

1 **TITLE**

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

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57 **ABSTRACT**

58 Secondary tropical forests play an increasingly important role for carbon budgets and  
59 biodiversity conservation. Understanding successional trajectories is therefore imperative for  
60 guiding forest restoration and climate change mitigation efforts. Forest succession is driven by  
61 the demographic strategies – combinations of growth, mortality and recruitment rates – of the  
62 tree species in the community. However, our understanding of demographic diversity in tropical  
63 tree species stems almost exclusively from old-growth forests. Here, we assembled  
64 demographic information from repeated forest inventories along chronosequences in two wet  
65 (Costa Rica, Panama) and two dry (Mexico) Neotropical forests to assess whether the range of  
66 demographic strategies present in a community shifts across succession. We calculated  
67 demographic rates for >500 tree species while controlling for canopy status to compare  
68 demographic diversity in early successional (0-30 years), late successional (30-120 years) and  
69 old-growth forests. We quantified demographic diversity using two-dimensional hypervolumes  
70 of pairs of demographic rates and assessed whether shifts in demographic strategies were  
71 caused by intra-specific changes in demographic rates across succession or by species turnover.  
72 We expected that demographic strategies would shift from faster life-histories (fast growth,  
73 high mortality, high recruitment) in early successional forests to slower life histories (slow  
74 growth, low mortality, low recruitment) in old-growth forests and that shifts would be stronger  
75 in wet than in dry forests due to more pronounced differences in environmental conditions  
76 between early successional and old-growth forests. We also expected that demographic  
77 diversity would increase with succession. We found that demographic strategies largely  
78 overlapped across successional stages and that early successional stages already covered the  
79 full spectrum of demographic strategies found in old-growth forests. An exception was a group  
80 of species characterized by exceptionally high mortality rates that was confined to early  
81 successional stages in the two wet forests. Demographic diversity did not increase with  
82 succession. Our results suggest that current understanding of demographic strategies of tropical

83 tree species, which has been generated mostly from long-term forest monitoring plots in old-  
84 growth forests, is largely representative of demographic diversity in general, and that  
85 demographic diversity recovers quickly during succession.

86 **KEYWORDS**

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

## 89 INTRODUCTION

90 Tropical forests store almost half of global forest carbon and harbor a large proportion of the  
91 world's biodiversity (Pan *et al.* 2011, Slik *et al.* 2015, FAO 2020). With only one third of  
92 tropical forests being undisturbed primary forests and rates of deforestation remaining high  
93 (Pan *et al.* 2011, FAO 2020), secondary tropical forests regrowing after land abandonment are  
94 of increasing importance for carbon storage and sequestration as well as biodiversity  
95 conservation (Chazdon *et al.* 2016, Arroyo-Rodríguez *et al.* 2017, Lewis *et al.* 2019, Rozendaal  
96 *et al.* 2019). Understanding successional trajectories is therefore imperative for guiding efforts  
97 of forest management and global change mitigation. Amongst a variety of factors, successional  
98 dynamics in a community are driven by the demographic strategies (or life-history strategies)  
99 of the component tree species (*sensu* Finegan 1996). However, empirical knowledge of how  
100 community-wide variation in demographic strategies changes along successional gradients  
101 remains limited.

102 Demographic strategies emerge from trade-offs that all organisms are faced with when  
103 allocating limited resources between fast growth, high survival or reproductive success (Stearns  
104 1992, Metcalf & Pavard 2007) and that constrain the range of viable combinations of these  
105 demographic rates (Salguero-Gómez *et al.* 2016, Rüger *et al.* 2018). Recently, comparative  
106 analyses of life-history variation have improved our understanding of the consistency of  
107 demographic trade-offs structuring tropical forest communities (Kambach *et al.* 2022, Russo *et al.*  
108 *et al.* 2021). However, most of our knowledge on demographic strategies stems from old-growth  
109 forests and it remains unknown how demographic diversity (i.e., community-wide variation in  
110 demographic strategies) in secondary forests compares to old-growth forests. Specifically, it is  
111 unclear whether certain demographic strategies are confined to certain successional stages.

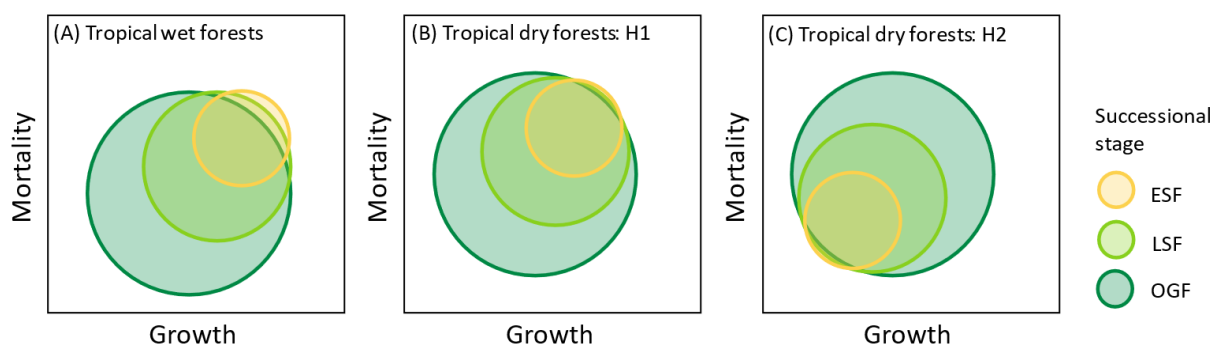
112 As an example, Finegan (1996) describes Neotropical forest succession as the consecutive  
113 replacement of species with different life-history strategies, where early successional pioneer

114 species will dominate the very first decades of succession but disappear later in succession.  
115 While we know that some early successional species can also occur in treefall gaps in old-  
116 growth forests (Schnitzer & Carson 2001), it is unclear whether there are species with unique  
117 demographic strategies that rely on large-scale disturbances for regeneration and therefore  
118 occur uniquely in early successional forests. If so, they might remain undetected when  
119 focussing tree demographic research exclusively on old-growth forests and important  
120 ecological processes might be overlooked.

