



Expected adult lifespan in tropical trees: Long-term matrix demography in a large plot

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ABSTRACT

Background: Documenting the entire lifetime of long-lived organisms requires splicing together short-term observations. Matrix demography provides a tool to calculate lifetime statistics, but large samples from juvenile to adult are needed, and few such studies have been done in tropical trees because high species diversity limits sample sizes. The 50-ha plot at Barro Colorado in Panama was designed to provide large samples, and with 30 years of censuses, accurate population matrices can be constructed.

Methods: In 31 abundant species, I divided all individuals ≥ 1 cm dbh into 4 or 5 size class in each of seven censuses. Movements of stems between size classes over two censuses are termed transitions, and I constructed complete transition matrices for each species. From the matrices, I derived analytic solutions for lifetime demographic statistics. Expected adult lifespan from the sapling stage was the key statistic.

Results: Expected adult lifespan from the sapling stage varied 100-fold over the 31 species, from 0.5 to 50 years, and maturation time varied from 19 to nearly 200 years. Species with the highest growth rates also had high death rates, and theoretical calculations of reproductive lifespan show that the fast-growing pioneer species have short expected adult lifespans relative to the average slow-growing, shade-tolerant species. Within the slow-growth category, however, there was high variation in expected adult lifespan, and several shade-tolerant species under-performed the pioneers in terms of adult lifespan.

Conclusions: Analytical solutions from population matrices allow theoretical analyses that integrate short-term growth records into lifespans of tropical trees. The analyses suggest that pioneer species must reproduce more successfully than shade-tolerant species to persist in the Barro Colorado forest. My next goal is to incorporate seed production and germination into lifetime matrix demography to test this hypothesis.

1. Background

Lifetime demography of tropical forest trees means tracking the fate of juveniles until they become reproductive adults. But trees live longer than research projects, so complete life-tables can only be created by splicing together short-term measurements from trees monitored in census plots (Usher, 1966; Condit et al., 1993; Chien et al., 2008; Zuidema et al., 2010; Picard and Liang, 2014). Though tree-ring studies of tropical trees have proliferated, producing lifetime growth trajectories (Brienen and Zuidema, 2006; Brienen et al., 2010; Rozendaal and Zuidema, 2011; Alfaro-Sánchez et al., 2017), these cannot address survival and thus do not provide complete life-tables. Long-term and large-scale plot samples are needed. The Barro Colorado 50-ha plot in Panama was designed to create complete life-tables.

Short-term plot measurements have generated hypotheses about demographic guilds of tropical trees, focusing on how species with varying growth and mortality co-exist (Hartshorn, 1980; Denslow, 1980; Stearns, 1999; Salguero-Gómez, 2017; Rüger et al., 2018). Hypotheses about coexistence are necessarily about lifetime demography, yet the lifetime impact of tradeoff between growth and survival has not been examined. Here I test the impact of the growth-mortality tradeoff on reproductive lifespan using transition matrices constructed from observations in the Barro Colorado plot. I demonstrate analytical solutions to lifetime demographic parameters from the matrices, then examine how these parameters vary across the full spectrum of growth and survival rates (Rüger et al., 2011a,b).

The primary question is whether tree species across the fast-slow life history axis are in demographic balance. I examine this by calculating the

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expected adult lifespan of saplings at 1 cm dbh. The expected adult lifespan is a key demographic trait because it determines the potential reproductive output for the average juvenile entering the population. To be in balance, the fast growth rate of pioneer trees must overcome their high death rates, leading to an adult lifespan equal to slow-growing, shade-tolerant species. I also calculate two other demographic results closely related to the expected adult lifespan: the probability of reaching adulthood (maturation probability) and the time it takes to reach adulthood (maturation time), both for the average 1-cm sapling. Markov chain theory offers analytical formulations for a sapling's expected adult lifespan and probability of reaching adulthood (Kemeny and Snell, 1960; Iosifescu, 1980).

Analytical solutions allow theoretical analyses of elasticity, relating the key demographic outcomes to variation in transition parameters. In particular, I use theoretical predictions of adult lifespan along the observed growth-mortality tradeoff (Rüger et al., 2020) to examine whether the upper end of the axis (fast growth) achieves expected adult lifespan equal to the lower end (slow growth). This extends existing work on matrix demography, which seldom includes analytical results (Franco and Silvertown, 2004; Doak et al., 2021).

2. Transition matrix demography

2.1. Overview

Matrix models are a standard tool in plant demography, from the Lefkovich matrix to Integrated Projection Models, and there are many varieties of matrices (Lefkovich, 1965; Caswell, 2001; Ellner and Rees, 2006; Doak et al., 2021). In order to make theoretical predictions about the growth-survival tradeoff, I maintain that a simplified approach best reveals the basic underlying demographic consequences of a growth-survival tradeoff. For this reason, I omit reproduction and focus on expected adult lifespan, and I construct matrices with a small number of classes between which growth probabilities are near constant.

The demographic matrix starts by dividing individuals into categories based on stem diameter. This defines the population as a vector N_i , the number of individuals in each size class i . Given two successive measurements, a transition probability between any two size classes is estimated by counting the proportion of N_i that advance to a larger size class, $j > i$ (growth), remain in class i (stasis), and how many die. The Barro Colorado 50-ha plot was designed to include large sample sizes of many tree species, and for the most important species of the forest, demographic estimates are strong (Hubbell and Foster, 1983; Condit, 1998). Moreover, multiple censuses provide replicate transition estimates (Condit et al., 2017).

From a standard transition matrix, I calculate three lifetime demographic parameters, all expectations for the average 1-cm sapling: 1) adult lifespan, 2) maturation probability, and 3) maturation time. I then explicitly address two common concerns about population matrices (Picard et al., 2003; Zuidema et al., 2009; Doak et al., 2021): 1) that results are dependent on the size classes defined, and 2) that the matrix approach omits temporal autocorrelation in the demographic parameters. To address these concerns, I tested whether lifetime estimates were robust to variation in size classes, and I devised a new approach that allows transition matrices to include autocorrelation as memory of prior transitions.

