RESEARCH ARTICLE

Successional shifts in tree demographic strategies in wet and dry Neotropical forests

Nadja Rüger[1,2,3] | Markus E. Schorn[1,2] | Stephan Kambach[4] | Robin L. Chazdon[5,6] | Caroline E. Farrior[7] | Jorge A. Meave[8] | Rodrigo Muñoz[8,9] | Michiel van Breugel[10,11,12] | Lucy Amissah[13] | Frans Bongers[9] | Dylan Craven[14] | Bruno Hérault[15,16,17] | Catarina C. Jakovac[18] | Natalia Norden[19] | Lourens Poorter[9] | Masha T. van der Sande[9] | Christian Wirth[1,20,21] | Diego Delgado[22] | Daisy H. Dent[3,23,24] | Saara J. DeWalt[25] | Juan M. Dupuy[26] | Bryan Finegan[22] | Jefferson S. Hall[12] | José L. Hernández-Stefanoni[26] | Omar R. Lopez[3,27]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[2]Department of Economics, Institute of Empirical Economic Research, University of Leipzig, Leipzig, Germany

[3]Smithsonian Tropical Research Institute, Ancón, Panama

[4]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

[5]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA

[6]Tropical Forests and People Research Centre, University of the Sunshine Coast, Maroochydore DC, Queensland, Australia

[7]Department of Integrative Biology, University of Texas at Austin, Austin, Texas, USA

[8]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, Mexico

[9]Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, The Netherlands

[10]Yale-NUS College, Singapore, Singapore

[11]Department of Geography, National University of Singapore, Singapore, Singapore

[12]ForestGEO, Smithsonian Tropical Research Institute, Ancón, Panama

[13]CSIR-Forestry Research Institute of Ghana, Kumasi, Ghana

[14]Centro de Modelación y Monitoreo de Ecosistemas, Facultad de Sciencias, Universidad Mayor, Santiago, Chile

[15]CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Côte d'Ivoire

[16]Forêts et Sociétés, Université Montpellier, CIRAD, Montpellier, France

[17]Institut National Polytechnique Félix Houphouët-Boigny, INP-HB, Yamoussoukro, Côte d'Ivoire

[18]Departamento de Fitotecnia, Centro de Ciências Agrárias, Universidade Federal de Santa Catarina, Florianópolis, Brazil

[19]Programa de Ciencias Básicas de la Biodiversidad, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia

[20]Systematic Botany and Functional Biodiversity, Institute for Biology, Leipzig University, Leipzig, Germany

[21]Max-Planck Institute for Biogeochemistry, Jena, Germany

[22]Forests and Biodiversity in Productive Landscapes, CATIE, Turrialba, Costa Rica

[23]Biological and Environmental Sciences, University of Stirling, Stirling, UK

[24]Department of Environmental Systems Science, Institute of Integrative Biology, ETH-Zürich, Zürich, Switzerland

[25]Clemson University, Clemson, South Carolina, USA

[26]Centro de Investigación Científica de Yucatán (CICY), Unidad de Recursos Naturales, Mérida, Yucatán, Mexico

[27]Instituto de Investigaciones Científicas y Servicios de Alta Tecnología (INDICASAT), Ciudad del Saber, Clayton, Panama

Correspondence
Nadja Rüger, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, 04103 Leipzig, Germany.
Email: nadja.rueger@idiv.de

Handling Editor: Margaret Morrow Mayfield

Abstract

Aim: Tropical forest succession and associated changes in community composition are driven by species demographic rates, but how demographic strategies shift during succession remains unclear. Our goal was to identify generalities in demographic trade-offs and successional shifts in demographic strategies across Neotropical forests that cover a large rainfall gradient and to test whether the current conceptual model of tropical forest succession applies to wet and dry forests.

Location: Mexico and Central America.

Time period: 1985–2018.

Major taxa studied: Trees.

Methods: We used repeated forest inventory data from two wet and two dry forests to quantify demographic rates of 781 tree species. For each forest, we explored the main demographic trade-offs and assigned tree species to five demographic groups by performing a weighted principal components analysis to account for differences in sample size. We aggregated the basal area and abundance across demographic groups to identify successional shifts in demographic strategies over the entire successional gradient from very young (<5 years) to old-growth forests.

Results: Across all forests, we found two demographic trade-offs, namely the growth–survival trade-off and the stature–recruitment trade-off, enabling the data-driven assignment of species to five demographic strategies. Fast species dominated early in succession and were then replaced by long-lived pioneers in three forests. Intermediate and slow species increased in basal area over succession in all forests, but, in contrast to the current conceptual model, long-lived pioneers continued to dominate until the old-growth stage in all forests. The basal area of short-lived breeders was low across all successional stages.

Main conclusions: The current conceptual model of Neotropical forest succession should be revised to incorporate the dominance of long-lived pioneers in late-successional and old-growth forests. Moreover, the definition of consistent demographic strategies that show clear dominance shifts across succession substantially improves the mechanistic understanding and predictability of Neotropical forest succession.

KEYWORDS
demographic strategies, growth-mortality tradeoff, life-history strategies, long-lived pioneer, principal components analysis, stature-recruitment tradeoff, species classification

1 | INTRODUCTION

In recent decades, land abandonment following the expansion of croplands and pastures has initiated the regrowth of vast areas of secondary forests across the Neotropics (Aide et al., 2013). Secondary forests are estimated to cover 28% (2.4×10^6 km²) of the Neotropics (Chazdon et al., 2016) and have considerable potential for climate change mitigation (Chazdon et al., 2016; Hall et al., 2022) and biodiversity conservation (Rozendaal et al., 2019). We are

beginning to understand how community-level metrics, such as biomass, species composition or functional composition, recover during forest succession (Poorter et al., 2021) and to assess the role of macroclimate in forest recovery at continental scales. In contrast, our predictive understanding of shifts in dominance of different demographic strategies across succession, which arise from differences in demographic rates of the multiple tree species that compose local communities (Lai et al., 2021; Rüger et al., 2020), remains limited (Chazdon, 2014; Norden et al., 2015).

