

Predicting Population Trends from Size Distributions: A Direct Test in a Tropical Tree Community

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ABSTRACT: Forest ecologists often evaluate how well the species composition of saplings in the understory matches that of the canopy: absence of juveniles suggests that a tree species is suffering population decline. Here we offer a theoretical and empirical test of this assertion using data from a 50-ha census plot in Panama. Theory indicates that higher rates of population change, λ , lead to more steeply declining size distributions (more juveniles relative to adults). But other parameters also affect the size distribution: lower growth rate of juveniles and lower survival at any size produce more steeply declining size distributions as well. Empirical evaluation of 216 tree populations showed that juvenile growth was the strongest predictor of size distribution, in the direction predicted by theory. Size distribution did correlate with population growth, but weakly and only in understory species, not canopy species. Size distribution did not correlate with the growth rate of larger individuals nor with survival. Results suggest that static information on the size distribution is not a good predictor of future population trends, while demographic information is. Fast-growing species will have fewer juveniles in the understory than slow-growing species, even when population growth is equal.

Keywords: tropical forest, population change, size distribution.

Ecologists often use size distribution to indicate the health of a population. If there are large numbers of ju-

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veniles relative to adults, this is taken to indicate that a population is stable, perhaps growing, but few juveniles can be seen as a warning that the population is in decline. In the absence of direct estimates of population size through time, this seems a reasonable shortcut. It is often very easy to get estimates of size distribution from a population but much harder to record long-term population trends.

One main goal of forest ecology is to infer past changes and predict future changes in species composition, and examining the diameter distributions of canopy species is often used toward this end (Lorimer 1980; Knowles and Grant 1983; Ogden 1985; Hart et al. 1989; Franklin et al. 1993; Read et al. 1995). When canopy species are well represented among saplings, the forest is often considered to have reached a climax state. Species in the process of being eliminated from the forest—perhaps during succession—fail to reproduce and thus lack sufficient advanced regeneration. “The lack of congruence between overstory and understory in these stands is both an indicator of change as well as a major concern for conservation” (Foster et al. 1996, p. 420). In the tropics, the use of diameter distributions to project community change has been especially important in Africa, and several early studies suggested that dominant canopy species in African forests do not produce juveniles in the immediate area. This led to the idea of cyclical succession, or the mosaic theory of regeneration (Richards 1952). Swaine and Hall (1988) and Newbery and Gartlan (1996) provide in-depth analyses of these ideas, using extensive quantitative data on size distributions.

But the underlying assumption—that populations with low juvenile density relative to adult density are in decline—has not been explicitly tested. Here we address two ways of making this test. We first employ a theoretical approach, examining quantitative population models to determine how size distribution relates to population growth. Then we proceed with a direct, empirical test using records of population change over 13 yr in a tree community. In all 216 species abundant enough to analyze, we assessed a simple correlation: Are steeper size

distributions—those with lots of juveniles relative to adults—associated with better population growth?

The Theory

Two different theoretical approaches can provide insight into how size distribution relates to population growth. One employs a stage-based life table to examine the form of the size distribution resulting from a given set of demographic parameters and their associated population growth rate. The second is a continuous approach to a diffusion equation of population growth and size distribution, and we show briefly that this leads to the same results as the discrete life-table model.

A Life Table Based on Size Classes

In trees, discrete stages in a life table are typically stem-diameter classes (Usher 1966; Enright and Ogden 1979; Platt et al. 1988; Newbery and Gartlan 1996). Transition terms in the life table are based on the mortality of trees in each size (diameter) class, the growth of trees from one size class to the next, and reproduction by adults to produce juveniles in the smallest size class, each per unit time. Let $N_{i,t}$ be the number of individuals alive in size class i at time t , s_i the fraction of those individuals that survive to time $t + 1$, and g_i the fraction that grow to size class $i + 1$ by $t + 1$. For the sake of simplicity, we assume none grow to class $i + 2$ —in a real population, size classes and time intervals could be defined to assure this. We also assume no plants shrink. The fraction of $N_{i,t}$ that remain alive but do not grow is $s_i - g_i$. Notice that s and g are not dependent on t —we assume time invariance.

The survival, growth, and reproduction terms form a transition matrix, \mathbf{T} , whose dominant eigenvalue gives the population growth rate, λ , once a stable size distribution is achieved. That size distribution is the eigenvector, \hat{N} , with one element \hat{N}_i for each size class. What we seek is a relationship between \hat{N} , \mathbf{T} , and λ . It would be possible to write a general equation relating the eigenvector to the transition matrix; however, we felt that in the general case, the relation would not be very informative since it would consist of large and unwieldy polynomials in the demographic terms. Instead, we focus on the relationship between two successive size classes, which is easy to calculate because the life table only includes one-step transitions (most elements of \mathbf{T} are 0).

To do so, we start with a basic result from life-table theory and matrix algebra. When the population reaches its stable size distribution (which it will if the demographic parameters remain constant for long enough),

each \hat{N}_i as well as the whole population N will be increasing (through time) at the same rate λ . That is,

$$\lambda = \frac{N_{t+1}}{N_t} = \frac{N_{i,t+1}}{N_{i,t}}. \quad (1)$$

The number $N_{i+1,t+1}$ is easy to calculate from $N_{i,t}$:

$$N_{i+1,t+1} = g_i N_{i,t} + (s_{i+1} - g_{i+1}) N_{i+1,t}. \quad (2)$$

This is a standard life-table calculation—the number of individuals in the larger size class in the next time period is equal to those that grew from the smaller size class ($g_i N_{i,t}$) plus those that stayed in the larger size class [$(s_{i+1} - g_{i+1}) N_{i+1,t}$]. Once at the steady state, equation (1) gives

$$N_{i+1,t+1} = \lambda N_{i+1,t}, \quad (3)$$

and this can be substituted into equation (2) to produce

$$\frac{N_{i+1}}{N_i} = \frac{g_i}{\lambda - s_{i+1} + g_{i+1}} = x_i. \quad (4)$$

This gives the ratio of individuals in size class $i + 1$ to individuals in size class i , which we call x_i . At the steady state, x_i is time independent, so the subscript t has been removed.

Across all i , the ratio x_i represents the shape of the size distribution. Usually $x < 1$ and the larger size class has fewer individuals than the smaller. When x_i is slightly < 1 , the larger size class has nearly as many individuals as the smaller, and if this is true across all i , we refer to it as a flat size distribution, since a plot of N_i versus i is nearly level (N_i decreases only slightly with increasing size). On the other hand, if $x_i \ll 1$ for all i , then successively larger size classes have far fewer individuals and the size distribution is steep. It is also possible for x_i to be > 1 so that N_i increases with size, and with many size classes, distributions can (at least in theory) have a mixture of steep, flat, positive, and negative sections.

If survival and growth are constant across all size classes, then the form of the size distribution is exponential with respect to size class: a plot of $\log(N_i)$ versus i is a straight line. In most cases, $x_i < 1$, and it is a negative exponential. Every size class will have a constant fraction of individuals less (or more) than the prior size class.

More specifically, if s_i and g_i are constant across all i , and successive size classes are linear increments of diameter such as 0–10, 10–20, 20–30 cm, then a plot of $\log(N_i)$ versus dbh (diameter at breast height, a forester's abbreviation for stem diameter) would be a straight line. But if s_i and g_i are constant across i when size classes are defined to be exponentially increasing, such as 1–2, 2–4, 4–8, and 8–16 cm dbh, then a plot of $\log(N_i)$ versus $\log(\text{dbh})$ would be a straight line. Notice that if g_i is con-

stant but size classes are expanding, then absolute growth rate must increase with size, since larger trees have to grow further to reach the next size class.

Predictions

Equation (4) leads to several relevant predictions about the relationship between the shape of the size distribution and demographic parameters. First, the steepness of the size distribution correlates with population growth. All else being equal, if λ is increased, x_i must decrease, meaning the size distribution becomes more steeply negative. Notice, however, that survival and growth also affect the size distribution.

Second, high survival should correlate with higher values of x_i and thus flatter size distributions (as long as $x_i < 1$). If other parameters are held equal and survival increases across all size classes, then the entire size distribution becomes flatter. If survival is increased in some size classes but not others, the effect on the size distribution is more complex but still easy to interpret. For example, if survival is low at small sizes but higher at large sizes, then the size distribution starts steep but becomes flatter.

