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Lifespan of tropical trees from seed to 1-cm diameter

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ABSTRACT

Background: The full lifespan of long-lived trees includes a seedling phase, during which a seed germinates and grows to a size large enough to be measured in forest inventories. Seedling populations are usually studied separately from adult trees, and the seedling lifespan, from seed to sapling, is poorly known. In the 50-ha Barro Colorado forest plot, we started intensive censuses of seeds and seedlings in 1994 in order to merge seedling and adult demography and document complete lifespans.
Methods: In 17 species abundant in seedling censuses, we subdivided populations into six size classes from seed to 1 cm dbh, including seeds plus five seedling stages. The smallest seedling class was subdivided by age. Censuses in two consecutive years provided transition matrices describing the probability that a seedling in one stage moved to another one year later. For each species, we averaged the transition matrix across 25 censuses and used it to project the seedling lifespan, from seed until 1 cm dbh or death.
Results: The predicted mean survival rate of seeds to 1 cm dbh varied 1000-fold across species, from 2.9×10^{-6} to 4.4×10^{-3}; the median was 2.0×10^{-4}. The seedling lifespan, or the average time it takes a seed to grow to 1 cm dbh, varied across species from 5.1 to 53.1 years, with a median of 20.3 years. In the median species, the 10% fastest-growing seeds would reach 1 cm dbh in 9.0 years, and the slowest 10% in 34.6 years.
Conclusions: Combining seedling results with our previous study of lifespan after 1 cm dbh, we estimate that the focal species have full lifespans varying from 41 years in a gap-demanding pioneer to 320 years in one shade-tolerant species. Lifetime demography can contribute precise survival rates and lifespans to forestry models.

1. Background

The lifetime of a tree includes two strikingly different phases. At one extreme, there are mobile seeds that germinate into fragile seedlings, most of which die. The few that persist grow on to become much different organisms: inperturbable giants that dominate ecosystems. The contrast between the two phases carries over into the research that tree biologists pursue. Studies of seedlings involve experimental manipulation, transplants and fertilization, and produce results within a few weeks. Mature trees, in contrast, are studied with observations that capture snapshots of the life cycle. Indeed, tree research seldom covers seeds, seedlings, and mature trees within a single project. Our goal is to close this gap, combining the tree lifespan from tiny seed to canopy giant in a single demographic story.

The importance of seedlings in the tree life cycle was highlighted by Grubb (1977), who argued that regeneration niches at the seedling stage can explain niche-partitioning among species that share the same habitat as adult trees. Illustrating Grubb's point, numerous models of species coexistence hinge on seed and seedling demography (Janzen, 1970; Connell, 1971; Chesson and Warner, 1981; Moles and Westoby, 2004; Muller-Landau, 2010; Comita et al., 2014). Yet observations of seedling niches invariably last only one or a few years (Kobe, 1999; York et al., 2011; Metz, 2012; Chang-Yang et al., 2013; Inman-Narahari et al., 2014; Browne et al., 2021), and no seedling study has addressed the duration of the seedling lifespan. If seedlings take decades to recruit as saplings, short-term observations might miss important phases. One study that tracked seedlings for 30 years found slow growth and did not observe a single sapling recruit (Connell and Green, 2000).

Our goal here is to document the entire seedling lifespan, from seed to 1-cm sapling, based on direct observations of every stage, then to combine this with already published demography of saplings to adults (Condit, 2022). We can address seedling demography at Barro Colorado Island in Panama because we added annual seed and seedling surveys (Wright, 2002; Comita et al., 2007) to the long-term census of saplings and large trees (Hubbell and Foster, 1985; Condit et al., 2017). We now monitor every life stage of 300 tree species in the 50-ha plot. Using 25

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years of seed and seedling censuses, including 85,531 seedlings and 1,349,569 seeds, we produce here a lifetable for 17 common tree species that starts with the number of seeds falling and tracks their fate until they enter the tree census at 1 cm diameter at breast height (dbh). The lifetables lead to transition matrices defined by discrete seed and seedling stages.

Transition matrices are designed to project future size distributions of populations. Any starting population, meaning the number of individuals in each size category, can be converted into a predicted population one year later. This is accomplished by multiplying the current population by elements of the transition matrix (Caswell, 2001). For our purposes, we needed to start with a population of seeds only and project it into the future as individuals advance in size. After a sufficient number of steps, all individuals either die or reach 1 cm dbh. At that point, we have estimates of the seedling lifespan, providing answers to several basic questions about seedling demography. How many seeds are needed to produce a single 1-cm sapling? How long is the seedling lifespan, i.e., the time it takes the average seed to reach 1 cm dbh? How variable is the seedling lifespan within and between species? This is the first time any of these questions have been addressed in tropical forests, because tree-ring chronologies omit the reproductive and seedling stage. We conclude by merging the seedling results with matrix analyses of adult demography (Condit, 2022) to ask how well seedling dynamics match adult dynamics (Kambach et al., 2022, 2025). This also allows us to estimate how long an average adult tree at Barro Colorado Island lives, the first complete lifespans of tropical trees.

2. Field methods

2.1. Plot and census

The 50-ha plot on Barro Colorado Island is a long running census of trees ≥ 1 cm dbh, initiated in 1981 (Hubbell and Foster, 1983; Condit, 1998; Condit et al., 2017). Starting in 1994, additional censuses of seeds and seedlings were added (Wright, 2002; Comita et al., 2010, 2023), so we now have demographic observations based on marked individuals of trees at all sizes plus counts of seed production.

The seedling censuses include several components. The first is the Wright study of seeds and seedlings, begun in 1994 and ongoing (Wright, 2002; Wright et al., 2005, 2016). All seeds, fruits, and flowers falling into 200 nylon mesh traps, each 0.5 m^2, are counted weekly, and all seedlings of any size are counted once a year in 600 adjacent quadrats, each 1 m^2. In addition, seedlings ≥ 50 cm tall are counted in 5 m × 5 m quadrats at the same locations. The 200 locations are spaced regularly along permanent trails through the 50-ha plot, with distance from a trail chosen at random (Harms et al., 2000; Wright, 2002). Seedlings are marked with unique numbers, identified to species, and measured from ground to the highest growing tip. Diameters of those ≥ 50 cm tall are measured at the ground plus 1.3 m above the ground (dbh) when tall enough, but for seedlings < 50 cm tall, no diameter is recorded.

A separate project is the Comita-Hubbell census of all seedlings ≥ 20 cm tall in a larger sample of 1 m^2 quadrats, one at the center of every 5 m × 5 m grid cell in the 50-ha plot (Comita et al., 2007, 2010, 2023). There are 20,000 such cells in the plot, but locations on trails or overlapping the Wright census were omitted, leaving a total of 19,313 quadrats. A census was completed in most years over 2001–2018, but 2005, 2010, 2015 were skipped to avoid the main (≥ 1 cm dbh) census, and 2007 was also skipped. Height was measured as in the Wright censuses, and every seedling tall enough had a dbh recorded.

The Wright censuses have the advantage of being completed every year from 1995 to 2019 (though the separate census ≥ 50 cm tall started in 1998), and they include every plant above the ground. But the Wright censuses cover a relatively small area, 600 m^2 for all seedlings and 5,000 m^2 for those ≥ 50 cm tall. The Comita-Hubbell census included a larger area, nearly 20,000 m^2, but omitted seedlings < 20 cm tall. Moreover, the years skipped by the Comita-Hubbell census reduce the number of annual transitions available to seven, because each year skipped loses two transitions.