The dominant paradigm of tropical forest succession describes a shift in dominance (typically measured as relative basal area or biomass) from shade-intolerant species to shade-tolerant species driven by changes in light availability at the forest floor (Chazdon, 2014; Finegan, 1996). Shade-intolerant species are characterized by functional traits associated with resource acquisition, whereas shade-tolerant species maximize resource conservation, and the corresponding shifts in functional composition have been documented (Craven et al., 2015; Lohbeck et al., 2013, 2015; Poorter et al., 2019). In demographic terms, shade-intolerant species (or "pioneers") are species with a fast demographic strategy (henceforth "fast" species). They grow and die quickly, need light for successful recruitment and dominate early successional stages (Figure 1). In contrast, shade-tolerant species are characterized by a slow demographic strategy (henceforth "slow" species). They grow slowly, survive well, can regenerate in the shaded understorey and are more abundant in late-successional stages (Figure 1).

However, several studies suggest that tropical tree communities might be structured not only by this fast–slow continuum of life histories or growth–survival trade-off, but also by another orthogonal trade-off axis: the stature–recruitment trade-off (Kambach et al., 2022; Kohyama et al., 2003; Rüger et al., 2018). The stature–recruitment trade-off distinguishes long-lived pioneers (LLP) that grow fast and live long, and thus reach a tall stature, but recruit poorly, from short-lived breeders (SLB) that grow slowly and die fast, and hence remain short in stature, but produce many recruits.

Finegan (1996) hypothesized that LLP species recruit only at the onset of succession, reach a peak in biomass between 20 and 80 years following land abandonment and then gradually disappear from the forest (Figure 1). Along the one-dimensional fast–slow continuum, LLP species have often been considered as having intermediate shade tolerance, and the presence of large LLP trees is often interpreted as evidence that the forests are still undergoing successional change (Knight, 1975). However, LLP species comprised more

FIGURE 1 Conceptual model of Neotropical forest succession. Continuous lines correspond to a model suggested by Finegan (1996). Dashed lines and questions marks represent hypotheses. Each line can be interpreted as the trajectory of basal area of a typical species representing the different demographic strategies and as the sum of basal area of all species belonging to a given demographic strategy.
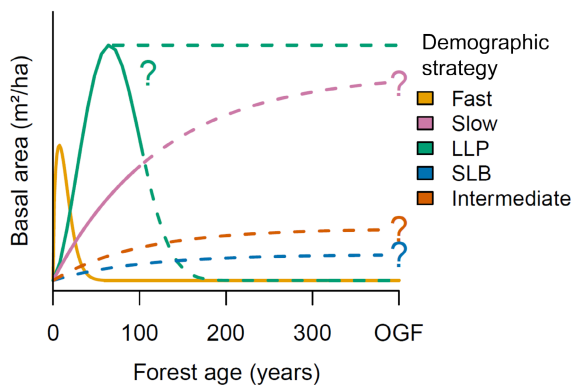
basal area than slow species in an old-growth wet forest in Costa Rica (Chazdon et al., 2010) and an old-growth moist forest in Panama (Rüger et al., 2020). Thus, it is unclear whether the current paradigm of dominance shifts from light-demanding to shade-tolerant species is an adequate description of tropical forest succession.

Likewise, it is unclear whether SLB species show consistent shifts in dominance across forest succession. Given that SLB species in Panama were mostly shade-tolerant understorey treelets and shrub species (Rüger et al., 2018), we expect them to be associated with old-growth forest, but to remain at low levels of basal area (Figure 1). Finally, species with intermediate growth, survival and recruitment can be assigned to a separate demographic group of intermediate species (Rüger et al., 2020). Given that intermediate species were neither very abundant nor very tall in Panama, we expect them to remain at low levels of basal area throughout succession (Figure 1).

The dominant conceptual model of secondary forest succession assumes that light is the most limiting resource, but water is the most limiting resource in dry forests, especially during early succession (Lebrija-Trejos et al., 2011; Pineda-García et al., 2013). Therefore, dry forests might not show the same dominance shifts of demographic groups during succession as wet forests. For example, traits reflecting greater resource conservation and drought tolerance (e.g., high wood density, leaf dry matter content) decreased during succession in dry tropical forests, while values of leaf traits related to light capture (e.g., specific leaf area, leaf thickness) shifted from acquisitive to conservative during succession (Buzzard et al., 2016; Lohbeck et al., 2013; Poorter et al., 2019). Moreover, dry forests are generally less structurally complex (i.e., they have fewer canopy layers) than wet tropical forests (Holl, 2007). Therefore, in dry forests, different demographic trade-offs and strategies might emerge than in wet forests.

In a dry forest in Bolivia, where demographic groups were defined based on assessments of shade tolerance (short-lived pioneers, long-lived pioneers, partly shade tolerant or shade tolerant), LLP species dominated the first decades of succession and co-dominated in mature forest, together with "shade-tolerant" species (Kennard, 2002). However, it is unclear how well these shade-tolerance groups correspond to the demographic strategies outlined above. Thus, to reach a more comprehensive understanding of tropical forest succession, we need a quantitative, standardized approach to classifying tree species based on their demographic rates.

Here, we assemble a unique dataset of repeated forest inventories along long successional gradients (<5 years after land-use abandonment to old-growth forests) in four Neotropical forests that range from the driest (900 mm/year rainfall) to the wettest (3900 mm/year rainfall) forests found in the Neotropics (Table 1). We calculate growth and survival rates for each tree species in three canopy layers to account for differences in tree size and light availability, in addition to recruitment rates. Based on these seven demographic rates, we examine demographic trade-offs and classify tree species into demographic groups using a weighted Principal component analysis (wPCA) (Rüger et al., 2018). We then evaluate shifts in demographic composition across succession in terms of basal area

TABLE 1 Location, mean annual temperature, mean annual precipitation, length of dry season (<100 mm rainfall per month), number of species with ≥10 individuals in the sampled plots that were included in the analysis, average old-growth forest canopy height, number of canopy layers and length of the chronosequences.