2.2. Lifetime demographic results from the transition matrix

I first illustrate the two main matrices I used and state formulae for the key demographic results. Appendices 1-2 include full derivations of the formulae and add descriptions of alternative matrix constructions. Since I use derivations from Markov chain analysis of transition matrices

(Kemeny and Snell, 1960), I follow conventions in the Markov-chain literature, using row-stochastic matrices (Caswell, 2001). This means that the fate of an individual is found along a row, and the sum of transition probabilities along a row is 1; this is the transpose of a Leslie matrix (Leslie, 1945).

For the basic matrix, I divided trees into four size classes, three juvenile and one adult. A Leslie matrix would stop at four classes, but a full transition process requires one more, because dead trees must be included, leading to a 5×5 transition matrix, T . Size categories 1–4 are labeled with boldface and D is the category for dead trees:

$$T = \begin{pmatrix} & \mathbf{1} & \mathbf{2} & \mathbf{3} & \mathbf{4} & D \\ \mathbf{1} & r_1 & g_1 & g'_1 & 0 & m_1 \\ \mathbf{2} & 0 & r_2 & g_2 & g'_2 & m_2 \\ \mathbf{3} & 0 & 0 & r_3 & g_3 & m_3 \\ \mathbf{4} & 0 & 0 & 0 & r_4 & m_4 \\ D & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad (1)$$

Element t_{ij} of T , at row i and column j , is defined as the probability that a tree in size class i in one census transitions to class j in the next census. The diagonal of the matrix has stasis probabilities, each a probability that a tree in class i remains there one census later; $t_{ii} = r_i$ (r for *remain* to emphasize that it differs from survival). Elements above the diagonal are growth transitions, and the final column is the death transition, so $t_{i5} = m_i$, with m for mortality ($j = 5$ is the D class).

A common simplification in demographic transitions is to restrict growth. I assume no shrinking, so $t_{ij} = 0$ when $j < i$. I also restrict growth to one or two steps. Define g_i as one-step growth from class i , then $g_i = t_{ij}$ when $j = i + 1$, and growth by two steps as $g'_i = t_{ij}$ where $j = i + 2$. In the bottom right corner, $t_{55} = 1$ to indicate that once trees are dead, they remain dead. Class 4, the adult class, is the final size class, so there is no growth in the fourth row: trees either remain as adults or die. Since the sum of row entries must be 1, $r_i + g_i + g'_i + m_i = 1$ for $i < 4$ and $r_4 + m_4 = 1$. Designate N as a vector of the number N_i alive in class i at time x . Then the population vector at $x + 1$ is $N' = N \cdot T$.

Equation 1 describes an absorbing Markov process because all trees are eventually absorbed into the death state, enforced by row 5 in the matrix. The demographic questions are about the pathway trees follow before death: how long it takes to die, what proportion live until adulthood, and expected lifespans. It is a Markov process because the transitions at one time step are independent of past times. There is no memory. Kemeny and Snell (1960) and Iosifescu (1980) give many examples of transition matrices, some non-absorbing, others with multiple absorbing states. By adding additional categories, it is not a difficult step to a Markov process that includes memory.

2.3. A transition matrix with memory

The demographic flaw in a Markov process is that trees might have unrealistically high growth. This can happen because a tree that grows from class 1 to class 2 at one time step might immediately grow from 2 to 3 at the next step. Zuidema et al. (2009) and Picard and Liang (2014) examined fast growth due to consecutive transitions. They reached opposite conclusions, so here I test explicitly the impact of adding memory to the transition process while retaining the Markov assumption. This is possible if the matrix has two subclasses within each size class, one for trees that just grew there and another for trees that were already there. This means a 9×9 transition matrix to cover four size classes:

$$T_m = \begin{pmatrix} & 1.1 & 1 & 2.1 & 2 & 3.1 & 3 & 4.1 & 4 & D \\ 1.1 & 0 & r_1 & f_1 & 0 & 0 & 0 & 0 & 0 & 1 - r_1 - f_1 \\ 1 & 0 & r & f & 0 & 0 & 0 & 0 & 0 & 1 - r - f \\ 2.1 & 0 & 0 & 0 & s_1 & g_1 & 0 & 0 & 0 & 1 - s_1 - g_1 \\ 2 & 0 & 0 & 0 & s & g & 0 & 0 & 0 & 1 - s - g \\ 3.1 & 0 & 0 & 0 & 0 & 0 & t_1 & h_1 & 0 & 1 - t_1 - h_1 \\ 3 & 0 & 0 & 0 & 0 & 0 & t & h & 0 & 1 - t - h \\ 4.1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & u_1 & 1 - u_1 \\ 4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & u & 1 - u \\ D & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix} \quad (2)$$

Within the first size class are two subclasses, labeled **1.1** and **1**, and likewise for classes **2** – **4**. When a tree first grows from one size to the next, it arrives in the **.1** subclass and it remains there for one time step (or dies). All transition probabilities must also be split into two, and here I redefine symbols in order to avoid double subscripts. Growth probabilities for size classes **1**, **2**, **3** are labeled f , g , and h , and each has a subscript **1** for trees that just arrived in a class (g_1 , f_1 , h_1) and no subscript for trees already in a size class. The residence probabilities, for remaining in each size class, are r , s , t , and u , and these likewise are paired, with and without subscripts. The final column has death probabilities, here written as one minus the sum of growth and residence to reduce the number of symbols.

Consider the example of a tree starting life as a new sapling, in subclass **1.1**. It has probability f_1 of growing, which means entering subclass **2.1**, the initial subclass in size class **2**. It has probability r_1 of remaining in size class **1**, but that means graduating from **1.1** to **1**. Or it might die with probability $1 - r_1 - f_1$. Once it is in category **1**, it can reside there with probability r or grow to **2.1** with probability f . The same rules repeat once a tree reaches **2.1**, using probabilities g , g_1 for growth and s , s_1 for residence, and so forth.

This same approach can accommodate three subcategories per size class, and this is written out in [Appendix 2](#). It could be extended to more subcategories, but I stopped at three.