Both Wright and Comita-Hubbell datasets include a record for each living seedling in every census, with a tag number used to identify individuals, the species name, a single height measurement, and a date; a subset includes dbh measurements. When seedlings were found dead, usually when a tag was observed with no plant, a note was included; seedlings and their tags sometimes disappeared, however, and death had to be inferred. For every seedling, we analyzed the full sequence of measurements and found the first and last years alive. This identified a few cases in which intermediate measurements were missed, i.e., a seedling was not measured but was alive in both earlier and later censuses. Occasional misses are not surprising given the small size of seedlings and the frequent litterfall from tall trees. Unlike diameter measurements in larger trees, there is every reason to include shrinkage in seedling heights: small stems can easily be clipped by animals or break when crushed (Alvarez-Clare and Kitajima, 2009). Every backward transition revealed by the measurements was accepted. We also allowed all upward transitions as observed. Complete details about censuses and calculations are given in Appendix 1.

2.2. Species

We focused on species with populations large enough to estimate transition rates from seed through 1 cm dbh. In Condit (2022), demography of canopy tree species at sizes ≥ 1 cm dbh was analyzed, using 31 species with large samples and reproductive sizes above 1 cm. Our goal was to use the same 31 species, but several had to be omitted due to small sample sizes of seeds or seedlings, leaving 16 of the species from Condit (2022). To augment the sample, we added one species having large seed and seedling samples (*Faramea occidentalis*), excluded in Condit (2022) because its reproductive size is only slightly above 1 cm dbh (Wright et al., 2015a). We thus had 17 species with adequate sample sizes throughout seed, seedling, and tree censuses (Table 1). Total sample sizes for these species over the study period included 27,437 newly germinated seedlings (whose age is known), 4,351 seedlings in the Wright census ≥ 50 cm, and 53,743 in the Comita-Hubbell census (7 years, 2003–2017), for a total sample of 85,531.

The focal species offer a wide range of adult demographic rates. Three of the 17 are classified as gap-demanding pioneers based on growth and survival after 1 cm dbh, while the others are shade-tolerant as saplings (Rüger et al., 2009; Condit and Rüger, 2024). For the sake of brevity, we refer to 15 of the 17 species by genus alone; two species in the genus *Protium* must be named to species. In figures, the 17 species are labeled

Table 1

Definitions of seed, seedling, and sapling stages for matrix demography, based on height and dbh. All stages **I** were defined using height and age, with subdivisions for exact ages **1**, **2**, **3**, …plus one terminal class **T** for ages $\geq T$. Terminal age was assigned differently for each species, from $T = 2$ years to $T = 10$ years, depending on sample sizes (Appendix 2). Stages **II** and **III** were defined using height alone. Stage **V** was based on dbh alone if the dbh was recorded, regardless of height; seedlings lacking the dbh measurement that were ≥ 240 cm tall were placed in Stage **V**. Stage **IV** had a lower height limit and an upper dbh limit (because there was no sapling with $H < 80$ cm and $D \geq 1$ cm, the stages are mutually exclusive). Blank entries indicate criteria not included in defining a category.

Stage	Category	height (H, cm)	dbh (D, cm)	age (yr)
O	Seed	–	–	0
I.1	Seedling	$0 \leq H < 20$	–	1
I.2	Seedling	$0 \leq H < 20$	–	2
I.3	Seedling	$0 \leq H < 20$	–	3
etc.	Seedling	…		
I.T	Seedling	$0 \leq H < 20$	–	$\geq T$
II	Seedling	$20 \leq H < 50$	–	–
III	Seedling	$50 \leq H < 80$	–	–
IV	Seedling	$H \geq 80$	$D < 1$	–
V	Sapling	$H \geq 240$	$D \geq 1$	–

Table 2
The 17 study species. Below each species name is the six-letter abbreviation used in figures, and a shortened family name (e.g. Rubi = Rubiaceae). The number of adults is the count of individuals above the minimum reproductive size across 50 ha in the census of year 2000. The number of seeds is the count from 200 seed traps summed over 25 years. The number of germinants (germs.) is the count of newly germinated seedlings summed over 25 years. Fecundity is the modeled seed production per adult per year, estimated from counts of seeds and adults (see Methods). Pioneer species are indicated with asterisks. Powers of 10 are given in computer notation for brevity, i.e., E6 means 10^6.

Species	Adults	Seeds	Germs.	Fecundity
Alseis blackiana alsebl (Rubi.)	**533**	**8.75·E5**	**234**	**1.06·E6** (6.6·E5, 1.7·E6)
Beilschmiedia tovarensis beilpe (Laur.)	**118**	**2.40·E3**	**2108**	**1.37·E4** (7.5·E3, 2.6·E4)
Drypetes standleyi drypst (Putranjiv.)	**167**	**9.25·E2**	**131**	**9.25·E2** (2.7·E2, 3.0·E3)
Eugenia oerstediana eugeoe (Myrt.)	**187**	**1.99·E3**	**1143**	**7.78·E3** (4.8·E3, 1.3·E4)
Faramea occidentalis faraoc (Rubi.)	**20393**	**1.94·E4**	**12432**	**4.75·E2** (2.1·E2, 1.1·E3)
Garcinia recondita gar2in (Clusi.)	**112**	**6.19·E2**	**165**	**9.64·E2** (3.1·E2, 2.8·E3)
Guarea guidonia guargu (Meli.)	**369**	**2.56·E3**	**334**	**2.47·E3** (1.0·E3, 5.6·E3)
Heisteria concinna heisco (Olac.)	**289**	**2.08·E3**	**969**	**3.74·E3** (2.1·E3, 6.7·E3)
Hirtella triandra hirttr (Chrysobalan.)	**719**	**1.19·E3**	**360**	**1.44·E3** (1.0·E3, 2.0·E3)
*Inga marginata** ingama (Fab.)	**63**	**1.47·E3**	**981**	**2.01·E4** (1.2·E4, 3.3·E4)
*Miconia argentea** micoar (Melastomat.)	**75**	**3.25·E5**	**268**	**3.50·E6** (2.1·E6, 5.8·E6)
Pouteria reticulata poutre (Sapot.)	**125**	**9.66·E2**	**517**	**2.50·E3** (9.9·E2, 6.1·E3)
Protium stevensonii tet2pa (Burser.)	**205**	**4.57·E3**	**1150**	**1.53·E4** (9.6·E3, 2.4·E4)
Protium tenuifolium protte (Burser.)	**393**	**8.80·E2**	**165**	**1.49·E3** (8.4·E2, 2.6·E3)
Quararibea asterolepis quaras (Malv.)	**348**	**2.96·E4**	**2019**	**7.40·E4** (4.9·E4, 1.1·E5)
*Simarouba amara** simaam (Simaroub.)	**126**	**1.61·E3**	**142**	**8.81·E3** (5.0·E3, 1.5·E4)
Trichilia tuberculata tri2tu (Meli.)	**824**	**4.92·E4**	**4725**	**5.29·E4** (3.3·E4, 8.6·E4)

with six-letter abbreviations, in 16 cases beginning with the genus name and thus readily recognizable. The exception is caused by a taxonomic revision that moved *Tetragastris panamensis* to *Protium stevensonii* (Condit et al., 2020); we must maintain the original abbreviation, tet2pa, in our databases (Condit et al., 2014).

