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Estimating Demographic Rates of Long-Lived Trees

Abstract

Long-lived species, such as many Pacific Northwest trees, pose special problems for studies in demography. A demographic model is presented that combines knowledge of current age distribution with detailed information of past environmental conditions gained from stand reconstruction techniques. The model makes simple assumptions about the influence of environmental factors on year-to-year survivorship. Multiple regression analysis then allows the direct estimation of birth rates and age-specific and environment-specific survival rates for the population. This new analytic tool should be useful for investigating environmental control of tree population dynamics.

Introduction

Birth and death rates provide basic information about populations. When these rates are specific to age and environment, they encapsulate much of the dynamics of a population and help reveal the mechanisms controlling population size. Unfortunately, most methods for estimating demographic parameters, including cohort and current life table analysis, are inadequate for studying the long-lived tree species common in the Pacific Northwest. Current (static) life tables are constructed from short-term observations of the births and deaths of an entire, multi-aged population. Demographic rates estimated from the analysis of current life tables are valid only if the age distribution of the population is stationary (Pielou 1977), but this condition seldom holds for field populations responding to a changing environment. Constructing cohort life tables, on the other hand, requires following individuals born within the same time interval throughout each of their lifetimes. Thus, only short-lived organisms are suitable for study as cohorts (e.g., Leverich and Levin 1979, Mack and Pyke 1983, Silvertown 1985).

The goal of this paper is to present a new method of demographic analysis suitable for the study of long-lived trees. The method combines information on a population's current age structure with reconstruction of past environmental conditions to produce estimates of birth rates and age-specific and environment-specific survival rates.

Model Development

Consider a general demographic model of the survivorship of a long-lived species:

$$N_x = N_0 \cdot S_1 \cdot S_2 \cdot \ldots \cdot S_x \qquad (1)$$

where N_0 is the total number of individuals born in a certain time interval, N_x is the number alive of age x, and each S_i is the proportion surviving from age class i-1 to i. The relative values of N_x for a population at a particular time describes its age structure. The units of x could be single years, 5 years, or another convenient interval.

The actual age-specific survival rates (S_i) result from the interaction of the population's potential or inherent age-specific survival under optimal environmental conditions with the constraint imposed on survival by an unfavorable environment. For a single environmental factor j, this relationship between population potential and environmental constraint can be described as

$$S_i(t) = \hat{S}_i \cdot C_{ij}(t) \qquad (0 \le C_{ij}(t) \le 1) \qquad (2)$$

where $S_i(t)$ is the actual survival rate for age class i at time t, $\hat{S}_i$ is the potential survival rate for age class i, and $C_{ij}(t)$ is the constraint imposed on survival of age class i by the environmental factor at time t. The constraint on survival is larger when $C_{ij}(t)$ is smaller; for example, $C_{ij}(t) = 1.0$ means that survival is not reduced by the environmental condition. It is useful to define $e_j(t)$ as the effect on survival of environmental factor j at time t. Then the relative favorableness ($F_j(t)$) of factor j at time t is

$$F_j(t) = \frac{e_j(t)}{\max e_j},$$

where $e_j(t) \ge 0$ and $\max e_j$ is the most favorable state in which factor j occurs. (The relationship between environment and favorableness, as depicted in the e_j values, ideally should be determined from prior studies.) A simple, albeit arbitrary way to relate relative favorableness (F) to environmental constraint (C) on survival is

$$C_{ij}(t) = F_j(t)^{\beta ij} \qquad (\beta \geq 0) \qquad (3)$$

where β_{ij} is a parameter specific for age class i and environmental factor j. With this power-function form, different values of the single parameter in equation 3 (β) allow the relationship between environmental favorableness and constraint to range between severe constraint on survival under any suboptimal conditions (β very large) to no constraint under any environmental condition ($\beta = 0$) (Figure 1).

