al., 1999; Hulshof & Umaña, 2023; Lobo & Dalling, 2014; Martinez-Ramos et al., 1988). These patches and shifts in light availability at the forest floor are often created by gaps resulting from branch or tree falls and are recognized as a common form of natural disturbance in Neotropical forests (Chazdon, 2014; Hubbell et al., 1999; Tomlinson & Zimmermann, 1978; Wright, 2002). Following these small-scale gap disturbances, tree competition for newly available light occurs within forest patches. Gaps can maintain diversity in Neotropical forests by providing competitive relief to shade-intolerant species from higher canopy layers (Schnitzer & Carson, 2001; Wright, 2002).

Due to differences in performance in light and shade, tree species have long been classified into so-called 'fast' (pioneer) and 'slow' (shade-tolerant) strategies (Denslow, 1987; Schnitzer & Carson, 2001). Heterogeneity in light leads to a demographic turnover from shade-intolerant, fast-growing strategies to shade-tolerant, slow-growing strategies following gap creation (Drury & Nisbet, 1973; Finegan, 1996; Horn, 1974). As a fundamental axis of species variation, the growth-survival trade-off underlies patterns

of niche differentiation with spatial heterogeneity in resource availability, favouring the recruitment of pioneer species in early succession and the recruitment of shade-tolerant species in late succession (Baraloto et al., 2005; Rüger et al., 2023; Wright et al., 2010). In particular, changes in light availability inherent to gap dynamics can allow for tree species with high growth rates but low survival abilities in the shade to establish when high-intensity light reaches the forest floor in an otherwise 'slow' dominated understory (Grady et al., 2024; Huston & Smith, 1987).

Recently, there has been evidence favouring the addition of a stature–recruitment trade-off to this growth–survival trade-off (Rüger et al., 2018). This trade-off between both growth and survival—leading to large stature—versus recruitment is found as an orthogonal dimension of variation in demographic rates, observed in several forests (Kambach et al., 2022; Rüger et al., 2018; Salguero-Gómez et al., 2016). That is, species with superior growth and survival suffer from poor recruitment, while those with exceptionally high recruitment rates generally have low growth and low survival. Further, summarizing the variation among species along the two trade-off axes into five demographic groups has been shown to more accurately capture successional and old-growth Panamanian forest dynamics than the single growth–survival trade-off axis alone (Rüger et al., 2020). Specifically, the demographic groups across the trade-off axes that capture forest dynamics well are (1) low growth, high survival, average recruitment (slow), (2) high growth, low survival, average recruitment (fast), (3) high growth, high survival, low recruitment (long-lived pioneers, LLP), (4) low growth, low survival, high recruitment (short-lived breeders, SLB), and (5) average growth, survival and recruitment (intermediate) (Figure S1).

Previous models have sought to explain coexistence among species varying in their demography along trade-offs and in variable habitats maintained by disturbances (Parvinen & Meszéna, 2009). In these patch occupancy-style metapopulation models, coexistence can range from up to five species (Parvinen & Meszéna, 2009) to a potentially unlimited number of species (Tilman, 1994), depending on how the trade-off, dispersal, and space are characterized. Models that have included gap dynamics have shown the coexistence of shade-tolerant and shade-intolerant species (Gravel et al., 2010), with gap dynamics potentially enhancing the range of demographic space for which species can coexist (Kohyama, 1993). Models focusing on the persistence of specific combinations of demographic

strategies have shown that life history differences among species can allow for coexistence (Dettlo et al., 2022; Falster et al., 2017; Jops & O'Dwyer, 2023). Further, recent forest dynamics models that focus on a mechanistic implementation of how species compete for light have shown a theoretically large number of species to coexist along physiological trade-offs considering leaf mass per unit area and height at maturation (Falster et al., 2017), and along trade-offs between growth, mortality, recruitment, maturation, crown area expansion, and stem height growth (Dettlo et al., 2022). However, none of these models combined empirically derived trade-offs of growth, survival, and recruitment, or focused on explaining the maintenance of diversity solely through realistic competition for light by testing niche coexistence with comparisons to neutral coexistence.

Here we integrate forest dynamics data with simulation models to test the possibility for only competition for light and gap disturbances to maintain the coexistence of the observed differences in demographic groups in a well-studied neotropical forest (Barro Colorado Island (BCI) Panama; Rüger et al., 2018, 2020). We test whether competition for light and the varying light environments that come from small-scale gap disturbances within forests are enough to explain the coexistence of slow, fast, LLP and SLB demographic groups (defined above) with a simple metacommunity forest dynamics model. We incorporate individual-based competition for light within small forest patches subject to stochastic patch-clearing disturbances, connected through seed dispersal. We experiment with the parameterization of the recruitment process, grounded within empirical data. We find that, indeed, for some empirically reasonable recruitment parameter values, the four demographic groups following the growth-survival and stature-recruitment trade-offs (niche models) do coexist for significantly longer than sets of species with no demographic differences (neutral models) when gap dynamics are included, despite the model simplicity of competition for only a single resource (light). That is, competition for light and gap disturbances alone is capable of generating population-level conspecific negative density dependence and realistic successional dynamics among four demographic groups, allowing for their stable coexistence.

2 | MATERIALS AND METHODS

To explore the potential for stand-clearing gap disturbances and height-structured competition for light to enable the coexistence of species with different demographic groups observed on BCI, we both combine and extend previously published models. Specifically, we extend a simulation version of the PPA (Perfect Plasticity Approximation; Strigul et al., 2008) model that has discrete individuals, finite space and competition for light occurring in patches subject to disturbances (as in Farrior et al., 2016) to include multiple species (here demographic groups) and four canopy layers with differing growth, survival and recruitment rates (as in Rüger et al., 2020).

We also add a metacommunity structure. The simulated forest is constructed of patches within which competition for light occurs,

and by which stand-clearing disturbance can occur, but across which new individuals are evenly dispersed. Within patches, the model simulates (spatially-limited) height-structured competition for light. We add a mechanism of reproduction, whereby the abundance of each demographic group (or species) contributes to new individuals of that demographic group (or species) in the following timestep.

2.1 | Model structure

The model is discrete in time (year), space (by patch) and in trees (whole individual trees). Within each patch, for simulation efficiency, individuals are collected into cohorts defined by the size of the individuals, their canopy layer and their demographic group (or species). Individuals compete for light at the patch level. Thus, patch size and number can be important parameters.