Here we are isolating the effect of survival in a mathematical sense, not allowing other parameters in equation (4) to change. In the real world, changes in survival would generally lead to changes in λ , which would also affect the size distribution. But in a mathematical abstraction, survival can be increased without changing λ simply by reducing the reproductive rate by an appropriate amount.

Third, the relationship between growth and size distribution is not so obvious and is thus useful to examine with a partial derivative. Assume first that growth is independent of size class, so $g_{i+1} = g_i = g$ and take a partial derivative of x_i (eq. [4]) with respect to g :

$$\frac{\partial x_i}{\partial g} = \frac{\lambda - s}{(\lambda - s + g)^2}. \quad (5)$$

More often than not, $\lambda - s > 0$ and the derivative is positive, meaning that higher growth rates lead to higher x_i and thus flatter size distributions. But if $\lambda - s < 0$, the derivative is negative, but $x_i > 1$, so higher growth means a flatter positive size distribution. In all cases, simultaneous increase in g across all size classes leads to an x_i closer to 1 and a flatter size distribution.

Equation (5) also indicates that, if $g_{i+1} > g_i$, so that growth is increasing with size, x_i is reduced (relative to the case where $g_{i+1} = g_i$). Conversely, if $g_{i+1} < g_i$, x_i increases. If $g_{i+1} < g_i$ by a sufficient amount (if $g_i - g_{i+1} > \lambda - s$), then $x_i > 1$ even in a situation where the population is growing ($\lambda > 1$). These results mean that change

in growth in a single size class has an ambiguous impact on the overall size distribution: if g_i increases but nothing else changes, then x_{i-1} decreases but x_i increases.

This demonstrates an interesting contrast between plant life tables and animal life tables. In animal populations, size classes are usually equivalent to age classes. This is a special case of equation (4) where $g_i = s_i$: every individual that survives advances to the next class, so

$$x_i = \frac{N_{i+1}}{N_i} = \frac{s_i}{\lambda}. \quad (6)$$

This is a familiar result in animal ecology: survival rates can be estimated from the size distribution, assuming λ is known. Thus, in an age-class life table, $x_i > 1$ only in a declining population, but in a size-class life table, x_i can be >1 even in a growing population if growth rates decrease sufficiently with size. Platt et al. (1988) provided an illustration of this: in their population of *Pinus palustris*, there were more individuals in the 40–50-cm diameter class than in the 30–40-cm diameter class, caused by a sharp drop in growth rate between those size classes.

The fourth prediction is that reproductive rates have no direct impact on the size distribution. Mathematically, this is obvious because equation (4) includes no terms describing reproduction. Intuitively, however, it seems that an increase in fecundity should steepen the size distribution. But this is an indirect effect—higher reproduction improves population growth λ , which does appear in equation (4). (The prediction that fecundity has no direct impact on size distribution is dependent on the assumption that all juveniles start life in the smallest size class. If some start in larger size classes, then reproduction does have a direct impact on the size distribution.)

In conclusion, other things being equal, increasing populations should have steeper size distributions than decreasing populations (the first prediction). In general terms, this justifies the assumption that population health correlates with size distribution. However, the remaining predictions indicate that other factors affect size distribution, suggesting that population health cannot be assessed from the size distribution alone. Species with higher growth rates and higher survival rates will tend to have flatter size distributions than species with lower growth and survival, given the same population growth rate. More generally, if growth or survival vary with size class in different ways in two different species, size distributions could be very different even with equivalent population growth.

A Continuous Approach to the Size Distribution

An alternative approach toward these predictions is to describe the size distribution as a continuous function of

size, describing its change through time and across size classes with a partial differential equation. The analysis is borrowed from diffusion theory (Hara 1984; Kohyama 1992, 1993) although here we use no diffusion term. Let $N(t, d)$ be the abundance at size d and time t , and let $g(d)$ and $m(d)$ be growth and mortality as functions of d (assumed to be constant with respect to time). A partial differential equation describes how N changes with time (Kohyama 1993):

$$\frac{\partial N(t, d)}{\partial t} = \frac{\partial [g(d)N(t, d)]}{\partial d} - m(d)N(t, d). \quad (7)$$

On a plot of N versus d , the steepness of the size distribution is $[\partial N(t, d)]/\partial d$, and this can be derived from equation (7). First, decompose the derivative on the right side of the equation: $[\partial(gN)]/\partial d = g(\partial N/\partial d) + N(\partial g/\partial d)$. Then use the fact that the population growth rate λ is related to the derivative on the left of equation (7) in a simple way, $\partial N/\partial t = (\lambda - 1)N$. This holds when λ is fairly close to 1 (more generally, $\ln(\lambda) = \partial N/\partial t$). Equation (7) then rearranges to $(\partial N/\partial d) = -N\{[\lambda - 1 + m + (\partial g/\partial d)]/g\}$. Since survival $s = 1 - m$, this can be rewritten as

$$\frac{1}{N} \frac{\partial N}{\partial d} = -\frac{\lambda - s + \frac{\partial g}{\partial d}}{g}. \quad (8)$$

The left-hand side is now the derivative of $\ln(N)$.

We will not examine equation (8) in detail but will point out how similar it is to equation (4). Indeed, taking the natural logarithm of the left side of equation (4) gives $\ln(N_{i+1}) - \ln(N_i)$, which is approximately the derivative of $\ln(N)$. The logarithm of the right side of equation (4) is very similar to the right side of equation (8). Further examination of equation (8) shows it leads to the four predictions listed above from the discrete model. These theoretical results led us to an empirical test of how well growth, survival, and population growth correlate with size distribution in real populations of trees.

Empirical Methods

Study Site

The theory was put to the test using data collected in a tropical moist forest on Barro Colorado Island (BCI) in central Panama (for background, see Croat 1978; Leigh et al. 1982). Censuses of 50 ha of forest were carried out in 1981–1983, 1985, 1990, and 1995 (Hubbell and Foster 1983, 1990, 1992; Condit et al. 1992, 1995, 1996a, 1996b; we refer to the first census, which lasted 2 yr, as the 1982 census). Most of the plot is old-growth forest and not subject to major disturbances, and the structure of the

forest (density, size distribution) has been quite constant during the 13-yr census period (Condit et al. 1996a). All free-standing, woody stems ≥ 10 mm dbh were mapped to within 1-m accuracy, identified to species, and measured at breast height (1.3 m). If there were irregularities in the trunk there, the measurement was taken at the nearest lower point where the stem was cylindrical. The dbh of buttressed trees was taken above the buttresses, except during 1982, when dbhs were measured around buttresses. Full details of the methods are presented elsewhere (Condit 1998).

Size Distributions

For each species, all individuals were tallied in the following dbh classes: 10–19, 20–29, 30–39, 40–49, 50–99, 100–199, 200–299, 300–399, 400–499, 500–999, 1000–1499, 1500–1999, and ≥ 2000 mm. There were two reasons for using size classes that expand with size: first, since stem density declines rapidly with size, it better balanced the sample across size classes; second, finer divisions below 100 mm allowed distributions to be calculated for the smallest species, many of which are never larger than 50 or 100 mm. Because size classes varied in width, though, the number of stems N_i in size class i had to be divided by the width of the size class:

$$n_i = \frac{100N_i}{(\text{dbh}_{i+1} - \text{dbh}_i)}, \quad (9)$$

where n_i is the corrected abundance (plants per 100-mm dbh bracket). We refer to the midpoint of each diameter bracket as d_i .

We then calculated regressions between $\ln(n_i)$ and d_i , between $\ln(\ln(n_i))$ and d_i , and between $\ln(n_i)$ and $\ln(d_i)$. Classes for which $n_i = 0$ were omitted from regressions. As mentioned above, equations (4) and (8) show that simple life tables produce size distributions that decline exponentially with either d_i or $\ln(d_i)$. This gives some justification for using the formulations $\ln(n_i)$ versus d_i or $\ln(n_i)$ versus $\ln(d_i)$. Newbery and Gartlan (1996) and Poorter et al. (1996) also used various regressions of abundance on dbh to define size distributions.

