ARTICLE

Tree demographic strategies largely overlap across succession in Neotropical wet and dry forest communities

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Abstract

Secondary tropical forests play an increasingly important role in carbon budgets and biodiversity conservation. Understanding successional trajectories is therefore imperative for guiding forest restoration and climate change mitigation efforts. Forest succession is driven by the demographic strategies—combinations of growth, mortality and recruitment rates—of the tree species in the community. However, our understanding of demographic diversity in tropical tree species stems almost exclusively from old-growth forests. Here, we assembled demographic information from repeated forest inventories along chronosequences in two wet (Costa Rica, Panama) and two dry (Mexico) Neotropical forests to assess whether the ranges of demographic strategies present in a community shift across succession. We calculated demographic rates for >500 tree species while controlling for canopy status to compare demographic diversity (i.e., the ranges of demographic strategies) in early successional (0–30 years), late successional (30–120 years) and old-growth forests using two-dimensional hypervolumes of pairs of demographic rates. Ranges of demographic strategies largely overlapped across successional stages, and early successional stages already covered the full spectrum of demographic strategies found in old-growth forests. An exception was a group of species characterized by exceptionally high mortality rates that was confined to early successional stages in the two wet forests. The range of demographic strategies

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did not expand with succession. Our results suggest that studies of long-term forest monitoring plots in old-growth forests, from which most of our current understanding of demographic strategies of tropical tree species is derived, are surprisingly representative of demographic diversity in general, but do not replace the need for further studies in secondary forests.

KEYWORDS

demographic rates, growth, life-history strategies, mortality, old-growth forest, recruitment, secondary succession, survival

INTRODUCTION

Tropical forests store almost half of global forest carbon and harbor a large proportion of the world's biodiversity (FAO, 2020; Pan et al., 2011; Slik et al., 2015). With only one third of tropical forests being undisturbed primary forests and rates of deforestation remaining high (FAO, 2020; Pan et al., 2011), secondary tropical forests regrowing after land abandonment are of increasing importance for carbon storage and sequestration as well as biodiversity conservation (Chazdon et al., 2016; Lewis et al., 2019; Rozendaal et al., 2019). Understanding successional trajectories is therefore imperative for guiding efforts of forest management and global change mitigation. Tree demographic strategies (or life-history strategies) are an important driver of successional dynamics (sensu Finegan, 1996). However, empirical knowledge of how community-wide variation in demographic strategies changes along successional gradients remains limited.

Demographic strategies emerge from trade-offs that all organisms are faced with when allocating limited resources between fast growth, high survival or reproductive success (Stearns, 1992) and that constrain the range of viable combinations of these demographic rates (Rüger et al., 2018; Salguero-Gómez et al., 2016). Recently, comparative analyses of life-history variation have improved our understanding of the consistency of demographic trade-offs structuring tropical forest communities worldwide (Kambach et al., 2022; Russo et al., 2021). However, most of our knowledge of demographic strategies stems from old-growth forests.

Fast-growing and short-lived species typically dominate the first decades of succession and long-lived pioneers and slow-growing shade-tolerant species typically dominate later successional stages and old-growth forests (Finegan, 1996; Lai et al., 2021; Martínez-Ramos et al., 2021; Rüger et al., 2023). However, while we know that abundances, basal area and biomass of species with different demographic strategies shift during succession in these predictable ways (Rüger et al., 2023), it remains unknown whether the community-wide range of demographic strategies shifts in the same way during succession. To our knowledge, a systematic comparison of the range of demographic strategies between early successional, late successional, and old-growth forests has not been performed. Specifically, it is unclear whether certain demographic strategies are confined to certain successional stages. While some early successional species can also occur in tree fall gaps in old-growth forests (Schnitzer & Carson, 2001), others are dependent on large-scale disturbances for regeneration and therefore occur uniquely in early successional forests (Marra et al., 2014; Revilla et al., 2023). However, it is unclear whether these species are characterized by unique demographic strategies that might remain undetected based on tree demographic research conducted exclusively in old-growth forests. Furthermore, despite comparisons of functional traits of tree species during succession in wet and dry tropical forests (e.g., Letcher et al., 2015; Poorter et al., 2021), we lack comparisons of demographic strategies.

In tropical wet forests, early successional environments are characterized by high resource levels

(especially light; Montgomery & Chazdon, 2001). Species that occur abundantly in these environments are, thus, commonly thought to trade off high growth and recruitment for high mortality rates (Chazdon, 2014; Finegan, 1996; Tilman, 1988). These fast demographic rates are related to acquisitive values of functional traits such as low wood density or high specific leaf area and leaf nutrient content (Rüger et al., 2012, 2018; Wright et al., 2010). Conversely, species that are more abundant in late successional environments are expected to grow slowly but invest more resources in the ability to live for a long time, represented by trait values indicative of resource conservation such as high wood density or low specific leaf area.

Indeed, using functional traits as proxies, several studies have confirmed that, in tropical wet forests, tree species with acquisitive trait values tend to dominate in early successional stages, while species with more conservative trait values gain in dominance as succession proceeds (e.g., Becknell & Powers, 2014; Boukili & Chazdon, 2017; Lohbeck et al., 2013; Poorter et al., 2004). Under such a scenario, we expect that the ranges of viable demographic strategies gradually shift from acquisitive strategies (fast growth, high mortality, high recruitment) toward more conservative strategies (slow growth, low mortality, low recruitment) during succession in tropical wet forests (Figure 1a).

In tropical dry forests, where water is considered a more important resource in shaping forest communities than light availability, early successional stages are characterized by dry and hot conditions changing toward moister and cooler environments as succession proceeds (Lebrija-Trejos et al., 2011). Therefore, trait values have been found to reflect a shift from strategies associated with greater resource conservation and drought tolerance early in succession to more acquisitive strategies (e.g., lower wood density, leaf dry matter content) later in succession (Buzzard et al., 2016; Derroire et al., 2018; Lebrija-Trejos et al., 2010; Lohbeck et al., 2013; Poorter et al., 2019). However, acquisitive leaf trait values related to light capture efficiency (e.g., high specific leaf area) have also been found to decrease during succession (Derroire et al., 2018; Lohbeck et al., 2013), making it unclear whether successional shifts toward more conservative (H_1) or more acquisitive (H_2) demographic strategies should be expected in tropical dry forests (Figure 1b,c).