Site	Location	MAT (°C)	MAP (mm/year)	Length of dry season (months)	Number of species (n ≥ 10)	OGF canopy height (m)[a]	Number of canopy layers	Chrono-sequence length
Costa Rica	10°26′ N, 84°00′ W	26	3900	–	284	20–35	4	1–57 years + OGF
Panama	9°90′ N, 79°51′ W	27	2600	3	357	15–30	4	0–120 years + OGF
Yucatán (Mexico)	20°05′ N, 89°29′ W	26	1100	6	77	8–13	3	3–85 years (+ OGF)
Oaxaca (Mexico)	16°39′ N, 95°00′ W	28	900	7	63	7–8	3	4–70 years + OGF

Note: The sampling area differs substantially among sites (Supporting Information Table S1).

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature; OGF, old-growth forest.

[a]Canopy heights are from Clark et al. (2021; Costa Rica), Mascaro et al. (2011; Panama), Dupuy et al. (2012; Yucatán, Mexico) and Lebrija-Trejos et al. (2008; Oaxaca, Mexico).

and abundance, as measures of species dominance. Our objectives are twofold: (1) we ask whether consistent demographic trade-offs emerge from species differences within both wet and dry forests, and (2) whether the conceptual model described by Finegan (1996) (Figure 1) is an adequate description of forest succession in both wet and dry Neotropical forests.

Our results show that the current conceptual model of Neotropical forest succession needs to be revised to incorporate the dominance of long-lived pioneers in late-successional and old-growth forests and substantially enhance the mechanistic understanding and predictability of Neotropical forest succession (Rüger et al., 2020).

2 | METHODS

2.1 | Study sites

We conducted our study at four Neotropical lowland forest sites that differ greatly in rainfall (Table 1; Supporting Information Table S1). The forest in the Sarapiquí region (Costa Rica), where the Tirimbina Reserve and La Selva Biological Station are located, is a wet evergreen broadleaved forest with no dry season (Chazdon et al., 2010; Finegan et al., 1999). The forest is dominated by *Pentaclethra macroloba* and has a high proportion of canopy and subcanopy palms (Chazdon et al., 2010; Rozendaal & Chazdon, 2015). The forest in central Panama (Barro Colorado Nature Monument, Agua Salud) is a moist semideciduous forest with a 3 month dry season (Ogden et al., 2013). Secondary forests in both wet sites have regenerated after abandonment of cattle pastures, agriculture or forest clearing (Chazdon et al., 2010; Denslow & Guzman, 2000; van Breugel et al., 2013). Old-growth forests (OGFs) in both sites have not suffered major anthropogenic disturbances for the last 400–500 years (Fichtler et al., 2003; Piperno, 1990).

The two dry sites in Mexico with mostly deciduous dry forests have a shorter canopy than the wet forests (Table 1). The dry forest in Kaxil Kiuic Biocultural Reserve (Yucatán) is dominated in terms of basal area by *Bursera simaruba*, *Lysiloma latisiliquum* and *Caesalpinia gaumeri* (Dupuy et al., 2012). The dry forest in Nizanda (Oaxaca) has many arborescent cacti (Pérez-García et al., 2010). Secondary forests in both dry forests have regenerated after shifting agriculture (Lebrija-Trejos et al., 2008; Saenz-Pedroza et al., 2020). The few plots classified as OGF in Yucatán have not suffered agricultural land use for ≥100 years. In Oaxaca, there is no indication of previous anthropogenic disturbance in OGF.

We used forest inventory data from permanent plots in nine long-term monitoring projects at the four sites to calculate demographic rates (Supporting Information Table S1). Sampling design, number and size of plots, census intervals and minimum diameter thresholds differed between projects (Supporting Information Table S1; Figure S1). In general, all freestanding woody individuals above a plot-specific diameter threshold [e.g., 5 cm diameter at breast height (d.b.h.)] were measured, marked and remeasured annually or at

longer census intervals (range 1–10 years). Where measurements were repeated more frequently than every 5 years, we selected census intervals of c. 5 years (range 4–10 years).

2.2 | Canopy layer assignment

To account for differences in tree size and light availability, we calculated demographic rates in different canopy layers, which has proved useful in capturing life-history variation among co-occurring species (Bohlman & Pacala, 2012; Rüger et al., 2018) and in predicting forest succession (Rüger et al., 2020). We assigned all trees to canopy layers based on their size and the size of their neighbours (Bohlman & Pacala, 2012). To do this, we generally assigned individual trees to subplots of 625–1000 m^2 (in wet forest sites) and 100–125 m^2 (in dry forest sites, where the largest trees are generally smaller than in wet forests), based on their spatial coordinates or the predefined sampling design (for exceptions, see Supporting Information Table S1). Next, all trees within a subplot were sorted by their d.b.h. (or the d.b.h. of the largest stem, in case of multi-stemmed individuals). Starting from the largest tree, trees were assigned to the top canopy layer (layer 1) until the cumulative area of their crowns exceeded the subplot area. Crown area was estimated using site-specific allometric equations (Schorn, 2021). Smaller trees were assigned successively to lower canopy layers in the same way.

2.3 | Demographic rates

In wet sites, tree size was defined as the d.b.h. of the largest living stem of an individual (i.e., neglecting smaller stems of multi-stemmed individuals). In dry sites, multi-stemmed individuals were much more abundant, and individual stems were measured but not tagged. It was therefore not possible to calculate stem-level d.b.h. growth, and instead we used the sum of basal area of all stems of an individual as a measure of tree size. Given that multi-stemmed individuals were rare in the wet forests and classification into canopy layers controlled for tree size, species rankings in terms of growth rates should not be affected by the choice of the size measure in the wet sites. Individuals were deemed alive if at least one stem was alive and dead only if all stems were dead.

