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Demographic Variation and Demographic Niches of Tree Species in the Barro Colorado Forest

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ABSTRACT. A principal goal for the 50-ha plot on Barro Colorado Island has been to understand demographic variability across the entire community of tree species. Early work used a gap-shade dichotomy, but both recent improvements in statistical methods have quantified the response of growth, survival, and recruitment to light across the entire community. These studies document the trade-off between fast growth in high light and long life in deep shade: response of growth and recruitment to light are correlated with mortality across species. Here we add a matrix analysis of expected adult lifespan of 31 dominant canopy species spanning the range of growth-mortality variation and demonstrate that the trade-off between high growth and long lifespan does not lead to equal population fitness. Instead, we find that expected adult lifespan of saplings is shorter in fast-growing pioneers than in long-lived shade-tolerant species. If reproductive output were equal across the growth-mortality axis, pioneer species could not persist. This suggests that pioneers out-reproduce shade-tolerant species.

Keywords: tropical tree demography; lifespan; mortality; Barro Colorado 50-ha plot

INTRODUCTION

From the outset, the 50-ha plot on Barro Colorado Island (BCI) included the goal of understanding how the demography of different tree species responds to variation in light environment in the forest, thus testing how species partition the regeneration niche created by high light below canopy openings (Grubb, 1977; Hartshorn, 1980; Denslow, 1980). A familiar paradigm in tree life history contrasts species that are tolerant of deep forest shade with those that regenerate only in clearings formed when trees die. This contrast in life history offers a way for species to coexist along the light gradient from shade to small gap and large gap (Denslow, 1980; Brokaw, 1985; Pacala and Rees, 1998). With a 50-ha census of more than 200,000 individual trees, Hubbell and Foster (1985) intended to assess life-history niches in most of the forest species. In contrast, most attempts to examine life-history variation in diverse tropical forests include only a handful of species (e.g., Brokaw, 1987; Denslow, 1990; Brown and Whitmore, 1992; Kobe, 1999; Svenning, 2000; Dalling et al., 2004; Balderrama and Chazdon, 2005).

Understanding the regeneration niche required detailed measurements of the light environment, and Hubbell and Foster (1986) included a map of light gaps from the

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outset of the project, estimating the density of vegetation above each corner of a 5 × 5 m grid over all 50 ha. Using this map, Welden et al. (1991) compared recruitment, growth, and survival rates in gaps versus shade for more than half the species in the forest. The definition of a gap in Welden et al. was strictly dichotomous: gaps were sites with no vegetation more than 10 m above the ground, and everywhere else was non-gap. In Condit et al. (1996), Welden's index of gap preference based on recruitment was combined with growth and survival rates to assign tree species into demographic guilds reflecting shade-tolerance and growth rate, again including more than half of the plot's species.

Starting with Condit et al. (2006), we incorporated Bayesian methods to improve species-level estimates of demographic rates and to accurately estimate the variance of rates across the community. We studied the entire community simultaneously, estimating the distribution of demographic rates across all species. This allowed rare species to be included, and because sampling error was modeled explicitly, extreme rates in rare species were avoided so that community-wide variation was estimated without bias. We subsequently refined a three-dimensional map of light across the 50 ha by integrating the vegetation profile at any point both horizontally and vertically, leading to a continuous estimate of vegetation density and thus light as a percent of full sun at every location (Rüger et al., 2009). Using the new map of light, Rüger et al. (2009, 2011a, 2011b, 2012) applied the community-level approach to estimate recruitment, growth, and mortality as a continuous function of light for 90% of the species in the 50-ha plot. This allowed us to define niche axes based on complete demographic profiles (Rüger et al., 2018).

Here we summarize demographic axes that combine growth, mortality, and recruitment, and we include in a data supplement complete tables of the demographic parameters that describe species responses to light. These offer users demographic traits for close to 90% of the 300 species in the plot (Rüger et al., 2022). Many future studies of morphology, physiology, or population biology of BCI trees can start with these (Rüger et al., 2020).