3. Analytical methods

3.1. Seedling transitions

The matrix analysis required a series of discrete seedling stages between which annual transitions could be calculated (Lefkovitch, 1965). We defined size classes using divisions at 20, 50, and 80 cm in height, plus 1 cm dbh, meaning four seedling stages (Table 1). Stage **V** designated saplings ≥ 1 cm dbh, stage **O** seeds, and stage **D** dead plants. We further subdivided the smallest size, seedlings < 20 cm tall, by age (Caswell, 2012; Bernstein et al., 2018). This was possible because the Wright seedling census includes seedlings of known age. In 1994, every seedling was tagged, so that from 1995 to 2018 cohorts of newly germinated seedlings could be identified; as of 2019, seedlings of ages 1–24 years are included (defining age 1 as the first year a seedling was seen). To assess the importance of age in seedling demography, we examined growth and death transitions for seedlings in stage **I** (0−20 cm tall) and stage **II** (20−50 cm tall) as a function of their age. Because this identified a strong effect of age in stage **I**, but not stage **II**, we included both age and size in the transition matrices. Stage **I** subclasses were designated **I.1**, **I.2**, **I.3**, etc., where numbers after the period indicate age in years. Stage **II** seedlings (≥ 20 cm tall) were not subdivided into age categories.

Dividing the initial size class by age required a decision about the number of age subcategories. To maintain adequate samples for estimating transitions, we chose a terminal age class so that there were at least 50 individuals in each stage **I** subcategory. In the abundant *Faramea* and *Trichilia*, stages **I.1** through **I.9** were permitted, meaning all seedlings age 1−9 years were separated; stage **I.10** was terminal, meaning all seedlings < 20 cm tall and ≥ 10 years old. In species with smaller samples, the terminal stage was earlier; for example, stage **I** seedlings in the pioneers *Miconia* and *Simarouba* had just two subclasses, **I.1** for those in their first year and a terminal subclass **I.2** including all others. Appendix 2 gives terminal age classes for the 17 species.

Transitions are defined as movement between any pair of stages, including death. Growth means moving to a larger stage, while shrinkage means regressing to a smaller one; many seedlings remained in the same stage after one year. Define transition t_{ij} as the probability that a seedling in stage i during the census in year y appeared in stage j in year $y+1$. Both i and j could be age classes within size stage **I**, meaning a seedling remained < 20 cm tall but aged one year. Once ≥ 20 cm tall, transitions were based solely on size, with seedlings either shrinking, growing, or remaining the same size. A special case involved shrinking from stage **II** back to stage **I** when seedling age was not known; these plants were assigned the terminal age subclass, **I.T**. With known-age seedlings, backward transitions could go into a specific age subcategory, for example, a seedling could move from **I.5** − **II** − **I.7** over three years. Transition probabilities t_{ij} were estimated as ratios of integer counts in consecutive years. Our matrices were built with long-term averages, so N_i was defined as the sum of the number of seedlings in stage i alive in any year (except the last), and the subset N_{ij} of those in stage j a year later. Then $t_{ij} = N_{ij}/N_i$.

Those seedlings that were missed, i.e., not measured in one year but known to be alive in earlier and later censuses, were assumed to be in the same size class as the prior measurement. We examined this assumption relative to the alternative of omitting these seedlings and found only a small impact on results (Appendix 3). In addition, because Wright seedlings of known age did not have diameters measured, we used observations having both height and dbh to define a critical height when seedlings surpass 1 cm dbh. The estimation of this height, $h = 240$ cm, is described in Appendix 4. Since dbh was recorded in all seedlings in the Comita-Hubbell census, and in some ≥ 50 cm tall in the Wright census, large numbers of stage **IV** to stage **V** transitions were observed directly.

3.2. Seed to seedling transition

Seeds were defined as stage **O** (Table 1), so seed germination is the transition t_{0j}. For the vast majority of germinants, $j =$ **I.1**, because most new germinants were < 20 cm tall, thus in stage **I.1**. Germinants ≥ 20 cm tall required transition t_{02}, stage **O** to **II**, but only one species, *Beilschmiedia*, had large numbers; age was not considered because it was not part of the stage **II** definition. Individual seeds could not be followed to germination, so the rate was based on the count all seeds falling in year y and newly germinated seedlings in year $y+1$, taken from Wright seed traps and seedling quadrats. Because transition matrices were based on 25-year averages, t_{0j} was found as the sum of germinants (1995−2019) divided by the sum of seeds one year earlier (1994−2018). Since the seedling census covered a larger area than the seed census, a six-fold correction was needed (Appendix 1C).

The assumption that germinants in year $y+1$ were produced by seeds in year y is warranted because seeds of most forest trees at Barro Colorado do not persist in the soil beyond one year; two of the 17 species we included survived for several months in the seed bank, but at a low rate (Dalling et al., 1997). In the event that a small number of germinants came from seeds 2 years earlier, it would have little impact on our results.

In a single species, *Faramea occidentalis*, germination was based on years y and $y+2$ due to the timing of seedfall (see Appendix 1C for details about seed phenology).

3.3. Transition after 1 cm dbh

Completing the transition matrix required rates for saplings in class **V**, those ≥ 1 cm dbh. These were taken from the main 50-ha census, which has much larger samples than seedling censuses. We used all saplings with dbh ≥ 1 and < 4 cm in the 2010 census and their fates in 2015. In the transition matrix, t_{55} was set to the annualized survival rate of this group, and mortality $t_{5D} = 1 - t_{55}$ (Condit et al., 1995, 2017). These rates were necessary for matrix calculations but inconsequential to our results, which end once seedlings enter class **V**.

3.4. Combining datasets and years

We used only annual transition rates, those calculated from two consecutive annual censuses, averaged over 25 years. Both Wright and Comita-Hubbell seedling censuses were repeated at the same time every year, so seedling observations were close to one year apart. No Wright censuses were skipped, so data include all 24 annual intervals (21 intervals in those ≥ 50 cm tall). Since the Comita-Hubbell censuses skipped several years, there were only seven annual intervals, starting in 2003, 2008, 2011, 2012, 2013, 2016, 2017. We assume every annual interval provided an independent trial of a population of seedlings. This makes most sense for mortality rates, because death only happens once. Moreover, newly germinated seedlings appear only once. For growth rates after the first year, we recognize that some individual seedlings appeared repeatedly in the calculations. Ideally, we would account for repeated measures, but we do not see how this would work. Since survival rates were low in the smaller sizes, many seedlings appeared only once or twice in the calculations, and repeated measures may be unimportant. Regardless, only statistical confidence in transition matrices would be biased by repeated measures, not the estimates themselves.

Transitions starting at stage **II** could be calculated from both Wright and Comita-Hubbell data, and we simply combined the samples. This meant that a single average transition term was calculated by summing all samples across every census interval in both datasets. Prior to combining, we compared transition rates from the two datasets and found that they correlated reasonably well and had similar magnitudes (Appendix 5). There was one exception, a discrepancy in stage **III** seedlings for which the Wright data showed lower growth and higher shrinkage. We tested matrices with and without the Wright data for stage **III** and found little impact on the results (Appendix 5).