To calculate growth and survival rates of species, we used forest inventory data from all successional stages. Individual annual tree growth g_i was calculated as:

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

with size being d.b.h. in the wet sites and basal area in the dry sites in the first and second census, respectively, and t being the time elapsed between the two size measurements (in years). 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:

$$g_{j,l} = \text{median}(g_{j,l,i}).$$

Species-level annual survival rates per canopy layer ($s_{j,l}$) were calculated as:

$$s_{j,l} = \left(\frac{N_2}{N_1}\right)^{\frac{1}{t}},$$

with N_1 being the number of individuals that were alive in the first census and N_2 being the number of individuals remaining alive in the second census. We are aware that tree size distributions in the different canopy layers might differ across a chronosequence. However, for most canopy layer-specific growth and survival rates, there were no significant changes across chronosequences (Schorn, 2021). We included only individuals that were classified to species or morphospecies and life-forms for which stem growth (d.b.h. or basal area) can be calculated reliably (trees, shrubs and arborescent cacti), but excluded palms and hemi-epiphytes (e.g., strangler figs).

To calculate recruitment rates, we used data only from OGFs, except for Yucatán, where the sampling area in OGFs was too small to calculate recruitment rates for a reasonable proportion of the species. For Yucatán, we used recruitment rates in late-successional forests (30–120 years). We calculated recruitment rates per unit of basal area as the number of recruits that surpassed the 1 cm d.b.h. threshold per year and hectare, divided by the average basal area of the species per hectare in OGFs (Rüger et al., 2018). We considered other measures of recruitment success and timing of recruitment in succession, such as per-capita or per-basal-area recruitment in early- or late-successional forests, average per-basal-area recruitment across succession, and the percentage of recruits in early-successional forests. However, all these approaches are sensitive to species abundances, because many rare species do not have recruits or "basal area" at a particular successional stage. Thus, we decided to adhere to the design of an earlier analysis of demographic strategies in Panama that used OGF per-basal-area recruitment (Rüger et al., 2018), and we assigned species to demographic groups that predicted secondary forest succession accurately between 40 and 120 years (Rüger et al., 2020).

2.4 | Weighted principal components analysis

We performed a weighted Principal component analysis (wPCA; Delchambre, 2014) on growth and survival rates in three canopy layers and the per-basal-area recruitment ≥1 cm d.b.h. in OGF to explore the main demographic trade-offs (i.e., opposite loadings of demographic rates along the wPCA axes) across the species within the four sites (objective 1). Given that the dry forests had only three canopy layers, we omitted demographic rates in canopy layer 4 of the wet forests for consistency. However, we evaluated the effect of this omission and show results including four layers in the Supporting Information.

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Macroecology

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Our goal was to assign as many species as possible to demographic groups, because many species in tropical tree communities are rare, and including them in analyses is crucial for understanding tropical forest succession. Therefore, we performed a wPCA in which all species contributed information, weighted by the credibility of the estimates of their demographic rates (for the definition of weights, see below). Because of the low credibility in the estimates of demographic rates of very rare species, we excluded species with <10 individuals across the chronosequence. These species accounted for a low percentage of stems (ranging from 0.03% in Panama to 4.1% in Oaxaca) and basal area (ranging from 0.9% in Panama to 5.2% in Oaxaca), averaged across all successional stages.

Weights ($w_{j,l}$) represented the relative credibility of the estimates of the demographic rates within sites. They were proportional to the $\log_{10}$ of the number of observations per species and canopy layer that were used to calculate growth and survival rates ($n_{j,l}$) or to the number of observed recruits (Supporting Information Figure S2). The species with the largest sample size in a site was assigned a weight of one:

$$w_{j,l} = \frac{\log_{10}(n_{j,l}) + 1}{\max_{j}(\log_{10}(n_{j,l}) + 1)}.$$

Weights of demographic rates of species with no individuals in the respective canopy layer were assigned a very small value (1.0×10^{-6}).

All demographic rates were transformed before the wPCA to linearize their relationships and were standardized to a weighted mean of zero and a weighted standard deviation of one within sites. Growth and recruitment rates were ln-transformed. Given that some growth rates were negative, we added a small site- and canopy-layer-specific constant to all growth rates, such that all growth rates were positive before transformation. Survival rates were transformed to ln lifespan [$\ln(1/(1-s))$], which is equivalent to $-\ln(\text{mortality})$. Survival rates equal to one were replaced by a value larger than the maximum (less than one) observed survival rate of the other species in the same site and canopy layer. This affected mostly species with a small sample size in the respective canopy layer. Thus, these rates were associated with low weights and did not substantially affect the wPCA.

To include species lacking individuals in some canopy layers, we set the missing growth, survival and recruitment rates equal to the median value of the corresponding demographic parameter across the other species at the same site. Again, these arbitrary growth, survival and recruitment values were associated with a very low weight and did not affect the wPCA.

2.5 | Demographic groups and patterns of succession

We used species scores along the first (*x*) and second (*y*) wPCA axes to assign them to demographic groups. Given that wPCA axes corresponded to the same two demographic trade-offs at all sites (the growth–survival trade-off separating fast and slow species, and the stature–recruitment trade-off separating LLP and SLB species; Figure 2), we could assign the species to the same four demographic groups and an intermediate group with intermediate demographic rates. Given that the wPCAs were standardized, we used the same centre locations for the five demographic groups across sites. The demographic group centers are as follows: fast ($x = 1.5$, $y = 0$); slow ($x = -1.5$, $y = 0$); LLP ($x = 0$, $y = 1.5$); SLB ($x = 0$, $y = -1.5$); and intermediate ($x = 0$, $y = 0$), with x and y being the species scores on the first and second wPCA axis, respectively (Rüger et al., 2020). For Yucatán, we switched x and y coordinates because the wPCA axes were switched with respect to the other sites (see Results). The species within a site were assigned to the closest demographic group centre (Euclidean distance in wPCA space).