We then evaluate the fast-slow continuum of BCI trees by asking whether it works as a demographic equalizing axis. Equalization would mean that a high growth rate of pioneer species precisely compensates for their high death rate, so that saplings of pioneer and shade-tolerant species are equally likely to spend time at reproductive size. If so, and given equal reproductive output, the two groups of species would have equal population-level fitness. The general theory of a fast-slow life history continuum (e.g., Salguero-Gomez, 2017) appears to implicitly assume that high growth rate of pioneers compensates for their high death rates, allowing them to coexist with shade-tolerant species. This assumption can only be tested, however, by integrating lifetime growth and survival (Bruijning et al., 2017). We offer a test by estimating the reproductive lifetime of the average sapling in 31 abundant species, integrating lifetime growth and survival using matrix demography.

DEMOGRAPHIC RESPONSES TO LIGHT

We start by combining the results from Rüger et al. (2009, 2011a, 2011b) into axes describing the light response of recruitment, growth, and mortality (Fig. 1). The figures make it clear that there are no separate demographic categories: pioneers are simply species at the upper end of continuous variation, including the abundant *Miconia argentea* and *Cordia bicolor* (Fig. 1). Conversely, shade-tolerant species, such as *Prioria copaifera* and *Swartzia simplex*, are at the low end. Between those extremes, species are spread along the axis in ways that had not been appreciated. Forest dominants, such as *Trichilia tuberculata, Tabernaemontana arborea*, *Beilschmiedia tovarensis*, *Guatteria lucens*, and *Guarea guidonia*, all recruiting abundantly in the forest understory, are surprisingly divergent in demography (Fig. 1).

At the pioneer end of the axis, there are species having recruitment rates that increase >100-fold from shade (2% light) to high light (20%), and growth rates that increase by >6-fold (Fig. 1). Both recruitment and growth increased with light in nearly every species in the forest (Fig. 1). Even the tree species we know as shade-tolerant, including abundant canopy dominants, had recruitment and growth rates two- to four-fold higher in 20% light relative to shade (Fig. 1). We included a map in the supplement to Rüger et al. (2009) showing recruits to 1-cm diameter at breast height (dbh) of all species overlain on a map of light, and forest-wide recruitment is conspicuously concentrated in high light.

Previous studies on mortality of tropical trees in gap versus non-gap often reported higher mortality in shade (Augspurger, 1984; Kobe, 1999; Balderrama and Chazdon, 2005), but some results suggested the opposite (Fraver et al., 1998), and all considered seedlings only. The early study on gaps in the BCI plot (Welden et al., 1991) suggested higher mortality in gaps, although individual species did not have statistically significant responses. Our new results support Welden et al. (1991), demonstrating increased mortality with light in most species (Rüger et al., 2011). The mortality response to light was negatively correlated with growth and recruitment responses, meaning species with strong growth and recruitment responses tended to have smaller mortality responses, but mortality was elevated in response to light even in those light-demanding pioneers (Fig. 1c). A few highly shade-tolerant species, such as *Protium panamensis* and *Prioria copaifera*, had sapling mortality rates more than two-fold higher in 20% light compared with shade. Elevated mortality in high light could be caused by damage from tree or branch falls in gaps, and pioneer species might avoid the effect because they invade high light sites and grow upward quickly, avoiding the worst of the branch falls.

The correlation lines in Figure 1 depict primary axes of demographic variation, from slow to fast species (Stearns, 1999; Salguero-Gómez, 2017), and a trade-off between survival in the shade and growth (or recruitment) in high light (Reich, 2014; Rüger et al., 2018, 2020). There is a physiological understanding of the trade-off, because the shift to high growth requires traits