3.5. Seedling lifespan

We used numerical projections with observed transition matrices. As in Condit (2022), we defined the vector of population size as **N**, having elements N_i for the population in stage i. The two main questions are the proportion of seeds that survive to 1 cm dbh and the time it takes. Projections thus started with 1 seed and no other seedlings,

$$\mathbf{N} = \{N_0 = 1,\ N_{1.1} = 0,\ N_{1.2} = 0,\ \ldots,\ N_2 = 0,\ N_3 = 0,\ N_4 = 0,\ N_5 = 0,\ N_D = 0\}.$$

We also calculated survival from germination to 1 cm dbh, and for this we started projections with $N_{1.1} = 1$ and all other stages $N_i = 0$.

After 1 time step (1 year), the population vector is $\mathbf{N}' = \mathbf{NT}$, where **T** is the matrix of transitions t_{ij}; after y years it is $\mathbf{T}^y$ (Kemeny and Snell, 1960). The number of stage **V** saplings (≥ 1 cm dbh) at any time is N_5. From numerical projections, we found r_y, the number of stage **V** saplings recruiting in year y, and continued projections until $r_y \rightarrow 0$. Details appear in Condit (2022).

The total number recruiting, $R = \sum r_y$, is the fraction surviving, since the initial population was 1 seed (or 1 germinant). $P_y = r_y/R$ defines a probability distribution of the fraction recruiting at each time y. We found the median plus 10th and 90th percentiles of P_y in order to describe the time it takes a cohort of seeds to reach 1 cm dbh.

3.6. Statistical confidence in transition matrices

Transition matrices were calculated from samples of living seedlings in year y, and one row of a matrix was based on N_i seedlings alive in stage i. The observations were a multinomial trial, since every seedling in year $y+1$ belonged in one of several stages j, including $j = i$. To estimate statistical confidence in the transition matrix, we created random draws on the observed multinomial distributions to create a posterior distribution of the observations. In Condit (2022), multinomial draws were created using binomial approximations, but here we used true multinomial draws (Brown and Bromberg, 1984; Davis, 1993) to maintain the sample size for every stage (Appendix 6). Posterior draws of the observed multinomial distributions were used to create a posterior distribution of the transition matrix, and this in turn a posterior distribution of all calculations based on the matrices. The advantage of the Bayesian approach is that it propagates error from the original census data through every result.

3.7. Adult population and fecundity

The reproductive size of each species was defined from observations of flowering and fruiting individuals (Wright et al., 2015a; Visser et al., 2016). These appear in Table 1 of Condit (2022); for *Faramea*, which was omitted from the earlier paper, we set reproductive size at 2 cm dbh. Adult population density of a species was estimated as the number of reproductive-size trees alive in each five-year census from 1995 to 2015, divided by 50 ha. Forest-wide fecundity was estimated as the mean number of seeds of each species counted in traps per year over the study period, adjusted to a density per hectare. Individual fecundity was the seed density divided by the adult density in the census closest in time (for example, seedfall in 1997 census was related to adults in 1995, and seeds in 1998 to year 2000). Error in fecundity was estimated using annual variation in the seed count and a simple Bayesian approach. Denote mean fecundity per adult as $\widehat{f}$. We assumed the natural logarithm, $\widehat{L} = \log \widehat{f}$, was normally distributed across years, and that the number of seeds observed in year y was a negative-binomial observation on L_y. From this, we could estimate $\widehat{L}$ and its standard deviation using the Bayesian Metropolis search described in Condit et al. (2017). We assumed errors in adult population size and seed counts were low enough to ignore.

3.8. Full lifespan

By combining estimates of seedling lifespan in the current analysis with adult lifespans from Condit (2022), which began with 1-cm saplings, we generated estimates of the full lifespan. Table 1 in Condit (2022) includes a column for maturation time, defined as the expected time it takes a 1-cm sapling to reach adulthood; here we call it L_m. To get the full adult lifespan, we need to add to this the expected lifespan after

Table 3

Transition dynamics from seed to 1-cm sapling in the 17 study species. Germination is the ratio of new germinants to seeds counted. The other survival rates, germinant to 1 cm and seed to 1 cm, are based on matrix projections. The time it takes for seeds to reach 1 cm is given as the mean for all surviving seedlings, plus 10th and 90th percentiles of the distribution. Pioneer species are indicated with asterisks. Credible intervals for all estimates are given in Appendix 6.

Species	Survival rate			Time (year)		
	Germination	Seed to 1 cm	Germinant to 1 cm	10%	Mean	90%
Alseis blackiana	4.46·E−5	2.93·E−6	5.87·E−2	14.7	44.4	82.2
Beilschmiedia tovarensis	1.46·E−1	2.54·E−4	5.51·E−4	6.5	16.4	28.2
Drypetes standleyi	2.36·E−2	1.41·E−4	5.23·E−3	8.6	19.3	32.0
Eugenia oerstediana	9.59·E−2	5.23·E−4	5.03·E−3	11.9	29.1	50.2
Faramea occidentalis	1.07·E−1	1.37·E−4	1.21·E−3	9.4	21.9	36.0
Garcinia recondita	4.44·E−2	4.44·E−3	9.63·E−2	21.9	53.2	93.5
Guarea guidonia	2.17·E−2	2.04·E−4	8.07·E−3	9.0	19.7	32.1
Heisteria concinna	7.78·E−2	5.91·E−5	7.41·E−4	10.2	19.7	30.1
Hirtella triandra	5.05·E−2	2.57·E−4	4.41·E−3	8.4	20.2	34.2
*Inga marginata**	1.11·E−1	3.59·E−4	2.85·E−3	6.7	15.6	25.2
*Miconia argentea**	1.38·E−4	3.31·E−6	2.03·E−2	2.2	5.1	7.7
Pouteria reticulata	8.92·E−2	2.03·E−4	1.95·E−3	9.3	22.9	39.7
Protium stevensonii	4.20·E−2	8.91·E−4	1.82·E−2	9.9	26.7	47.9
Protium tenuifolium	3.12·E−2	1.29·E−3	3.79·E−2	10.4	24.4	41.3
Quararibea asterolepis	1.14·E−2	1.59·E−5	1.26·E−3	8.1	20.3	34.6
*Simarouba amara**	1.47·E−2	5.77·E−4	3.35·E−2	5.6	11.7	18.2
Trichilia tuberculata	1.60·E−2	1.99·E−5	1.18·E−3	8.6	21.7	36.1

becoming an adult, which is L_{jj} in Equation 6 (Condit, 2022). Table 1 (Condit, 2022) does not show L_{jj} but does have P_a (the probability that a 1-cm sapling reaches adulthood) and L_{1j} (the adult lifespan expected for the average sapling). Since $L_{jj} = L_{1j}/P_a$ (Eq. 7; Condit, 2022), we can calculate it directly from Table 1 of Condit (2022). For the focal species in the present study, we calculated total expected lifespan from seed to death for the average adult tree as the mean time it takes a seed to reach 1 cm dbh (Table 3, this paper) added to $L_m + L_{jj}$; since *Faramea* was not included in Condit (2022), we have only 16 species. We set aside for future work analyses of variance and error in the estimates of the full lifespan.