These regressions were performed using 1985 data from 216 species in the BCI plot (we used 1985 and not 1982 data because of the problems with measurements around buttressed trees in 1982). All species with at least 15 individuals alive in 1985 were used, as in Newbery and Gartlan (1996). Excepted were all palms because they grow only in height, not diameter, and two nonpalms (*Psychotria limonensis* because all 17 individuals were < 20 mm dbh and *Inga ruiziana* because reevaluation of

all *Inga* in 1997 suggested that most of the 67 *I. ruiziana* were misidentified *Inga quaternata*).

An r^2 was calculated for each of the 216 species with each of the three regressions. The $\ln(n_i)$ versus $\ln(d_i)$ regression performed best (highest r^2) in 86 species, $\ln(n_i)$ versus d_i performed best in 66 species, and $\ln(\ln(n_i))$ versus d_i performed best in 59 species (there were ties in five species). The r^2 from the ln-ln regression was ≥ 0.8 in 189 of the 216 species. In addition, the ln-ln regression performed best ($r^2 = 0.965$) for data from the entire 50-ha plot (all species combined).

Because r^2 values were high, the slope of this ln-ln regression can be used to summarize—in a single number—the shape of a size distribution. Thus, we chose to define the size distribution for each species using this slope, which we call L . The slope was usually negative (214 of 216 species), meaning larger size classes had fewer individuals. Species with many small and few large individuals had steep slopes, meaning large negative numbers, whereas species with few small stems had flat distributions, meaning negative slopes close to 0.

We also considered two alternative indices of size distribution—the fraction of adults in each species and the coefficient of skewness of the distribution. The first was based on notes assembled over the years on reproductive status of individuals, from which we made qualitative estimates of the minimum size at which each species produced substantial quantities of fruit. We then counted all individuals greater than this cutoff and divided by the total population for each species. The skewness coefficient was $[N\sum(d_k - \bar{d})]/[(N-1)(N-2)] \times 1/SD^3$, where d_k is the dbh of individual k , \bar{d} is the mean dbh, N is the total number of individuals, and SD is the standard deviation of the distribution of d_k .

Both the fraction of adults and the skewness coefficient were correlated with the slope L of the size distribution, and the main results reported below were similar whichever of the three indices was used. Thus we report results from just one of the three, and because the slope provides an intuitive description of a size distribution and because it can easily be applied in other studies, we chose it.

Life Tables

To evaluate how size distributions were dependent on demographic parameters, complete life tables were calculated for individual species. Since age is unknown, the life tables had to be stage dependent (Lefkovitch 1965; Hubbell and Werner 1979), a common approach in tree population models (Usher 1966; Enright and Ogden 1979; Piñero et al. 1984; Platt et al. 1988; Alvarez-Buylla and García-Barríos 1991). Stages were defined as 50-mm brackets of dbh (10–49, 50–99, 100–149, 150–199 mm,

etc.), and the terminal stage was all individuals ≥ 400 mm or when a bracket was reached with < 5 individuals. No species was considered if it had < 5 individuals in any class up to 250 mm or < 5 individuals above 250 mm dbh, since not much of a size distribution can be calculated with < 5 size classes. This restriction also meant that all demographic parameters were calculated on the basis of at least five individuals.

Transition probabilities g_{ij} were calculated as the fraction of individuals in size class i during one census that had shifted to class j by the next. In the theoretical formulation above, transition could only occur from i to $i + 1$, but in real life tables, all transitions were allowed (even backward transitions, such as when a tree breaks and sprouts a smaller stem). In practice, the vast majority of transitions were one stage upward, except in a few fast-growing species where two-step transitions were common. The transition probability g_{ii} is the fraction of plants remaining in the same size class. The survival probability s_i is simply $\sum_j g_{ij}$, or the fraction of individuals in stage i that were still alive in the next census (regardless of whether they grew or not).

Reproduction in the life table was defined in the simplest possible way. The number of recruits in the second census in size class i was divided by the number of adults during the previous census to give a fecundity term. Recruits were individuals that appeared for the first time in the second census, and adults were all individuals in the terminal size class (we refer to the terminal size class as a , $a = 5, 6, 7, 8, \text{ or } 9$). These fecundity terms give the transitions g_{ai} . In general, g_{ai} can be > 0 for any i , but in practice it was nonzero only for $i = 1$ (dbh < 50). We did not delete any transitions from the data though; if there were recruits in larger size classes i , we allowed $g_{ai} > 0$.

Thus, we assumed for all species that only the terminal size class was reproductive. We could have allowed differences between species, and we could have assumed smaller size classes were reproductive, but we made the assumption that these adjustments would not alter by much the stable size distribution nor the population growth rate resulting from a transition matrix. If smaller size classes were deemed reproductive, the estimated g_{ai} would be lower, but because more size classes reproduced, total reproduction would be similar and population growth unaffected. (It would only be affected if the simulated size distribution among the reproductive size classes was dramatically different from the observed, and in general this proved not to be the case.)

The matrix of transition probabilities T can be multiplied successively by the vector of abundance N to simulate population growth. For each species, these projections were carried out numerically until the population growth rate $\lambda = N_{t+1}/N_t$ reached an equilibrium value

(changed by $<10^{-6}$). At this point, the size distribution was assumed to have reached its steady state. Simulations were repeated using 1985–1990 and 1990–1995 transition probabilities.

Correlates of Size Distributions

The fundamental empirical question we wished to address was whether size distribution correlated with population growth. To test this, we ran a regression of the slope of the size distribution L (calculated for each species from 1985 data) versus $\lambda = N_{1995}/N_{1982}$. Separate regressions were done for four different growth forms: large trees (maximum height >20 m), midsized trees (10–20 m), treelets (4–10 m), and shrubs (1–4 m). Parametric regression was used, but Spearman rank correlations were also run. Results from the latter will be given in cases where it gave markedly different results from the former.

The theoretical analysis indicated how other demographic parameters should affect size distribution as well. Thus we examined correlations between size distribution and growth and survival probabilities. Since survival probabilities were fairly constant across size classes, we used the average of s_1 , s_2 , and s_3 as a survival index, \bar{s} . For growth, we used two stages, g_1 and g_3 , separately, because growth generally increased quite a bit from the first to the third stage. A stepwise multiple regression was run, with the slope of the size distribution L as the dependent variable and λ , \bar{s} , g_1 , and g_3 the independent variables. The regression was done separately on each growth form. In all regressions, the 5% probability level was considered statistically significant.

Since ultimately we are interested in predicting population change, we also carried out a stepwise regression with a different arrangement of variables. In this case, λ was the dependent variable and the remaining four the independent variables.

Life tables and transition probabilities were not calculated for shrub species since these seldom had dbhs >50 mm. We could have recalculated life tables using narrower size classes, perhaps 10–19, 20–29 mm dbh, and so forth, but we decided not to out of concern that our data set misses important features of the size distribution of shrubs: since the minimum dbh included in the study was 10 mm dbh, most are mature adults by the time they enter the census. We show the initial correlation between size distribution and population growth in shrubs but have not calculated life tables.

Dbh Distribution Classifications

Because of the substantial amount of work done on size distributions of tree species in Africa, we thought it

would be interesting to compare the BCI forest with sites there. Newbery and Gartlan (1996) provided an opportunity to do so because they classified species' size distributions in a quantitative way. In two forests in Cameroon, they defined species as group 1 if 1% of individuals were ≥ 500 mm dbh; group 2 if at least 1% were ≥ 500 mm but fewer than 1% were ≥ 700 mm; group 3 if at least 1% were ≥ 700 mm but fewer than 1% were ≥ 900 mm; group 4 if at least 1% were ≥ 900 mm. In addition, a group 5 was defined as a subset of groups 3 and 4, including any species that had more individuals in size classes ≥ 400 mm dbh than in size classes of 100–400 mm. Since Newbery and Gartlan only had censuses of trees ≥ 100 mm dbh, we classified the BCI species after excluding all individuals 10–99 mm dbh, and we only used species that had at least 15 individuals ≥ 100 mm dbh in 1985.