With each timestep, individuals within cohorts grow and die following the parameters of their group and their canopy layer. Growth, given canopy layer status, is deterministic, while both individual-level and patch-level mortality are stochastic. Patches are subject to a constant probability (μ) of all individuals dying (small-scale, 'gap' disturbances). Individuals are subject to mortality probabilistically, according to demographic group (or species) and canopy layer (Table S1).

2.2 | Competition for light

We use an analytically tractable and relatively realistic, spatially limited version of the spatially implicit PPA (Perfect Plasticity Approximation; Farrior et al., 2016; Strigul et al., 2008) model to determine light availability to individual trees. Specifically, we do not track the location of individual trees within a patch because trees are good at foraging horizontally for light. Instead, we assign individuals to a canopy layer based on their size and the size of the other trees in the patch alone. Each canopy layer is filled with tree crowns in order of tree height, in discrete canopy layers. Individuals are either in full sun (canopy layer 1) or covered by one, two or three layers of tree crowns or more (canopy layers 2, 3 and 4, respectively). This PPA algorithm captures the effect of trees' abilities to forage for light horizontally through the placement of their crowns and incorporates the limits of this plasticity through patch size. Farrior et al. (2016) showed that this variation (limited patch size for competition for light, and patch-level disturbances) on the original PPA (Strigul et al., 2008) could explain the emergent size structure of trees in the BCI forest dynamics plot and provide a simple hypothesis for the similarities among tropical forests in their size distributions (Enquist & Niklas, 2001).

Despite the cohort structure of the model, canopy layer assignment works at the level of the individual. If only some of the crowns of individuals of a given tree height (here equal to their rank by height because all trees have the same allometries) can fit into a canopy layer, the individuals that can fit in the canopy

are selected at random among all individuals with the same size, across all demographic groups (or species). See [Appendix S2](#) for further details.

2.3 | Recruitment

Individuals contribute to the generation of new individuals of their demographic group (or species) in the next time step according to their recruitment parameter, crown area and canopy layer. The original PPA model (Strigul et al., [2008](#)) assumes that only trees in full sun can reproduce. We find this assumption to be too restrictive for our purposes here as some of the demographic groups spend very little time in full sun yet have high observed recruitment rates. Some degree of limitation of the reproductive success of an individual by light availability, however, is realistic and necessary to keep the forest from growing to an infinite number of individuals or dying out entirely.

To incorporate a realistic dependence of reproduction on light, we assume that individuals in the top three canopy layers reproduce (those in full sun and shaded by one and two layers of trees, respectively), but that a unit of crown area in each more shaded canopy layer contributes less to the next generation than the layer before. For simplicity, we assume this decreasing proportion is the same across demographic groups (or species). Specifically, we assume that the crown area of a tree that is shaded by one canopy layer (layer 2) generates 30% of what the same amount of crown area of a tree of the same demographic group (species) would contribute if it were in full sun (layer 1). The crown area of an individual that is shaded by two layers of individuals (layer 3) contributes 10% of what that same crown area would contribute to reproduction if it were in full sun, and individuals in layers greater than 4 do not reproduce (see [Appendix S2](#) for further explanation).

The number of recruits ($R_i(t+1)$) of demographic group (or species) i in a patch at year $t+1$ of the model run is given by:

$$R_i(t+1) = \text{RandRound} \left[\frac{F_i(CA_{i,1}(t) + 0.3 CA_{i,2}(t) + 0.1 CA_{i,3}(t))}{N} \right], \quad (1)$$

where F_i is the demographic group-specific constant governing recruitment (defined by [Equation \(2\)](#) below, individuals/crown area m^2 /year), $CA_{i,j}(t)$ is the total crown area of demographic group (or species) i in canopy layer j across all patches at year t of the run, N is the total number of patches in the metacommunity, and RandRound turns the value into an integer in an unbiased way ([Appendix S2](#)).

2.4 | Model parameterization

Following Farrior et al. ([2016](#)), we set the patch size to $1000m^2$ ($31.62m \times 31.62m$) and the patch-level stand-clearing gap disturbance rate to 0.0097 year^{-1} (μ ; half of the observed canopy tree

mortality rate, [Table S2](#); Bohlman & Pacala, [2012](#); Condit et al., [1995](#); Farrior et al., [2016](#)). We use a metacommunity size of 50 patches (N , 5-ha total).

The growth and mortality rates by canopy layer are taken from the demographic groups found in BCI forest dynamics data ([Table S1](#), the five-group case of Rüger et al., [2020](#)). Individual-level mortality rates, however, are decreased by the patch-level mortality rate (stand-clearing gap disturbance rate) to a minimum of zero to yield the correct total mortality. We assume any individual that falls into a canopy layer greater than 4 shares the growth and mortality parameters of layer 4.

We calculate the demographic group-specific F_i 's (new recruits produced per unit of demographic groups' crown area per year, [Equation 1](#)) by assuming that the BCI forest dynamics plot is in equilibrium at the scale of these demographic groups:

$$F_i = \frac{r_i}{ca_{i,1} + (0.3 ca_{i,2}) + (0.1 ca_{i,3})}, \quad (2)$$

where r_i is the observed total recruitment rate of individuals of the i 'th demographic group (individuals/ha ground area/year, as calculated by Rüger et al., [2020](#)), and $ca_{i,j}$ is the observed crown area of the i th demographic group of canopy layer j (m^2 crown area/ha ground area). Because these are rough estimates, the specific estimates of $ca_{i,j}$ used for the demographic groups (slow, fast, LLP, SLB and intermediate) are explained in the Section [2.5.4](#) below.

For simplicity, regardless of the demographic group, we assume that all individuals follow a single height and crown area allometry with diameter. The diameter (dbh, cm) to crown area (m^2) allometry that is used throughout this paper follows that of Rüger et al. ([2020](#); crown area = $0.7854 \times dbh^{1.24}$, following Martínez Cano et al., [2019](#); [Table S2](#)).

2.5 | Model run settings

2.5.1 | Gap versus no gap models

To test for the effect of gaps and competition for light on species coexistence, we run models with and without gaps. When models are run without gaps, individual mortality rates are returned to those of Rüger et al. ([2020](#), as the stand-clearing disturbance rate here is zero).