2.4. Deriving expected lifespan

The primary question about adult lifespan is about a tree starting as a sapling, in class **1**. Given a population of $N_1 = 100$ saplings, what is their expected time spent as adults? This expectation is an average of two groups: trees that die before adulthood, and thus have an adult lifespan of zero, and trees that reach adulthood and spend at least one time step there. The mean adult lifespan might be a small number, much less than 1 if most of the 100 saplings die before adulthood.

The expected adult lifespan of a sapling has a straightforward analytical solution from the transition matrix **T** ([Kemeny and Snell, 1960](#)), and if two-step growth is zero, it extends to any number of size classes. There are also exact solutions for matrices with one- or two-step memory, though extending those to > 5 size classes is more complicated.

Define L_{ij} as the expected lifespan in size class j for an individual starting in size class i . One of the basic calculations from [Kemeny and Snell \(1960\)](#) leads to the expected lifespan in any of the size classes for an individual starting in class **1**:

$$L_{1j} = \frac{1}{1 - r_j} \prod_{k=1}^{j-1} \frac{g_k}{1 - r_k}, \quad (3)$$

assuming no two-step growth, that is $g' = 0$ (Eq. 1). With four size classes, L_{14} is the expected time that a sapling will spend as an adult ($j = 4$), but

the formula also works for $j = 5$ or more. With two-step growth, g'_i , and the 4-class model, the expected adult lifespan becomes

$$L_{14} = \frac{g_1 g_2 g_3 + g_1 g'_2 (1 - r_3) + g_3 g'_1 (1 - r_2)}{\prod_{k=1}^4 (1 - r_k)}, \quad (4)$$

which collapses to Equation 3 with $g'_i = 0$ and $j = 4$. The comparison with Equation 3 demonstrates that adult lifespan increases in proportion to two-step growth, since the g' terms are linear. Extending Equation 4 to more size classes is complicated, as the number of terms expands quickly. I show the solution for $j = 5$ classes in [Appendix 1](#) (Eq. A16), but have not gone further.

There is also an analytical solution for expected adult lifespan of a sapling in the matrix with memory (Eq. 2):

$$L_{1.1,4.1} + L_{1.1,4} = \frac{\alpha \beta \delta (1 - u + u_1)}{(1 - r)(1 - s)(1 - t)(1 - u)}, \quad (5)$$

where $\alpha = fr_1 + f_1(1 - r)$, $\beta = gs_1 + g_1(1 - s)$, and $\delta = ht_1 + h_1(1 - t)$. The two terms $L_{1.1,4.1}$ and $L_{1.1,4}$ are needed because adults include the last two subclasses, **4.1** and **4** (Eq. 2). Equation 5 gives the expected adult lifespan of a sapling just entering category **1.1**. I show analytical solutions for matrices with memory using only four size classes and one-step growth.

Comparing Equations 3 and 5 suggests how adult lifespan will change with the addition of memory. In slow growing trees, it is reasonable to consider the immediate growth terms f_1 , g_1 , $h_1 \sim 0$. Then the numerator in Equation 5 is left with $\alpha \beta \delta = fgh$, the product of all growth terms, as in Equation 3, plus an extra $1 - u + u_1$. Denominators in the two equations are identical. The growth terms f , g , h should be increased relative to growth in the original matrix (no memory), while empirical results suggest $1 - u + u_1 < 1$, because trees that just grew usually have lower death rates than resident trees. The resulting adult lifespan from Equation 5 is thus neither obviously increased nor decreased relative to Equation 3. My analysis should be compared closely with [Picard and Liang \(2014\)](#).

2.5. Deriving maturation probability

The probability that a sapling reaches adulthood, or maturation probability, is a straightforward derivation because the expected adult lifespan after reaching adulthood, L_{jj} (where j is the adult class), is easy to calculate. It requires no matrix theory because mortality rate as an adult remains constant, so

$$L_{jj} = \frac{1}{m_j} = \frac{1}{1 - r_j}. \quad (6)$$

This is the mean of a geometric distribution whose rate is the survival probability, $r_j = 1 - m_j$. It holds with or without two-step growth in Equation 1, but there is a small adjustment in the matrix with memory ([Appendix 2](#)). Given L_{jj} , the probability of reaching adulthood is

$$P_a = P_{1j} = \frac{L_{1j}}{L_{jj}}, \quad (7)$$

where L_{1j} is the expected adult lifespan of a sapling (from Eqs. 3–5). This follows from the definition of average expected lifespan, which declines from L_{jj} to L_{1j} in proportion to the fraction of saplings that never become adults, all of which have an adult lifespan of zero ([Appendix 1](#)).

2.6. Deriving maturation time

The final calculation is the time it takes for a sapling to reach adulthood, or the maturation time. I have not found this published ([Kemeny and Snell, 1960](#); [Iosifescu, 1980](#); [Caswell, 2001](#)), and I do not have an analytical solution for the matrices in Equations 1 and 2. There is an analytical solution, however, for a simpler matrix with constant growth g

and residence r , where $g_i = g$ and $r_i = r$ in every size class, and omitting two-step growth. Then the mean number of time steps it takes a sapling to reach adult class j is

$$\hat{S}_{ij} = \frac{j-1}{1-r}. \quad (8)$$

Appendix 1 gives the derivation. This remarkably simple way of estimating maturation time should provide many insights into matrix demography and lifespan, but I do not pursue it here.