Results

Size Distributions and Life Tables

Concrete examples of size distributions and life tables serve to illustrate predictions of the theory. At one end of the size distribution spectrum are species with large numbers of juveniles relative to adults. Examples are shown in figures 1 and 2: both *Trichilia tuberculata* (Meliaceae) and *Tetragastris panamensis* (Burseraceae) were among the most numerous canopy species in the plot (Condit et al. 1996b). Like most of the common tree species, they are shade tolerant and had high survival rates at all sizes, very low growth rates in small size classes, but much higher growth rate at larger sizes (figs. 1, 2). They also had very steep size distributions, with more than 70% of all individuals in the 10–49-mm size class. In *Tetragastris*, the slope L from the ln-ln regression was -2.04 , in *Trichilia*, -2.25 ; these values fall in the steepest (most negative) quartile among large tree species.

According to the third prediction from the theory, the sharp increase in growth across the first four size classes caused the steep size distributions. In addition, growth rates were fairly low at all sizes, which predicts steep size distributions. High survival rates should flatten the distributions, but the impact of survival was apparently overridden by growth. *Tetragastris* had a rapidly increasing population ($\lambda = 1.26$ over 13 yr), whereas *Trichilia's* was barely declining ($\lambda = 0.99$). Thus, population growth was apparently not instrumental in determining the size distributions.

A contrast can be found in fast-growing pioneer species, all of which were much less common than *Tetragastris* or *Trichilia* (Condit et al. 1996a, 1996b). Two of the most common pioneers that had among the highest growth rates in the plot were *Cecropia insignis* (Mora-

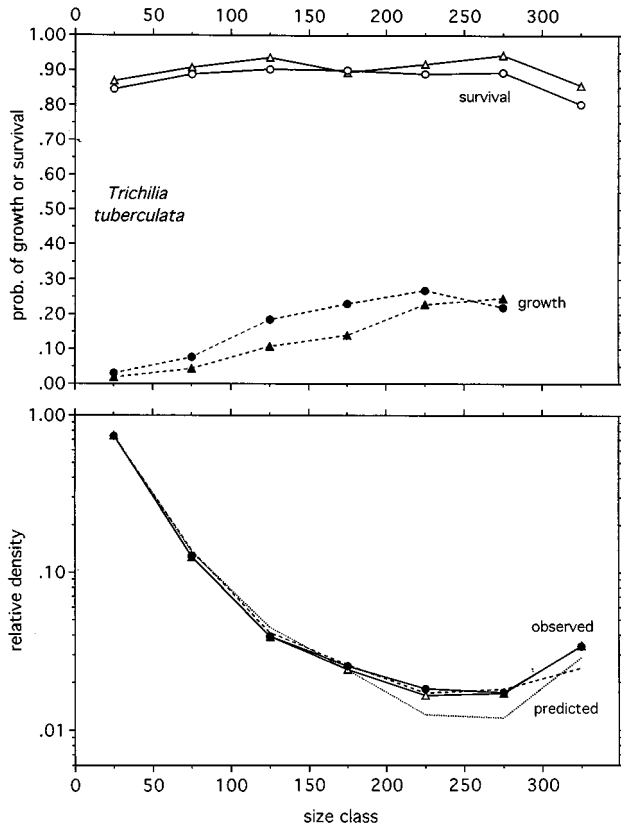


Figure 1: Size distribution and demographic parameters for *Trichilia tuberculata*. The top panel gives growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). Growth here is the sum of all transition probabilities from a given dbh class to any larger class over a 5-yr period (in *Trichilia*, nearly all growth was by a single size class). There was no growth rate for the terminal size class, since there was no larger size class. Survival was the fraction that survived the 5-yr period. Data from 1985–1990 interval indicated by circles, 1990–1995 by triangles. The bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species. The vertical scale is logarithmic. Solid lines are observed distributions (circles = 1990 data; triangles = 1995 data). Dashed lines are those predicted from simulation of the life table (large dashes = 1985–1990 data; fine dashes = 1990–1995 data).

ceae) and *Zanthoxylum belizense* (Rutaceae; Condit et al. 1996a). Both species had much higher growth rates than *Tetragastris* or *Trichilia*, with the greatest contrast in the smallest size class (figs. 3, 4). Growth did increase with size class in these species but not as sharply as in *Tetragastris* or *Trichilia*; in *Cecropia*, for instance, growth increased by about 2.5-fold from the smallest to largest size class (from 0.22 to 0.53), while in *Trichilia*, the increase was ninefold (from 0.03 to 0.27). Survival rates were low in the fast-growing species, but survival in the larger size

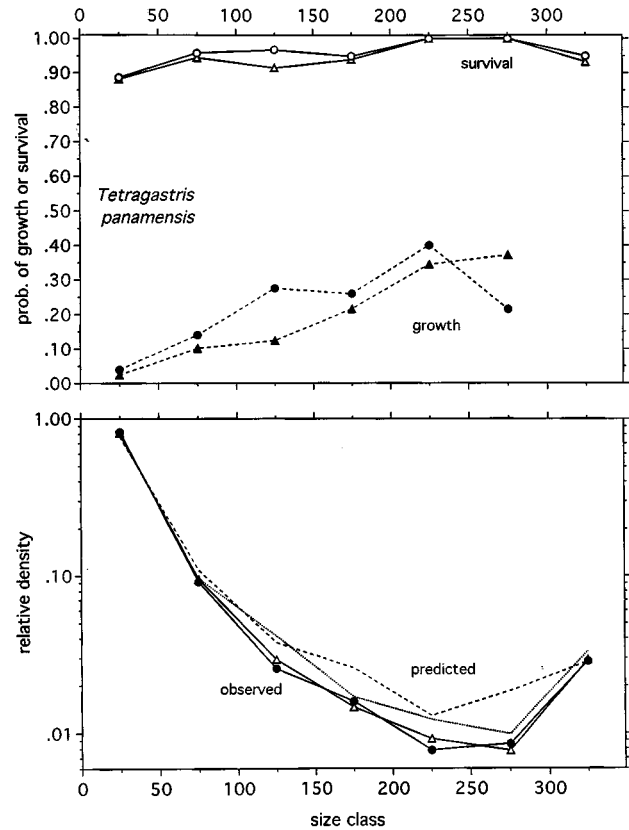


Figure 2: Size distribution and demographic parameters for *Tetragastris panamensis*. All symbols are identical to those in figure 1. As with *Trichilia*, most growth was by a single size class. The top panel gives growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). The bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species.

classes approached that found in the shade-tolerant species (figs. 3, 4). Both *Cecropia* ($\lambda = 0.74$) and *Zanthoxylum* ($\lambda = 0.94$) had declining populations.

Cecropia and *Zanthoxylum* had flat size distributions, with slopes of -0.85 and -1.31 , respectively. The former was very close to the flattest for large trees. The flat size distributions can be attributed to very high growth and population decline (second and third predictions); however, *Zanthoxylum* and *Trichilia* were only slightly different in population growth yet had very different size distributions. Notice the extreme example of a flat size distribution in *Zanthoxylum*: there were fewer stems 200–250 mm dbh than 250–300 mm, associated with a drop in growth rate between these classes (as in Platt et al. 1988 and our third prediction).

In all four species, the final size class had more individuals than prior size classes. This is a trivial result of defining the terminal class as open-ended (all larger indi-

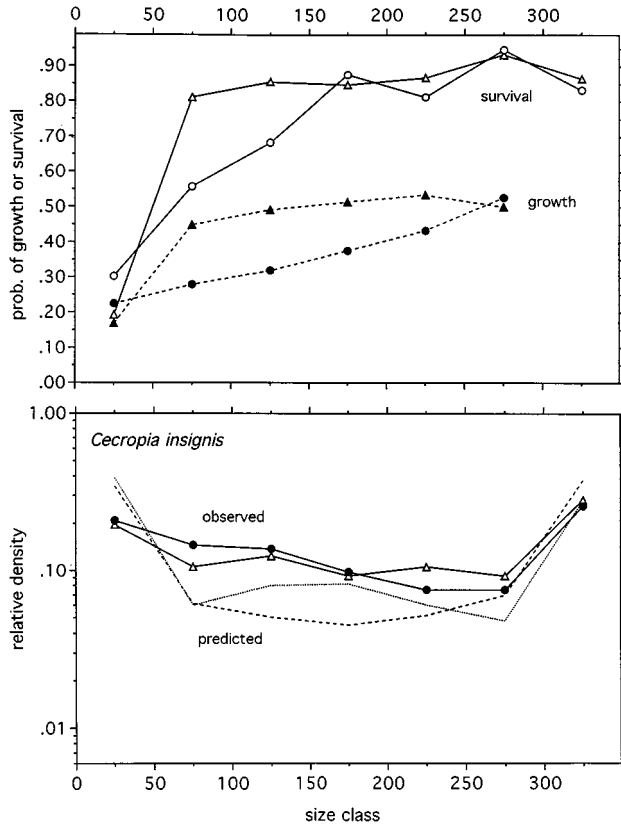


Figure 3: Size distribution and demographic parameters for *Cecropia insignis*. All symbols are identical to those in figure 1. Unlike *Trichilia* and *Tetragastris*, many individuals grew by two or even three size classes in this species. The top panel shows growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). The bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species.

viduals). However, the result can also be viewed in the light of the third prediction from equation (4): growth was 0 in the terminal size class (by definition), so growth declined sharply from the subterminal to the terminal class. In *Zanthoxylum*, this decline was the greatest, and the number of individuals in the terminal size class was very high relative to prior classes.