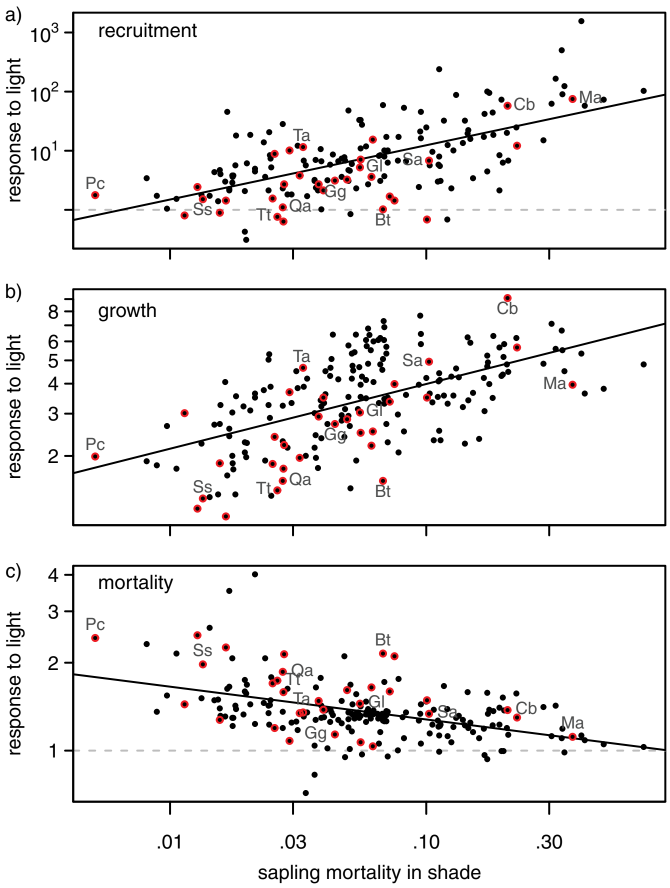

FIGURE 1. Demographic response to light as a function of mortality rate in the shade in the Barro Colorado Island 50-ha plot. The vertical axes are ratios of recruit density, dbh growth, or mortality at 20% versus 2% light; values >1 mean higher rates in high light. Mortality is the death rate of 1-cm saplings at 2% light. (**a**) Recruitment response to light for 165 tree species. (**b**) Growth response of 1-cm saplings to light for 197 species. (**c**) Mortality response of 1-cm saplings to light for 203 species. All species reaching 12 m height for which estimates could be made are included; 163 species appear on all three panels. The horizontal dashed line at 1 indicates no response (it is outside the graph in panel b). In (a) and (c), a few species have responses <1, indicating higher recruitment (mortality) in the shade, but no species had higher growth in the shade. Axes are logarithmic. Solid lines are regressions, and all three were highly significant (based on log-transformed values). The 31 species used in lifetable calculations are highlighted by red circles, and 11 are identified: Bt = *Beilschmiedia tovarensis* (formerly *B. pendula*), Cd = *Cordia bicolor*, Gg = *Guarea guidonia*, Gl = *Guatteria lucens* (formerly *G. dumetorum*), Ma = *Miconia argentea*, Pc = *Prioria copaifera*, Qa = *Quararibea asterolepis*, Sa = *Simarouba amara*, Ss = *Swartzia simplex var. grandifolia*, Ta = *Tabernaemontana arborea*, and Tt = *Trichilia tuberculata*.

that mitigate against high survival (Kitajima, 1994; Poorter, 1999; Sack and Grubb, 2001; Wright et al., 2010; Philipson et al., 2014). Physiology alone, however, cannot, explain community dynamics, and what the fast-slow axis means to population fitness, or net demographic performance, is crucial. An analysis of lifetables constructed from observed growth and mortality can account for continuous variation along the axis as well as the spread above and below the axis.

VARIANCE AROUND THE MAIN AXIS

Rüger et al. (2018, 2020) extended observations of demographic trade-offs by considering variation around the primary axis of fast versus slow demography. The Bayesian analysis accounts for the variance caused by sampling error, which is high in rare species, and the remaining variance that Figure 1 reveals is the true difference between species. Despite the importance of the growth-mortality trade-off, many species fall far off the line, such as *Alseis*, *Protium*, and *Tabernaemontana* above versus *Beilschmiedia*, *Quararibea*, and *Trichilia* below (labeled in Fig. 1b). In terms of net demographic performance, those two groups are expected to be very different.

INTEGRATING DEMOGRAPHIC VARIATION

On the surface, the qualitative link between high growth and high death rates might appear to equalize the net fitness of all the species, where fitness refers to integrated lifetime per capita population growth. But fitness is a quantitative trait requiring quantitative comparisons of lifetime demography across the entire spectrum of variation (Fig. 1). Here we review a matrix population analysis that provides a test based on demography of trees above 1 cm dbh (Condit, 2022).

A matrix approach to demography is an analysis of a Markov transition process that allows the size distribution of trees in a population to be projected through time, allowing the maturation time from sapling to adulthood and the length of the reproductive period to be quantified (Caswell, 2001). It requires a description of the state of the population at one time as the number of individuals in several dbh categories and a transition matrix that converts the population state from one time to the next.