2.7. Numerical estimates

In order to calculate the key demographic traits numerically, from any transition matrix, I used numerical projections with observed matrices. Since the questions are about the fate of saplings in class 1, the vector of initial population size, N , had $N_1 = 1$ and $N_i = 0$ for $i > 1$. The population vector at step x is $N' = NT^x$, since the transition matrix after x steps is T^x , meaning T raised to the x th power (Kemeny and Snell, 1960). The number of adults at time x is N'_a , where a is the adult (terminal) size class. I calculated maturation time and maturation probability by finding the fraction of saplings recruiting to class a in each time step. The number of adults recruiting between $x-1$ and x is

$$a_x = N'_a - r_a N_a, \quad (9)$$

where N'_a is the number of adults at step x , N_a the number at $x-1$, and r_a is the residence probability in class a . This is the difference between the number in class a at time x and those that were already in class a at time $x-1$ and remained until x . In the matrix with memory, the calculation is easier, because newly recruited adults are only in subclass $a.1$ and the

Table 1

The 31 species included in matrix analyses. Adult size is the minimum dbh at which many trees were reproductive. N is total population ≥ 1 cm dbh in 1990. Adult life expectancy includes the three key demographic traits calculated from transition matrices: 1) *as sapling* is the mean adult life expectancy in years for the average sapling of 1 cm dbh, based on the analytical calculation with two-step growth in pioneers and one step growth in the others; 2) *probability* is the maturation probability, or the probability that a sapling reaches adult size, also based on the analytical solutions; and 3) *maturation* is the average time in years it takes a sapling to grow from 1 cm to adult size, based on numerical calculations. Mean transitions are the average growth and mortality transitions across all size classes of the transition matrix, i.e. the probability any tree grows to the next size class (or dies) during one 5-year census interval. Pioneer species are indicated with *p*.

Species (Family)	N	Adult size	Adult life expectancy			Mean transitions	
			As sapling	Probability	Maturation	Growth	Mortality
<i>Alseis blackiana</i> (Rubiaceae)	8412	200	10.7	0.072	124.9	0.055	0.074
<i>Beilschmiedia tovarensis</i> (Lauraceae)	2748	300	1.3	0.023	117.4	0.073	0.099
<i>Brosimum alicastrum</i> (Moraceae)	920	300	4.8	0.080	188.3	0.060	0.055
<i>Chrysophyllum argenteum</i> (Sapotaceae)	688	300	3.0	0.025	137.3	0.061	0.078
<i>Cordia bicolor</i> (Cordiaceae) ^p	1043	100	5.6	0.099	24.3	0.190	0.264
<i>Cordia lasiocalyx</i> (Cordiaceae)	1695	100	1.8	0.078	48.1	0.131	0.181
<i>Drypetes standleyi</i> (Putranjivaceae)	2279	150	15.5	0.140	107.0	0.075	0.066
<i>Eugenia coloradoensis</i> (Myrtaceae)	838	200	1.2	0.051	74.5	0.077	0.148
<i>Eugenia oerstedia</i> (Myrtaceae)	2343	100	2.3	0.085	52.4	0.125	0.168
<i>Garcinia recondita</i> (Clusiaceae)	4289	100	8.3	0.181	99.9	0.085	0.076
<i>Guarea guidonia</i> (Meliaceae)	1963	100	9.9	0.146	67.9	0.122	0.092
<i>Guatteria lucens</i> (Annonaceae)	1469	200	0.6	0.022	56.3	0.080	0.185
<i>Heisteria concinna</i> (Olacaceae)	984	100	50.5	0.548	61.8	0.199	0.046
<i>Hirtella triandra</i> (Chrysobalanaceae)	5026	100	22.6	0.282	70.6	0.142	0.074
<i>Inga marginata</i> (Fabaceae) ^p	717	200	1.1	0.066	27.9	0.212	0.318
<i>Lonchocarpus heptaphyllus</i> (Fabaceae)	894	300	0.5	0.022	94.9	0.083	0.153
<i>Maquira guianensis</i> (Moraceae)	1502	100	9.9	0.298	78.7	0.127	0.085
<i>Miconia argentea</i> (Melastomataceae) ^p	900	100	0.5	0.033	18.8	0.207	0.428
<i>Ocotea whitei</i> (Lauraceae)	754	300	1.7	0.034	53.0	0.159	0.205
<i>Poulsenia armata</i> (Moraceae)	2120	300	0.3	0.014	60.6	0.106	0.200
<i>Pouteria reticulata</i> (Sapotaceae)	1767	200	5.3	0.044	73.7	0.076	0.123
<i>Prioria copaifera</i> (Fabaceae)	1439	400	31.5	0.219	151.1	0.093	0.042
<i>Protium stevensonii</i> (Burseraceae)	4114	200	5.0	0.057	109.2	0.055	0.082
<i>Protium tenuifolium</i> (Burseraceae)	3015	100	11.0	0.207	58.6	0.149	0.102
<i>Quararibea asterolepis</i> (Malvaceae)	2349	300	13.4	0.171	118.5	0.110	0.060
<i>Simarouba amara</i> (Simaroubaceae) ^p	1289	200	1.3	0.050	37.6	0.142	0.240
<i>Swartzia simplex</i> (Fabaceae)	2573	100	42.8	0.301	138.1	0.075	0.038
<i>Tabernaemontana arborea</i> (Apocynaceae)	1430	200	14.7	0.255	69.7	0.136	0.082
<i>Trichilia tuberculata</i> (Meliaceae)	13284	200	0.7	0.022	90.3	0.047	0.127
<i>Unonopsis pittieri</i> (Annonaceae)	790	100	6.7	0.154	47.3	0.162	0.144
<i>Virola sebifera</i> (Myristicaceae)	2080	100	8.1	0.210	47.6	0.183	0.125

second term in Equation 9 is unnecessary.

The number of adults recruiting is $A = \Sigma a_x$, summed over time steps until $a_x \rightarrow 0$. The maturation probability is $P_{1j} = A/N_1$, and the maturation time is the mean of the distribution a_x . The expected adult lifespan for all N_1 saplings at the start can then be found using Equation 7.

Numerical calculations are possible on any transition matrix, with no restrictions on growth steps, with or without memory. The only limitation was that I did not calculate transition matrices with two-step memory in the larger tree species (Table 1).

3. Field methods

3.1. Plot and census

The 50-ha plot on Barro Colorado Island was first censused in 1981–1982, then recensused every 5 years from 1985 through 2015. All stems ≥ 1 cm diameter-at-breast-height (dbh) were mapped, measured, and identified in each census (Hubbell and Foster, 1983; Condit, 1998; Condit et al., 2017). A total of 423,617 individual trees have been tagged over 35 years, where the individual is defined as a genetic unit, meaning all stems from one base. Though all stems were measured, here I only used the largest stem per individual. Stems were measured at breast height, 1.3 m above the ground, except where the stem was swollen or misshapen at that height. Growth rates are included here only when the same stem was measured at the same height in consecutive censuses; I refer to stem diameter as dbh (diameter-breast-height), even if it was not 1.3 m. Trees were considered dead when all stems within an individual died. In 1982 and 1985, stems < 55 mm dbh were measured with a precision of only 5 mm, but starting in 1990, every measurement was recorded to the nearest millimeter.