121 In tropical wet forests, early successional environments are characterized by high resource  
122 levels (especially in terms of light availability; Montgomery & Chazdon 2001). Species that  
123 occur abundantly in these environments are, thus, commonly thought to trade off high growth  
124 and recruitment for high mortality rates (Tilman 1988, Finegan 1996, Chazdon 2014). These  
125 fast demographic rates are related to acquisitive values of functional traits such as low wood  
126 density or high specific leaf area and leaf nutrient content (Wright *et al.* 2010, Rüger *et al.* 2012,  
127 Rüger *et al.* 2018). On the other hand, species that are more abundant in late successional  
128 environments are expected to grow slowly but invest more resources in the ability to live for a  
129 long time, represented by trait values indicative of resource conservation such as high wood  
130 density or low specific leaf area (Tilman 1988, Finegan 1996, Chazdon 2014).

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

139 In tropical dry forests, where water is considered a more important resource in shaping forest  
140 communities than light availability, early successional stages are characterized by dry and hot  
141 conditions changing towards moister and cooler environments as succession proceeds (Lebrija-  
142 Trejos *et al.* 2011, Pineda-García *et al.* 2013). Therefore, trait values have been found to reflect  
143 a shift from strategies associated with greater resource conservation and drought tolerance early  
144 in succession to more acquisitive strategies (e.g. lower wood density, leaf dry matter content)  
145 later in succession (Lebrija-Trejos *et al.* 2010, Lohbeck *et al.* 2013, Buzzard *et al.* 2016,  
146 Derroire *et al.* 2018, Poorter *et al.* 2019). However, acquisitive leaf trait values related to light  
147 capture efficiency (e.g. high specific leaf area) have also been found to decrease during  
148 succession (Lohbeck *et al.* 2013, Derroire *et al.* 2018), making unclear whether successional  
149 shifts towards more conservative (H1) or more acquisitive (H2) demographic strategies should  
150 be expected in tropical dry forests ( **Figure 1B & C**).



151 **Figure 1:** Hypotheses for potential shifts of the ranges of demographic strategies from early successional forests  
152 (ESF) to late successional forests (LSF) and old-growth forests (OGF) for (A) tropical wet forests and (B, C) tropical  
153 dry forests. H1 (B) and H2 (C) represent opposing hypotheses for tropical dry forests. It is not clear whether shifts  
154 from acquisitive to conservative demographic strategies or vice versa are to be expected since wood density and  
155 leaf dry matter content have been found to shift from conservative to acquisitive values, whereas specific leaf  
156 area has been found to shift from acquisitive to conservative values. Axis labels can be any combination of  
157 growth, mortality or recruitment since e.g. high values for all three demographic rates are expected in wet ESF.  
158

159 Environmental differences between early and late successional tropical dry forests are thought  
160 to be less pronounced compared to wet forests mainly due to greater canopy openness (Ewel  
161 1977, Lebrija-Trejos *et al.* 2011). Indeed, Letcher *et al.* (2015) have observed a trend towards  
162 less successional habitat specialization among tree species in certain tropical dry forests. Based  
163 on this, we hypothesize that potential shifts in demographic strategies may be less pronounced

164 in dry than in wet forests. However, as the horizontal and vertical heterogeneity of light  
165 availability increases across succession in both forest types, we hypothesize that the range of  
166 viable demographic strategies extends as succession progresses ( **Figure 1**).

167 Here, we assemble a unique chronosequence dataset of repeated forest inventories from four  
168 Neotropical forests varying in rainfall. We calculate demographic rates for >500 tree species  
169 and use hypervolumes to quantify demographic diversity in three successional stages. We  
170 address the following questions: (a) Do ranges of demographic strategies shift across  
171 succession in wet and dry tropical forests? (b) If so, are these shifts due to intra-specific changes  
172 in demographic rates across succession or due to species turnover? (c) Does demographic  
173 diversity increase with succession? Answers to these questions will reveal to what degree our  
174 understanding of demographic diversity gained from old-growth forests can be extended to  
175 secondary forests, for which much less information on demographic rates and strategies is  
176 available. This information will enhance our understanding of underlying mechanisms and  
177 improve our ability to predict successional dynamics in tropical forests with the help of  
178 demographic forest models.

## 179 **MATERIALS AND METHODS**

### 180 **Study sites and forest inventory data**

181 We used inventory data from nine long-term forest monitoring projects along chronosequences  
182 from four Neotropical lowland forest sites located in Costa Rica, Panama and Mexico. The sites  
183 differ in rainfall with mean annual precipitation ranging from 3,900 mm without any dry season  
184 to 900 mm with 90 % of annual rainfall occurring within 5.5 months of the year (**Table 1**). The  
185 forest in Costa Rica is a tropical wet evergreen broadleaved forest with a high proportion of  
186 palms (Clark & Clark 2000, Chazdon *et al.* 2007, Letcher & Chazdon 2009). The forest in  
187 Panama is a semideciduous tropical moist forest with a 3-month dry season (Denslow &  
188 Guzman 2000, van Breugel *et al.* 2013, Condit *et al.* 2019). The predominant natural



189 disturbance regime in both wet sites are occasional windthrows and lightning strikes. The two  
 190 sites in Mexico are both deciduous tropical dry forest differing from the wet sites in shorter  
 191 stature, higher canopy openness and lower species richness (**Table 1**; Letcher *et al.* 2015).  
 192 Forests in the Yucatán peninsula have undergone anthropogenic influences since ancient Mayan  
 193 times and experience regular strong wind storms (Rico-Gray & García-Franco 1991,  
 194 Hernández-Stefanoni *et al.* 2014, Saenz-Pedroza *et al.* 2020). The forest in Oaxaca is shorter in  
 195 height, has arborescent cacti and has been only mildly affected by human disturbances (Lebrija-  
 196 Trejos *et al.* 2008, Pérez-García *et al.* 2010, Gallardo-Cruz *et al.* 2010).

197 **Table 1:** Location, mean annual temperature (MAT), mean annual precipitation (MAP), dry season length  
 198 (<100mm precipitation per month), number of species, number of species with 10 or more individuals, average  
 199 old-growth forest (OGF) canopy height and length of the chronosequences used in this study. Note that the  
 200 sampling area differs strongly between sites and the number of species included in the analyses may not be  
 201 indicative of total species richness.