In the lower panels of figures 1–4, size distributions based on life-table simulations are given along with observed size distributions. The simulated output closely matched observed, especially in *Tetragastris* and *Trichilia* (figs. 1, 2). Simulations clearly predicted the flatter distributions in *Cecropia* and *Zanthoxylum*, but in both pioneers, observed distributions were even flatter than predicted (figs. 3, 4). For 44 species with the most complete life tables (≥ 5 individuals in all size classes to 400 mm dbh and ≥ 400 mm dbh), we correlated the simulated

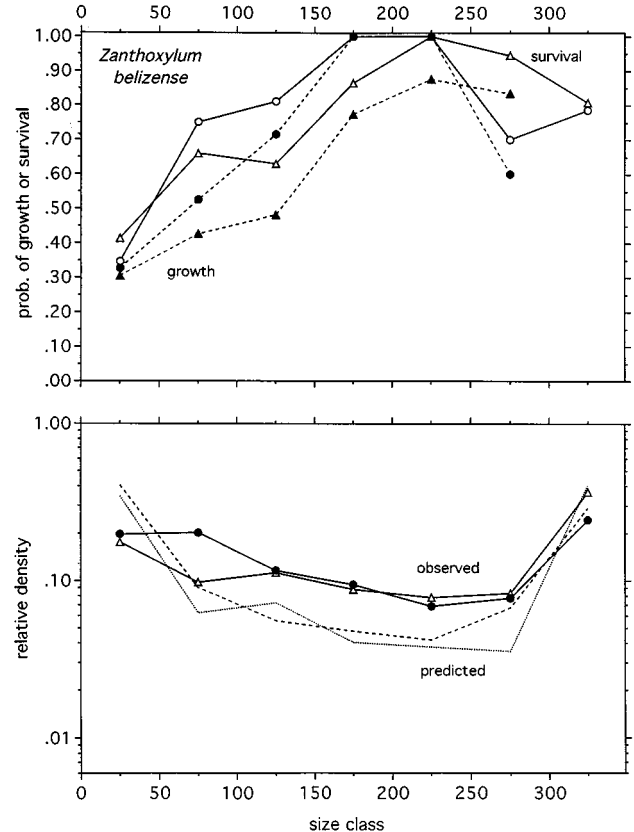


Figure 4: Size distribution and demographic parameters for *Zanthoxylum belizense*. All symbols are identical to those in figure 1. As with *Cecropia*, many individuals of *Zanthoxylum* grew by two or more size classes. The top panel shows growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). The bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species.

slope L against observed L and simulated λ against observed λ . Predictions were good (fig. 5).

Correlates of Size Distribution

As predicted by theory, population growth correlated negatively with the slope of the size distribution (fig. 6). Species toward the right-hand side of each graph in figure 6 had flatter size distributions (less negative L), with fewer small stems relative to large stems, and in most cases, also had shrinking populations ($\lambda < 1$). According to parametric regression, the relationship was significant only in treelets, not in large and midsized trees (fig. 6); however, nonparametric Spearman correlations were significant in all three groups. In shrubs, the correlation between L and λ was positive but nonsignificant (fig. 6).

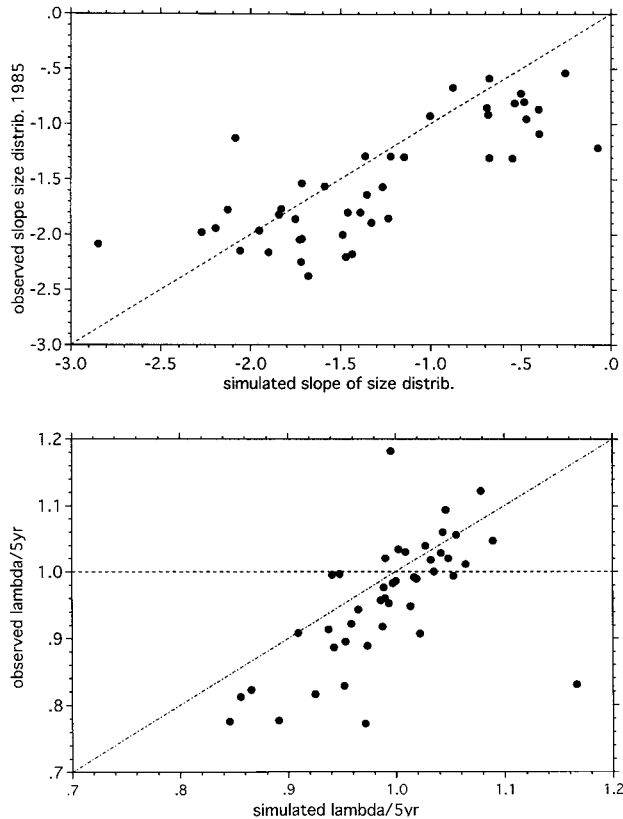


Figure 5: Predictions of life-table simulations versus real data. Top panel, observed slope L of size distribution versus prediction from life table. Bottom panel, observed versus predicted population growth rate λ . Predicted λ from life tables was per 5-yr interval, so observed λ over 1982–1995 was converted by raising to the five-thirteenth power. The diagonal line in each figure is not a regression line but is drawn at $Y = X$, where prediction and observation matched. The bottom frame also has a horizontal line at $\lambda = 1$. Only 44 species were used in these comparisons—all that had at least five individuals in all size brackets up to 400 mm dbh, and at least five ≥ 400 mm. The simulations were based on the average of 1985–1990 and 1990–1995 transition probabilities.

Size distribution was much more strongly related to g_1 , the growth probability of the smallest size class (fig. 7). A highly significant correlation was found in all three groups of trees (fig. 7; recall that this analysis was not done in shrubs). In a multiple regression including four demographic parameters—survival, growth of the first size class, growth of the third size class, and λ — g_1 was significantly associated with L in all three groups. In large and midsized trees, it was the only variable appearing in the model, whereas in treelets, λ was the first variable in the regression and g_1 the second. Neither growth of the larger size class nor survival was significantly associated in any group.

In both large and midsized trees, inclusion of g_1 in the regression model eliminated any correlation between λ and L (fig. 5). After regressing L against g_1 , we took residuals of L and plotted them against λ and found no relationship. But in treelets, the relationship did persist even after correcting for g_1 .

Further Examples

In view of the weak association between size distribution and population growth, we extracted two examples to illustrate how species with flat size distributions can have increasing populations and vice versa (figs. 8, 9). *Heisteria concinna*, a midsized tree in the Chrysobalanaceae, had $\lambda = 1.10$ and $L = -1.4$, thus a size distribution well flatter than the median (fig. 6). Fewer than 50% of its stems were in the smallest size class (fig. 8). Its relatively flat size distribution can be attributed to very high survival rates and growth rates that did not increase much with size (fig. 8). *Guarea* sp., a still unnamed midsized tree in the Meliaceae, was an interesting contrast. With $L = -2.6$, it had among the steepest size distributions, despite $\lambda = 0.79$, and had relatively low survival and extremely poor growth at all sizes (fig. 9).