3.2. Species

I analyzed demography for 31 dominant tree species of the 50-ha plot. All had populations of at least 750 trees < 10 cm dbh and at least 80 trees ≥ 10 cm dbh in 1990, and had at least one tree measured taller than 16 m (Wright et al., 2010). The abundance criteria were chosen to include several of the fast-growing pioneers (Table 1). The 50-ha plot had 172 species ≥ 16 m tall in 1990, and the 31 focal species comprised 53% of all individuals of those species.

I estimated adult size from a large dataset of fruit observations in individual trees (Wright et al., 2015; Visser et al., 2016). I defined reproductive size as the first multiple of 50 mm dbh above which many trees were reproductive. Seven species that qualified by the height and abundance criteria were excluded from the study because they reproduced at < 50 mm dbh, or had few saplings or few adults.

3.3. Defining size categories

In each species, the largest size class was defined as all trees $\geq$ adult size (Table 1). Juvenile trees were divided into three classes, defined flexibly in order to create near-constant growth transitions. I used an optimization algorithm to adjust two juvenile dbh cutoffs until the three growth transitions were as constant as possible. The resulting dbh classes are roughly logarithmic with respect to dbh, because diameter growth increases as diameter increases. In those species with adult size ≥ 300 mm dbh, I used four juvenile categories. Appendix 3 gives the size categories.

It is not possible to adjust dbh classes to balance mortality rates. At Barro Colorado, however, mortality declined only slightly from saplings to large trees, from 2.4% to 2.0% (Condit et al., 1995, 2017). The growth-adjusted dbh categories thus lead to matrices whose transition probabilities are reasonably constant. This simplifies theoretical predictions about adult lifespan.

To test the impact of varying size class boundaries, I also created transition matrices in which juveniles were divided into 10 classes of equal width. With adult size = 200 mm dbh, the narrow classes were 21.1 mm wide, so 10–31.1, 31.1–52.2 mm, etc.

3.4. Estimating transition matrices

For the 31 selected species, transition matrices were calculated using seven censuses from 1985 to 2015, meaning six different transition matrices, one for each interval of 5 years (I omitted the first interval since it was only 3 years). In each census, all individuals were assigned one of the 4 (or 5) size classes based on dbh, and probabilities of death, growth, and residence were calculated as the fraction of trees that moved between classes by the next census. The six transition matrices were then averaged. The transition calculations required several assumptions about stems that broke but survived and stems that shrunk to a smaller size class, detailed in Appendix 4.

Calculating transitions with memory (Eq. 2) from one census pair requires the earlier census as well, since all trees had to be separated into two subclasses depending on the earlier size. This required more assumptions about cases where stems shrunk or broke in one or both intervals (Appendix 4), and only five replicate transition matrices were available. For two-step memory, four consecutive censuses are needed for one transition, reducing the number of replicates to four. Matrices with memory required large samples, since the number of trees in the immediate-growth category was small; matrices with one step of memory were calculated for 28 of 31 species (omitting *Brosimum alicastrum*, *Chrysophyllum argenteum*, *Lonchocarpus heptaphyllus* due to small adult samples), and those with two steps of memory were not calculated for any of the species with adult size of 300 mm (Table 1). The entire set of transition matrices, including all growth steps, with and without

memory, are available in digital format in a separate data archive (Condit, 2022).

For every matrix, three lifetime demographic statistics were calculated: the expected adult lifespan for saplings (Eqs. 3–5), the maturation probability (Eq. 7), and the maturation time (Eq. 8). Every analytical calculation was checked against numerical estimates. Demographic results based on different matrix structures were compared in three ways: 1) results from matrices including only one-step growth versus those with two-step growth, 2) results from matrices without memory to those with one- or two-step memory (all limited to one-step growth), and 3) results from matrices with 4–5 size classes versus those with 11 size classes (all limited to one-step growth without memory).

3.5. Credible intervals

To estimate statistical confidence in the transition matrices and their demographic results, I estimated Bayesian posterior distributions for all matrix terms. Because transition probabilities are calculated from proportions, it is natural to describe them as binomial variables. This is not quite the case, because they are in fact multinomial, however, binomial probabilities give good approximations to multinomial variables (Fitzpatrick and Alastair, 1987). A posterior distribution of observed transitions was generated with random draws from a binomial distribution using the observed sample size and fraction transiting, using the R function *rbinom* (R Core Team, 2021). I created 400 random transition matrices for each census interval, then averaged across the six intervals, leading to 400 random matrices. These represent posterior draws of the observed matrix. From each random matrix, all demographic statistics were calculated, and the 5th and 95th percentiles were used as 95% credible intervals.

4. Theory of demographic tradeoff and performance

I compared lifetime demographic performance across the range of growth and mortality rates observed in the 31 species. For each species, I created a simplified matrix with constant transitions across size classes by averaging growth and death transitions, $g = g_i$, $m = m_i$, and calculated the expected adult lifespan from those (Eq. 3). I extended these calculations over an entire demographic space, using Equation 3 with all growth-mortality pairs (g, m) from $g = (0.03, 0.04, \dots, 0.24, 0.25)$, $m = (0.03, 0.04, \dots, 0.49, 0.50)$ i.e. increments of 0.01. Given the lifespan $L(g, m)$ over g - m space, I created a surface with contours showing lines of equal L using the *contour* function in R (R Core Team, 2021). This theoretical exploration allows the demographic consequences of the growth-mortality tradeoff to be evaluated. If the tradeoff is demographically equalizing, the growth-mortality axis will have constant adult lifespan throughout, i.e. fall on a contour of L . To test this, I estimated a linear correlation between mean g and m probabilities across species, added 95% credible intervals using a Bayesian parameter-fitting method (Condit et al., 2017), then compared expected adult lifespan along the resulting correlation line.