	Location	MAT (°C)	MAP (mm)	Length of dry season (months)	Number of species (N ≥ 10)	OGF canopy height* (m)	Chronosequence length
<b>Costa Rica</b>	10°26' N, 84°00' W	26	3.900	-	485 (355)	20-35	1-57 years + OGF
<b>Panama</b>	9°90' N, 79°51' W	27	2.600	3	470 (391)	15-28	0-120 years + OGF
<b>Yucatán, Mexico</b>	20°05' N, 89°29' W	26	1.100	6	154 (106)	8-13	3-85 years
<b>Oaxaca, Mexico</b>	16°39' N, 95°00' W	28	900	7	125 (90)	7-8	4-70 years + OGF

202 \*Canopy heights are from Clark *et al.* (2021), Mascaro *et al.* (2011), Dupuy *et al.* (2012) and Lebrija-Trejos *et al.*  
 203 (2008).

204 The four chronosequence sites comprised a total of 252 secondary forest plots and 23 old-  
 205 growth forest plots ranging in size from 0.04 ha to 50 ha (Table S1, Figure S1). Plots are located  
 206 in complex landscapes mainly consisting of fragments of old-growth and second-growth forest,  
 207 plantations, agricultural land and pastures. Most secondary forest plots were established on  
 208 abandoned agricultural land used primarily for low-intensity crop farming or cattle ranching  
 209 (Denslow & Guzman 2000, Chazdon *et al.* 2007, Letcher & Chazdon 2009, Lebrija-Trejos *et al.*  
 210 *et al.* 2011, van Breugel *et al.* 2013). Some plots were only clear cut but not farmed (Chazdon *et*

211 *al.* 2007, Letcher & Chazdon 2009). In general, previous forest vegetation was completely  
212 removed, yet in a few cases some remnant trees remained, which we excluded from the  
213 analyses. The age of the youngest plots ranged from 0 to 4 years across sites, whereas the oldest  
214 secondary forest plots ranged from 57 to 120 years after agricultural abandonment (Figure S2).  
215 All free-standing woody individuals above the plot-specific size threshold (generally 1 or 5 cm  
216 diameter at breast height (dbh); range: 1-10 cm dbh, Table S1) were measured, marked and  
217 remeasured 1 to 10 years later. We selected census intervals of 5 years, if possible (range: 4-10  
218 years, Table S1). In the wet sites (Costa Rica, Panama), only the largest stem of an individual  
219 was measured in some plots. In the dry sites (Yucatán, Oaxaca), where resprouting is an  
220 important mode of regeneration and, thus, multi-stemmed individuals are abundant (Vieira &  
221 Scariot 2006), all stems of an individual were measured, but not individually marked.  
222 We assigned all census intervals to one of three successional stages (Figure S2). Census  
223 intervals from secondary forest plots ending less than 30 years after abandonment were  
224 classified as early successional forests (ESF) and intervals ending less than 120 years after  
225 abandonment were classified as late successional forests (LSF), although most plots were not  
226 older than 90 years. Census intervals from old-growth forest plots were classified as old-growth  
227 forests (OGF). Data from old-growth forests in Yucatán was not available to sufficient extent.

## 228 **Canopy layer assignment**

229 Growth and mortality rates of individual trees depend on their size and light availability. To  
230 account for these differences, we assigned trees to discrete canopy layers based on their size  
231 and the size of their neighbors following the Perfect Plasticity Approximation approach of  
232 Purves *et al.* (2008) and Bohlman & Pacala (2012). To do this, we first divided all plots into  
233 subplots that were either predefined by the sampling design, or trees were assigned to subplots  
234 based on their spatial coordinates. The size of these subplots ranged from 625-1000 m<sup>2</sup> in wet  
235 sites (except for a 100 m<sup>2</sup> plot in a <20 year old forest) depending on the sampling design and

236 plot sizes (Table S1). In the dry sites, where trees are generally smaller than in wet forests,  
237 subplot sizes ranged from 100-125 m<sup>2</sup> except for some 400 m<sup>2</sup> plots in Yucatán (Table S1).  
238 Next, we sorted trees by dbh of the largest living stem within subplots. We then estimated the  
239 crown area for all trees using allometric equations (see SI Methods). Starting from the largest,  
240 we assigned trees to the top canopy layer (layer 1) as long as the cumulative estimated area of  
241 their crowns did not exceed the subplot area. Smaller trees were successively assigned to lower  
242 canopy layers in the same way. Calculating demographic rates in discrete canopy layers has  
243 proven useful in capturing variance in demographic strategies between co-occurring species  
244 (Bohlman & Pacala 2012, Rüger *et al.* 2018) and in predicting forest dynamics (Rüger *et al.*  
245 2020).

#### 246 **Demographic rates**

247 We calculated demographic rates for species with interpretable stem growth, i.e. excluding  
248 palms and hemi-epiphytes. We determined dbh increment and mortality for all observations  
249 and subsequently calculated species-level annual growth and mortality rates for each canopy  
250 layer and successional stage. Individual annual tree growth  $g_i$  was calculated as

(Equation 1) 
$$g_i = \frac{size_2 - size_1}{t}$$

251 with *size* being the dbh of the largest living stem of an individual in wet sites and dbh equivalent  
252 of the total basal area (ba) of all living stems of an individual in dry sites in the first and second  
253 census, respectively, and  $t$  being the time elapsed between the two size measurements in years.  
254 We used dbh equivalent of the total basal area as the measure of size because in the dry sites,  
255 stems were not individually marked and, thus, stem-level dbh growth could not be calculated.  
256 Species-level growth rates per canopy layer ( $g_{j,l}$ ) were calculated as the median growth of all  
257 individuals  $i$  of species  $j$  in layer  $l$ :

(Equation 2) 
$$g_{j,l} = \text{median}(g_{j,l,i})$$

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

(Equation 3)

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

259 with  $N_1$  being the number of living individuals in the first census,  $N_2$  being the number of  
260 individuals remaining alive in the second census and  $t$  being the mean census interval length in  
261 years (measured to the nearest day). Multi-stemmed individuals were deemed alive if at least  
262 one stem was alive and dead if all stems were dead.