Predicting Population Change

To determine what variables can be used to predict population change, we rearranged the multiple regression so that λ was the dependent variable, with \bar{s} , g_1 , g_3 , and L the independent variables. In large and midsized trees, survival was the only significant associate in the stepwise regression, and its association was not strong ($r^2 < 0.14$ in both). High survival predicted increasing population growth. In treelets, the results were rather different: size distribution (L), growth of size class 3 (g_3), and survival (s) were all significantly associated with population growth; only growth of class 1 (g_1) was not. Higher survival, faster growth, and steeper size distributions all predicted better population growth.

Dbh Distribution Categories

Of 135 species that qualified for the comparison with African forests, 16 fell in group 3, 16 in group 4, and seven in group 5. There were clearly fewer group 5 species at Barro Colorado Island than in Cameroon. At BCI, group membership had no significant association with population growth; however, all seven group 5 members had declining populations (table 1). Not surprisingly, group membership was associated with the slope of the size dis-

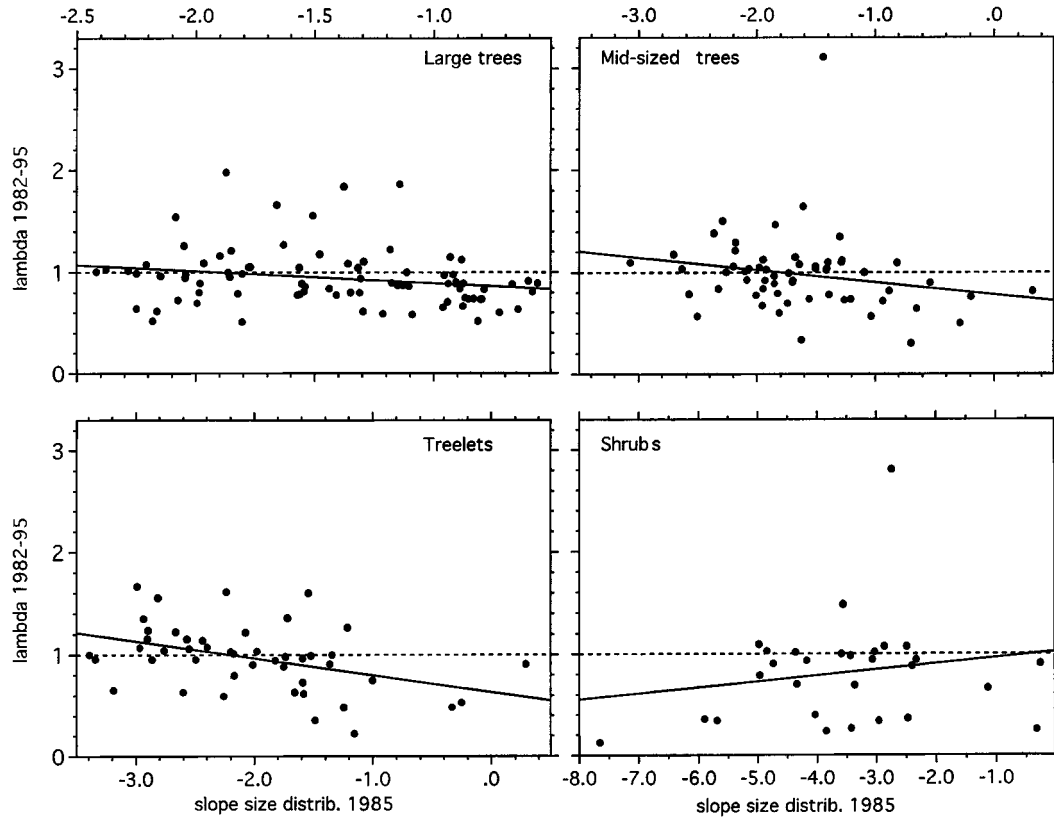


Figure 6: Correlations between size distribution (L) and population change (λ) in four growth forms: large trees, mid-sized trees, treelets, shrubs. The solid lines are regression lines; the horizontal dashed lines are at $\lambda = 1$, indicating a stable population. Standard parametric regression revealed statistical significance only in treelets ($P = .0035$), although almost so in trees ($P = .056$ in large trees, $P = .119$ in mid-sized trees). The nonparametric rank correlation revealed a significant relationship in all three groups. No correlation was significant in shrubs.

tribution—group 1 species had steep distributions, group 5 very flat distributions (table 1).

The group 5 species—*Anacardium excelsum* (Anacardiaceae), *Cavanillesia platanifolia* (Bombacaceae), *Ceiba pentandra* (Bombacaceae), *Dipteryx panamensis* (Leguminosae), *Hyeronima alcheornoides* (Euphorbiaceae), *Hura crepitans* (Euphorbiaceae), and *Platypodium elegans* (Leguminosae)—include the biggest trees in the forest. In 1995, the 14 largest diameters in the 50-ha plot belonged to *Ceiba*, *Hura*, *Cavanillesia*, and *Anacardium*, and 40 out of the 46 individuals with dbh > 1,500 mm were in group 5. The other six included four species of *Ficus* (Moraceae) and *Pseudobombax septenatum* (Bombacaceae).

Discussion

The main conclusion is that size distribution was a poor predictor of population performance. Only in treelets did it work at all, whereas in canopy species, there was only

a very weak association, which disappeared when growth rates were taken into account. Growth of the smallest size class was a strong predictor of size distribution in both understory and canopy species: faster growing species had fewer stems in juvenile classes. Swaine and Hall (1988) echoed the view that size distribution is not necessarily a predictor of population change, but they did not examine how size distribution is affected by other life-table parameters. The general conclusion is that static information about the size distribution was not a good predictor of population dynamics.

These associations were well supported by theory. Growth in the smallest size class should correlate with size distribution because, in this size class, increases in growth should always flatten the distribution (third prediction). In larger size classes, higher growth should not correlate with a flatter distribution, and it did not. The theory predicted an association between survival and size distribution, but the data did not support this. This is probably because survival did not vary much across spe-

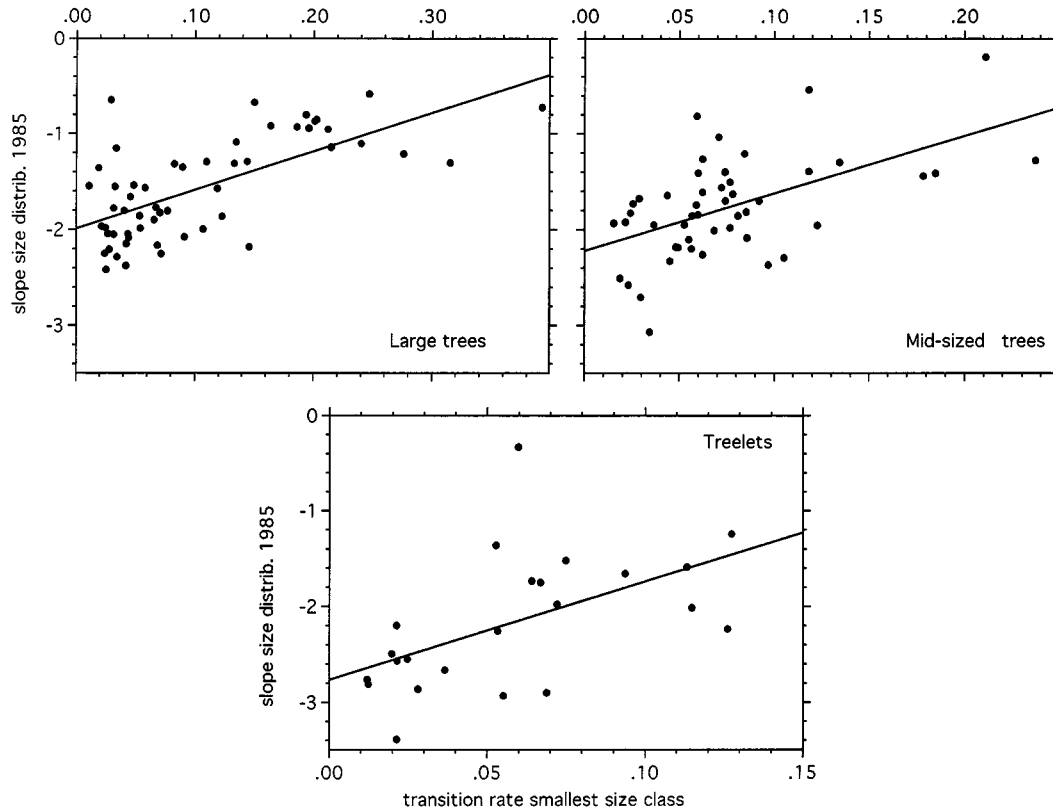


Figure 7: Correlations between size distribution (L) and growth probability of the smallest size class, for three growth forms: large trees, mid-sized trees, treelets. Solid lines are regression lines. In all three, parametric regressions were highly significant ($P < .0001$ for large and mid-sized trees; $P = .008$ for treelets). Rank correlations were also highly significant.

cies: a considerable majority of species had annual mortality rates between 1% and 6% per year (Condit et al. 1995), meaning 5-yr survival of 70%–95%. Growth of the small size class was much more variable, frequently being <3% over 5 yr but sometimes as high as 30% (figs. 1–4, 8, 9).