Environmental differences between early and late successional tropical dry forests are thought to be less pronounced compared with wet forests, mainly due to greater canopy openness (Ewel, 1977; Lebrija-Trejos et al., 2011). Indeed, Letcher et al. (2015) observed a trend toward less successional habitat specialization among tree species in certain tropical dry forests. Based on this, we hypothesize that potential shifts in demographic strategies may be less pronounced in dry than in wet forests. However, as light availability becomes more heterogenous during succession in both forest types, we hypothesize that the range of viable demographic strategies expands as succession progresses (Figure 1).

Here, we assemble a unique chronosequence dataset of repeated forest inventories from four Neotropical forests varying in rainfall. We calculate growth, mortality, and recruitment rates for >500 tree species and use hypervolumes (i.e., the area occupied by species in the two-dimensional case of pairs of demographic rates) to quantify demographic diversity in three successional stages. In this study, we used the term demographic diversity only to refer to the range of demographic
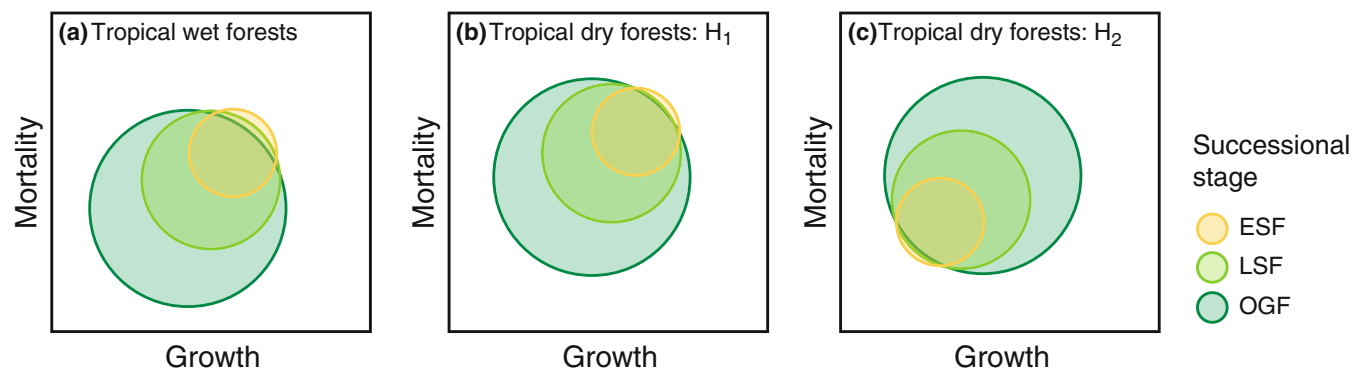
FIGURE 1 Hypotheses for potential shifts of the ranges of demographic strategies from early successional forests (ESF) to late successional forests (LSF) and old-growth forests (OGF) for (a) tropical wet forests and (b, c) tropical dry forests. H_1 (b) and H_2 (c) represent opposing hypotheses for tropical dry forests. It is not clear whether shifts from acquisitive to conservative demographic strategies or vice versa are to be expected because wood density and leaf dry matter content have been found to shift from conservative to acquisitive values, whereas specific leaf area has been found to shift from acquisitive to conservative values. Axis labels can be any combination of growth, mortality or recruitment since for example high values for all three demographic rates are expected in wet ESF.

strategies present in a tree community (Needham et al., 2022). Successional changes in the abundance and basal area of different demographic strategies in the same forests have been studied by Rüger et al. (2023). We addressed the following questions: (1) Are there changes in demographic diversity during succession in wet and dry tropical forests? We specifically ask: (1a) Do ranges of demographic strategies shift as hypothesized during succession in wet and dry tropical forests? (1b) Are there demographic strategies, that are exclusive to particular successional stages? (1c) Do ranges of demographic strategies expand during succession? (2) If we detect any changes, we ask whether they are caused by intraspecific changes in demographic rates or by species turnover?

Answers to these questions will reveal to what degree our understanding of demographic diversity gained from old-growth forests can be extended to secondary forests, for which much less information on demographic rates and strategies is available. This information will enhance our understanding of the mechanisms underlying succession and improve our ability to predict successional dynamics in tropical forests with the help of demographic forest models.

MATERIALS AND METHODS

Study sites and forest inventory data

We used inventory data from nine long-term forest monitoring projects along chronosequences from four Neotropical lowland forest sites located in Costa Rica, Panama and Mexico. The sites differ in rainfall with mean annual precipitation ranging from 3900 mm without any dry season to 900 mm with 90% of annual rainfall occurring within 5.5 months of the year (Table 1). The forest in

Costa Rica is a tropical wet evergreen broadleaved forest with a high proportion of palms (Chazdon et al., 2007; Clark & Clark, 2000; Letcher & Chazdon, 2009). The forest in Panama is a semideciduous tropical moist forest with a 3-month dry season (Condit et al., 2019; Denslow & Guzman, 2000; van Breugel et al., 2013). The predominant natural disturbance regimes in both wet sites are occasional windthrows and lightning strikes. The two sites in Mexico are both deciduous tropical dry forests differing from the wet sites in shorter stature, higher canopy openness and lower species richness (Table 1; Letcher et al., 2015). Forests in the Yucatán peninsula have undergone anthropogenic influences since ancient Mayan times and experience regular strong wind storms (Hernández-Stefanoni et al., 2014; Rico-Gray & García-Franco, 1991; Saenz-Pedroza et al., 2020). The forest in Oaxaca is shorter in height, has arborescent cacti and has been only mildly affected by human disturbances (Gallardo-Cruz et al., 2010; Lebrija-Trejos et al., 2008; Pérez-García et al., 2010), but it is also regularly subjected to strong wind (Dechnik-Vázquez et al., 2016).