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

(Equation 4)

$$r_j = \frac{N_{j,r}}{N_j}$$

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

### 273 **Quantification of demographic diversity**

274 We used two-dimensional hypervolumes based on gaussian kernel density estimations (Blonder  
275 *et al.* 2014) to represent and quantify diversity of demographic strategies spanning pairs of  
276 demographic rates: growth vs mortality, growth vs recruitment and mortality vs recruitment.  
277 Because many species did not occur in all canopy layers and species with non-observed values  
278 cannot be included in hypervolume analyses, we calculated hypervolumes using only growth  
279 and mortality rates from a single canopy layer. Only species with at least 10 or 5 observations

280 for mortality per canopy layer were included in the analyses for wet and dry sites, respectively.  
281 Species with mortality rates of 0 or 1 or with recruitment rates of 0 were excluded from the  
282 respective hypervolumes. A total of 353, 503 and 463 species met the criteria for inclusion in  
283 the analyses in canopy layers 1, 2 and 3, respectively. We used growth and mortality rates from  
284 canopy layer 2 to maximize the number of species included in the analyses (Tables S3-S5). To  
285 ensure representability, we also examined hypervolumes using growth and mortality rates from  
286 canopy layers 1 and 3.

287 We natural log transformed all demographic rates to ensure approximate gaussian multivariate  
288 distributions. We estimated kernel bandwidths (the parameter defining the smoothness of the  
289 probability densities) for each hypervolume per site using the cross-validation method (Duong  
290 2007, Blonder *et al.* 2014). We used the same bandwidths for all successional stages per site to  
291 ensure comparability among sites (Blonder 2018). Hypervolume boundaries represent the  
292 smallest volume that captures 80% of the total probability densities. All species contributed  
293 equally to the hypervolume calculations. We used the *hypervolume* R package (version 3.0.4)  
294 for all analyses (Blonder *et al.* 2014). We also report demographic spaces with underlying  
295 abundance heatmaps to indicate observed shifts in the dominance of certain demographic  
296 strategies.

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

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

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

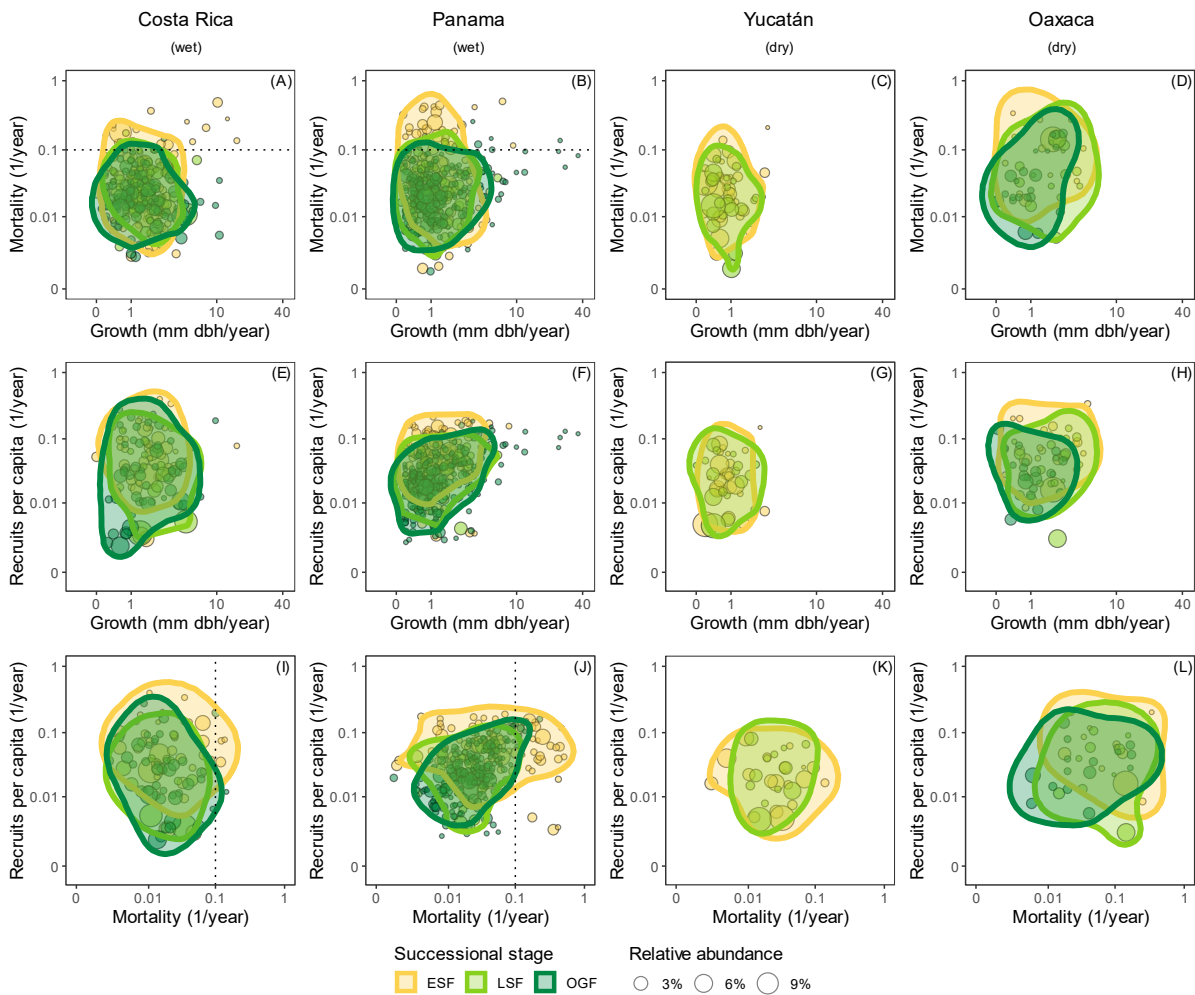
## 317 **RESULTS**

318 We used 1,385,018 observations from 352,243 individual trees to calculate demographic rates  
319 for a total number of 503 species from 77 families. The number of individual trees ranged from  
320 3,302 in Oaxaca to 312,328 in Panama (Table S2).