To determine successional shifts in demographic strategies across forests (objective 2), we aggregated basal area and abundance by demographic group in 10-year age classes (1–10, 11–20 years, etc.) and OGF. All analyses were carried out in R v.3.6.2 (R Development Core Team, 2019).

3 | RESULTS

3.1 | Demographic trade-offs and strategies

In all sites except Yucatán, the first axis of demographic variation separated species with fast growth and low survival (fast species) from species with slow growth and high survival (slow species; Figure 2; Supporting Information Table S2). This axis accounted for ≥40% of demographic variation (Costa Rica, 41%; Panama, 44%; Oaxaca, 44%). In Yucatán, the growth–survival trade-off appeared on the second axis and accounted for less variation (25%). In all sites except Yucatán, the second axis of demographic variation separated species with fast growth and high survival but low recruitment (LLP species) from species with slow growth and low survival but high recruitment (SLB species). This axis accounted for *c.* 30% of demographic variation (Costa Rica, 28%; Panama, 33%; Oaxaca, 23%). In Yucatán, the stature–recruitment trade-off appeared on the first axis and accounted for more variation (40%).

In Costa Rica, recruitment loaded only very weakly on the second axis. This is likely to be because the sampling area and number of censuses for trees ≥1 cm d.b.h. in OGFs in Costa Rica was much smaller than in Panama (1.12 vs. 300 ha; Supporting Information Figure S1), and 75% of the species in Costa Rica had no observed recruits or no individuals (hence basal area) in OGFs (214 of 284 species) compared with 28% in Panama (99 of 357 species). Likewise, in the two dry sites, the number of species without estimates of recruitment rates was high (Yucatán, 68%; Oaxaca, 57%).

The consistent importance of the growth–survival and stature–recruitment trade-offs (as wPCA axes 1 and 2) in all four forests allowed us to assign tree species to five demographic groups based on their position in the two-dimensional demographic space. These groups are fast, slow, LLP, SLB and intermediate species (Figure 2). The five groups show clear differences in growth, survival,
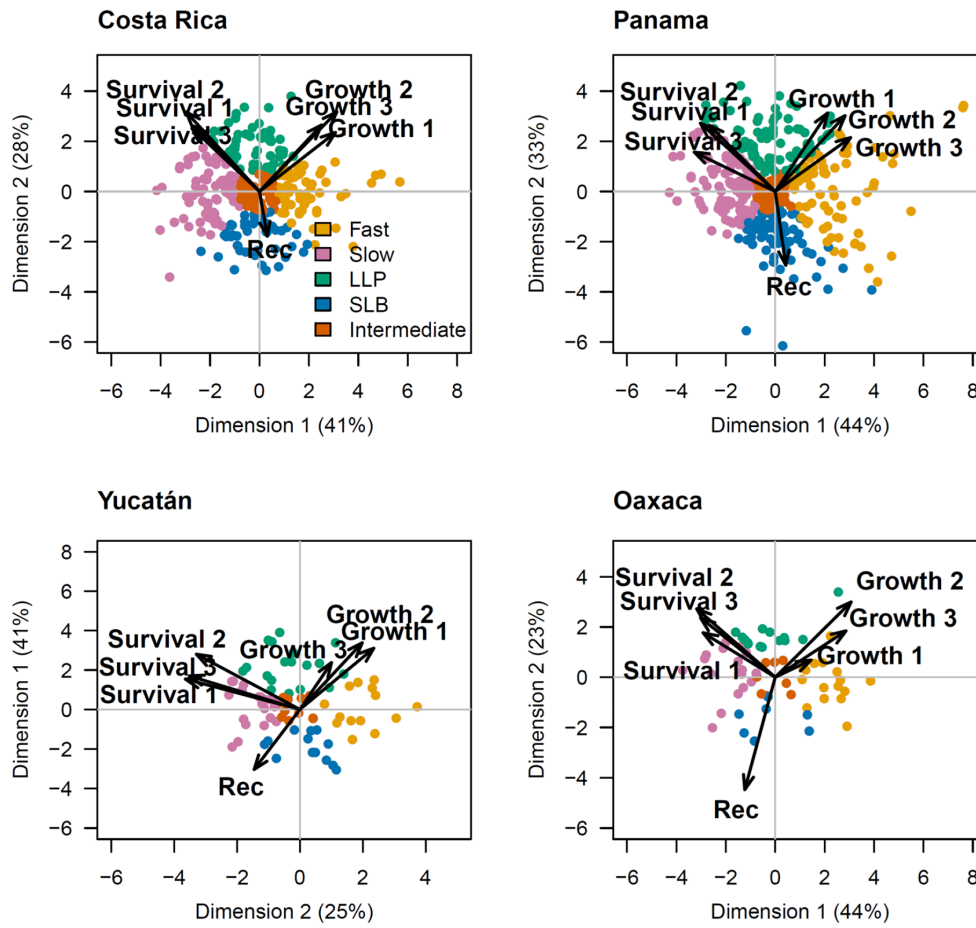
FIGURE 2 Demographic strategies in four Neotropical forest sites. Loadings of seven demographic rates [growth and survival rates of individuals ≥1 cm diameter at breast height (d.b.h.) in three canopy layers and the number of sapling recruits ≥1 cm d.b.h. per m² of basal area in old-growth forest (OGF)] in weighted Principal component analysis. Species assignment to demographic groups is shown by the colour of the dot. For Yucatán, the first and second demographic dimensions are switched to increase comparability with the other sites.

recruitment and size (i.e., maximum d.b.h.; Supporting Information Figures S3–S6). An exception was Costa Rica, where demographic groups were not clearly differentiated with respect to recruitment (Supporting Information Figure S5). In the wet and dry forests, respectively, growth and survival rates in the demographic groups were comparable (Supporting Information Figures S3 and S4).