The four chronosequence sites comprised a total of 252 secondary forest plots and 23 old-growth forest plots ranging in size from 0.04 to 50 ha (Appendix S1: Table S1; Appendix S1: Figure S1). Plots were located in complex landscapes mainly consisting of fragments of old-growth and second-growth forests, plantations, agricultural land and pastures. Most secondary forest plots were established on abandoned agricultural land used primarily for low-intensity crop farming or cattle ranching (Chazdon et al., 2007; Denslow & Guzman, 2000; Lebrija-Trejos et al., 2011; Letcher & Chazdon, 2009; van Breugel et al., 2013). Some plots were only clear-cut but not farmed (Chazdon et al., 2007; Letcher & Chazdon, 2009). In general, previous forest vegetation was completely removed, yet in a few cases some remnant

TABLE 1 Location, mean annual temperature (MAT), mean annual precipitation (MAP), dry season length (<100 mm precipitation per month), number of species, number of species with 10 or more individuals, average old-growth forest (OGF) canopy height and length of the chronosequences used in this study.

Location	Latitude and longitude	MAT (°C)	MAP (mm)	Length of dry season (months)	No. species (N ≥ 10)	OGF canopy height[a] (m)	Chronosequence length
Costa Rica	10°26′ N, 84°00′ W	26	3.900	...	485 (355)	20–35	1–57 years + OGF
Panama	9°90′ N, 79°51′ W	27	2.600	3	470 (391)	15–28	0–120 years + OGF
Yucatán, Mexico	20°05′ N, 89°29′ W	26	1.100	6	154 (106)	8–13	3–85 years
Oaxaca, Mexico	16°39′ N, 95°00′ W	28	900	7	125 (90)	7–8	4–70 years + OGF

Note: The sampling area differs strongly between sites and the number of species included in the analyses may not be indicative of total species richness.
[a]Canopy heights are from Clark et al. (2021), Mascaro et al. (2011), Dupuy et al. (2012) and Lebrija-Trejos et al. (2008).

trees remained, which we excluded from the analyses. The age of the youngest plots ranged from 0 to 4 years across sites, whereas the oldest secondary forest plots ranged from 57 to 120 years after agricultural abandonment (Appendix S1: Figure S2). All free-standing woody individuals above the plot-specific size threshold (generally 1 or 5 cm diameter at breast height (dbh); range: 1–10 cm dbh; Appendix S1: Table S1) were measured, marked and remeasured 1 to 10 years later. We selected census intervals of 5 years, if possible (range: 4–10 years; Appendix S1: Table S1). In the wet sites (Costa Rica, Panama), only the largest stem of an individual was measured in some plots. In the dry sites (Yucatán, Oaxaca), where resprouting is an important mode of regeneration and, thus, multistemmed individuals are abundant (Vieira & Scariot, 2006), all stems of an individual were measured, but not individually marked.

We assigned all census intervals to one of three successional stages (Appendix S1: Table S1; Figure S2). Census intervals from secondary forest plots ending less than 30 years after abandonment were classified as early successional forests (ESF) and intervals ending less than 120 years after abandonment were classified as late successional forests (LSF), although most plots were not older than 90 years. Census intervals from old-growth forest plots were classified as old-growth forests (OGF). Available data from OGFs in Yucatán were not sufficient to be included in the analysis.

Canopy layer assignment

The growth and mortality rates of individual trees depend on their size and light availability. To account for these differences, we assigned trees to discrete canopy layers based on their size and the size of their neighbors following the Perfect Plasticity Approximation approach of Purves et al. (2008) and Bohlman and Pacala (2012). To do this, we first divided all plots into subplots that were either predefined by the sampling design, or trees were assigned to subplots based on their spatial coordinates. The size of these subplots ranged from 625 to 1000 m^2 in wet sites (except for a 100 m^2 plot in a <20-year-old forest) depending on the sampling design and plot sizes (Appendix S1: Table S1). In the dry sites, where trees are generally smaller than in wet forests, subplot sizes ranged from 100 to 125 m^2 except for some 400 m^2 plots in Yucatán (Appendix S1: Table S1). Next, we sorted trees by dbh of the largest living stem within subplots. We then estimated the crown area for all trees using allometric equations (see Appendix S1). Starting from the largest, we assigned trees to the top canopy layer (layer 1) as long as the cumulative estimated area of their crowns did not exceed the subplot area. Smaller

trees were successively assigned to lower canopy layers in the same way. Calculating demographic rates in discrete canopy layers has proven useful in capturing variance in demographic strategies between co-occurring species (Bohlman & Pacala, 2012; Rüger et al., 2018) and in predicting forest dynamics (Rüger et al., 2020).

Demographic rates

We calculated demographic rates for species with interpretable stem growth, that is, excluding palms and hemi-epiphytes (Appendix S1: Table S2). We determined dbh increment and mortality for all observations and subsequently calculated species-level annual growth and mortality rates for each canopy layer and successional stage. Individual annual tree growth g_i was calculated as

$$g_i = \frac{size_2 - size_1}{t}, \tag{1}$$

with size being the dbh of the largest living stem of an individual in wet sites and dbh equivalent of the total basal area (ba) of all living stems of an individual in dry sites in the first and second censuses, respectively, and t being the time elapsed between the two size measurements in years. We used the dbh equivalent of the total basal area as the measure of size in the dry sites, because there were many individuals with multiple stems that were not individually marked and, thus, stem-level dbh growth could not be calculated. The dbh equivalent (dbh$_e$) is the dbh that a single stem would have with the same basal area as all the stems of a multistemmed individual together:

$$dbh_e = \sqrt{\frac{4}{\pi} ba}. \tag{2}$$

Species-level growth rates per canopy layer ($g_{j,l}$) were calculated as the median growth of all individuals i of species j in layer l:

$$g_{j,l} = median\left(g_{j,l,i}\right). \tag{3}$$

Species-level annual mortality rates per canopy layer ($m_{j,l}$) were determined as

$$m_{j,l} = 1 - \left(\frac{N_2}{N_1}\right)^{\frac{1}{t}}, \tag{4}$$

with N_1 being the number of living individuals in the first census, N_2 being the number of individuals remaining alive in the second census and t being the mean census interval length in years (measured to the nearest day).