The theory also predicted an association between population growth and size distribution, as was born out in treelets but not larger trees. Again, it seems likely that the reason we did not find an association in larger trees is that λ varied much less than growth rate: most species had annual population changes <5% per year (Condit et al. 1996b). So our primary conclusion must be that growth rate of small stems is the strongest correlate of size distribution across species, resulting from the fact that it is the most variable of the demographic parameters that associate with size distribution.

The predictions generated by equations (1)–(4) are based on a life-table model. The key assumption underlying this model is that growth and mortality of a stem depend only on its current size class, not its prior history, and that there is no density dependence in the model. We also assumed time invariance in vital statistics. We

know that these assumptions are violated—current mortality and current growth both depend on prior growth (Pacala et al. 1993; Terborgh et al., in press), density dependence in growth, mortality, and recruitment have been documented at Barro Colorado Island (Condit et al. 1992, 1994; Wills et al. 1997), and demographic parameters vary (Condit et al. 1995). Nevertheless, simulation of these simple life tables produced good matches for actual size distributions and population change. Since life-table theory underlies equation (4), we can take the accurate simulations as evidence for the validity of the theoretical derivations. We suggest that variation among individuals in local environment may average out over larger periods, and in this old-growth forest subject to no catastrophic disturbances, population parameters are fairly constant over long enough periods. Platt et al. (1988) also found excellent agreement between observed size distributions and those predicted from a life table, and their analysis nicely illustrates several of the theoretical conclusions derived here.

The regression analysis did not offer clear ways to predict population trends in canopy species. Only survival rate was a predictor of population change in larger trees,

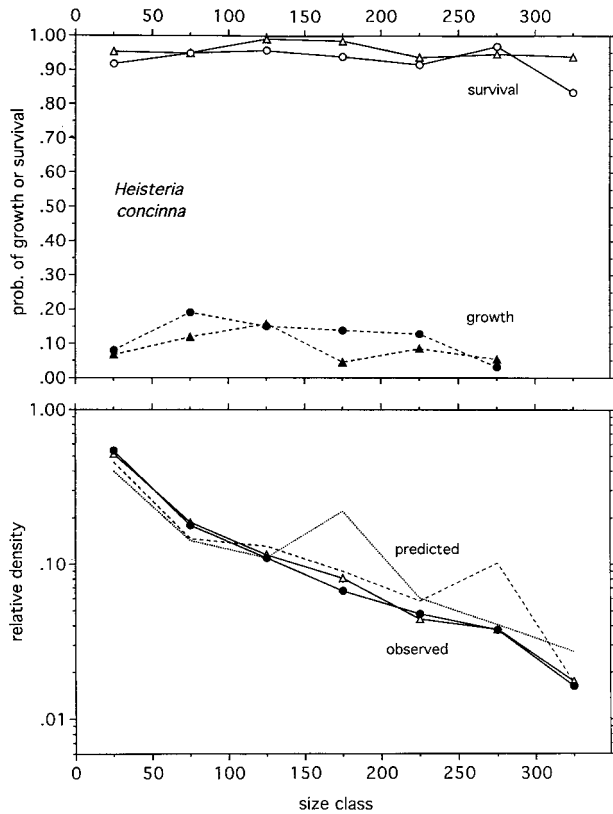


Figure 8: Size distribution and demographic parameters for *Heisteria concinna*. All symbols are identical to those in figure 1. Top panel gives growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). Bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species.

although survival and size distribution did work in treelets. Species with low survival rates are declining in abundance in the BCI plot. We believe this is a result specific to Barro Colorado Island: pioneer species have been in steady decline since the plot began (Hubbell and Foster 1990, 1992; Condit et al. 1996*b*). This is possibly because areas adjacent to the plot were cleared in the nineteenth century and have since reforested. Invasive species were undoubtedly extremely abundant just outside the plot during this recovery and pumped large numbers of seeds into the old forest; now they are gradually being lost (Hubbell and Foster 1990, 1992).

The trend for pioneer species to be declining apparently underlies the weak correlation observed between size distribution and population change in canopy species. Pioneers, which had decreasing populations, tend to have high growth (Condit et al. 1996*a*) and, thus, flatter size distributions. Thus, there was a weak association between population change and size distributions in canopy species, but it disappeared when the effect of growth rate

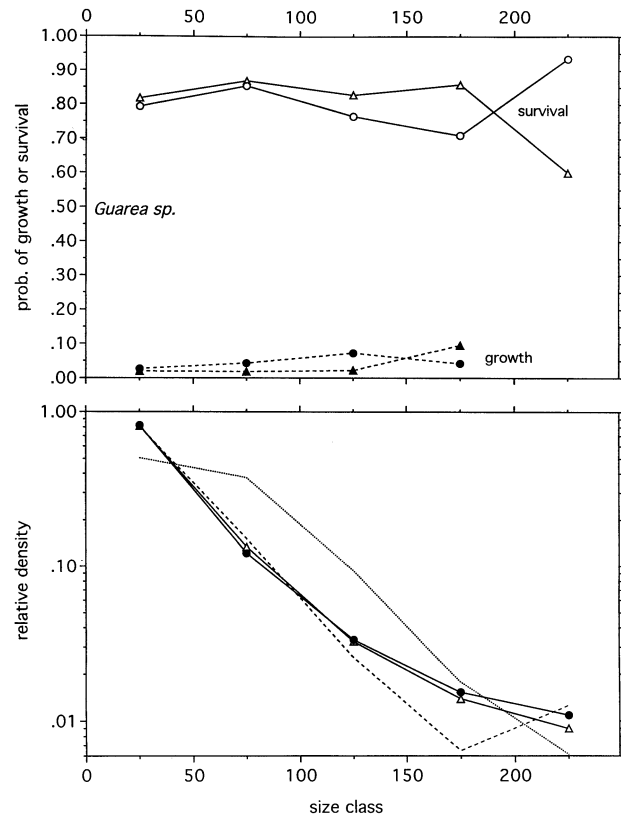


Figure 9: Size distribution and demographic parameters for *Guarea sp.* All symbols are identical to those in figure 1. Top panel gives growth and survival probabilities for each 50-mm dbh bracket (10–49, 50–99 mm, etc.). Bottom panel shows number of individuals in each 50-mm dbh class divided by the total number of individuals of that species.

was subtracted. Each of these correlation links left a substantial amount of unexplained variance, and this explains why some of the associations were not significant. For example, although high survival was significantly related to population change (this study) and to growth rate (Condit et al. 1996*a*), growth rate was not significantly associated with population change.

Regardless of these details, we can say that we found no unequivocal shortcuts for predicting population changes. Static and short-term data on a population are not sufficient for predicting longer-term dynamics, at least in this forest.