3.2 | Demographic groups and successional trajectories

In Costa Rica, fast species dominated the first 60 years of succession (Figure 3; Supporting Information Figure S7), but in the OGF, LLP species clearly dominated in terms of basal area. Slow and intermediate species increased to only low levels of basal area in OGF. In terms of abundance, LLP, slow and intermediate species co-dominated in OGF.

In Panama, fast species dominated the first 50 years, LLP species dominated between 40 and 90 years, and slow and intermediate species increased in basal area across succession (Supporting Information Figure S8). LLP and slow species dominated in OGF in terms of basal area and abundance, respectively. These results

were robust to the number of canopy layers included in the wPCA (Supporting Information Figures S9 and S10).

In Yucatán, fast species dominated the first 30 years of succession, but species of other demographic groups, including SLB and slow species, also reached high basal area and abundance during the first decades of succession. In general, the successional pattern in Yucatán was less clear. In terms of basal area, fast, LLP and slow species co-dominated during mid successional stages and in the OGF (Supporting Information Figure S11). In terms of abundance, LLP and slow species dominated in later successional stages and the OGF.

In Oaxaca, fast species dominated the first 50 years, LLP species dominated thereafter, and slow species increased in basal area over succession (Supporting Information Figure S12). The basal area of slow species remained low, and the OGF was clearly dominated by LLP species. In terms of abundance, LLP and slow species co-dominated the OGF.

4 | DISCUSSION

We used demographic rates of 781 tree species from two wet and two dry Neotropical forests to explore demographic trade-offs and
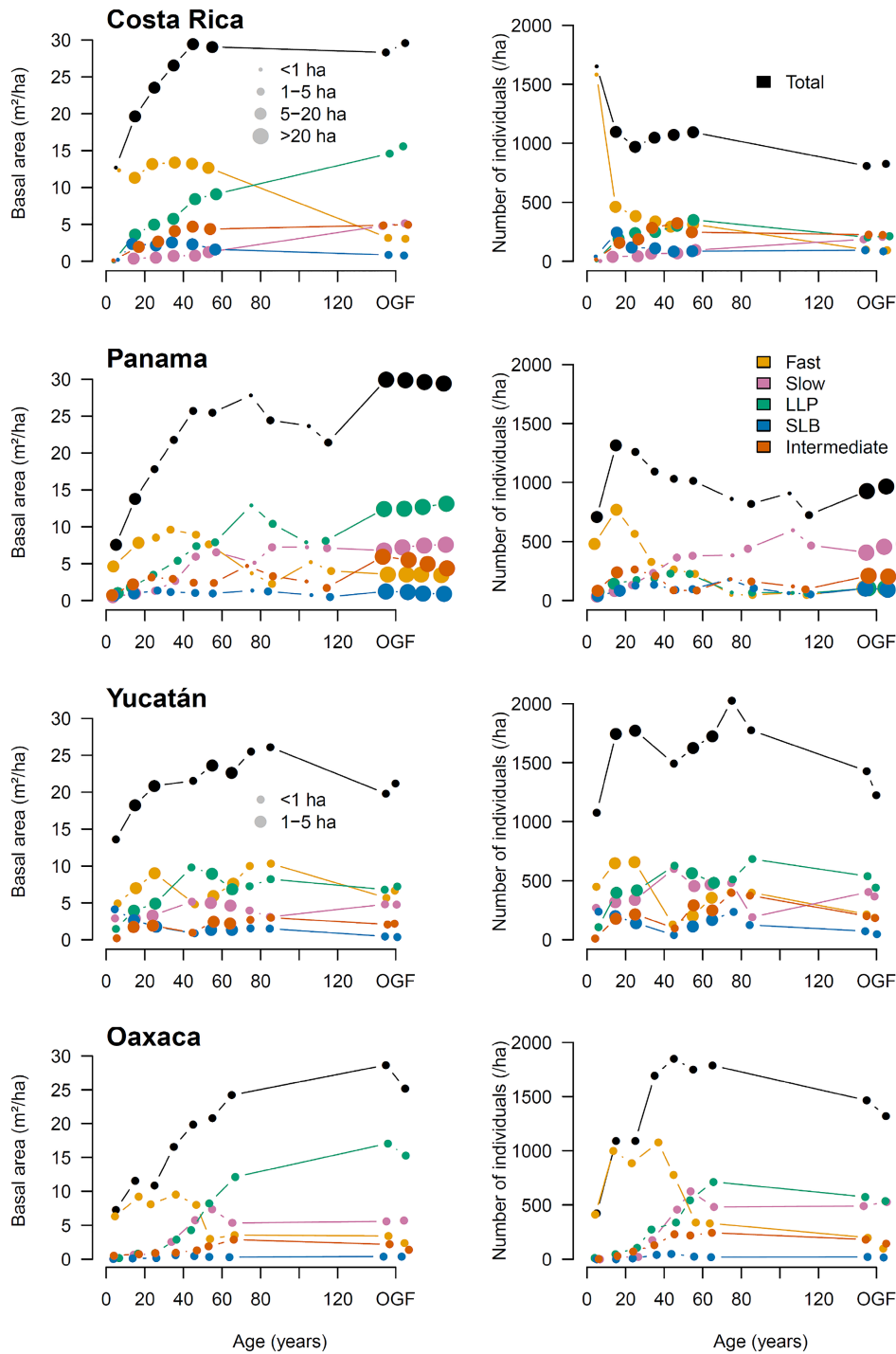
FIGURE 3 Shifts of demographic strategies during succession in four Neotropical forest sites. Basal area (left panels, ≥1 cm d.b.h.) and abundance (right panels, ≥5 cm d.b.h.) of different demographic groups across succession. Repeated inventories in old-growth forest (OGF) are shown separately to indicate whether OGF composition is in equilibrium. The sampling area is indicated by dot size.