Multistemmed individuals were deemed alive if at least one stem was alive and dead if all stems were dead.

Species-level per capita recruitment rates for each successional stage were determined as

$$r_j = \frac{N_{j,r}}{N_j}, \qquad (5)$$

with $N_{j,r}$ being the mean number of recruits per hectare that surpassed the 1 cm dbh threshold between two consecutive censuses divided by the mean census interval length in years and N_j being the average number of individuals per hectare of the respective species in the respective successional stage across plots. Only plots or subplots with a minimum dbh threshold of 1 cm were used to determine $N_{j,r}$, whereas all plots of the respective successional stage were used to determine N_j. In some successional stages, only a few small plots had a minimum dbh threshold of 1 cm, which limited our ability to assess recruitment rates. However, recruitment over the 1 cm dbh threshold is a more frequent event than recruitment over the 5 cm dbh threshold. Thus, recruitment rates could be quantified for more species using the lower threshold.

Quantification of demographic diversity

We used two-dimensional hypervolumes based on Gaussian kernel density estimations (Blonder et al., 2014) to represent and quantify the range of demographic strategies spanning pairs of demographic rates: growth versus mortality, growth versus recruitment and mortality versus recruitment. Because many species did not occur in all canopy layers and species with nonobserved values cannot be included in hypervolume analyses, we calculated hypervolumes using only growth and mortality rates from a single canopy layer. That means, we quantified demographic diversity separately for canopy trees (layer 1), subcanopy trees (layer 2), and understory trees (layer 3). We focused on growth and mortality rates from canopy layer 2 to maximize the number of species included in the analyses (Appendix S1: Tables S3–S5). To ensure representativity, we also examined hypervolumes using growth and mortality rates from canopy layers 1 and 3. Only species with at least 10 or 5 observations for mortality per canopy layer were included in the analyses for wet and dry sites, respectively. Species with mortality rates of 0 or 1 or with recruitment rates of 0 were excluded from the respective hypervolumes (see Appendix S1: Tables S3–S5). In total, 353, 503 and 463 species met the criteria for inclusion in the analyses in canopy layers 1, 2 and 3, respectively.

We natural log-transformed all demographic rates to ensure approximate Gaussian multivariate distributions. We estimated kernel bandwidths (the parameter defining the smoothness of the probability densities) for each hypervolume per site using the cross-validation method (Blonder et al., 2014; Duong, 2007). We used the same bandwidths for all successional stages per site to ensure comparability among sites (Blonder, 2018). Hypervolume boundaries represent the smallest volume that captures 80% of the total probability densities. All species contributed equally to the hypervolume calculations. We used the *hypervolume* R package (version 3.0.4) for all analyses (Blonder et al., 2014).

To quantify the overlap of demographic strategies in different successional stages, we calculated overlap statistics for all hypervolumes using the "hypervolume_overlap_statistics" function. We used bootstrapping and rarefaction techniques ($r = 100$ replicates, $n = 10$ species per replicate) to account for differences in the number of species included and to obtain 95% confidence intervals. Likewise, we derived volumes of all two-dimensional hypervolumes (i.e., areas) to quantify the amount of demographic diversity using the "hypervolume_gaussian" function. We assumed statistically significant differences if the confidence intervals did not overlap.

Quantification of the causes of shifts in demographic diversity

To evaluate whether shifts in the range of demographic strategies were due to intraspecific variation in demographic rates across successional stages, we performed major axis regressions between species' demographic rates in different successional stages. To evaluate whether shifts in the range of demographic strategies were due to species turnover, we assessed successional trends in the abundance of species that exhibited a demographic strategy that was exclusive to one particular successional stage. As we only found unique demographic strategies in the early successional stage, we modeled abundances per ha of the species with this unique strategy as a function of stand age with the form: Ln(abundance) $= a \times$ stand age^b. Parameters a and b were estimated using the "nls" R function. For parameter estimation, we only used data points from the point in time when species reached their highest abundance onwards.

All analyses were carried out in R version 4.2.2 (R Core Team, 2022). Taxonomy was standardized according to The Plant List version 1.1 (http://www.theplantlist.org) using the *Taxonstand* package (Cayuela et al., 2012).

RESULTS

We used 1,550,171 observations from 352,243 individual trees (of this total, 101,777 observations were from 80,317

individual trees in secondary forests) to calculate demographic rates for a total number of 503 species from 77 families. The number of individual trees ranged from 3302 in Oaxaca to 312,328 in Panama (Appendix S1: Table S2).

Do ranges of demographic strategies shift during succession?