5. Data availability

The entire set of plot data from eight censuses is available in a published archive (Condit et al., 2019). All original transition matrices for the 31 focal species appear in another archive (Condit, 2022).

6. 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.

7. Results

7.1. Adult life expectancy of saplings

The expected adult lifespan for the average sapling varied nearly 100-fold in the 31 species, from 0.54 years in the pioneer *Miconia argentea* to 50.5 years in the shade-tolerant *Heisteria concinna* (Table 1). Nearly half the species (14 of 31) had expectations < 4 years, but several were > 10 years and three extremes were > 30 years (Fig. 1a, Table 1).

Expected adult lifespan was strongly correlated with maturation probability, which varied 40-fold (Fig. 1a), and weakly correlated with maturation time, which varied from 19 to 188 years (Fig. 1b). Mortality rate was closely associated with expected adult lifespan (Fig. 2a) but growth rate was not (Fig. 2b).

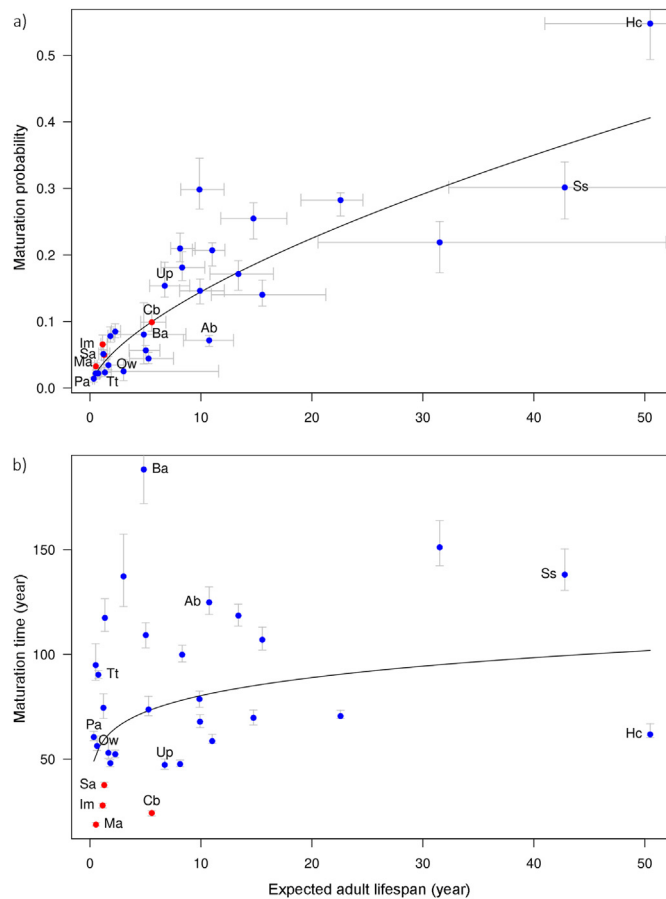


Fig. 1. Maturation probability and maturation time (years) versus expected adult lifespan (years) for the average sapling at 1 cm dbh for 31 dominant tree species in the Barro Colorado 50-ha plot. a) y-axis is the maturation probability for the average sapling. b) y-axis is the maturation time, or mean time (years) it takes the average sapling to reach adult size. Expected adult lifespan is on the x-axis in both panels. Red points mark the four pioneer species, and other species mentioned in the text are labeled as well: pioneers (Cb = *Cordia bicolor*, Im = *Inga marginata*, Ma = *Miconia argentea*, Sa = *Simarouba amara*); and non-pioneers (Ab = *Alseis blackiana*, Ba = *Brosimum alicastrum*, Hc = *Heisteria concinna*, Ow = *Ocotea whitei*, Pa = *Poulsenia armata*, Ss = *Swartzia simplex*, Tt = *Trichilia tuberculata*, Up = *Unonopsis pittieri*). Gray bars, horizontal and vertical, show 95% credible intervals; in a), both are shown, but in b), those for adult lifespan are omitted, since they are identical to a). Curves are based on linear regressions of log-transformed values, but axes are untransformed. In a) the regression is highly significant ($p = 3 \cdot 10^{-12}$, $r^2 = 0.82$); in b) it is weakly significant ($p = 0.034$, $r^2 = 0.15$). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

7.2. The growth-mortality tradeoff and adult life expectancy

The 31 species demonstrated the expected tradeoff between growth and mortality, having high growth significantly associated with high mortality (Fig. 3). The observed tradeoff, however, did not match theoretical contours of equal expected adult lifespan: contours were steeper than the tradeoff (Fig. 3). The mismatch means that traversing the tradeoff axis from low growth and mortality toward high (right along the dashed line in Fig. 3) moves down the 'hill' of adult lifespan, and that conclusion was supported across credible intervals of the growth-mortality trend. For example, two species at opposite extremes, *Swartzia simplex* and *Miconia argentea*, are both close to the tradeoff line, but *Swartzia* had a much longer adult lifespan. At the lowest mortality, the contours were nearly vertical (Fig. 3), thus adult lifespan was nearly independent of growth at low mortality.

7.3. Impact of two-step growth

In most species, matrices with or without two-step growth produced similar demographic outcomes: in 26 of the 31 species, omitting two-step growth reduced the lifespan < 10% (i.e. comparing Eqs. 3 and 4). In two