successional shifts in demographic strategies. The same two trade-offs among demographic rates emerged across all forests, allowing us to define five demographic groups that correspond to fast species (fast growth and low survival), slow species (slow growth and high survival), long-lived pioneer (LLP) species (fast growth, high survival and low recruitment rates), short-lived breeder (SLB) species (slow growth, low survival and high recruitment rates) and intermediate species with intermediate demographic rates. These groups showed clear shifts in basal area and abundance across forest succession. As expected from the conceptual model (Figure 1), fast species dominated early-successional stages in all four forests, and LLP species dominated in mid-successional stages in three of the four forests. However, in contrast to this model, LLP species were a dominant component of the OGF in all sites.

4.1 | Demographic trade-offs and strategies

The same two trade-offs among demographic rates emerged in wet and dry sites. The first is the well-known growth–survival trade-off (Russo et al., 2021; Wright et al., 2010). The second is the stature–recruitment trade-off between fast growth and high survival (hence tall adult stature) versus high recruitment rates per unit of basal area in the OGF (Kambach et al., 2022). Recruitment rates per unit of basal area exhibit strong negative correlations with basal area, which is, in turn, correlated with tree stature. Thus, our measure of recruitment is also an implicit measure of tree stature. Together, the two trade-offs captured by the first two principal components accounted for *c.* 70% of the demographic variation among tree species. In Yucatán, the importance of the two trade-offs was reversed, and demographic variation was more strongly structured by the negative correlation between recruitment and growth, and to a lower degree survival. This might be because, in Yucatán, the ability to resprout (hence recruit) is a key trait owing to the long history and high frequency of recurring natural and human disturbance (Rico-Gray & García-Franco, 1991), and typical fast-growing species (high light requirements and low wood density) tend to be poor resprouters (Poorter et al., 2010; Vandermeer et al., 1995).

The largest uncertainty in assigning tree species to demographic groups defined by the two orthogonal axes of demographic variation lies in the estimation of recruitment rates. Tree recruitment over a certain size threshold is a relatively infrequent event, and the larger the size threshold, the less frequent it is. Therefore, we used recruitment rates over the 1 cm d.b.h. threshold. However, for most forests only a small sample area was monitored with this size threshold. In Costa Rica, where only 1.1 ha OGFs were monitored for trees ≥1 cm d.b.h., only 25% of the tree species had observed recruits. Given that reproduction and performance at early life stages are important components of the life cycle of a tree species, we recommend forest ecologists to continue efforts to measure small trees (e.g., through a nested sampling design that balances sample sizes across different size classes).

4.2 | Demographic groups and trajectories of forest succession

In three of the four forests, the five demographic groups showed clear successional shifts (i.e., changes in basal area and abundance across succession). As expected, the first decades of forest succession were dominated by fast species in all forests (cf. Chazdon, 2014; Finegan, 1996). In Yucatán, SLB species were also most abundant during the first decades and then declined, possibly owing to their higher resprouting ability or their higher drought tolerance (Guillemot et al., 2022). Interestingly, the SLB demographic group (slow growth, low survival and high recruitment) is composed of species that are characteristic of very early successional stages that disappear within a few decades of land abandonment (e.g., *Vismia* spp., *Conostegia* spp. and *Neomillspaughia emarginata*; Dupuy et al., 2012, Schorn, 2021),

in addition to understorey shrubs and treelets that are characteristic of OGFs (e.g., *Piper* spp., *Psychotria* spp. and *Eugenia axillaris*; Dupuy et al., 2012; Rüger et al., 2018; Saenz-Pedroza et al., 2020). The slow growth of SLB species could be explained, in part, by their shade intolerance, which could lead to slow growth once the forest canopy closes or their short stature (i.e., individuals were probably monitored close to their maximum size, where they already showed decreasing growth rates).

As expected, after 40–70 years, LLP species had reached dominance in terms of basal area in all forests (Finegan, 1996). However, in contrast to our expectations, LLP species did not decline during succession, but clearly dominated or co-dominated in later succession and OGFs in terms of basal area in all four forests. One reason could be that the forests might not yet have reached the old-growth stage, and LLP species could be survivors from initial cohorts after past disturbance (van Gemerden et al., 2003). However, our results suggest that plots classified as OGF are in equilibrium in the sense that their composition in terms of demographic groups remains stable (Figure 3), and there is ample evidence that the forests in Costa Rica and Panama have not suffered major disturbances for the last 400–500 years (Fichtler et al., 2003; Piperno, 1990).

An exception is Yucatán, where the high frequency and long history of human disturbance and hurricanes might have altered the original species pool by eliminating the most shade-tolerant late-successional species (Rico-Gray & García-Franco, 1991). This might be the cause for the lack of clear successional shifts of the remaining species and the continued dominance of the fast species in terms of basal area until the OGF.

If the dominance of LLP species is not attributable to remnant individuals of initial cohorts, many LLP species must continue to regenerate in canopy gaps and be able to maintain populations in OGF by compensating low mortality rates through sparse but sufficient recruitment (Kohyama et al., 2015; Rüger et al., 2020). Thus, the term "long-lived pioneer" is probably misleading, and we suggest that these species should be termed "tall" species for the purpose of predicting forest succession based on demographic strategies. Consequently, SLB species should be called "short". Previously, many LLP species might have been defined as "successional generalists" (i.e., species that occur at similar abundances in secondary forest and OGF; e.g., *Pentaclethra macroloba* in Costa Rica; Chazdon et al., 2011).