4. Data availability

The complete Comita-Hubbell seedling data and the main plot data ($\geq$ 1 cm, eight censuses) are available in public archives (Comita et al., 2023; Condit et al., 2019). Since the Wright censuses are ongoing, existing archives (Wright et al., 2015a,b) are incomplete; to support our current analyses, we provide the data used in a supplement (Hernández et al., 2025). All transition matrices for the 17 focal species are archived in Condit (2024); the same archive includes the adult matrices from Condit (2022).

5. Results

5.1. Transition rates

5.1.1. Variation with age

In stage **I** seedlings, those $<$ 20 cm tall, age was an important predictor of transition rate. Growth probability increased with age in most species, from $<$ 5% at age 1 to 10%–20% in older seedlings (Fig. 1a). In several species with large samples, growth increased continuously from age 1 to age 9 (Fig. 1a). Among all 17 species, 12 had at least one significant growth increase with age. *Beilschmiedia* (beilpe) was an exception, having high growth at age 1 but no increase through age 5 (Fig. 1a). Appendix 7 includes graphs of transition versus age for all 17 species, with sample sizes given.

Survival also increased with age in stage **I**, though for only 3 years (Fig. 1b). Annual survival probability was 40%–60% at age 1 then 70%–90% or higher by age 3 (Fig. 1b). Among all 17 species, there were 12 having at least one significant increase in survival with age (Appendix 7). Again, *Beilschmiedia* was exceptional, having low survival that did not increase with age (Fig. 1b).

Once seedlings reached stage **II**, surpassing 20 cm tall, age was not a significant predictor of growth nor of survival. In nine species having at least 50 stage **II** seedlings at more than one age, only one showed a significant increase in growth (*Beilschmiedia*) and one in survival (*Protium stevensonii*). Transitions in stage **II** are illustrated for every species in Appendix 7, with sample sizes shown.

5.1.2. Variation with size

Annual growth transitions in larger stages, **II**, **III**, and **IV** ($\geq$ 20 cm in height), were generally below 10% (Fig. 1a), and annual survival rates reached 80%–90% (Fig. 1b; Appendix 7). Full transition matrices are illustrated for four species (Appendix 8) and all matrices are provided in a data supplement Condit (2024).

5.2. Survival over the seedling lifespan

5.2.1. Germination rate

Germination rate of seeds – the ratio of new seedlings to seeds – was between 0.01 and 0.15 in most species, but two orders of magnitude lower in *Alseis* and *Miconia* (Table 3, Fig. 2). The median rate across species was 0.042, meaning 24 seeds were needed to produce one germinant.

5.2.2. Seedling to 1-cm dbh

Survival rate between germination and 1 cm dbh varied by 200-fold across species. The highest rate was in *Garcinia*, just below 0.1 (Table 3, credible intervals in Appendix 6), while the lowest was 5.5×10^{-4} in *Beilschmiedia*. The median was 5.0×10^{-3}, meaning 200 germinants were needed to produce a single 1-cm sapling. Survival after germination was negatively related to germination rate, but the significance of the relationship was driven by the two outliers having extremely low germination (Fig. 2). *Alseis* had the lowest germination rate but the second highest post-germination survival, while *Beilschmiedia*, with the highest germination rate, had the lowest survival (Fig. 2).

5.2.3. Seed to 1-cm dbh

Survival across the seedling lifespan, from seed to 1 cm dbh, varied 1000-fold across species (Table 3, credible intervals in Appendix 6). The rate was lowest, near 3×10^{-6}, in *Alseis* and *Miconia*, the two species with very low germination, while it exceeded 4×10^{-3} in *Garcinia* (Table 3, Fig. 3). For 10 of 17 species it was between 10^{-4} and 10^{-3}. Median survival across species was 2.0×10^{-4} (the rate in *Guarea*), meaning 5,000 seeds were needed to produce a single 1-cm sapling.

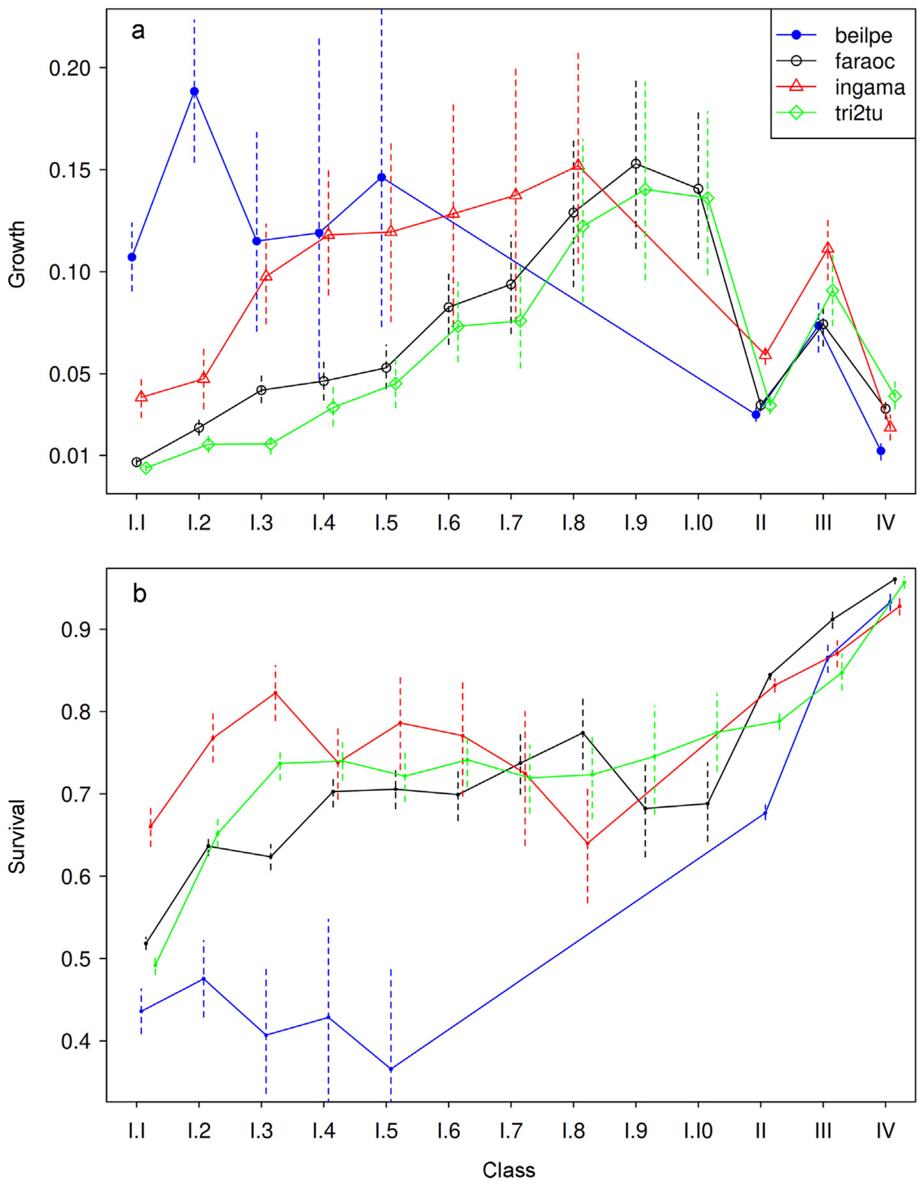

Fig. 1. Transition rates across age-size stages in four species, chosen for large sample sizes. In both panels, the horizontal axis shows all stages up to **IV**, excluding stage **V** ($\geq$ 1 cm). Classes **I.N** are ages (in years) within stage **I** (height < 20 cm); the last age combines all greater ages (e.g. **I.5** includes all seedlings $\geq$ 5 years of age in beilpe). **a)** Vertical axis shows fraction of individuals growing by one size class; for all stages **I.N**, this means growing to stage **II**. **b)** Vertical axis shows fraction surviving. *Beilschmiedia* (beilpe), *Faramea* (faraoc), and *Trichilia* (tri2tu) had the highest samples of germinants (Table 2); *Inga* (ingama) was included to illustrate a pioneer species, and it had the largest sample among the pioneers. The same graph appears for all 17 species in Appendix 7.