Define the population of trees in size class i as N_i, the vector of N_i as $\mathbf{N}$, and the transition matrix

$$T = \begin{pmatrix} r_1 & g_1 & h_1 & 0 & m_1 \\ 0 & r_2 & g_2 & h_2 & m_2 \\ 0 & 0 & r_3 & g_3 & m_3 \\ 0 & 0 & 0 & r_4 & m_4 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}, \qquad \text{Eq. 1}$$

is defined so that $\mathbf{N}' = \mathbf{N}T$. That is, multiplying current population $\mathbf{N}$ by T produces the population vector one time step later, $\mathbf{N}'$. The matrix of Equation 1 covers four size classes, plus a fifth class for dead trees (i.e., N_5 means the number dead). The matrix entries can be calculated from observed stem growth in repeat censuses: r_i terms are probabilities that a tree currently in size class i remains in size class i at the next census, g_i are probabilities that a tree in class i grows to class $i+1$, h_i means growth by two classes, and m_i are probabilities that a tree in class i dies in the next step. Class 4, the adult class, is terminal, with trees either remaining there (r_4) or dying (m_4). A 1 appears in the lower right corner because a tree in class 5, the dead class, has probability 1 of remaining dead. As an example, Equation 2 is a four-class transition matrix for *Trichilia tuberculata*:

$$T = \begin{pmatrix} 0.806 & 0.050 & 0.0007 & 0 & 0.144 \\ 0 & 0.845 & 0.043 & 0 & 0.113 \\ 0 & 0 & 0.846 & 0.048 & 0.106 \\ 0 & 0 & 0 & 0.853 & 0.147 \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}, \qquad \text{Eq. 2}$$

where probabilities refer to five-year transitions. The diameter classes are 10–34.4, 34.4–76.8, 76.8–200, and >200 mm; 200 mm was set as the approximate reproductive size in *Trichilia* (Visser et al., 2016), and the other sizes were chosen by an algorithm designed to equalize the growth probabilities g_i as closely as possible. The estimates were calculated from observed stem transitions in each five-year census interval of the 50-ha plot from 1985 to 2015, and then were averaged across the six intervals. Entries below the diagonal, those transitions representing a tree moving backward to a smaller class, are zero, although in fact, there were a few cases in which a small dbh error led to a tree shrinking below a class boundary. All those were assumed instead to be trees that remained in their earlier size class. Details of matrix construction and transition matrices for 31 species in the BCI plot are given in Condit (2022).

The advantage of the matrix approach is that it offers a direct calculation of one crucial demographic statistic: the expected adult lifespan of the average sapling. In the four-class model, it is the expected number of time steps a sapling starting in class 1 will spend as an adult, in class 4. This average must include the many saplings that die before adulthood, which is the average adulthood of those that do make it to adulthood discounted by zeroes for all those that do not. The time as a reproductive adult is crucial because, if the population is to persist, the length of time a sapling will spend reproducing must be sufficient to replace itself. If the primary axis of demographic variation, from slow to fast species (Fig. 1b), is also an axis of demographic equalization, then the expected adult lifespan should be equal along the full axis, from slow to fast species.

The expected adult lifespan has a straightforward analytic formulation in the absence of two-step growth ($h = 0$) and assuming no shrinkage. Define L_j as the expected lifespan in the largest reproductive size class of a sapling starting in class 1. Then based on a matrix like Equation 1, but with an arbitrary number of size classes j (i.e., j can be >4),

$$L_j = \frac{1}{1-r_1}\prod_{k=2}^{j}\frac{g_{k-1}}{1-r_k}, \qquad \text{Eq. 3}$$

There is an analytical solution that includes h as well, although it does not generalize easily beyond $j = 5$. Another useful result is the probability that a sapling reaches adulthood, or the maturation time. It has an analytical formulation,

$$P(A) = \prod_{k=1}^{j-1}\frac{gk}{1-r_k}, \qquad \text{Eq. 4}$$

A third result is the maturation time, M, or the mean number of steps required for a sapling to reach adulthood. There is not an analytical formulation for M from the matrix in Equation 1, but there is for a simplified matrix, in which g_i and r_i are constant. Then, with $r_i = r$,

$$M = \frac{j-1}{1-r}. \qquad \text{Eq. 5}$$

L_j, $P(A)$, and M can also be calculated numerically by raising the transition matrix, T, to successive powers, because T^X is the transition matrix for x time steps (Kemeny and Snell, 1976; Condit, 2022). Complete derivations of Equations 3–5 are given in appendices of Condit (2022).