2.5.2 | Niche versus neutral models

To test whether the differences among species in demography along the growth-survival and stature-recruitment trade-offs promote species coexistence, we compare the coexistence times of demographic groups as species with differing parameters (niche models) to neutral versions of the model, where all of the two or four simulated species are equal and are parameterized by the demographic parameters of one demographic group.

For the niche models, four-group models include all four of the demographic groups, and two-group models include the trade-offs independently, that is slow and fast or LLP and SLB. Note: niche models do not include the intermediate demographic group. We did not include the intermediate group because the coexistence of the other groups with this group of non-specialization or intermediate niche poses slightly different theoretical questions. We leave the understanding of the coexistence of the four specialist demographic groups with the intermediate group to be explored in future work. We run separate neutral models for parameterizations where all two or four species have the demographic rates of only one of the following demographic groups: slow, fast, LLP, SLB or intermediate.

2.5.3 | Initialization and model run length

To avoid a bias towards early-successional groups, we initialize all model runs with the number and diameters of trees within a randomized selection of 50, 1000 m² patches from the 3rd census of the BCI forest dynamics data (not from bare ground). The assignment of the initial individual trees into demographic groups was selected at random (Appendix S3). For each model run, we used the same initialization of trees to provide a controlled comparison between neutral and niche model runs.

The model is stochastic due to individual-level mortality, patch-level disturbance, the canopy layer assignment of equally sized individuals at layer boundaries, and the rounding of recruitment numbers. We run each model setting 40 times.

2.5.4 | Exploring the recruitment parameter space

The recruitment parameters of the model are likely the least well-grounded in the data. We cannot connect the recruits within the 50-ha plot directly to the abundance of individuals of the same group within the plot. Many of the observed recruits are likely produced by individuals existing over longer timescales and larger spatial scales than those observed in the plot inventory data. Further, the coexistence of demographic groups within model runs is likely to be highly sensitive to the F_i parameters, as they capture the basic reproductive population dependence that, without competition, would generate exponential growth or decay of a demographic group's abundance.

To investigate the potential for our model structure and the observed qualitative demographic trade-offs to generate stable species coexistence, we explore the coexistence times for a range of the recruitment parameters (F_i ; Equation 2; Figure 1; Appendix S4). We consider the plausible range of F_i parameterizations to be that generated by calculating the F_i parameters (Equation 2) given the crown area by canopy layer for each of the 50, 1-ha square patches of the plot while keeping the recruits per unit forest area (r_i) constant from all 50-ha of data. For these calculations, within each 1-ha sample,

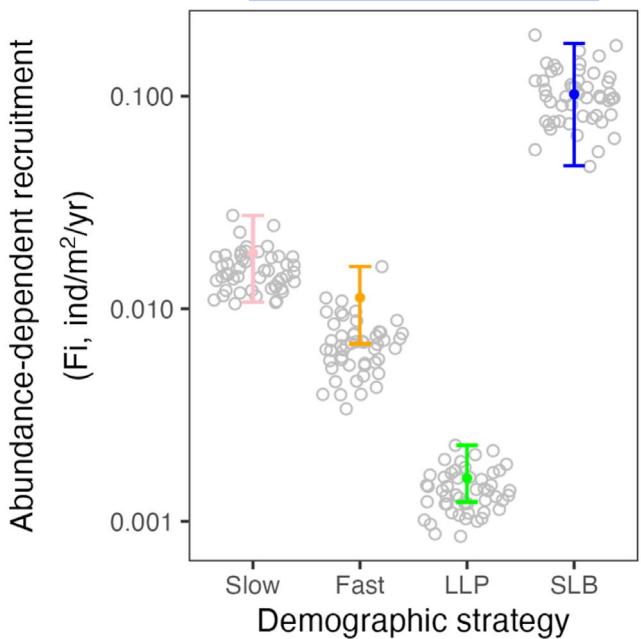


FIGURE 1 The empirically reasonable variation in recruitment parameters (F_i , Equation 2) as derived from the variation in size and abundance of trees in the demographic groups in 1-ha patches across the Barro Colorado Island forest dynamics plot (grey points; see Section 2.5.4). Coloured bars indicate the range of F_i parameters that have produced simulations resulting in long-term coexistence of all four demographic groups (coexistence of 150,000 years for two out of two independent simulations). Combinations of the four parameters spread evenly in log-space from the minimum to the maximum observed (grey points) generated 500^4 possible combinations, 100,000 of which were selected randomly for testing for the possibility of long-term coexistence, and 751 of which generated long-term coexistence. Note that not all combinations of parameters within the space marked by the bars lead to coexistence, as there is interdependence among the parameters that can generate coexistence of all four demographic groups. The specific combinations that lead to coexistence are presented graphically in a four-dimensional plot in Figure S4.1. The points marked in solid colours is the F_i parameter combination used in the rest of the main text (Figures 2–5).

we use 9,111 m² patches (in 3 × 3 orientation) for the canopy layer assignments. We then average the crown areas ($ca_{i,j}$; Equation 2) across censuses 3–8 of the BCI forest dynamics data (Condit, 1998; Condit et al., 2019; for simplicity, we excluded the censuses 1 and 2 from our analyses due to differences in methods of measuring small and large trees.). Thus, the variation in F_i parameters we explore is due to spatial variation in the (assumed to be) reproducing trees across the plot.

To investigate the effect of the F_i parameter space systematically, we take the minimum and maximum F_i values (out of 50) for each demographic group and divide their range into 500 parameters spaced evenly along a base-10 logarithmic scale (Figure 1), generating 500^4 empirically reasonable F_i parameter combinations. We then select 100,000 of these combinations at random from this set to test for long-term coexistence in the niche models with and without

gaps. Given the variability we see in the model runs, below, we count a parameter combination as being capable of generating 'long-term' coexistence if it supports coexistence of all four demographic groups for the maximum runtime of 150,000 years in two out of two independent runs.

Hereafter, we choose one F_i parameter combination (closest in Euclidean distance to the mean points of all the parameters of each group that generate 'long-term' coexistence, see Figure S4.1) to present in the two- and four-group niche and neutral models in the main paper ($F_{\text{Slow}}=0.018267073$ ind/m²/year, $F_{\text{Fast}}=0.011276210$ ind/m²/year, $F_{\text{LLP}}=0.001596888$ ind/m²/year, $F_{\text{SLB}}=0.102122161$ ind/m²/year). Key results are also presented for two other sets of parameters (Appendix S4).