5.2.4. *Observed transitions from seed to 1-cm dbh*

There were 20 different known-age seedlings that surpassed a height of 240 cm by 2019 and thus surpassed 1 cm dbh, found in 11 of the 17 study species. The youngest was a *Miconia* that germinated at 428 cm tall and was thus already 1 cm dbh at 1-year old. The others reached 240 cm tall between age 6 and age 20. There were 7,431 seedlings that survived $\geq$ 20 years without reaching 240 cm tall, though 221 were still alive in 2019 and thus still might reach it.

5.2.5. *Adult fecundity and seed survival to 1-cm dbh*

Mean annual fecundity per adult was negatively related to survival from seed to 1 cm dbh across species. Indeed, the relationship was close to inverse, i.e. survival was approximately one over fecundity (Fig. 3). In *Trichilia*, for example, mean adult fecundity was 52,916 seeds, while 1 out of 50,136 seeds would survive to 1 cm dbh. Towards the extremes, adults of the highly fecund *Alseis* produced over 1 million seeds per year, but < 3 per million survived to 1 cm; *Protium tenuifolium* had fecundity 1000-fold lower but survival 1000-fold higher (Table 3). The four most fecund species were above the inverse line, while species with low fecundity were scattered around it, such as *Faramea* well below and *Garcinia* above (Fig. 3).

5.3. *Lifespan*

5.3.1. *Time to 1 cm dbh*

In *Quararibea*, the mean seedling lifespan to 1 cm dbh was 20.3 years (credible interval 18.4–22.4). This was the median for the 17 species; there was, however, 10-fold variation among species (Table 3). The fastest time to 1 cm was in the pioneer *Miconia*, in which the mean successful seed would reach 1 cm in 5.1 years (credible interval 4.5–5.8); the slowest was in *Garcinia* at 53.1 years (48.2–60.4). The two species with the longest time to 1 cm dbh were those with the highest survival rates after germination, *Alseis* and *Garcinia* (Fig. 2).

The time to 1 cm was also highly variable within species. In the median species, *Quararibea*, the 10% fastest growing seedlings would take 8.1 years to reach 1 cm (credible interval 6.2–9.4), while the 10% slowest would take 34.6 years (31.3–38.4). Indeed, most species varied approximately four-fold from the fastest to the slowest: in the fast-growing pioneer *Miconia*, the range was 2.2–7.7 years, while in *Garcinia*, it was 21.9–93.2 years (Table 3).

5.3.2. *Total lifespan*

In the three pioneer species, the expected total lifetime from seed

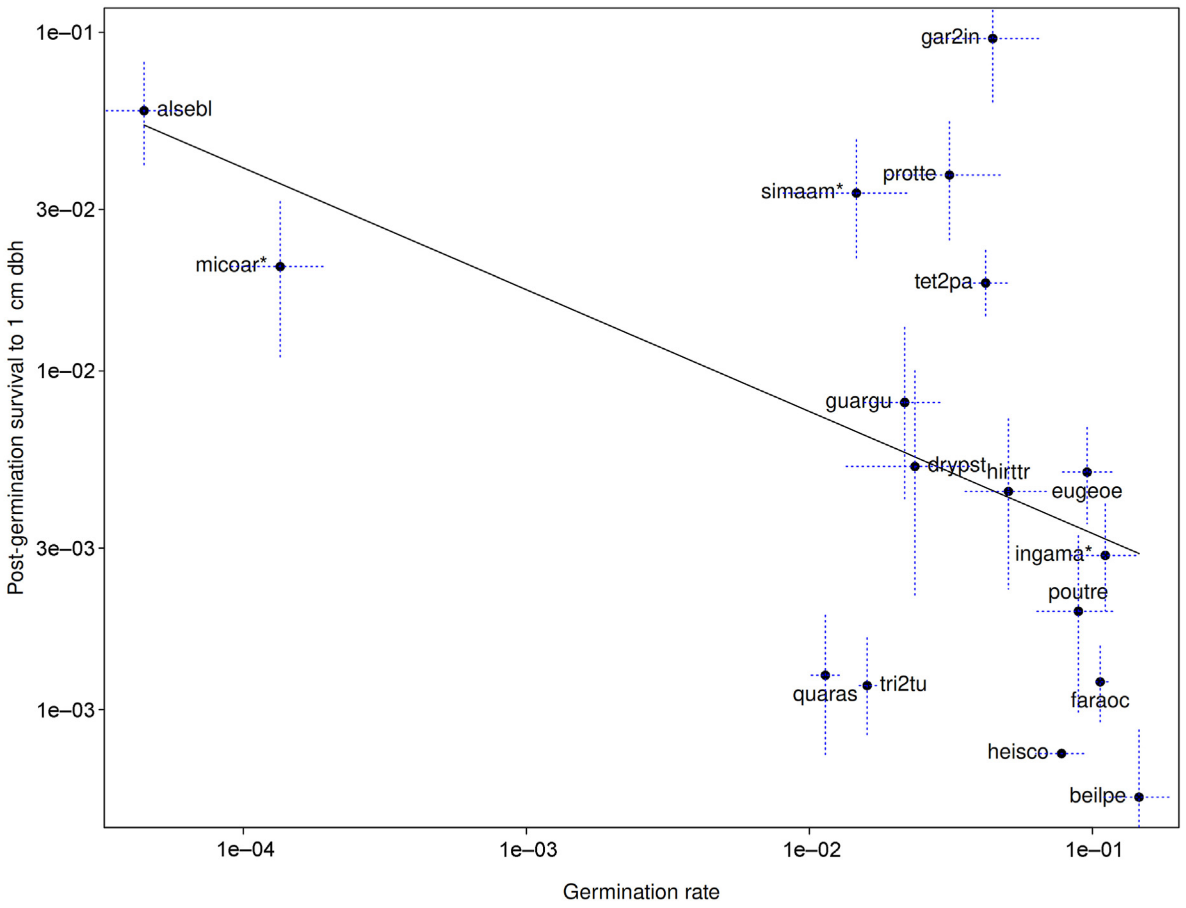

Fig. 2. Survival from germination to 1 cm dbh versus germination rate for the 17 study species. Axes are logarithmic. The solid line is a regression of log-transformed variables (slope $= -0.36$, $p = 0.04$, $r^2 = 0.20$). The negative regression is due to the two outliers at the far left, and without them is not significant ($p = 0.19$). Species names are abbreviated with 6-letter codes that are given in Table 2; all but one match genus names. Three pioneers are labeled with asterisks.

through adulthood was 41–75 years (Table 4). In the shade-tolerant species, it varied from 110 years in *Eugenia* to 320 years in *Alseis*. The percent of the lifespan in the seedling stage, from seed to 1-cm dbh, was a minimum of 8.1% (*Drypetes*) and a maximum of 26.8% (*Garcinia*); the average was 14.8%.