For the *Trichilia* transition matrix (Eq. 2), $L_4 = 0.15$ time steps, which is 0.75 years because there are 5 years per census interval. This means that the average *Trichilia* sapling can expect to live less than one year as an adult. The analytical solution for the maturation probability (the probability of reaching adulthood) is $P(A) = 0.022$, and maturation time $M = 18.1$ time steps (90.5 years), the latter of which is found by setting r to the mean of the diagonal, r_i (Eqs. 1, 2). Numerical solutions confirm the analytical results closely.

Condit (2022) produced a transition matrix for each of the 31 most abundant tree species in the 50-ha plot. The criteria used to select species were designed to include four fast-growing pioneers, ensuring that the sample is spread widely across the growth-mortality axis (Fig. 1). For those species with reproductive size of 300 mm dbh (Table 1), I used five size classes instead of four, always choosing the breaks between size classes to equalize growth transitions as closely as possible. Two of the fast-growing species, *Miconia argentea* and *Cordia bicolor*, had fairly frequent two-step growth transitions, and for those, I used the two-step version of Equation 3. In every other species, two-step transition probabilities were always less than 0.05 of one-step probabilities. I estimated maturation time M using the numerical method, which has no limitations about two-step transitions.

TABLE 1. Demographic results for 31 dominant species of the Barro Colorado Island 50-ha plot, taken (except for the demographic axis) from Condit (2022). Adult size is estimated reproductive size in mm dbh. *N* is the total number of individuals in the 1990 census. The x-axis is the position along the growth-mortality regression (Fig. 1), with high values for the fastest-growing species. Adult expectations: *Life span* is the expected adult life span for the average sapling of 1 cm dbh (Fig. 2a); *Probability* is the fraction of those saplings that live to adulthood (Fig. 2b); *Maturation* is the mean time it takes a successful sapling to reach adulthood (Fig. 2c). *Swartzia simplex* includes one of the two varieties distinguished in the plot, *S. s. var. grandifolia*. The four pioneer species deliberately included by judicious choice of the abundance criterion were *Cordia bicolor, Inga marginata, Miconia argentea,* and *Simarouba amara*. See Condit (2022) for details of matrix calculations.

		Adult	Demographic	Adult expectations from 1 cm		
Species (Family)	*N*	Size	Axis	Life span	Probability	Maturation
Alseis blackiana (Rubiaceae)	8,412	100	–0.14	10.74	0.072	124.9
Beilschmiedia tovarensis (Lauraceae)	2,748	100	0.32	1.35	0.023	117.4
Brosimum alicastrum (Moraceae)	920	100	–0.48	4.85	0.080	188.3
Chrysophyllum argenteum (Sapotaceae)	688	100	–0.21	3.03	0.025	137.3
Cordia bicolor (Cordiaceae)	1,043	100	0.92	5.57	0.099	24.3
Cordia lasiocalyx (Cordiaceae)	1,695	100	0.26	1.84	0.078	48.1
Drypetes standleyi (Putranjivaceae)	2,279	100	–0.17	15.53	0.140	107.0
Eugenia coloradoensis (Myrtaceae)	838	100	–0.09	1.21	0.051	74.5
Eugenia oerstediana (Myrtaceae)	2,343	100	0.00	2.28	0.085	52.4
Garcinia recondita (Clusiaceae)	4,289	100	–0.45	8.31	0.181	99.9
Guarea guidonia (Meliaceae)	1,963	100	0.08	9.91	0.146	67.9
Guatteria lucens (Annonaceae)	1,469	150	0.20	0.64	0.022	56.3
Heisteria concinna (Olacaceae)	984	200	–0.58	50.49	0.548	61.8
Hirtella triandra (Chrysobalanaceae)	5,026	200	–0.22	22.58	0.282	70.6
Inga marginata (Fabaceae)	717	200	0.96	1.14	0.066	27.9
Lonchocarpus heptaphyllus (Fabaceae)	894	200	0.27	0.52	0.022	94.9
Maquira guianensis (Moraceae)	1,502	200	–0.64	9.87	0.298	78.7
Miconia argentea (Melastomataceae)	900	200	1.24	0.54	0.033	18.8
Ocotea whitei (Lauraceae)	754	200	0.53	1.66	0.034	53.0
Poulsenia armata (Moraceae)	2,120	200	0.37	0.34	0.014	60.6
Pouteria reticulata (Sapotaceae)	1,767	300	0.21	5.28	0.044	73.7
Prioria copaifera (Fabaceae)	1,439	300	–1.08	31.52	0.219	151.1
Protium tenuifolium (Burseraceae)	3,015	300	0.03	11.01	0.207	58.6
Quararibea asterolepis (Malvaceae)	2,349	300	–0.17	13.38	0.171	118.5
Simarouba amara (Simaroubaceae)	1,289	400	0.54	1.28	0.050	37.6
Swartzia simplex (Fabaceae)	2,573	100	–0.56	42.79	0.301	138.1
Tabernaemontana arborea (Apocynaceae)	1,430	300	–0.07	14.73	0.255	69.7
Protium stevensonii (Burseraceae)	4,114	300	–0.16	5.03	0.057	109.2
Trichilia tuberculata (Meliaceae)	13,284	300	–0.20	0.75	0.022	90.3
Unonopsis pittieri (Annonaceae)	790	100	0.35	6.74	0.154	47.3
Virola sebifera (Myristicaceae)	2,080	200	0.14	8.12	0.210	47.6