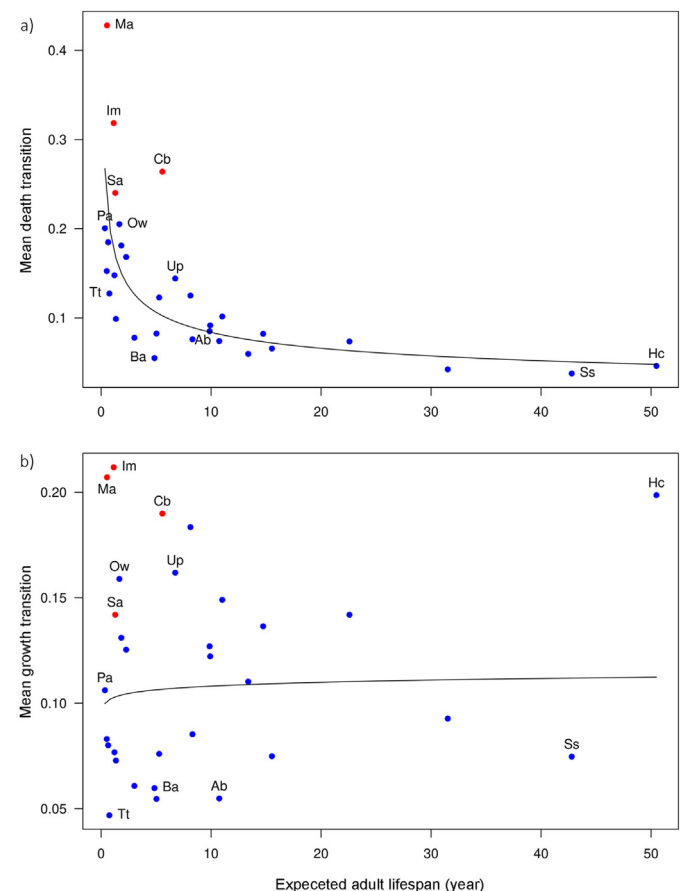


Fig. 2. Growth and death rates versus expected adult lifespan (years) for the average sapling at 1 cm dbh for 31 dominant tree species in the Barro Colorado 50-ha plot. a) y-axis is the mean growth transition across all size classes in the transition matrix, i.e. the probability a tree grows to the next size class in a 5-year census interval. b) y-axis is the mean mortality transition across all size classes, i.e. the probability a tree dies in 5 years. Expected adult lifespan is on the x-axis in both panels. The species labeled match those in Fig. 1. Curves are based on linear regressions of log-transformed values, but axes are untransformed. In a) the regression is highly significant ($p = 2 \cdot 10^{-7}$, $r^2 = 0.61$); in b) it is non-significant ($p = 0.64$, $r^2 < 0.01$).

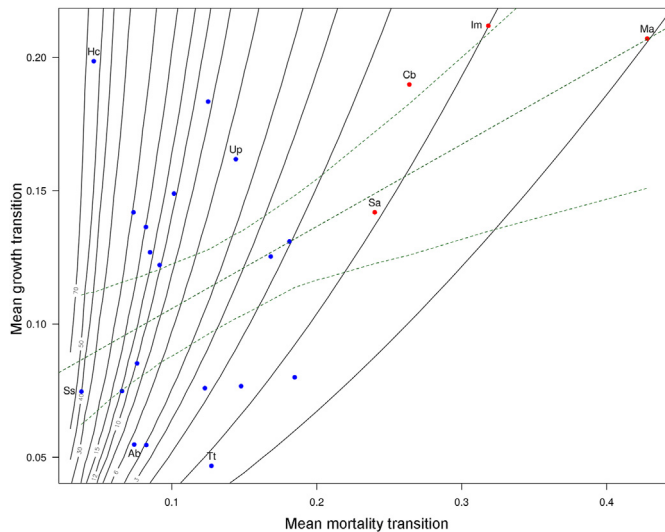


Fig. 3. The observed growth-mortality tradeoff versus theoretical contours of equal expected adult lifespan. Only the 23 species with four-class transition matrices are shown, because the contours differ with the number of size classes. Observed growth and mortality rates are the mean transition probabilities across the four size classes. The central dashed line is the linear regression between observed growth and mortality (statistically significant, $p < 0.01$); the dashed curves above and below it are 95% credible intervals around the regression. Species labels match Figs. 1 and 2.

pioneers, on the other hand (*Cordia bicolor*, *Miconia argentea*), many individuals grew by two size classes, and the expected adult lifespan with two-step growth was 90% and 60% higher than without. In three non-pioneers (*Ocotea whitei*, *Poulsenia armata*, *Unonopsis pittieri*), including two-step growth caused a 14–24% increase in adult lifespan.

7.4. Impact of transition with memory

The addition of memory to the transition matrices had minor impacts on estimated demographic outcomes. Expected adult lifespan for a sapling calculated from a matrix with no memory was highly correlated with lifespan based on one- or two-step memory (Fig. 4a). Adding one-step memory to the matrix led to < 3% reduction in expected adult lifespan. With two steps of memory, there was a more appreciable change, and adult lifespan was shortened by an average of 20% (Fig. 4a). Maturation probability was similarly affected by the addition of memory. Maturation time, however, was nearly unaffected: even with two-step memory, it increased only 3.5% relative to a matrix with no memory.

7.5. Impact of narrow size classes

Redefining size classes to be narrower, and evenly sized, had little impact on the expected adult lifespan of saplings (Fig. 4b). Maturation time and maturation probability were lifewise unaffected by the change in size classes.

8. Discussion

The demographic tradeoff between growth and survival, familiar in forests in general, is not equalizing at Barro Colorado. A growth-survival regression line from 31 abundant species was not parallel to theoretical contours of adult lifespan as expected from the sapling stage. Moving up the regression line, toward higher growth and survival, accompanied a decline in adult lifespan. I conclude that the average pioneer species at Barro Colorado has a shorter adult life expectancy than the average shade-tolerant species. Pioneers have high growth rates, and saplings reach adulthood quickly, however, their death rates are so high that few