In all forest sites, the ranges of demographic strategies present in the three successional stages largely overlapped (Figure 2). The ranges of growth rates were largely consistent across succession in all sites except Oaxaca, where they slightly shifted toward slower growth later in succession. In Costa Rica and Panama, the ranges of mortality rates were largest in ESF, where they extended further toward high mortality rates. In Oaxaca, the ranges of mortality rates shifted slightly toward lower mortality later in succession. The ranges of recruitment rates shifted slightly toward fewer recruits during succession in all sites except Yucatán. These results were robust to the choice of canopy layer (Appendix S1: Figures S3–S5) and were not biased by the number of species included (Appendix S1: Figure S6). The measured average hypervolume overlap across pairs of demographic rates between successional stages did not differ
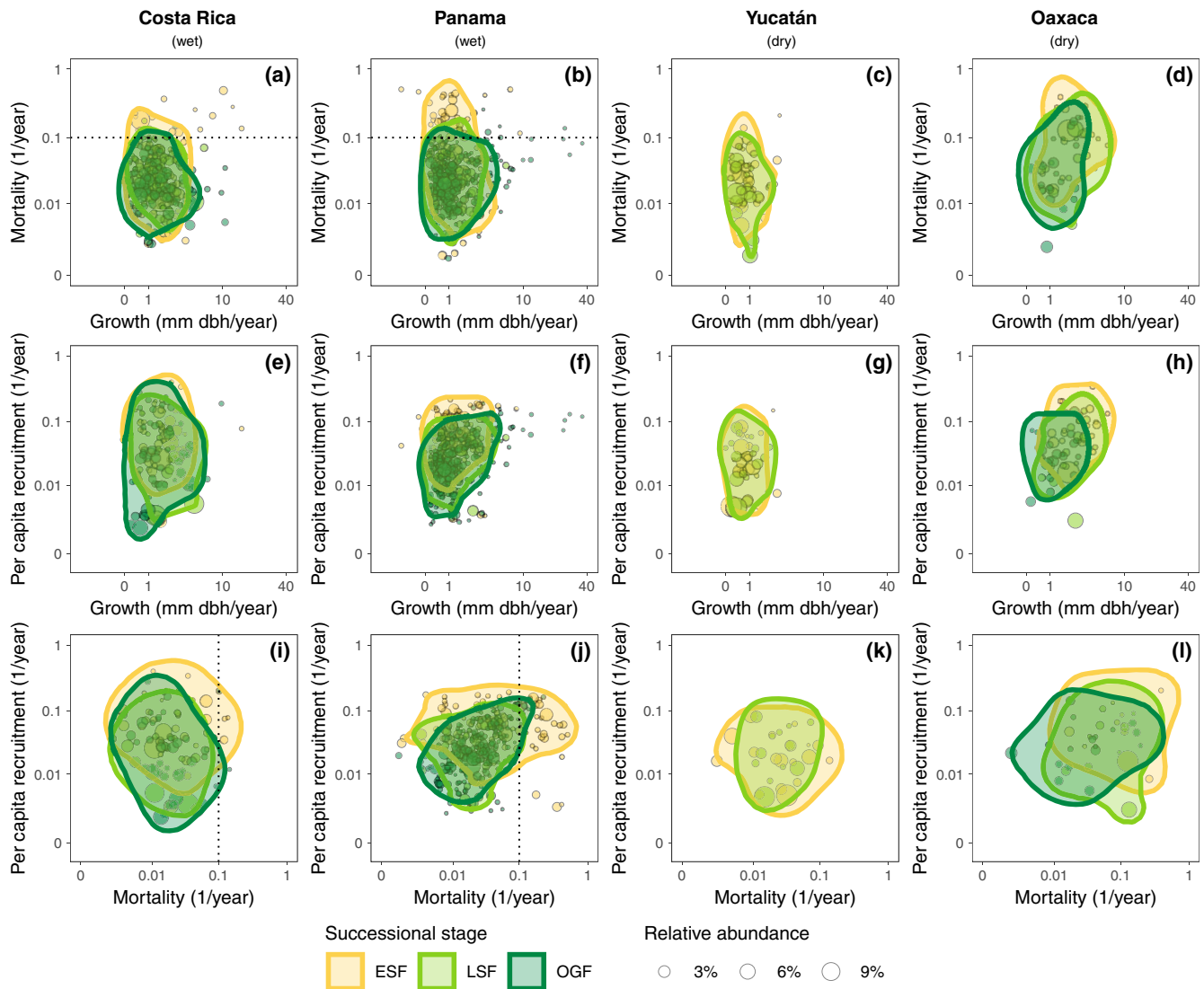

FIGURE 2 Two-dimensional hypervolumes representing ranges of demographic strategies for different pairs of demographic rates (a–d: growth–mortality, e–h: growth–recruitment, i–l: mortality–recruitment) for all sites and successional stages (ESF, early successional forest; LSF, late successional forest; OGF, old-growth forest). All axes are log-transformed (Ln). Growth and mortality rates are from individuals assigned to canopy layer 2 because this layer contains the most individuals and species. Hypervolume boundaries represent the smallest volume that captures 80% of the total Gaussian probability densities. All species contributed equally to the hypervolume calculation. Points represent species and point sizes indicate relative abundances within the successional stage. dbh, diameter at breast height.

across sites and was also similar among all successional stages within sites (Figure 3a; Appendix S1: Figure S7).

Are there demographic strategies that are exclusive to particular successional stages?

In the wet forests in Costa Rica and Panama, we found a demographic strategy exclusive to ESF, which was primarily associated with exceptionally high mortality rates of 10% or more (Figure 2a,b). This group of high mortality species consisted of 17 and 28 species in Costa Rica and Panama, respectively. Many of these species are typically considered pioneer species (e.g., *Cecropia insignis*, *Ochroma pyramidale*, *Trema integerrima*, *Byrsonima crassifolia*, *Conostegia xalapensis*, *Vernonanthura patens*, *Vismia baccifera*, *Vismia macrophylla*; see Appendix S1: Figures S8 and S9). Many species within this group did not grow particularly fast, especially in Panama. In Costa Rica, no recruits were recorded for most of the

species in this group (Figure 2i), whereas in Panama, most of these species had fairly high recruitment rates (Figure 2j).

Do ranges of demographic strategies expand during succession?

Demographic diversity (the area of the 2-dimensional hypervolumes) did not generally increase with succession, but tended to decrease in Panama and increase in the dry sites (Figure 3b; Appendix S1: Figure S10).

Are shifts in demographic strategies due to intraspecific variation or due to species turnover?