### 321 **Overlap in demographic strategies across succession**

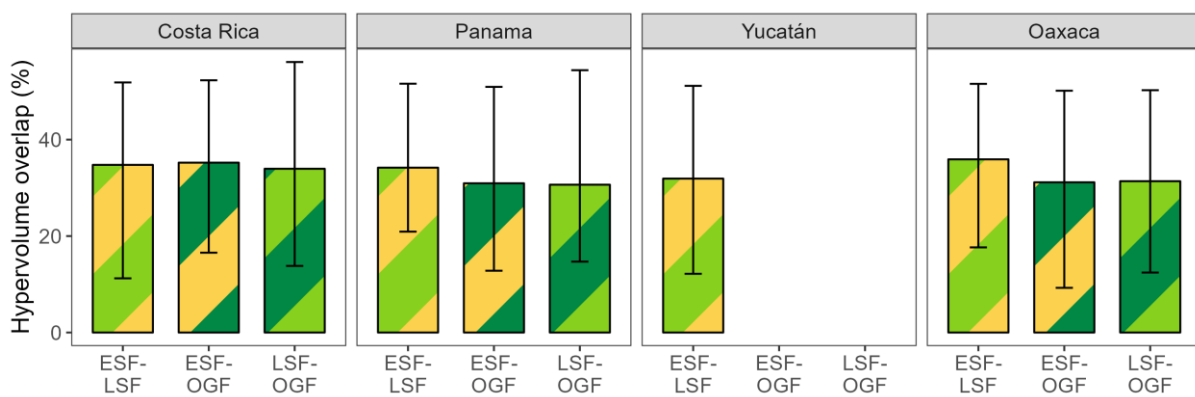
322 In all forest sites, the ranges of demographic strategies present in the three successional stages  
323 largely overlapped (**Figure 2**), except for recruitment rates that shifted slightly towards fewer  
324 recruits during succession in all sites except Yucatán. In the wet sites, we found a demographic  
325 strategy exclusive to early successional forests, which was primarily associated with  
326 exceptionally high mortality rates of 10% or more (**Figure 2A&B**). This group of high mortality  
327 species consisted of 17 and 28 species in Costa Rica and Panama, respectively. Many of these  
328 species are typically considered pioneer species (e.g. *Cecropia insignis*, *Ochroma pyramidale*,

329 *Trema integerrima*, *Byrsonima crassifolia*, *Conostegia xalapensis*, *Vernonanthura patens*,  
 330 *Vismia baccifera*, *Vismia macrophylla*; see Figures S15 & S16). Many species within this group  
 331 did not grow particularly fast, especially in Panama. In Costa Rica, no recruits were recorded  
 332 for most of the species in this group (**Figure 2I**), whereas in Panama, most of these species had  
 333 fairly high recruitment rates (**Figure 2J**).



345 slower growth during succession. In Oaxaca, but not in Yucatán, the range of mortality rates  
346 shifted slightly towards lower values in older forests. The range of growth and mortality rates  
347 was smaller in Yucatán compared to Oaxaca.

348 These results were robust to the choice of canopy layer (Figures S3-S5) and were not biased by  
349 the number of species included (Figure S6). The measured average hypervolume overlap across  
350 pairs of demographic rates between successional stages did not differ across sites and was also  
351 similar among all successional stages within sites (**Figure 3**Figure 6, Figure S7).



352

353 **Figure 3:** Mean overlap statistics of the two-dimensional hypervolumes representing the ranges of demographic  
354 strategies for all successional stages (ESF = early successional forest, LSF = late successional forest, OGF = old-  
355 growth forest). Colored bars represent the median rarefied and bootstrapped values, error bars represent 95%  
356 confidence intervals ( $r = 100$  replicates,  $n = 10$  species per successional stage). All values are means across pairs  
357 of demographic rates. Individual values per pair of demographic rates are given in Figure S7.

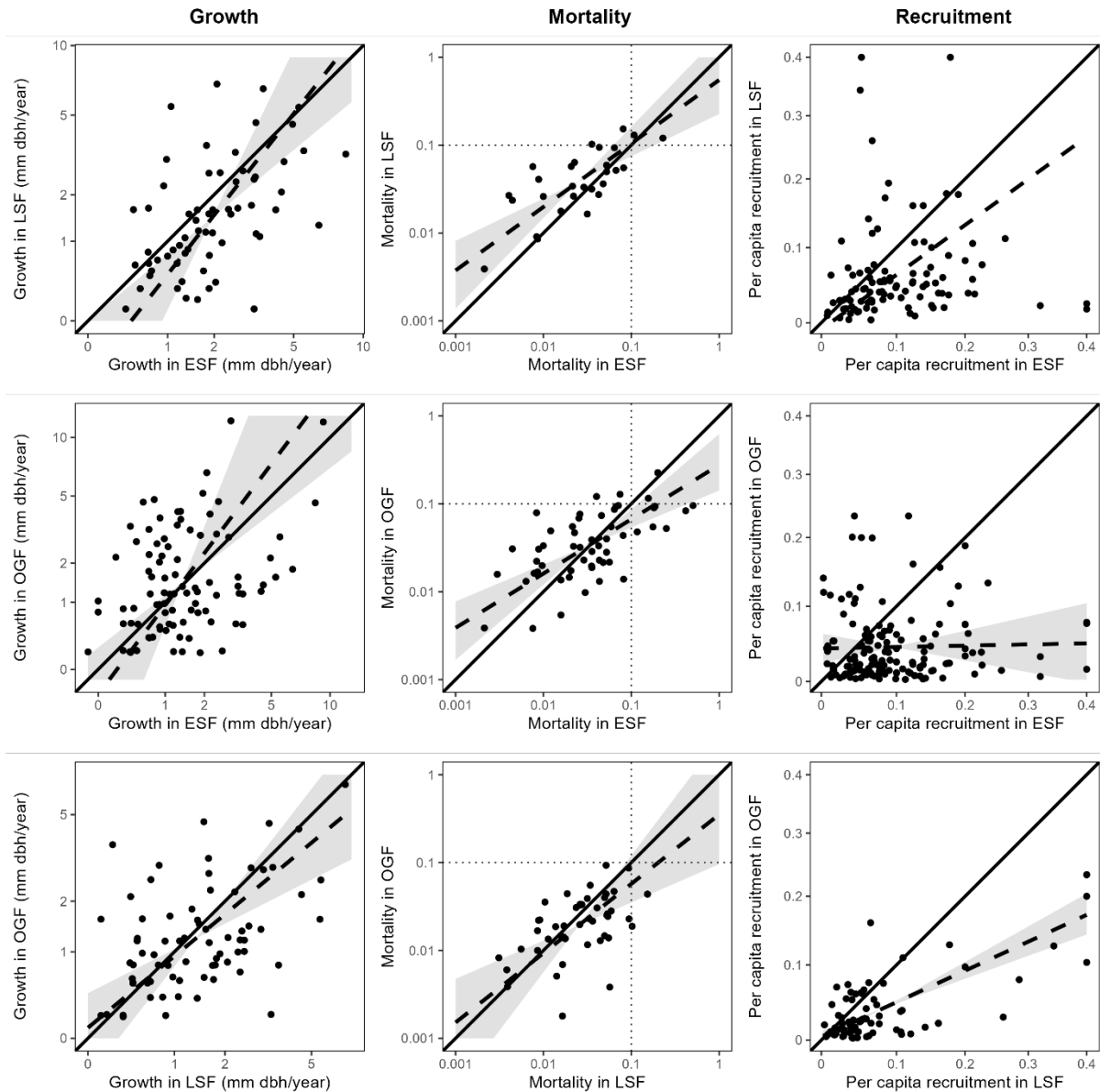
358 Except for Oaxaca, species abundance was more evenly distributed across the range of  
359 demographic strategies in early successional forests compared to later successional stages,  
360 where species with the highest abundances were more concentrated around conservative  
361 strategies (Figures S8-S11).