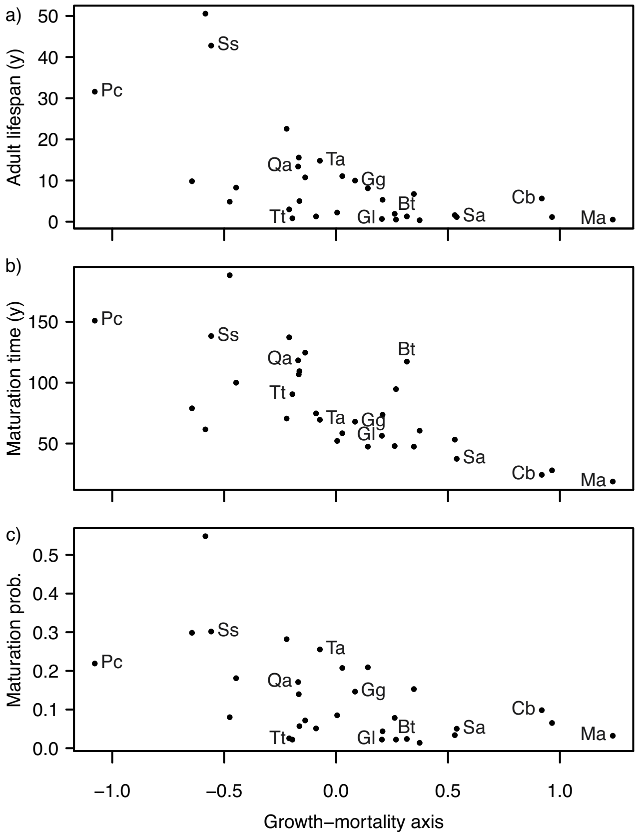

FIGURE 2. Lifetime demographic results (vertical axes) as a function of species' positions on the growth-mortality axis (horizontal axes) for 31 abundant tree species chosen to represent the full range of the axis. The position along the axis was calculated from the regression line (Fig. 1b): first the predicted growth response was calculated for each species from the regression, then the distance of that prediction from the overall mean growth response was calculated as the species' position. High positions are the fastest growing pioneers, to the right in Figure 1b. (**a**) Vertical axis is the expected adult lifespan (years) for a sapling calculated from the transition matrix (Eq. 2); in two fast-growing species, the two-growth version of the equation was used. The negative relationship is highly significant ($p = 0.003$). (**b**) Vertical axis is the probability a sapling reaches adulthood. The negative relationship is highly significant ($p < 0.001$). (**c**) Vertical axis is the mean time (years) it takes for a successful sapling to reach adulthood. The negative relationship is highly significant ($p = 0.002$). The 11 species identified in all three panels are the same as in Figure 1.

ADULT LIFESPAN AND THE GROWTH-SURVIVAL TRADE-OFF

The fast-growing pioneers performed poorly in the integrated demographic assessment, having short adult lifespans (Fig. 2a). A sapling of *Miconia argentea*, at the extreme, can expect to survive six months as an adult, and *Simarouba* and *Inga* less than two years (Table 1). *Cordia*, in contrast, had a nearly six-year expected adult lifetime (Table 1), demonstrating that pioneers can compensate for high mortality with fast growth (Fig. 1b). Several of the species at the slow end of the axis, *Prioria*, *Swartzia*, and *Heisteria concinna*, had expected adult lifespans >20 years. For many of the most common BCI tree species, those in the center of the growth-mortality axis, expected adult lifespan was highly variable. Some, including *Trichilia* and *Guatteria*, had expected adult lifespans <1 year, as low as pioneers, whereas *Alseis*, *Quararibea*, and *Tabernaemontana* had adult lifespans >10 years.