Overall, intraspecific variation in growth and mortality rates across succession was low in all sites (Appendix S1:
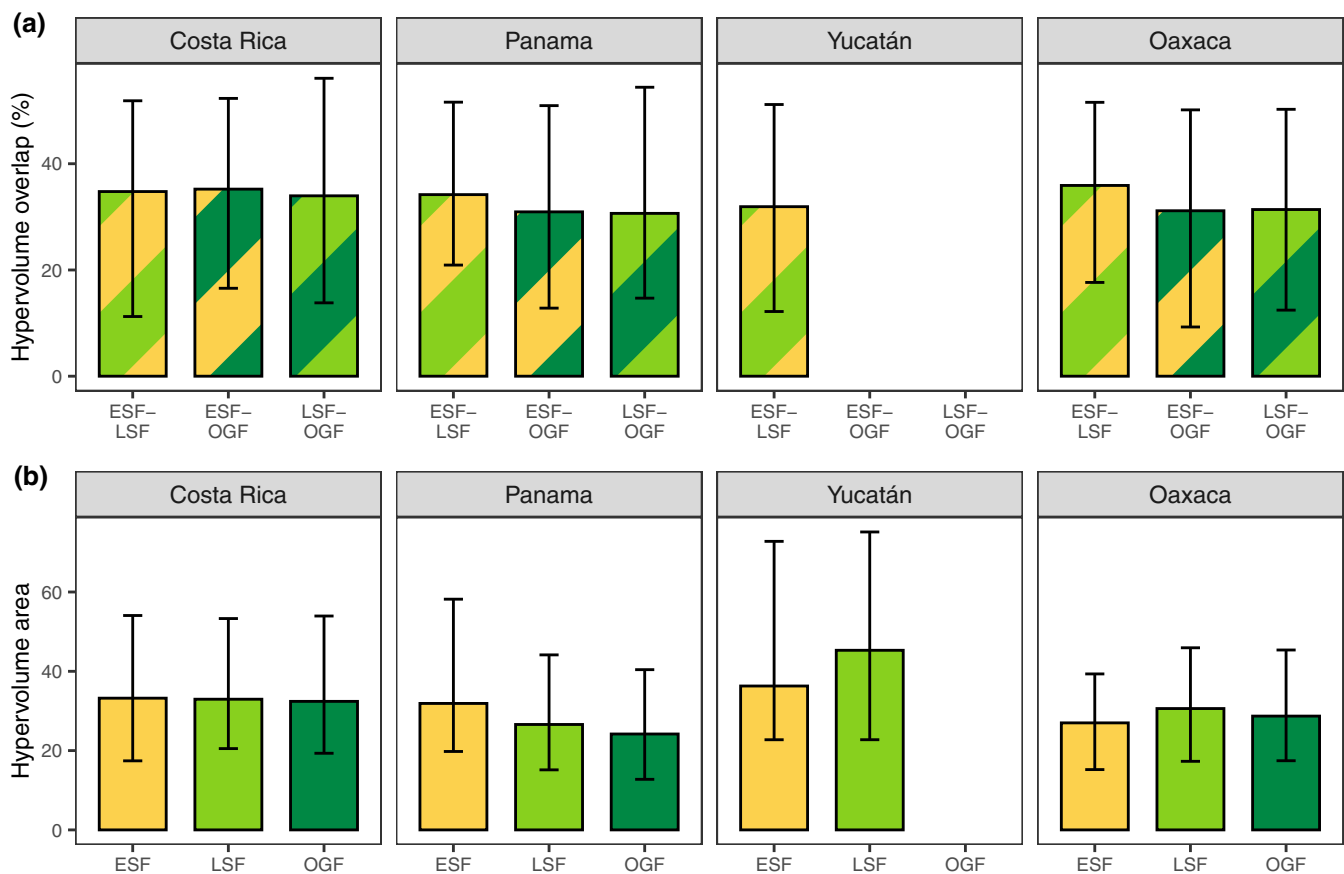

FIGURE 3 (a) Mean overlap statistics and (b) mean areas of the two-dimensional hypervolumes representing the ranges of demographic strategies for all successional stages (ESF, early successional forest; LSF, late successional forest; OGF, old-growth forest). Colored bars represent the median rarefied and bootstrapped values, error bars represent 95% confidence intervals ($r = 100$ replicates, $n = 10$ species per successional stage). All values are means across pairs of demographic rates. Individual values per pair of demographic rates are given in Appendix S1: Figures S10 and S11.

Figures S11–S14). In Panama and Oaxaca, recruitment rates were higher in secondary forests than in OGFs (Appendix S1: Figures S12 and S14), whereas in Costa Rica and Yucatán, results for the major axis regressions on recruitment rates were inconclusive (Appendix S1: Figures S11 and S13).

Most of the species that exhibited an exclusive demographic strategy (i.e., species with mortality >10% in wet ESF) decreased substantially in abundance during the first 30 years of succession (Figure 4; Appendix S1: Figures S8 and S9). In Costa Rica, only five out of the 17 species were also found in LSF (four species) or OGF (one species). In Panama, 11 out of the 28 species forming this group in ESF were also found in LSF (two species) or OGF (nine species), albeit at low abundances. Species from this group that were present in more than one successional stage generally had lower mortality rates in later successional stages (Appendix S1: Figures S11 and S12).

DISCUSSION

We used demographic rates from 503 woody plant species to compare ranges of demographic strategies along successional gradients in four Neotropical forests. Contrary to our expectations, we found not only that demographic strategies largely overlapped across successional stages,

but also that the amount of demographic diversity was similar along succession. Interestingly, we found a group of species with exceptionally high mortality rates that occurred exclusively in ESF in wet sites. Our results suggest that insights gained from analyses of demographic rates in OGFs are largely representative of forests of all successional stages, with the exception of a strategy associated with high mortality that only occurs in early successional wet forests.