362 **Are shifts in demographic strategies due to intra-specific variation or due to species**  
363 **turnover?**

364 Overall, intra-specific variation in demographic rates across succession was low in all sites  
365 (**Figure 4**, Figures S12-S14). Especially growth and mortality rates were generally consistent  
366 across successional stages. In Panama and Oaxaca, recruitment rates were higher in secondary



367 forests than in old-growth forests (**Figure 4**, Figure S14), whereas in Costa Rica and Yucatán,  
368 results for the major axis regressions on recruitment rates were inconclusive (Figures S12 &  
369 S13).

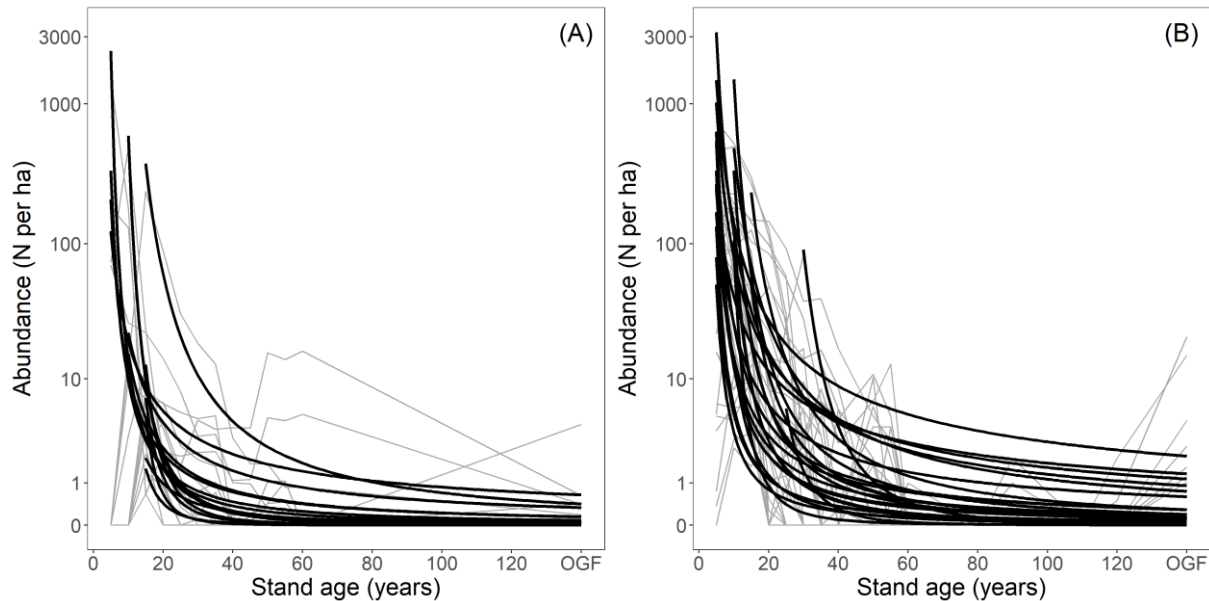


370

371 **Figure 4:** Major axis regressions for species' demographic rates in early successional forests (ESF), late  
372 successional forests (LSF) and old-growth forests (OGF) in Panama (for other sites see Figures S12-S14). Each  
373 point represents a species and its demographic rates in the respective successional stage. Solid lines represent  
374 the 1:1-line, dashed lines represent the major axis regression lines and areas highlighted in grey represent the  
375 confidence intervals. Growth and mortality rates are from canopy layer 2. Only species with at least 5  
376 observations for growth and survival in both successional stages were included, respectively. If no confidence  
377 intervals are given, the model was not statistically significant (i.e., the variables are unrelated,  $p \geq 0.05$ ).

378 Most of the species that exhibited an exclusive demographic strategy (i.e., species with  
379 mortality >10% in wet ESF) decreased substantially in abundance during the first 30 years of

380 succession (**Figure 5**, Figures S15 & S16). In Costa Rica, only five out of the 17 species were  
381 also found in LSF (four species) or OGF (one species). In Panama, eleven out of the 28 species  
382 forming this group in ESF were also found in LSF (two species) or OGF (nine species), albeit  
383 at low abundances. Species from this group that were present in more than one successional  
384 stage generally had lower mortality rates in later successional stages (**Figure 4**, Figure S14).