For comparisons of niche with neutral models, we always use the matching parameterizations of F_i . For the intermediate group neutral comparison, because there is no niche parameterization, this is not possible. Thus, we estimate the intermediate group's F_i parameter ($F_{\text{Intermediate}}=0.009895514$ ind/m²/year) in a way that follows the methods of finding the other parameters (see Appendix S5).

2.6 | Model analyses

2.6.1 | Species coexistence

We measure the coexistence time of species across the metacommunity as the time in years for which all demographic groups (or species) remain in the model run. If all demographic groups (or species) persist for the maximum run time of 150,000 years, for statistical analyses, we take its coexistence time to be 150,000 years, a conservative assumption given that the real coexistence time would have been higher.

2.6.2 | Conspecific negative density dependence

To explore stable coexistence in niche model runs, we compare the population-level conspecific negative density dependence (CNDD) of the four-group niche and neutral models with gaps.

Assuming that 200 years is enough to get an effectively independent sample within a run, once every 200 years (starting at year 0) for the total time of a run, we take a 10-year sample and calculate the crown area growth rate per unit crown area ($\text{CAg}_i(t)$) of each demographic group (or species) i in the whole metacommunity from year t to $t+10$ by:

$$\text{CAg}_i(t) = \frac{\text{CA}_i(t+10) - \text{CA}_i(t)}{\text{CA}_i(t)}, \quad (3)$$

where $\text{CA}_i(t)$ is the total crown area of demographic group (or species) i at year t , and $\text{CA}_i(t+10)$ is the total crown area of i at year $t+10$ (individuals/m²/year). Note the number of $\text{CAg}_i(t)$ and $\text{CA}_i(t)$ combinations resulting from a model run depends on the coexistence time of the run (explained above).

We then build independent, linear regressions between all crown area growth rates per unit crown area ($\text{CAg}_i(t)$, Equation 3) and initial crown area ($\text{CA}_i(t)$) values of a run by:

$$\text{CAg}_i(t) = \beta_0 + \beta_{\text{CNDD}} \text{CA}_i(t), \quad (4)$$

and take the best-fit slope of the regressions (β_{CNDD}) for each 40 model run as measures of the CNDD of a model setting (fit with the 'lm' function in version 4.3.3, R Core Team, 2024, using the ordinary least squares method of estimation).

In four-group niche models with gaps, we performed the $\text{CAg}_i(t)$ calculations and regressions separately for the slow, fast, LLP and SLB parameterized demographic groups from the same 40 model runs. In four-species neutral models with gaps (parameterized separately by slow, fast, LLP, SLB as well as the intermediate group), we picked one species out of the four represented in the model run for comparison. We calculate the CNDD for the exact model runs presented in Figure 3 (Equation 4).

2.6.3 | Successional dynamics

To examine patch-level successional dynamics, we analyse the dynamics of demographic group abundances within a focal patch in a four-group niche model run. We run the metacommunity until the metacommunity exhibits stable dynamics (year 2000), then select a focal patch where we initiate a disturbance event and observe the demographic groups' crown areas without another disturbance in the focal patch while the rest of the metacommunity remains under the model run scenario (with disturbances occurring as before and connected through dispersal as before). Due to model stochasticity, we repeat this process 40 times, each time with a new metacommunity model run and the same focal patch.

Code for the model, all specific initializations of model runs, and the calculations necessary for the presented results are provided in an online repository (Cinoğlu et al., 2025).

3 | RESULTS

To investigate whether demographic differences along the growth-survival and stature-recruitment trade-off axes could aid in stabilizing species coexistence, we test the coexistence of demographic groups that remain within the range of possible recruitment parameters as derived from the data (Figure 1). Specifically, we change the least well data-constrained parameters, the recruitment parameters (F_i ; Equation 2). We find that 751 out of the 100,000 tested F_i parameter combinations lead to long-term coexistence of all four demographic groups (reaching 150,000 years, the max run time for two independent simulations) in niche models with gaps (Figure S4.1). With the same process, we find that none of the 100,000 tested F_i parameter combinations lead to long-term coexistence for niche models without gaps (Appendix S6). For the rest of the analyses, we use the central F_i parameters of the empirically reasonable niche