Demographic strategies largely overlap across succession

In contrast with our hypotheses, we found a high degree of overlap of demographic strategies across successional stages in all four sites. Almost all demographic strategies that were present in OGFs were present in secondary forests after 30 years of succession in both the wet and dry tropical forests that we studied. This suggests that most species, regardless of their life-history strategies, can establish in ESF (Egler, 1954) and highlight the importance of stochastic processes for successional trajectories (Chazdon, 2008; Norden et al., 2015). At the same time, tropical wet forests recover quickly and the range of microsites that can develop during the first 30 years of succession may accommodate the full range of demographic
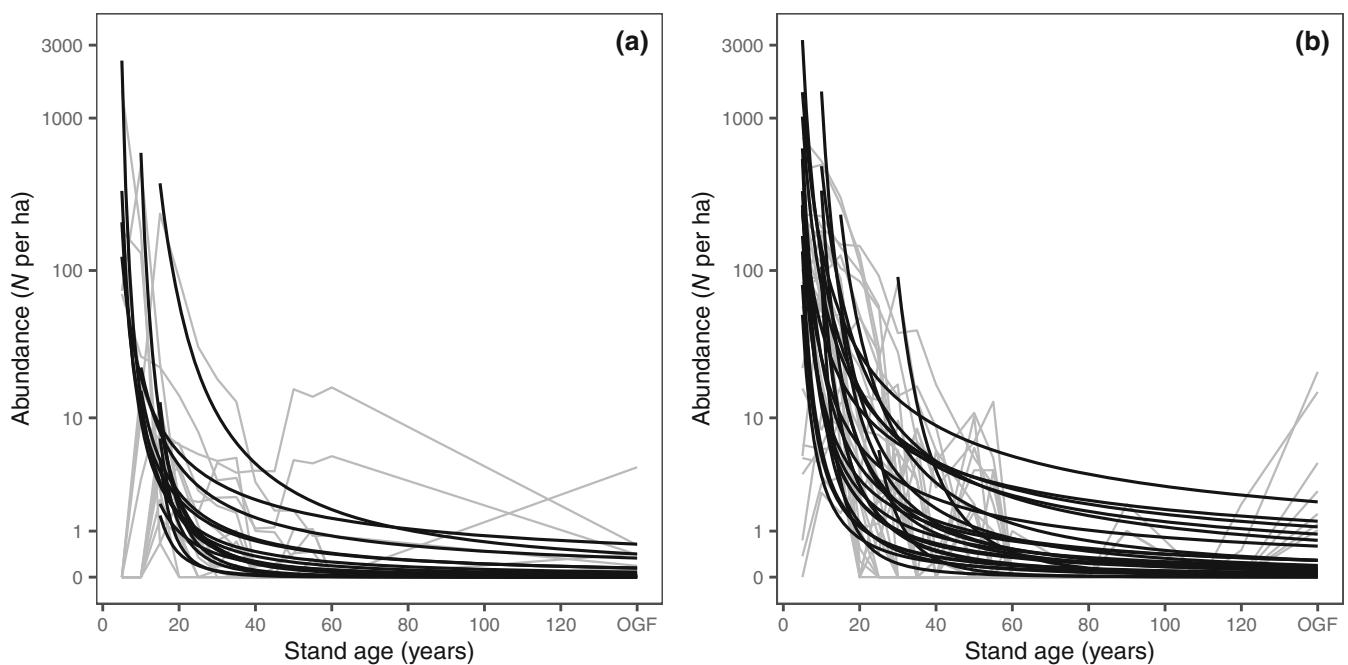

FIGURE 4 Observed (gray) and modeled (black) abundances >1 cm dbh over time of species with annual mortality >10% exclusive to wet early successional forests in (a) Costa Rica and (b) Panama. Models are of the form Ln(abundance) = $a \times$ stand age^b. Parameters a and b were estimated using the "nls" R function. The model did not converge for two species in Costa Rica and three species in Panama due to irregular patterns in abundance over time. The model does not accurately capture that one species in Costa Rica and seven species in Panama had increased abundances in old-growth forest (OGF). Individual models are shown in Appendix S1: Figures S8 and S9.

strategies exhibited by species that occur in older forests (Denslow & Guzman, 2000). This does not mean that the abundance of species with different demographic strategies does not shift across succession (Rüger et al., 2023), but here we focus on the presence or absence of demographic strategies.

Only for recruitment rates, we found the expected shift toward lower recruitment rates during succession in all sites except Yucatán. Recruitment rates strongly depend on seedling and sapling performance and, hence, on resource (primarily light) availability on the forest floor (Kupers et al., 2019; Montgomery & Chazdon, 2001). Because light availability at the forest floor decreases during succession (Denslow & Guzman, 2000), recruitment rates are predicted to do the same.

In Oaxaca, the driest forest site, the range of demographic strategies shifted slightly toward lower growth, mortality and recruitment rates, that is, toward more conservative life-history strategies during succession. In Yucatán, the second dry forest site, however, we detected a slight shift toward higher recruitment, hindering our ability to generalize more broadly from our results. The forest in Yucatán stands out in that it occurs in a landscape that has been shaped by human land use for many centuries (Rico-Gray & García-Franco, 1991). Thus, the pool of tree species might have been restricted over time to those species that are able to cope with frequent disturbance, including the ability to resprout (Rico-Gray & García-Franco, 1991; Sanaphre-Villanueva et al., 2017). This is also indicated by the smaller range of growth and mortality rates of the dry forest in Yucatán compared with that of Oaxaca.

High mortality strategy is exclusive to early successional stages in wet forests

We expected to find the most acquisitive demographic strategies with the highest growth, mortality and recruitment rates in early successional wet forests. Yet, the group of species exclusively observed in these forests was associated with high mortality (>10%) and moderately high recruitment rates, but not particularly with fast growth. Potentially, higher growth rates might be masked because the entire life cycle of these short-lived species is completed within the early successional stage (0–30 years since abandonment), including senescent stages when trees might reach their maximum stature and growth might decline (Cailleret et al., 2017; Martínez-Ramos et al., 2021).