The dominance of LLP species also meant that slow species did not play the expected dominant role in OGFs. Slow species often do not belong to the tallest species in a forest (Rüger et al., 2018), which might explain their lower basal area than LLP species. However, except for Panama, slow species also occur at similar or lower abundances than LLP and intermediate species in the OGF. One factor that could explain the low abundance and basal area of slow species in Costa Rica is the high abundance of palms (basal area 2 m^2/ha, 7% of stems). Many of the palm species could be classified as late-successional slow species, but palms were not included in our analysis. In Panama, palms are less abundant (0.5 m^2/ha, 1.8%).

Another factor could be that competition with dominant LLP species could impede the successful recruitment of slow species. In Costa Rica, Yucatán and Oaxaca, some mostly LLP species became so dominant in terms of basal area in the OGF that they could almost be called "super species" (i.e., species that combine advantageous life-history traits and are competitively superior to other species). For example, in Costa Rica, *Pentaclethra macroloba*, a legume, is extremely successful because of its fast growth (4.8 mm/year in canopy layer 1), high survival (>98%) and relatively high recruitment. It can recruit in pastures and in closed forests and makes up 9% of the individuals (≥5 cm d.b.h.) and 29% of the basal area in OGFs (Menge & Chazdon, 2016).

In the dry forests, also a few species stood out for their high basal area in the OGF: *Bursera simaruba* (fast), *Caesalpinia gaumeri* (LLP) and *Lysiloma latisiliquum* (fast) in Yucatán, and *Jacaratia mexicana* (LLP) and *Lysiloma divaricatum* (LLP) in Oaxaca. They are all found in the upper right corner of the demographic space (Supporting Information Figures S6, S7, S10 and S11), where species with fast growth are located. Some of them are N-fixing legumes like *P. macroloba* (*C. gaumeri*, *L. latisiliquum*, *L. divaricatum*). These highly successful species might have a competitive advantage that hampers the recruitment and growth of slow, intermediate and SLB species in Costa Rica, Yucatán and Oaxaca, because they probably cast more shade and take up more soil nutrients and water than less successful species. However, the strength of this competitive advantage might differ across forests. For example, N-fixing trees have been found to inhibit their neighbours more strongly than non-fixing trees in our study site in Costa Rica (Taylor et al., 2017), but not in our study site in Panama (Lai et al., 2018).

If forests are dominated by few species and these species are located close to the boundaries between demographic groups (in our case, between fast and LLP), the evaluation of successional patterns might be sensitive to uncertainties in the demographic rates of other tree species, because they might cause the dominant species to be placed on either side of the boundary. Thus, our findings have to be taken with care, especially in the dry forests where sample sizes were lower. Another caveat inherent to all chronosequence studies is that younger stands might not be representative for the younger stages of older stands, especially in the face of climate change that might alter species demographic rates and forest dynamics (Anderson-Teixeira et al., 2013; McDowell et al., 2020; Swenson et al., 2020). However, the sampling period was only *c.* 15 years in the dry sites and 30 years in the wet sites (Supporting Information Table S1). Taking into account the gradual progress of climate change and the long time-scales of forest succession, it is unlikely that the successional patterns that we found were substantially confounded by changing climate.

5 | CONCLUSIONS

Overall, the conceptual model (Finegan, 1996; Figure 1) is an adequate description of the first 50–100 years of succession in the two

wet forests and the dry forest in Oaxaca, in that fast species dominate early in succession and are then replaced by LLP species. In contrast to expectations, LLP species continue to dominate also in the OGF in terms of basal area, while slow species might dominate (Panama) or co-dominate (three remaining forests) in terms of stem numbers. Forest succession in Yucatán does not show clear successional shifts in demographic groups. This forest stands out because it occurs in a landscape that has been shaped by Mayan agriculture for several thousand years (Torrescano-Valle & Islebe, 2015). This suggests that there is no systematic difference in successional patterns between wet and dry forests, but rather between forests that experience disturbances of different intensity and frequency. Future studies will be able to test this hypothesis as more forest inventory data become available.

Given that LLP species seem to be an integral and dominant component of many late-successional and old-growth tropical forests, we should revise our conceptual understanding of forest succession to incorporate this finding and not rely on the complete disappearance of LLP species as a criterion for the definition of OGFs (Hartshorn, 1978; Wirth et al., 2009). Instead, we suggest a focus on structural criteria for the classification of a forest as "old-growth" (Mosseler et al., 2003). Most importantly, the definition of consistent demographic strategies that show clear dominance shifts across succession substantially improves the mechanistic understanding and predictability of Neotropical forest dynamics (Rüger et al., 2020).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data supporting the results (original and transformed demographic rates, sample sizes, weights, demographic group classification, abundance and basal area in 10-year time intervals for each species) are available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.2280gb5x4), and the related software is published at Zenodo (https://doi.org/10.5281/zenodo.7614822).

ORCID

Nadja Rüger https://orcid.org/0000-0003-2371-4172
Markus E. Schorn https://orcid.org/0000-0002-2510-3239
Robin L. Chazdon https://orcid.org/0000-0002-7349-5687
Jorge A. Meave https://orcid.org/0000-0002-6241-8803
Rodrigo Muñoz https://orcid.org/0000-0001-9434-0126
Michiel van Breugel https://orcid.org/0000-0003-2778-7803
Dylan Craven https://orcid.org/0000-0003-3940-833X
Bruno Hérault https://orcid.org/0000-0002-6950-7286
Lourens Poorter https://orcid.org/0000-0003-1391-4875
Masha T. van der Sande https://orcid.org/0000-0002-6845-2308
Daisy H. Dent https://orcid.org/0000-0002-1219-7344

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BIOSKETCH

This research team aims to gain a better understanding of how tropical forests recover after natural disturbances or the abandonment of agricultural land use. They combine empirical approaches and mechanistic modelling to uncover patterns, drivers and mechanisms of tropical forest succession, primarily in the Neotropics, but also in Africa and Asia.

SUPPORTING INFORMATION

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