The seven species with flat size distributions that qualify as Newbery and Gartlan's group 5 are an especially interesting set. All include immense trees—the largest in the plot—but very few juveniles. These characteristics have been the focus of much attention in Africa with discussion revolving around whether such dominant canopy species are replacing themselves. Here is a summary of what we know about the group at BCI: all are early suc-

Table 1: Classification of size distributions according to the system used in Africa by Newbery and Gartlan (1996)

Category	Species at BCI	Population trend at BCI		$\bar{X} \pm SE$ of slope of size distribution at BCI	Species at Korup	Species at Douala Edea
		Fraction decreasing	$\bar{X} \pm SE$ of λ			
Group 1	74	.57	.96 \pm .04	-1.82 \pm .08	93	48
Group 2	22	.73	.87 \pm .04	-1.57 \pm .11	40	30
Group 3	16	.63	.90 \pm .05	-1.24 \pm .12	19	12
Group 4	16	.44	1.07 \pm .09	-1.57 \pm .10	18	9
Group 5	7	1.00	.85 \pm .03	-.87 \pm .11	27	19
Total	135	.61	.95 \pm .03	-.63 \pm .06	197	118

Note: Barro Colorado Island (BCI) species include those with ≥ 15 individuals above 100 mm dbh, excluding palms, in 1985. Counts from the two forests in Cameroon (Korup and Douala Edea) are from Newbery and Gartlan (1996). Many species are common to the two African sites, but just one is common to BCI and Africa: *Symphonia globulifera* (Guttiferae) is in group 2 at BCI, group 5 at Douala Edea.

cessional species that are also very long-lived, and all have declining populations. Each of the species has recruited into the 10-mm class since 1982, but *Anacardium*, *Cavanillesia*, and *Hura* had just four recruits between them. It appears that at least some of the African species that Newbery and Gartlan (1996) assigned to group 5 are similar—for example, *Microberlinia bisulcata* (Leguminosae) is a giant, long-lived, invasive species. Other American forests have a “group 5” guild, for example, mahogany *Swietenia macrophylla* in Bolivia obviously fits the category (Gullison et al. 1996). Nevertheless, the cross-continent comparison suggests that Cameroonian forests have substantially more species of this guild than BCI.

Given that these long-lived, giant invaders are all declining in abundance, what will their long-term status be? One possibility is that they invaded during large-scale disturbances in the past and are now dropping out of the forest. At BCI, there were small clearings 600–800 yr ago where the plot is now; this is clearly within the life span of a giant *Ceiba* or *Anacardium*. Newbery and Gartlan (1996) favored this successional theory in Cameroon. But another reasonable possibility is that these species do occasionally recruit following large-scale natural disturbances, as *Swietenia* does on recent erosion gullies in South America (Gullison et al. 1996). The fact that the BCI species are all recruiting at least some to the 10-mm class favors this view. If adults live for centuries, successful recruitment events do not have to be common to maintain a quasi-stable population. Many temperate conifers maintain populations with very irregular recruitment in response to fire, and juveniles are often lacking in mature stands (Johnson and Fryer 1989; Clark 1996). A tropical dry forest we

have studied in India has few juveniles, and many species there may persist through episodic recruitment (Sukumar et al. 1992).

But for most tropical forest trees, populations are sustained by ongoing recruitment. In these, it cannot be concluded that size distribution alone is a good predictor of future population trends, since size distribution is also affected by other demographic variables that vary enormously between species. Growth rate of young stems in particular is strongly associated with flat distributions, that is, with few juveniles. This conclusion was predicted by straightforward theoretical population biology and confirmed by empirical observations of population change in a large number of species.

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Literature Cited

- Alvarez-Buylla, E. R., and R. García-Barríos. 1991. Seed and forest dynamics: a theoretical framework and an example from the neotropics. *American Naturalist* 137: 133–154.
- Clark, J. S. 1996. Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *American Naturalist* 148:976–996.
- Condit, R. 1998. A field guide to large forest censuses in the tropics: the Barro Colorado Island Project and a network of tropical forest plots. Landes, Austin, Tex.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist* 140:261–286.
- . 1994. Density dependence in two understory tree species in a neotropical forest. *Ecology* 75:671–705.
- . 1995. Mortality rates of 205 neotropical tree species and the responses to a severe drought. *Ecological Monographs* 65:419–439.
- . 1996a. Assessing the response of plant functional types in tropical forests to climate change. *Journal of Vegetation Science* 7:405–416.
- . 1996b. Changes in a tropical forest with a shifting climate: results from a 50 ha permanent census plot in Panama. *Journal of Tropical Ecology* 12:231–256.
- Croat, T. R. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, Calif.
- Enright, N., and J. Ogden. 1979. Applications of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. *Australian Journal of Ecology* 4:3–23.
- Foster, D. R., D. A. Orwig, and J. S. McLachlan. 1996. Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends in Ecology & Evolution* 11:419–424.
- Franklin, S. B., P. A. Robertson, J. S. Fralish, and S. M. Kettler. 1993. Overstory vegetation and successional trends of Land between the Lakes, USA. *Journal of Vegetation Science* 4:509–520.
- Gullison, R. E., S. N. Panfil, J. J. Strouse, and S. P. Hubbell. 1996. Ecology and management of mahogany (*Swietenia macrophylla* King) in the Chimanes Forest, Beni, Bolivia. *Botanical Journal of the Linnean Society* 122:9–34.
- Hara, T. 1984. A stochastic model and the moment dynamics of the growth and size distribution in plant populations. *Journal of Theoretical Biology* 109: 173–190.
- Hart, T. B., J. A. Hart, and P. G. Murphy. 1989. Mono-dominant and species-rich forests of the humid tropics: causes for their co-occurrence. *American Naturalist* 133:613–633.
- Hubbell, S. P., and R. B. Foster. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pages 25–41 in S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, eds. *Tropical rain forest: ecology and management*. Blackwell Scientific, Oxford.
- . 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Pages 522–541 in A. Gentry, ed. *Four neotropical rain forests*. Yale University Press, New Haven, Conn.
- . 1992. Short-term population dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* 63:48–61.
- Hubbell, S. P., and P. A. Werner. 1979. On measuring the intrinsic rate of increase of populations with heterogeneous life histories. *American Naturalist* 113: 277–293.
- Johnson, E. A., and G. I. Fryer. 1989. Population dynamics in lodgepole pine–Engelmann spruce forests. *Ecology* 70:1335–1345.
- Knowles, P., and M. C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. *Ecology* 64:1–9.
- Kohyama, T. 1992. Density-size dynamics of trees simulated by a one-sided competition multi-species model of rain forest stands. *Annals of Botany (London)* 70: 451–460.
- . 1993. Size-structured tree populations in gap-dynamic forests: the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology* 81: 131–143.
- Lefkovich, L. P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21:1451–1454.
- Leigh, E. G., Jr, S. A. Rand, and D. M. Windsor, eds. 1982. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 6:1169–1184.
- Newbery, D. McC., and J. S. Gartlan. 1996. A structural analysis of rain forest at Korup and Douala-Edea, Cameroon. *Proceedings of the Royal Society of Edinburgh B, Biological Sciences* 104:177–224.
- Ogden, J. 1985. Past, present and future: studies on the population dynamics of some long-lived trees. Pages 3–16 in J. White, ed. *Studies on plant demography*. Academic Press, London.

- Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements. I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* 23:1980–1988.
- Piñero, D., M. Martinez-Ramos, and J. Sarukhán. 1984. A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *Journal of Ecology* 72:977–991.
- Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131:491–525.
- Poorter, L., F. Bongers, R. S. A. R. van Rompaey, and M. de Klerk. 1996. Regeneration of canopy tree species at five sites in West African moist forest. *Forest Ecology and Management* 84:61–69.
- Read, J., P. Hallam, and J.-F. Cherrier. 1995. The anomaly of monodominant tropical rainforests: some preliminary observations in the *Nothofagus*-dominated rainforests of New Caledonia. *Journal of Tropical Ecology* 11:359–389.
- Richards, P. W. 1952. *The tropical rain forest*. Cambridge University Press, Cambridge.
- Sukumar, R., H. S. Dattaraja, H. S. Suresh, J. Radhakrishnan, R. Vasudeva, S. Nirmala, and N. V. Joshi. 1992. Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. *Current Science (Bangalore)* 62:608–616.
- Swaine, M. D., and J. B. Hall. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. *Journal of Tropical Ecology* 4: 253–269.
- Terborgh, J., C. Flores N., P. Mueller, and L. Davenport. In press. Estimating the ages of tropical trees from growth increments. *Journal of Tropical Ecology*.
- Usher, M. B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *Journal of Applied Ecology* 3:355–367.
- Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences of the USA* 94:1252–1257.

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