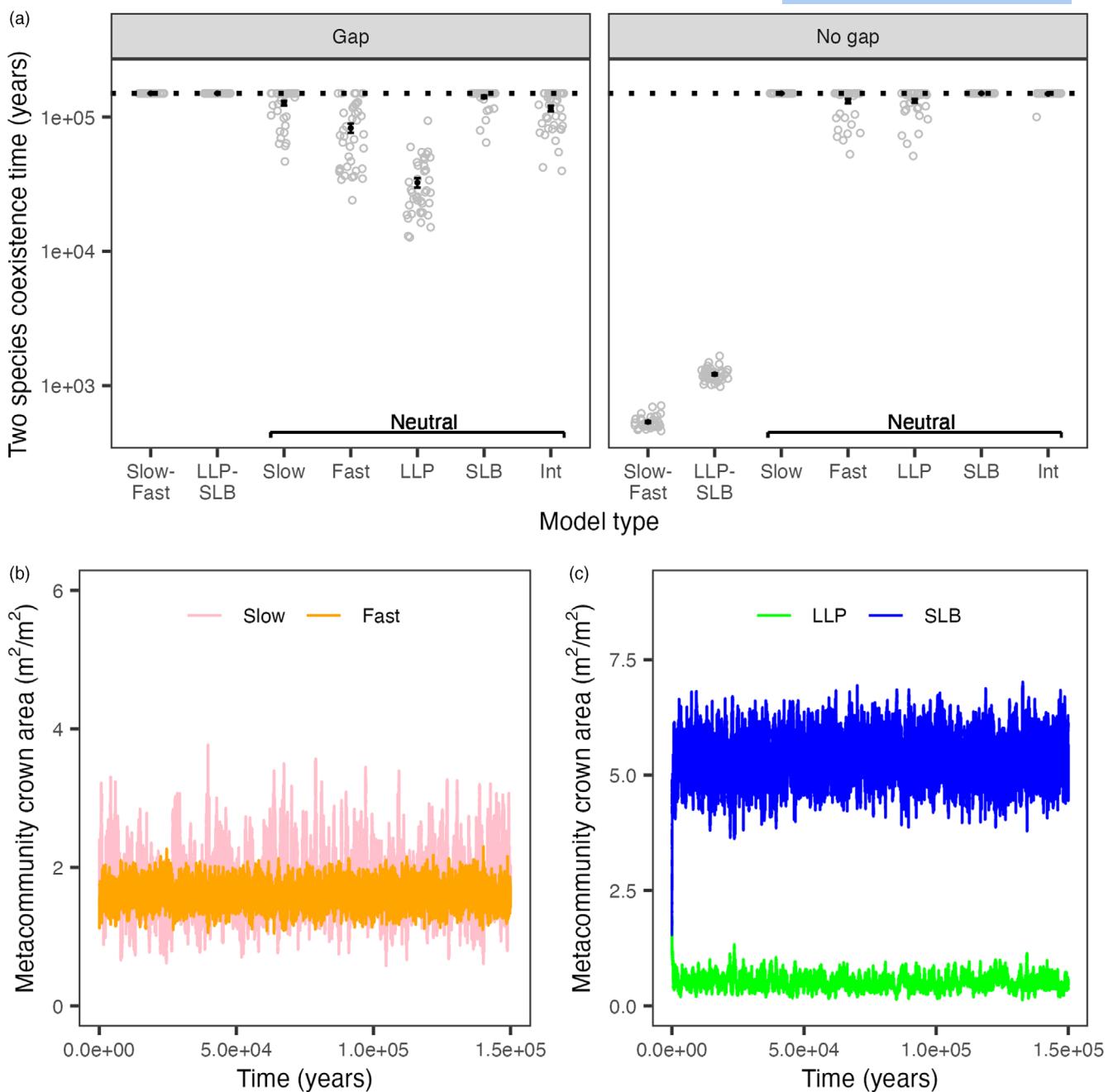


FIGURE 2 (a) Coexistence times for model runs with two demographic groups parameterized by slow and fast or LLP and SLB demographic parameters (niche models) and two species with the same parameters (neutral models, using the indicated demographic groups' parameterization), with and without patch-level disturbances (gaps). Grey points mark the coexistence time of demographic groups (or species) in 40 independent model runs of each model setting. The maximum run time for runs and thus maximum coexistence time is 150,000 years, which is indicated on the plot by a dotted horizontal line. Means (black dots) and standard errors (plotted but some not visible due to magnitude, see main text for values) are calculated under the conservative assumption that the coexistence time of runs that reached 150,000 years was 150,000 years (run time). (b, c) The abundance in the total crown area of each demographic group in one example run of the associated niche models, additional examples can be found in Figure S7.1. Demographic groups in two-group niche models with gaps coexist for significantly longer than the two-species neutral models with gaps and significantly shorter in two-group niche models without gaps (two-sample t-tests for each comparison between each niche model and all neutral models (those for the niche demographic groups as well as the intermediate), p -values <0.05). Without gaps, demographic groups coexist significantly longer in two-species neutral models than in two-group niche models (two-sample t-tests for each comparison between each niche model and all neutral models (those for the niche demographic groups as well as the intermediate), p -values <0.0001).

model runs with gaps that generate long-term coexistence (Figure 1). See Appendix S4 for key analyses with two other sets of F_i parameters (which also generate long-term coexistence). Because we limit our following analyses to parameter combinations that can generate long-term coexistence, the following results explore the possibilities of coexistence maintained by only competition for light and gaps, but are subject to some uncertainty due to our uncertainty in the recruitment parameters.

We find that demographic groups in the two- and four-group niche models with gaps coexist for significantly longer than all of their respective neutral models (two-sample t -tests, p -values < 0.05 , p -values < 0.0001 , respectively). That is, the differences among demographic groups promote their coexistence (niche models; Figures 2 and 3; Figure S4). Without gaps, these results change. The coexistence times of four-group niche models decrease from an average of 145,516 years (± 3676 SE) with gaps to 520 years (± 10 SE) without gaps, and the coexistence times of two-group niche models decrease from 150,000 years (± 0 SE) with gaps to 537 and 1216 years (± 9 SE, ± 22 SE) without gaps for the growth-survival trade-off and the stature-recruitment trade-off, respectively. For neutral models, coexistence is significantly longer in model runs without gaps (Figures 2 and 3, Appendix S7, increases from an average of 99,816 to 142,429 years in two-group runs without gaps and 46,783 to 103,334 years in four-group runs without gaps). Thus, differences among demographic groups can promote their coexistence only when gaps are present.

All demographic groups in the four-group niche model runs had significantly stronger population-level conspecific negative density dependence compared to four-species neutral models parameterized individually by the same demographic groups (two-sample t -test, p -value < 0.0001) as well as the intermediate group (two-sample t -test: p -value < 0.05 for niche—slow vs. neutral—int. and niche—SLB vs. neutral—int., and p -value < 0.0001 for niche—fast vs. neutral—int. and niche—LLP vs. neutral—int.; Figure 4; Figure S8).

Finally, we present within-patch successional dynamics following a gap. In four-group niche model runs, fast and SLB demographic groups peak in abundance before year 100 while the slow and LLP demographic groups take over in late succession (Figure 5).

4 | DISCUSSION

Here we present a metacommunity tropical forest dynamics model to investigate the role of gap disturbances and subsequent competition for light in maintaining the observed diversity of demographic groups in a neotropical forest. We find that there are empirically reasonable parameters where all four different demographic groups (slow, fast, LLP and SLB) coexist more strongly than if the same number of species in the model had identical demographic rates and were neutral. These parameterizations result in stronger emergent conspecific negative density dependence (CNDD) than neutral comparisons and yield realistic qualitative dynamics of the groups within patches, following their local disturbances. The demographic groups

with fast growth rates or high reproductive rates lose their competitive edge later in succession, while the demographic groups with high survival or large statures better resist shaded conditions. The greater coexistence of the demographic groups in the niche models in comparison to the species in the neutral models indicates that we have found a case of emergent negative density dependence for four demographic groups in a model with height-structured competition for light and its variation through time.