6. Discussion

Our quantitative analysis of seedling lifespans answers major questions in tropical forest demography that are seldom addressed. Matrix projections based on 25 years of seedling censuses predicted an average seedling lifespan, from seed to 1-cm dbh sapling, of 20 years in the median species. Across species, mean projected lifespan varied from 5 years in a fast-growing pioneer to 53 years in one long-lived, shade tolerant species.

The matrix projections also produced estimates of the variation within species of the seedling lifespan. In fact, we discovered a general pattern that held across species: there was a four-fold range between the fastest and the slowest times for a seed to become a 1-cm sapling. This wide variance in seedling lifespan within a species means that cohorts of saplings recruiting at the same time originate from decades of seedling cohorts. Highly variable seed production from year to year (Usinowicz et al., 2012) may be smoothed away by the sapling stage. This tends to undermine the theory that species coexist based on distinct temporal niches (Chesson and Warner, 1981; Kelly and Bowler, 2002).

Matrix projections also generated estimates for the number of seeds it takes to produce a single sapling at 1 cm dbh. For the median species, survival from seed to sapling was 2×10^{-4}, meaning 5,000 seeds would be needed per sapling, but this varied three orders of magnitude among species. In *Alseis*, 345,000 seeds would be needed, but only 225 in *Garcinia*. Moreover, we discovered that seed survival to 1 cm dbh was close to the inverse of annual adult fecundity, meaning that the average adult produces approximately one sapling per year. It follows that the adult lifespan must be the inverse of the probability that a sapling reaches adulthood to maintain a population. We set aside for another study an analysis of lifetime demography.

Our predictions of seed survival will be difficult to test via direct observation because of long seedling lifespans. We observed 20 newly germinated seedlings that grew to 240 cm tall during our observations, representing a fraction of 7×10^{-4} of the 27,437 observed germinants. The predicted survival of germinants to 1 cm dbh was 5×10^{-3}, an order of magnitude higher, but our observations spanned only 25 years, far shorter than predicted seedling lifespans. Indeed, new germinants censused through 2019 will not finish recruiting as saplings until the year 2113 in *Garcinia*. This demonstrates that seedlings' lifespans can only be fully documented by projecting current demography.

We know of few studies of matrix demography covering the entire lifespan of trees. Piñero et al. (1984) and Silva Matos et al. (1999) did so in two palm species but did not estimate the lifespan of seedlings (nor adults). Cochran and Ellner (1992) reanalyzed data from Piñero et al. (1984) and reported that the probability a seedling would reach maturity was 0.001–0.004, but they did not calculate the same probability from the seed stage. Horvitz and Schemske (1995) showed a matrix from seed to adult for a large tropical herb, and we reanalyzed it, finding that a seed's probability of reaching medium adult size would be 5×10^{-3}, at the upper end of probabilities we found for a seed to reach 1 cm dbh. Tree

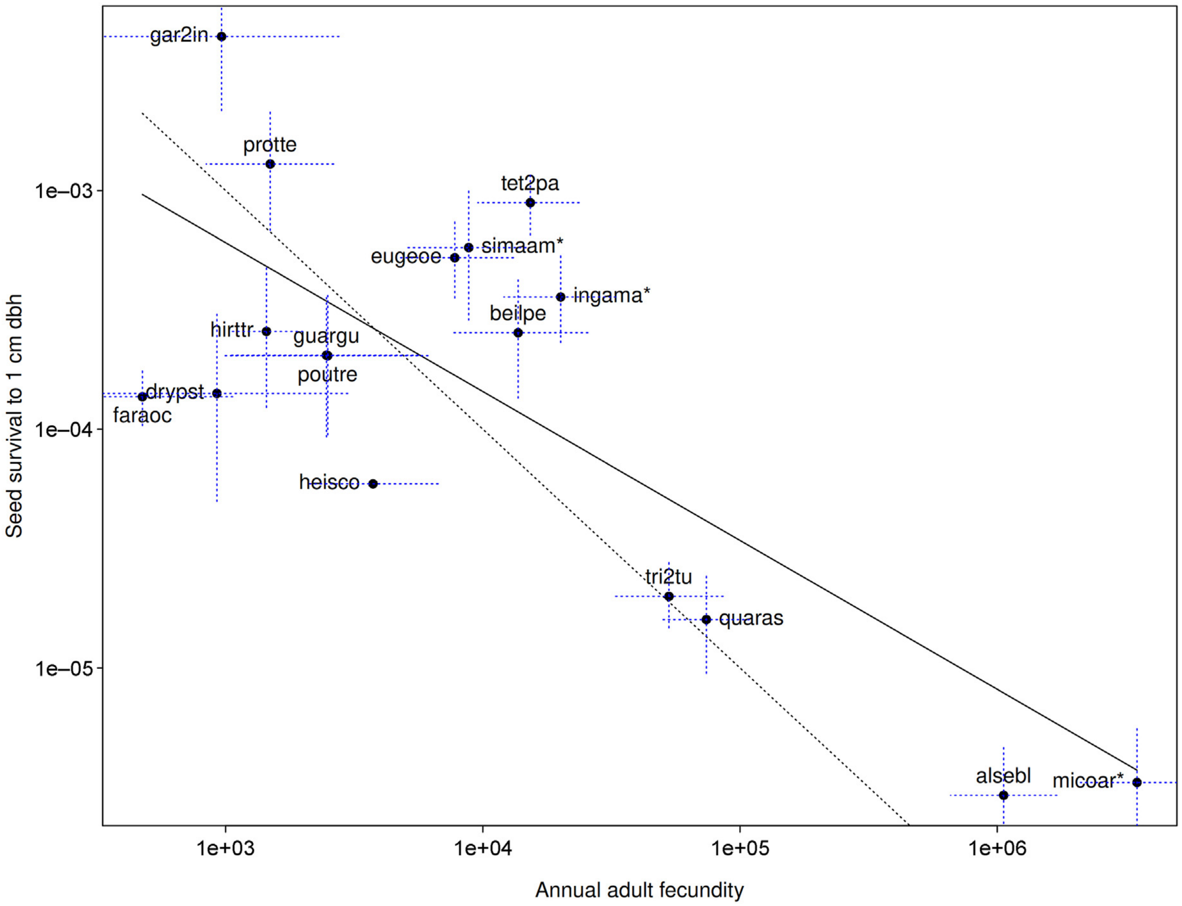

Fig. 3. Survival rate from seed to 1-cm dbh versus annual adult fecundity. Axes are logarithmic. A solid line is the regression of log-transformed variables (slope $= -0.62$, $p = 0.0004$, $r^2 = 0.56$). The two rates are nearly inverse, and the dashed line is included to show exactly where survival = 1/fecundity. Species abbreviations are given in Table 2; three pioneers are labeled with asterisks.