Although some of these high-mortality species were highly abundant in ESF, no recruits were recorded for most of them in Costa Rica. Here, recruitment rates might be less informative than in other forests because

only a few plots that were 12 years or older had information on trees ≥1 cm dbh and met our criterion for the calculation of recruitment rates (Appendix S1: Table S1). Additionally, recruitment in the plots at the La Selva Biological Station (referred to in Appendix S1: Table S1 as Sarapiquí) is known to be affected by collared peccaries (Huanca-Nuñez et al., 2023; Kuprewicz, 2013). Given their high abundance during the first ~15 years of succession, many of the high-mortality species might actually have similarly high recruitment rates in ESF as many of the high-mortality species in Panama, where data availability was more consistent throughout the chronosequence. Hence, in contrast with common assumptions, early successional specialist demographic strategies in these forests might indicate a trade-off of high mortality and high recruitment rather than consistently high growth rates. However, as mentioned above, high early growth rates of species with short lifespans might be left undetected in this study integrating over the first 30 years of succession.

The fact that the high-mortality strategy was restricted to the ESF was primarily due to species turnover, as projected by Finegan (1996). Most of the species were either completely absent after 30 years of succession or persisted at very low abundance. However, the few species from this group that were present in OGFs exhibited lower mortality rates there, indicating that intraspecific variation in mortality rates also contributes to this shift (Umaña et al., 2018). The same pattern has also been observed for some species in other tropical rainforests (Martínez-Ramos et al., 2021).

In the dry sites, we did not find an exclusive demographic strategy in ESF. In tropical dry forests, species that are present in ESF can persist for a longer time and do not have a unique demographic strategy. Because of a lower and (seasonally) more open canopy, early and late successional environments are less distinct in dry compared with wet forests (Lebrija-Trejos et al., 2011; Letcher et al., 2015). Moreover, many resprouting species in ESF might in fact be species that were abundant predisturbance and therefore follow demographic strategies associated with late-successional environments (Boucher et al., 2001; Lebrija-Trejos et al., 2008). Additionally, resprouting trees in ESF are likely to rely on belowground carbohydrate reserves of the old root system and therefore might have similar demographic rates as in OGFs (Poorter et al., 2010).

Ranges of demographic strategies do not expand during succession

Contrary to our expectations, we did not find a general pattern of increasing diversity in demographic strategies during succession. Indeed, demographic diversity seems

to recover to OGF values within the first 30 years of succession. Similarly, Poorter et al. (2021) found that structural heterogeneity and species richness in secondary tropical forests recovered to 90% of OGF values at around 30 years after abandonment, whereas species composition only recovered after more than a century. Although we did not examine shifts in the relative abundance of demographic strategies (but see Rüger et al., 2023), this may nevertheless indicate that demographic diversity (defined solely as the range of demographic strategies employed in a forest) is more closely linked to species richness than to species composition and that many different species exhibit similar demographic strategies and have similar demographic niches.

Limitations

When interpreting our results, it should be noted that we used a chronosequence approach that substitutes space for time and thus infers temporal trends from static data (Walker et al., 2010). Moreover, data availability as well as data collection methodologies varied widely across sites (Appendix S1: Figure S1), and plots within each chronosequence also varied in extent and minimum dbh threshold (Appendix S1: Table S1). Last, it should be noted that only a small number of plots was measured down to 1 cm dbh, especially in the dry sites. This precluded the reliable calculation of recruitment rates. While our results are robust to this heterogeneity and independent of the number of species included (e.g., Appendix S1: Figure S6), this emphasizes the need for more permanent monitoring plots with small dbh cut-offs in ESF.

CONCLUSION

Overall, we found that the secondary forests in our study harbored similar levels of demographic diversity as the OGFs, indicating that early successional stages (0–30 years since abandonment) contain the full spectrum of life-history strategies found in OGFs. Based on these findings, demographic data from OGFs is surprisingly informative for understanding the diversity of demographic strategies in these tropical forests. An exception was a group of species with exceptionally high mortality rates that was confined to early successional stages in the wet forests. This suggests that studies of demographic diversity of OGFs might be more informative than previously thought, but that they do not obviate the need for further demographic studies in secondary forests. These results also imply that accurate predictions of early

successional dynamics in tropical wet forests need to account for this demographic strategy that occurs uniquely during the first 30 years of succession. However, predictions of forest recovery and successional changes in the dominance of different demographic strategies in tropical dry forests, and after the first decades in wet forests, can likely be based on information on the diversity of demographic strategies from OGFs (Rüger et al., 2020, 2023). These findings enhance our understanding of the mechanisms underlying tropical forest succession across rainfall gradients and improve our ability to predict successional dynamics in tropical forests with the help of demographic forest models (Purves et al., 2008; Rüger et al., 2020).

AUTHOR CONTRIBUTIONS

The idea for this study was conceived during a workshop attended by Lucy Amissah, Frans Bongers, Robin L. Chazdon, Dylan Craven, Caroline E. Farrior, Bruno Hérault, Catarina C. Jakovac, Stephan Kambach, Jorge A. Meave, Rodrigo Muñoz, Natalia Norden, Lourens Poorter, Nadja Rüger, Markus E. Schorn, Michiel van Breugel and Masha T. van der Sande. Robin L. Chazdon, Dylan Craven, Daisy H. Dent, Diego Delgado, Saara J. DeWalt, Juan M. Dupuy, Bryan Finegan, Jefferson S. Hall, José L. Hernández-Stefanoni, Omar R. Lopez, Jorge A. Meave, Rodrigo Muñoz, and Michiel van Breugel contributed data. Markus E. Schorn, Nadja Rüger and Stephan Kambach prepared forest inventory data for analysis and calculated demographic rates. Markus E. Schorn analyzed the data. Markus E. Schorn wrote the first draft of the manuscript with support from Nadja Rüger. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Schorn et al., 2024) are available in Dryad at https://doi.org/10.5061/dryad.f7m0cfz4h.

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SUPPORTING INFORMATION

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

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