4.1 | Demographic groups across two main trade-off axes

Previous work organized trees on BCI into three functional groups as pioneers, building phase and shade-tolerant species (Condit et al., 1996) using data on demography, growth form, phenology and moisture requirements. More recent work used continuous functional trait measurements from BCI to show that tree species cluster into three functional groups: species with short stature, intermediate wood density and low leaf area; tall species with high wood density and low leaf area; and tall species with low wood density and high leaf area (Rubio & Swenson, 2022). Rüger et al. (2020) complement this body of literature with an analysis of the growth, mortality and recruitment rates and their dependence on individual tree estimated light availability from the BCI forest dynamics plot. They found that five groups, spanning the growth–survival and stature–recruitment trade-offs, have the potential to capture forest dynamics more robustly than the parameterization from all 282 species at BCI or just one trade-off. The empirical prevalence of these growth–survival and stature–recruitment trade-offs has also been shown in multiple other tropical forests (Kambach et al., 2022). Our work here further supports the importance of these two trade-off axes by showing their potential to maintain this diversity with the simple and unavoidable mechanisms of small-scale gaps and subsequent competition for light. We leave the understanding of the continuum of species that exist across these trade-off axes to future work.

4.2 | Stable coexistence

Coexistence within the PPA forest modelling framework (Strigul et al., 2008) has been addressed in different ways. Adams et al. (2007) derived the necessary conditions for coexistence, given an equilibrium forest without gaps. These conditions involve a dependence of demographic rates on the abundance of species, whereby species perform more poorly when they are dominant. Lichstein and Pacala (2011) showed that in a metacommunity, patches that promote the dominance of different species can lead to within-patch diversity when there are disturbances and dispersal. Dettlo et al. (2022) investigated the possibilities of successional diversity by examining one trade-off axis at a time and making several simplifying assumptions (that we do not make) to make analytical results possible.

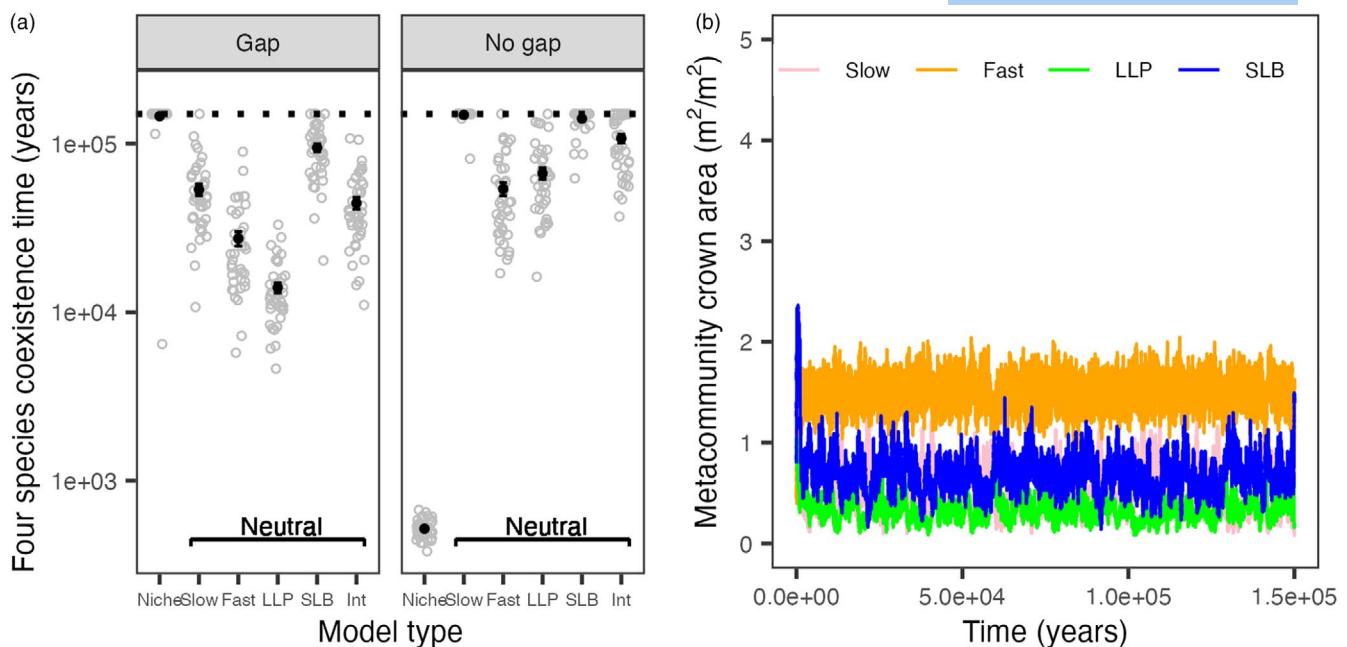


FIGURE 3 (a) Coexistence times for model runs with all four demographic groups, slow, fast, LLP and SLB (niche models), and model runs with four species with the same parameters (neutral models, with all species parameterized identically by indicated demographic groups), with and without patch-level disturbances (gaps). Grey points mark the coexistence time of demographic groups (or species) in 40 independent model runs of each model setting. The dotted line indicates the maximum run time (150,000 years). Means and standard errors (plotted but some are not visible due to magnitude, see main text for values) are shown in black for model runs with and without gaps. (b) Metacommunity-level species dynamics for one run of the niche model with gaps (see Figure S7.2 for additional examples). The demographic groups in four-group niche models with gaps coexist for significantly longer than the species in four-species neutral models with gaps and significantly shorter in four-group niche models without gaps (two-sample *t*-tests for all comparisons between the niche model and the neutral models, *p*-value < 0.0001). Without gaps, species coexist for significantly longer in neutral models than in niche models (two-sample *t*-tests for all comparisons between the niche model and the neutral models, *p*-value < 0.0001). Figure S4.4 shows these results for two additional F_i parameterizations, providing additional evidence of longer coexistence in the niche models than the neutral models when gaps are included.

Other models have also found that species that differ in their life history can generate successional niches that can coexist through time (including Falster et al. (2017) and Kohyama (1993)). The work here is different from previous efforts in that we are working with the empirically derived parameters and an already validated model for the forest from which these parameters are obtained. That is, we are providing another angle on this research theoretically as inspired by the data and previous data-model integrations for this forest.

4.3 | A strong test of stabilizing forces

To test whether it is the differences among the demographic groups that allow them to coexist stably in this stochastic model, we have compared our niche models to neutral models (Figures 2–4). For the neutral models, we assume that all species have the same demographic parameters. This allows us to make a clear comparison, but it is worth noting that the comparison may rightly be considered a strong test of stable coexistence. That is, a neutral model with exactly equal parameters will have quite strong coexistence, and it is unlikely that such strictly equal strategies would ever be possible in nature. The more equal these demographic rates are, the longer the species will coexist, as neutrality is a strong mechanism of coexistence (Chisholm & Pacala, 2010; Hubbell, 2001) and the

amount of coexistence predicted in a model with species that have exactly equal rates may be an unfairly high bar in testing for stabilizing mechanisms. Relaxing the rigid neutrality of species may well increase the regions of parameter space where these specific differences among species improve their coexistence.