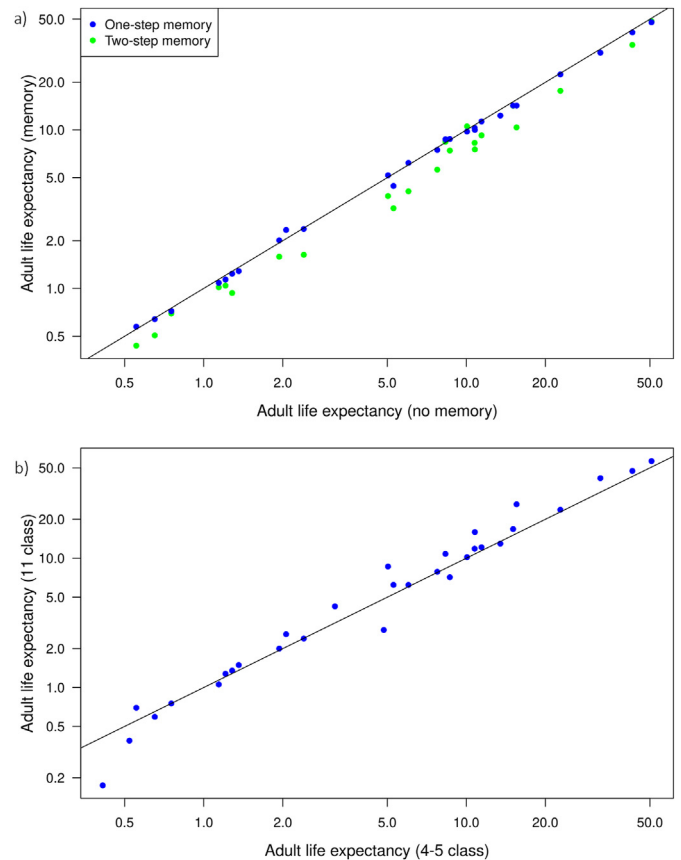


Fig. 4. Impact of altering matrix structure on key demographic results. a) Results based on transition matrices that include memory compared to those without memory. The vertical axis is the expected adult lifespan estimated from a matrix with one- or two-step memory, the horizontal axis is the same parameter from a matrix with no memory. The 1:1 line is shown (not a regression line); both linear regressions (log-transformed values) had $r^2 > 0.98$. b) Results based on transition matrices with narrow size classes compared to broad size classes, again based on expected adult lifespan. The vertical axis is the result when matrices had 10 evenly-sized juvenile size classes, the horizontal axis from matrices with 3 or 4 expanding juvenile classes. The 1:1 line is shown; the regression $r^2 = 0.96$. All results in both panels are from numeric estimates of adult lifespan, in order to isolate the impact of varying matrix structure independent of assumptions behind analytical results.

survive that long. The theoretical contours of equal lifespan demonstrate how the tradeoff could be balancing. Pioneers would need to have lower death rates by a substantial margin. In *Cordia bicolor*, for example, the observed mean death rate of 28% per 5 years would have to be lowered to 15% for its adult lifespan to reach 4 years, matching that of the very slow growing *Alseis blackiana*. If reproductive output were similar across the demographic axis, the pioneer group would decline in abundance relative to many of the shade tolerant species.

There was considerable additional variation in adult lifespan around the growth-survival regression. *Alseis blackiana* and *Trichilia tuberculata* are conspicuous examples. Both are abundant canopy trees, and both grow slowly, but their expected adult lifespans differed by 12-fold, and *Swartzia simplex*, another slow-growing species, had an expected adult lifespan another four-fold higher. Assuming similar reproductive output, *Trichilia* cannot persist.

The contours of equal adult lifespan show that death rate has a greater impact on adult lifespan than does growth, especially at the low end of the growth-mortality axis. Given low mortality, increases in growth have little impact on adult lifespan. This means elasticity of growth is lower than that of survival (Franco and Silvertown, 2004). Selection favoring higher growth rates is thus weak in long-lived forest tree species: traits

lowering mortality would have more impact on adult lifespan, and thus reproductive output, than traits raising growth. At the highest growth rates, however, increasing growth and decreasing death have similar impacts on adult lifespan.

These conclusions about sapling to adult lifetimes were robust to key assumptions underlying the matrix method. Adding memory to the transition matrices did not effect the main results, though two-step memory did reduce expected adult lifespan by 20% and increase maturation time slightly. This demonstrates the effect described by Zuidema et al. (2009) whereby a transition matrix can overestimate the fastest growth. That the effect of memory was small supports conclusions of Picard and Liang (2014), who argued that the matrix method also underestimates growth rates at the low end, tending to balance rapid transitions.

One of my goals using matrices with few, broad size classes was to the reduce the impact of growth errors. In previous work, I excluded extreme negative and positive outliers in growth rates. Here, I discounted negative growth by assuming it meant stasis, and I overcame positive errors by omitting two-step growth; in most species, demographic results from one-step growth differed little from those with two-step growth, though in some pioneers, growth by two size classes had to be included. I also checked results from the broad size classes against matrices based on many narrow size classes and found no differences, supporting conclusions in Doak et al. (2021). In general, matrices with only four or five broad classes provided consistent and reliable results on maturation time and expected adult lifespan of saplings. By adjusting size class boundaries, I was able to equalize growth transitions across size classes, an advantage for the theoretical analyses behind the adult lifespan contours. Large sample sizes in abundant species of the 50-ha plot foster the success of my combined empirical-theoretical approach.

Whether the growth-survival tradeoff is equalizing across the entire life cycle remains unknown until reproduction is added to the analysis. Thirty years of data on seed output and germination in the 50-ha plot are available (Wright et al., 2005, 2015, 2016), and my next goal is build transition matrices that start from seeds. I will then be able to examine expected lifetime reproductive output across the growth-survival tradeoff, and I will examine aspects of demography that account for fluctuations in abundances over the 30 years of observations (Condit et al., 2017).

9. Conclusions

I applied methods from matrix demography to derive lifetime demographic parameters in 31 of the dominant species of a 50-ha forest plot in Panama. Using analytical solutions to matrix projections, I calculated expected adult lifespan for a sapling across a wide range of growth and survival rates. I then estimated the growth-survival regression in those species and overlaid theoretical predictions of adult lifespan across the breadth of demographic variation. Predicted adult lifespan is not constant along the regression line, rather, the upper end of the growth-survival axis, representing the fast-growing pioneer tree species, had relatively short reproductive lifespan compared to the low end, with shade-tolerant, climax species. This leads to the hypothesis that pioneer species produce more seeds or seedlings while they are reproductive than do climax species. I plan to test this by extending the matrix approach to fruits and seedlings and generate theoretical results on the entire life cycle, from seed to adult and back.

Declaration of competing interest

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

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Appendices. Supplementary material

Appendices with matrix derivations and supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2022.100053>.

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