Pioneers matured rapidly, and expected time for a 1-cm dbh sapling to reach adult size was <20 years in *Miconia*. In contrast, *Beilschmiedia* and *Prioria* needed >150 years to reach adulthood (Table 1, Fig. 2b). The probability of reaching adulthood was low in pioneers and high in the long-lived species, but species in the middle of the axis were highly variable, and *Trichilia* had a lower probability of reaching adulthood than several pioneers (Fig. 2c).

Condit (2022) produced a theoretical analysis of variation in adult lifespan relative to the growth-survival demographic axis. The axis is not parallel to contours of adult lifespan: the upper end of the growth-survival axis yields an adult lifespan much shorter than the lower end. Two species illustrate this well. *Miconia argentea* and *Swartzia simplex* both fall on the growth-survival axis, but their adult lifespans differ by nearly 100-fold (Table 1).

CONCLUSION

The demographic axis describes a growth-mortality trade-off that is not demographically equalizing. The expected adult lifespan of saplings in species at the fast end of the axis, the pioneers, is short relative to many slow-growing species. Although pioneers grow rapidly to adulthood, it is not sufficient to overcome high mortality rates. To persist in the forest, pioneers must have a reproductive advantage—that is, by producing more seedlings and saplings during their reproductive life than long-lived species do. Rüger et al. (2018, 2020) and Kambach et al. (2022) pursued this possibility by including recruitment rate at the 1-cm size in analyses of demographic axes. This leads to the suggestion that species below the growth-mortality axis in Figure 1 persist in the forest by recruiting well (Rüger et al., 2018). Alternatively, it may be that the pioneer species are so concentrated in areas of high light that the only demography that matters is their maximum growth, not the average growth across the plot. Perhaps a lifetable constructed from only those saplings in high light would lead to sufficient adult lifetimes. Moreover, we know that the community of species abundances in the 50-ha plot is far from stable, with many species increasing or decreasing by substantial amounts (Chisholm et al., 2014; Condit et al., 2017), and the variation in adult lifespan revealed in Figure 2a should predict those fluctuations.

An overarching question is whether the demographic tradeoff axis is stabilizing in the sense that species abundances are held in a narrow range, thus fostering coexistence (Grubb, 1977; Hubbell et al., 1999; Chesson, 2000; Silverton, 2004). Stable coexistence of two species, one at the upper end of the axis and one at the lower, is easy to understand, and demographic variation may be an important coexistence mechanism in low-diversity temperate forests. The question at BCI is whether the coexistence of hundreds of species based on a demographic tradeoff is plausible. Tilman (2004) argued that many species spread uniformly along a single resource axis could persist in a stable community. The principal argument against this hypothesis is that stabilizing differences among hundreds of species would be trivially small, almost certainly smaller than population drift (Condit et al., 2012). Moreover, the observed spacing of species along the demographic axis counters the Tilman prediction, because most species are clustered in the center (Fig. 1; Condit et al., 2006). Even with a second axis of moisture variation within the BCI plot, there are too many species for stable coexistence through local niche partitioning. At much wider scales, the issue reopens, because climatic and soil variation are much greater, and seeds can disperse widely. Species that are demographically equivalent within the BCI plot could be maintained by dispersal from sites where they differ (Condit et al., 2013).

Future studies need to go beyond the documentation of species differences and focus on demographic consequences of those differences. This analysis moves in that direction, and the further step of incorporating reproduction and seedling demography into the lifetables must follow. There are now 30 years of seed and seedling demography (Wright et al., 2005, 2015, 2024) to go with 30 years of the main census (Condit et al., 2017). Combining these findings can provide the precise estimates of lifetime demography needed for understanding the consequences of species differences, as Bruijning et al. (2017) did for species grouped by breeding system. In the meantime, we offer now, for the first time, complete demographic profiles calculated for individual species in the BCI 50-ha plot (Rüger et al., 2022).

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