With direct comparisons of four-group niche and neutral models, we find that differences in demography increase coexistence. This is further supported by the stronger conspecific negative density dependence we have observed for the demographic groups in the four-group niche models compared to species in the four-species neutral models that are parameterized by the respective demographic group parameters and the intermediate group. Note that we observed significant CNDD in four-species neutral models (although less strong compared to four-group niche models), due to the negative density dependence imposed by competition for light in the forest stand itself. That is because there is a limited amount of crown area to be filled in total (the plot area); when one species becomes very abundant (relatively likely with only four species), this non-CNDD (generic all-plant negative density dependence) will be present in the CNDD measurements. Additionally, the differences between the measured strength of CNDD between niche and neutral models were not as strong as the differences in coexistence times. This is likely due to the challenges of measuring CNDD at the appropriate temporal and spatial scale for the mechanism of gap-successional

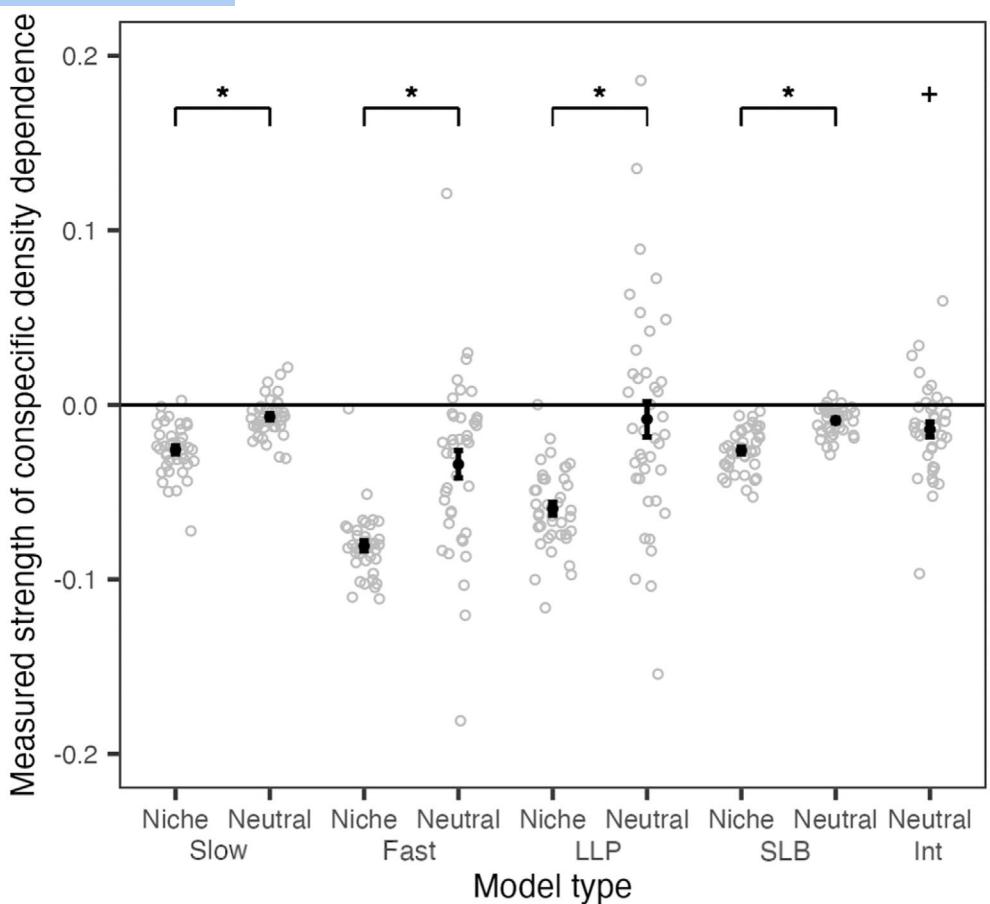


FIGURE 4 Comparisons of metacommunity-level conspecific negative density dependence (CNDD, [Equation 4](#)) for demographic groups parameterized by the indicated demographic group in both niche (in competition with the other three demographic groups) or neutral (in competition with species with the same demographic parameters) model types (shown with grey points for each model run). All models shown here include gaps. Means and standard errors are shown in black. Demographic groups in the four-group niche model runs have stronger CNDD than their respective four-species neutral models with the same demographic group parameterization (two-sample t-test, p -value < 0.0001 shown with *). + The demographic groups in the four-group niche model runs with gaps all have stronger CNDD than the neutral models of the intermediate group (two-sample t-test: p -value < 0.05 for niche—slow vs. neutral—int. and niche—SLB vs. neutral—int., and p -value < 0.0001 for niche—fast vs. neutral—int. and niche—LLP vs. neutral—int). See [Figure S8](#) for examples of the regressions that go into calculating the β_{CNDD} for different model settings ([Equation 4](#)).

coexistence. For instance, various demographic strategies may be negatively impacted by an overabundance of individuals with different time scales or at different life and forest stages, further contributing to the complex feedback between CNDD and the entire forest stand, which is likely relevant to the challenges of finding an empirical link between the strength of CNDD and diversity (Hülsmann et al., [2024](#); LaManna et al., [2017](#)).

4.4 | Variation in light availability through time is the stabilizing force promoting the coexistence of demographic groups

Classic ecological theory states that no more species can stably coexist than the number of limiting resources (Gause, [1934](#); Tilman, [1982](#)). Although we have only incorporated competition for a single resource, light, in our models, we are capable of explaining the stable coexistence of four species because the species are

competing for the amount of light at different time points following a gap disturbance. It is the variation in competition for the single resource that makes coexistence possible when assuming competition only for it (Armstrong & McGehee, [1980](#); Tilman, [1982](#)). The importance of this temporal variation is seen in the comparisons between models with and without gaps. When there are no gaps, we do not see a benefit of the differences among species in demographic strategies for their coexistence as we do when gaps are included (demographic groups in niche models coexist for less time than in their neutral models when there are no gaps, [Figures 2–3](#)).