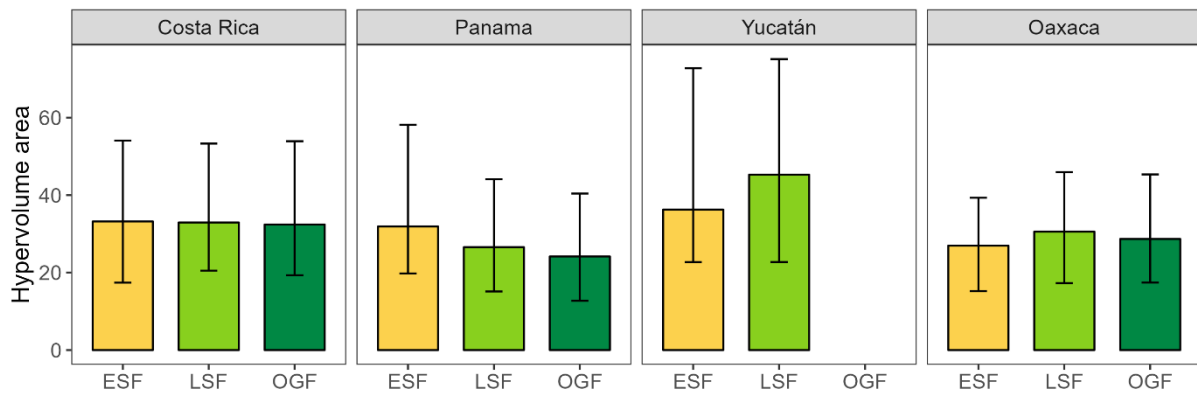


385

386 **Figure 5:** Observed (grey) and modelled (black) abundances > 1 cm dbh over time of species with annual mortality  
387 >10% exclusive to wet early successional forests in (A) Costa Rica and (B) Panama. Models are of the form  
388  $\ln(\text{abundance}) = a * \text{stand age}^b$ . Parameters *a* and *b* were estimated using the *nls* R function. The model did not  
389 converge for two species in Costa Rica and three species in Panama due to irregular patterns in abundance over  
390 time. The model does not accurately capture that one species in Costa Rica and seven species in Panama had  
391 increased abundances in OGF. Individual models are shown in Figures S15 and S16.

### 392 **Demographic diversity does not increase with succession**

393 We found that demographic diversity (quantified as the area of the 2-dimensional  
394 hypervolumes) did not increase with succession (**Figure 6**, Figure S17). In the wet sites,  
395 demographic diversity tended to decrease, but not significantly. In the dry sites, demographic  
396 diversity tended to increase, but not significantly.



397

398 **Figure 6:** Mean areas of the two-dimensional hypervolumes representing the ranges of demographic strategies  
399 for all successional stages (ESF = early successional forest, LSF = late successional forest, OGF = old-growth  
400 forest). Colored bars represent the median rarefied and bootstrapped values, error bars represent 95%  
401 confidence intervals ( $r = 100$  replicates,  $n = 10$  species per successional stage). All values are means across pairs  
402 of demographic rates. Individual values per pair of demographic rates are given in Figure S17.

## 403 DISCUSSION

404 We used demographic rates from 503 woody plant species to compare ranges of demographic  
405 strategies along successional gradients in four Neotropical forests. Contrary to our expectations,  
406 we found not only that demographic strategies largely overlapped across successional stages,  
407 but also that the amount of demographic diversity was similar along succession. Interestingly,  
408 we found a group of species with exceptionally high mortality rates that occurred exclusively  
409 in early successional forests in wet sites. Our results suggest that insights gained from analyses  
410 of demographic rates in old-growth forests are largely representative for forests of all  
411 successional stages, with the exception of a strategy associated with high mortality that, in wet  
412 forests, only occurs in early successional forests.

### 413 **Demographic strategies largely overlap across succession**

414 In contrast to our expectations, we found large amounts of overlap of demographic strategies  
415 across successional stages in all four sites. Almost all demographic strategies that were present  
416 in old-growth forests were present in secondary forests after 30 years of succession in both wet  
417 and dry tropical forests. This could suggest that most species, regardless of their life-history  
418 strategies, can establish in early successional forests as long as their seeds reach the site, and  
419 highlight the importance of stochastic processes in general and of dispersal limitation in

420 particular for successional trajectories (Chazdon 2008, Norden *et al.* 2015, Dent & Estrada-  
421 Villegas 2021). At the same time, tropical wet forests recover quickly and the range of  
422 microsites that can develop during the first 30 years of succession may accommodate the full  
423 range of demographic strategies exhibited by species that occur in older forests. This does not  
424 mean that abundances of species with different demographic strategies do not shift across  
425 succession (Rüger *et al.* 2022), but here we focus on the presence or absence of demographic  
426 strategies.

427 We found a shift towards lower recruitment rates during succession in all sites except Yucatán.  
428 Recruitment rates strongly depend on seedling performance and, hence, on resource (primarily  
429 light) availability at the forest floor (Montgomery & Chazdon 2001, Kitajima *et al.* 2013,  
430 Kupers *et al.* 2019). Because light availability at the forest floor decreases during succession  
431 (Denslow & Guzman 2000), recruitment rates are predicted to do the same.

432 In Oaxaca, the driest forest site, the range of demographic strategies shifted slightly towards  
433 lower growth, mortality and recruitment rates, i.e., towards more conservative life-history  
434 strategies during succession. In Yucatán, the second dry forest site, however, we detected a  
435 slight shift towards higher recruitment, hindering our ability to generalize more broadly from  
436 our results. The forest in Yucatán stands out in that it occurs in a landscape that has been shaped  
437 by human land use for many centuries. Thus, the pool of tree species might have been restricted  
438 over time to those species that are able to cope with frequent disturbance, including the ability  
439 to resprout (Rico-Gray & García-Franco 1991, Kammesheidt 1999, Sanaphre-Villanueva *et al.*  
440 2017). This is also indicated by the smaller range of growth and mortality rates of the dry forest  
441 in Yucatán compared to that of Oaxaca.