Table 4
Expected lifespan from seed for all trees surviving into adulthood. Seed to 1 cm lifespan comes from Table 2 in this paper; 1 cm to adult is the maturation time from Table 1 in Condit (2022). The expected lifespan as an adult is also based on Table 1 in Condit (2022), using the expected adult lifespan as a sapling and the probability of reaching adulthood (see Methods). Pioneer species are indicated with asterisks.

Species	Expected lifespan (year)			
	Seed to 1 cm	1 cm to adult	Adulthood	Total
Alseis blackiana	44	125	150	320
Beilschmiedia tovarensis	16	117	58	192
Drypetes standleyi	19	107	111	237
Eugenia oerstediana	29	52	28	110
Garcinia recondita	53	100	46	199
Guarea guidonia	20	68	74	161
Heisteria concinna	20	62	93	174
Hirtella triandra	20	71	81	171
*Inga marginata**	16	28	17	61
*Miconia argentea**	5	19	17	41
Pouteria reticulata	23	74	119	216
Protium stevensonii	27	109	89	225
Protium tenuifolium	24	59	55	138
Quararibea asterolepis	20	119	79	217
*Simarouba amara**	12	38	26	75
Trichilia tuberculata	22	90	34	146

ring chronologies show that adults of tropical trees commonly live 100–250 years (Brienen and Zuidema, 2006; Brienen et al., 2010; Alfaro-Sánchez et al., 2017), similar to our projections, but rings cannot address expected lifespan, which is crucial for demographic analysis, and omit the seedling stage. Our estimates are the first we know that address expected lifespans of trees from the seed stage that include more than a single species.

The hypothesis that tree species partition a regeneration niche hinges on variation in recruitment along the gradient from high light under treefalls to deep forest shade. Transient canopy gaps offer the light pioneer species demand, allowing them to coexist with shade-tolerant dominants (Grubb, 1977; Brokaw, 1985; Denslow, 1987). Based on demography above 1 cm dbh, we described this partitioning as a demographic axis that extends from pioneers, with high growth but low survival in gaps, to shade-tolerators with high survival but low growth (Hubbell and Foster, 1986; Condit et al., 1996; Condit, 2022; Condit and Rüger, 2024; Rüger et al., 2018, 2020; Kambach et al., 2022). But it is seedling demography that defines the regeneration niche, and we discovered that seedlings do not easily conform to this growth-survival tradeoff. In particular, seedlings of the pioneers *Inga* and *Simarouba* behaved like seedlings of the shade-tolerant species, with good germination and survival. The third pioneer we studied, *Miconia*, was much different, with low germination followed by rapid growth to 1 cm dbh. The other exceptional species was *Alseis*, which behaved like the pioneer *Miconia* in its low germination and high fecundity, but unlike *Miconia* it shifted to high survival after germination, and had one of the longest seedling lifespans (see Dalling et al., 2001 for more on *Alseis* life history). The regeneration niche is evidently more complex than a single axis, and must account for a variety of demographic adaptations in seeds and seedlings (Kambach et al., 2025).

Some of the differences in seedling strategy are explained by seed size: *Inga* and *Simarouba*, though pioneers as adults, have seeds over 0.1 g in dry mass, similar to many shade-tolerant species (Sautu et al., 2006; Pritchard et al., 1995; Wright et al., 2010). Both *Miconia* and *Alseis*, however, have tiny seeds, not even 0.1 mg, accounting for their enormous fecundity. Remarkably, both species managed higher than average survival once germinated: they overcame tiny germination probability and achieved high production of saplings per adult. *Beilschmiedia*, on the other hand, has enormous seeds at 3.9 g and germinated well, but seedlings immediately had low survival. An inverse correlation between seed size and seedling survival is surprising, but also reported by Visser et al. (2016) in an analysis across the Barro Colorado tree community. The question posed in Moles and Westoby (2004) about whether the low fecundity of large-seeded species is offset by longer lifespan can only be answered by tracking seeds through to adulthood, which has seldom been done, but the question is simplistic in that seed size has only a brief impact on a very long lifespan.

We believe these demographic results are a reasonable representation of seedling demography of the entire community, because we selected 17 species that come close to spanning the range of tree growth and survival rates (Condit et al., 1995; Rüger et al., 2011a, 2011b; Condit and Rüger, 2024). However, the abundant, fast-growing genus *Cecropia* could not be included because its seeds are too tiny to count, while long-lived giants in the genera *Prioria* and *Cavanillesia* had too few seeds to analyze. It will be interesting to find ways of analyzing seedling demography of these extremes in life history.

Combining our seedling results with lifespans from sapling to adulthood from Condit (2022), we now have a full estimate for the lifespan of tropical trees. Three pioneer species had lifespans below 75 years, with a minimum of 41 years in *Miconia*, while shade-tolerant species had lifespans over 100 years, and beyond 300 years in *Alseis*. These are average lifespans – expected lifespans starting from a seed – of all trees that survive to adulthood. This is the best way to assess lifespans of trees. Ages based on tree-ring chronologies are also based on trees surviving to adulthood, since only larger trees are included, but they omit the seedling period (Brienen and Zuidema, 2006). On average, we found that seedling development to 1 cm added 15% to the lifetime, up to 27% in some species. Trees can live much longer than 300 years (Piovesan and Biondi, 2021), but maximum lifespans have little relevance in demography.

Using transition matrices based on discrete categories has drawbacks owing to the assumption that all individuals within a category are identical. This means, for example, that seedlings entering size class **II** at one step are just as likely to advance to class **III** as those already in class **II** for many steps. In the analysis here, we addressed this concern for the smallest seedlings, stage **I**, because their ages were considered, and age was important, but age was not a predictor of transitions at stage **II**. Larger sizes could not be divided by age. In future work, we will carry out explicit tests of the matrix approach by comparing projections with direct observations of long-lived seedlings and saplings, possible given censuses that have continued for 25 years.

7. Conclusions

Our results provide the first rigorous estimates in tropical trees of the lifespan of seedlings, from seed to sapling. In the fastest growing species, seedlings reached sapling size in 5 years, while other species took over 50 years. Within species, the time to 1 cm dbh varied four-fold, meaning that 1-cm saplings alive at any one time arose from decades of seedfall. Such quantitative precision in seedling demography can inform models of the importance of the regeneration niche, currently based on approximate seedling lifespans (Pacala et al., 1996; Hubbell, 2001; Usinowicz et al., 2012; Stump and Comita, 2020), as well as models of forest growth and yield (Weiskittel et al., 2011). Combined with the adult demography presented in Condit (2022), it gives us a complete description of the lifespan of the dominant tropical tree species at Barro Colorado Island.

CRediT authorship contribution statement

Richard Condit: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Andrés Hernández:** Methodology, Investigation. **Oswaldo Calderón:** Methodology, Investigation. **Rolando Pérez:** Methodology, Investigation. **Salomón Aguilar:** Methodology, Investigation. **Liza S. Comita:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Stephen P. Hubbell:** Resources, Methodology, Investigation, Conceptualization. **S. Joseph Wright:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Ethics approval and consent to participate

The research involved no human subjects. The forest on Barro Colorado Island is used solely for research purposes under an agreement between the Panama Government and the U.S. Government.

Declaration of competing interest

The author declares that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100309.

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