4.5 | Stable coexistence with empirically grounded parameters

We find several parameter combinations that promote long-term coexistence ([Figure 1](#); [Appendix S4](#)). These parameters represent a relatively narrow hypervolume of the possible parameter space

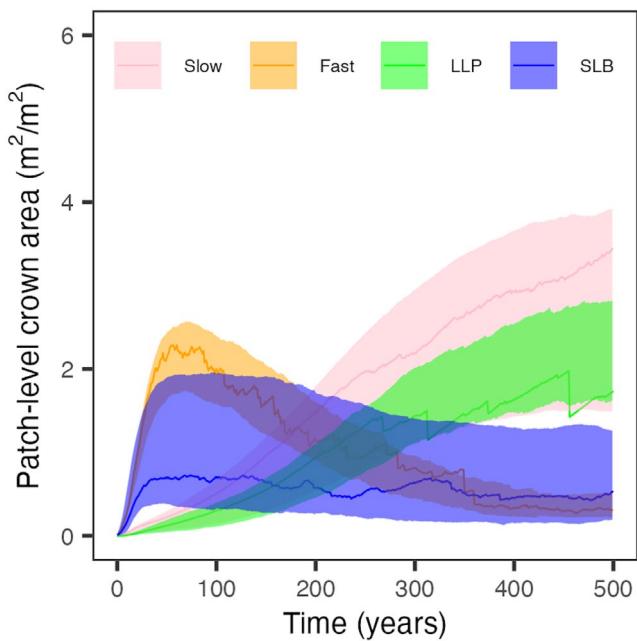


FIGURE 5 Patch-level post-gap crown area trajectories in the four-group niche models. Lines correspond to a single run. Highlighted areas around the lines show one standard deviation around the mean of 40 focal patches, each from an independent metacommunity simulation. Standard deviation areas are shown only for positive values.

we calculated using 1-ha subsets of the forest data. However, the parameters that generate stronger coexistence are beneficial to individuals of these different groups, improving their persistence as evidenced by their longer coexistence. This means that, if such parameters are feasible, they should eventually arise in the community and successfully invade. Thus, there is reason to expect species to have the parameters that allow for their stronger coexistence, if they are physiologically possible.

We note that our recruitment parameterization is largely a theoretical exercise. We assume that the production of new recruits is proportional to crown area and is dependent on the canopy layer status of trees (a m^2 of full sun crown area generates the most recruits, followed by a m^2 of crown area shaded by one layer, and then a m^2 of crown area shaded by two layers). Even though we have relaxed the rigid assumption of the original PPA that only canopy trees can reproduce, there is little empirical grounding for the exact amount each layer should contribute to recruitment and how this varies by demographic group. These assumptions, along with other simplifying assumptions (for example, all demographic groups have the same allometries) were made so that we could focus on the question of whether gap disturbances and competition for light can generate the coexistence of species with different growth, mortality and recruitment rates. Other interesting differences among species that represent these groups can potentially contribute to even greater diversity through competition for other resources and other species interactions (with pollinators, seed dispersers, herbivores, etc.) that have not been represented here (Wright, 2002). These differences

could be detected through additional trade-offs in growth and fecundity concerning seedling-to-adult survival (Umaña et al., 2023), along ontogeny (Clark & Clark, 1992), and in shade versus dry season intensity performance (Kupers et al., 2019).

We note that the simulated crown areas of the demographic groups in our four-group niche models do not match the crown areas of groups in the BCI forest dynamics plot quantitatively or in rank of abundance. This could be due to the above-listed simplifications within the model and shows that for a model with population size-dependent recruitment, the inclusion of important missing mechanisms such as differences in allometry, differences in germination rates by light availability (Dalling & Denslow, 1998), and feedback with other trophic levels may be necessary for accurate quantitative predictions of the forest dynamics (Wright, 2002).

5 | CONCLUSIONS

We find that small-scale disturbances, competition for light and differences among species across both growth-survival and stature-recruitment trade-off axes can promote stable species coexistence. This work is motivated by the data and structure of the Barro Colorado Island forest dynamics plot. A mechanism as universal as competition for light explaining tree demographic strategy coexistence is exciting. The seeming ubiquity of the growth-survival and stature-recruitment trade-offs (Kambach et al., 2022) offers strong support that it could be generating a fundamental form of diversity axes upon which further diversification may multiply the number of coexisting species, generating the wealth of diversity in real forests. We look forward to further explorations to test the validity of our recruitment parameterization necessary to get these results, and to understand the potentially interacting roles of additional mechanisms in promoting the hundreds of coexisting species in these forests through a combination of equalizing and stabilizing mechanisms.

AUTHOR CONTRIBUTIONS

Damla Cinoğlu and Caroline E. Farrior designed the study. Damla Cinoğlu analysed the model and wrote the manuscript with support from Caroline E. Farrior. All authors provided feedback on the model and contributed to the writing of the manuscript.

ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation (NSF DEB 1939559). We thank Annette Ostling, the Farrior and Wolf laboratory members at the University of Texas at Austin for helpful discussions. The BCI forest dynamics research project was founded by S.P. Hubbell and R.B. Foster and is now managed by R. Condit, S. Lao, and R. Perez under the Center for Tropical Forest Science and the Smithsonian Tropical Research Institute in Panama. Numerous organizations have provided funding, principally the U.S. National Science Foundation. We acknowledge the Texas Advanced Computing Center (TACC) at The University of Texas at Austin for

providing HPC resources that have contributed to the research results reported within this paper (<http://www.tacc.utexas.edu>).

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

R code and data for the results are available at <https://doi.org/10.6084/m9.figshare.27055204.v1> (Cinoğlu et al., 2025). Empirical parameters are shared in the [Supporting Information](#).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. The demographic groups.

Appendix S2. Additional model details.

Appendix S3. Run initialization with BCI data.

Appendix S4. Testing coexistence for the range of empirically reasonable recruitment parameters.

Appendix S5. Calculation of crown area by demographic group and canopy layer for the intermediate demographic group's recruitment parameterization.

Appendix S6. Niche models without gaps.

Appendix S7. Additional trajectory examples from Figures 2 and 3.

Appendix S8. Conspecific negative density dependence.

How to cite this article: Cinoğlu, D., Rüger, N., Decker, R. R., & Farrior, C. E. (2025). Small disturbances and subsequent competition for light can maintain a diversity of demographic strategies in a neotropical forest: Results from model–data integration. *Journal of Ecology*, 00, 1–14. <https://doi.org/10.1111/1365-2745.70118>