#### 442 **Species with high mortality rates are exclusive to early succession in wet forests**

443 We expected to find the most acquisitive demographic strategies with highest growth, mortality  
444 and recruitment rates in early successional wet forests. Yet, the group of species exclusively

445 observed in these forests was associated with high mortality and moderately high recruitment  
446 rates, but not particularly with fast growth. Potentially, higher growth rates might be masked  
447 because the entire lifecycle of these short-lived species is completed within the early  
448 successional stage (0-30 years since abandonment), including senescent stages when growth  
449 might decline.

450 Although some of these high-mortality species were highly abundant in early successional  
451 forests, no recruits were recorded for most of them in Costa Rica. Here, recruitment rates might  
452 be less informative than in other forests because only a few plots that were 12 years or older  
453 had information on trees  $\geq 1$  cm dbh and met our criterion for the calculation of recruitment  
454 rates (Table S1). Additionally, recruitment in the plots at the La Selva Biological Station  
455 (referred to in Table S1 as Sarapiquí) is known to be affected by collared peccaries (Kuprewicz  
456 2013). Given their high abundance during the first ~15 years of succession, many of the high-  
457 mortality species might actually have similarly high recruitment rates in early successional  
458 forests as many of the high-mortality species in Panama, where data availability was more  
459 consistent throughout the chronosequence. Hence, in contrast to common assumptions, early  
460 successional specialist demographic strategies might trade off high mortality for high  
461 recruitment rather than consistently high growth rates.

462 In tropical dry forests, species that are present in early successional forests can persist for a  
463 longer time and do not have a unique demographic strategy. Because of a lower and (seasonally)  
464 more open canopy, early and late successional environments are less contrasting in dry  
465 compared to wet forests (Lebrija-Trejos *et al.* 2011, Letcher *et al.* 2015). Moreover, many  
466 resprouting species in early successional forests might in fact be species that were abundant  
467 pre-disturbance and therefore follow demographic strategies associated with late successional  
468 environments (Boucher *et al.* 2001, Lebrija-Trejos *et al.* 2008). Additionally, resprouting trees  
469 in early successional forests likely rely on belowground carbohydrate reserves of the old root

470 system and therefore might have similar demographic rates as in old-growth forests (Poorter *et*  
471 *al.* 2010).

### 472 **Shifts in demographic strategies are mainly due to species turnover**

473 The shifts that we identified mainly relate to the loss of a group of species with exceptionally  
474 high mortality rates (>10%), that is present only in early successional tropical wet forests. The  
475 majority of species within this group did not persist in later successional stages, suggesting that  
476 their disappearance is primarily due to species turnover as projected by Finegan (1996).  
477 However, the few species from this group that are present in old-growth forests do exhibit lower  
478 mortality rates there, indicating that both species turnover as well as intra-specific variation  
479 contribute to this process.

### 480 **Demographic diversity does not increase with succession**

481 Counter to our expectations, we did not find a general pattern of increasing diversity in  
482 demographic strategies during succession. Indeed, demographic diversity seems to recover to  
483 old-growth forest values within the first 30 years of succession. Similarly, Poorter *et al.* (2021)  
484 found that structural heterogeneity and species richness in secondary tropical forests recovered  
485 to 90% of old-growth forest values at around 30 years after abandonment, whereas species  
486 composition only recovered after more than a century (Poorter *et al.* 2021). This suggests that  
487 demographic diversity is more closely linked to species richness than to species composition,  
488 indicating that many different species exhibit similar demographic strategies and fill similar  
489 demographic niches.

### 490 **Limitations**

491 When interpreting our results, it should be considered that we use a chronosequence approach  
492 that substitutes space for time and thus infers temporal trends from static data (Foster & Tilman  
493 2000, Johnson & Miyanishi 2008, Walker *et al.* 2010). Moreover, data availability as well as  
494 data collection methodologies varied widely across sites (Figure S1), and plots within each

495 chronosequence also varied in extent and minimum dbh threshold (Table S1). Nevertheless, our  
496 results are robust to this heterogeneity and independent from the number of species included  
497 (e.g. Figure S6).

## 498 **CONCLUSION**

499 Overall, we find that secondary forests harbor similar levels of demographic diversity as old-  
500 growth forests, indicating that early successional stages already contain the full spectrum of  
501 life-history strategies found in old-growth forests, and that demographic data from old-growth  
502 forests is surprisingly informative for understanding the diversity of demographic strategies in  
503 tropical forests in general. Our results also suggest that the recovery of demographic diversity  
504 is more closely linked to species richness than to species composition. Lastly, our results  
505 indicate that, contrary to common assumptions, early successional specialists in tropical wet  
506 forests trade off high mortality for high recruitment rates rather than consistently fast growth,  
507 at least when integrating over 30 years of successional development.

508 Our results enrich the current understanding of tropical secondary succession by using a  
509 demographic perspective that evaluates mechanisms that underpin succession. As ranges of  
510 demographic rates are similar and species-specific demographic rates are largely consistent  
511 across succession, we argue that demographic information from old-growth forests can be used  
512 to predict successional changes in the dominance of different species or species groups and to  
513 estimate future tropical forest carbon stocks with the help of demographic forest models (Purves  
514 *et al.* 2008, Rüger *et al.* 2020), especially for tropical dry forests. Accurate predictions of early  
515 successional dynamics in tropical wet forests, however, likely rely on information about  
516 demographic strategies that occur uniquely during the first 30 years of succession.

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#### 546 **CONFLICT OF INTEREST**

547 The authors declare no competing interests.

#### 548 **AUTHOR CONTRIBUTIONS**

549 The idea for this study was conceived during a workshop attended by LA, FB, RLC, DC, CEF,  
550 BH, CCJ, SK, JAM, RM, NN, LP, NR, MES, MvB and MTvdS. RLC, DC, DHD, DD, SJD,  
551 JMD, BF, JSH, JLHS, ORL, JAM, RM, and MvB contributed data. MES, NR and SK prepared  
552 forest inventory data for analysis and calculated demographic rates. MES analysed the data.  
553 MES wrote the first draft of the manuscript with support from NR. All authors contributed  
554 critically to the drafts and gave final approval for publication.

#### 555 **DATA AVAILABILITY STATEMENT**

556 Should the manuscript be accepted, the data supporting the results will be archived in an  
557 appropriate public repository (e.g. Dryad) and the data DOI will be included at the end of the  
558 article.

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