Field populations, of course, are influenced by more than one environmental factor at a time. Moreover, exposure to one stress can sometimes predispose or harden a plant to another (Levitt 1980). Nevertheless, a useful first approximation is to assume that constraints on survival of multiple environmental factors act independently of one another. Under this assumption, the overall environmental constraint ($C_i(t)$) on the survival of age class i is

$$C_i(t) = C_{i1}(t) \bullet C_{i2}(t) \bullet \ldots \bullet C_{iv}(t) \qquad (4)$$

$$C_i(t) = \prod_{j=1}^{v} C_{ij}(t)$$

where v is the total number of environmental factors being described. Substituting into equation 4 the relationship between single environmental factors and constraints on survival described in equation 3 produces

$$C_i(t) = \prod_{j=1}^{v} F_j(t)^{\beta ij}. \qquad (5)$$

The extension of equation 2 for the case of several environmental factors is then

$$S_i(t) = \hat{S}_i \prod_{j=1}^{v} F_j(t)^{\beta ij}. \qquad (6)$$

At this point, the general demographic model described in equation 1 can be rewritten to include the constraints on survival developed in equations 2 through 6:

$$N_x(t) = N_0(t\text{-}x)\prod_{i=1}^{x} S_i(t\text{-}x+i) \qquad (7a)$$

$$N_x(t) = N_0(t\text{-}x)\prod_{i=1}^{x}\left\{\hat{S}_i\prod_{j=1}^{v} F_j(t\text{-}x+i)^{\beta ij}\right\}. \qquad (7b)$$

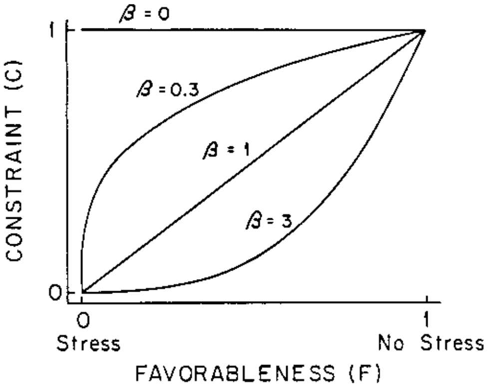

Figure 1. The relationship between relative environmental favorableness and constraint on survival rates described by equation 3. Large values of C mean that the survival rate is close to the rate that would occur under optimal environmental conditions. The shape of the relationship depends on the value of β. If β is large, then unfavorable conditions strongly decrease survival. If $\beta = 0$, survival is unaffected by the state of the environmental factor.

Equation 7b describes the expected number of individuals of age x at time t that had experienced a particular sequence of environmental conditions. This sequence corresponds to a time series of variables F_j. For example, for $j = 2$ environmental factors, a sequence of environmental conditions over three time periods can be written as

$$\{F_1(t\text{-}2),F_2(t\text{-}2)\},\ \{F_1(t\text{-}1),F_2(t\text{-}1)\},\ \{F_1(t),F_2(t)\}.$$

Different environmental histories would have different sequences of F values. Many of these sequences would undoubtedly be necessary to account for the heterogeneous environmental histories of most ecosystems. Thus, the final demographic model is actually a series of equations, each of the form shown in equation 7b. Each equation describes the relationship between a unique temporal sequence of environmental conditions (seen in the different values of F_j through time) and the number of individuals alive of age x ($N_x(t)$) that have lived through the environmental sequence. Although each equation differs in the values of the independent variables (the F_j) and the dependent variables (the N_x values), they partially share some parameters (the N_0, $\hat{S}_i$, and β_{ij} values).

The number of equations in the final model is potentially very large. For $x = 1$ (the first age class), the number of unique environmental sequences would be the number of distinct, current environmental conditions (v). For older age classes ($x > 1$), the possibility of permutations of different environmental conditions occurring in different sequences over time means that the potential number of unique sequences is substantial ($= v^x$). In practice, however, most sequences will not occur. For example, litter depth in forests should increase steadily through time except for occasional, rapid consumption by fire. Irregular fluctuations in litter depth are improbable and the actual number of unique environmental sequences in this example would be much less than the potential number.

Application

The use of the final model in demographic analysis requires relating the information on the current tree age structure ($N_x(t)$) with past environmental conditions. The first step in field application is to divide the study area into patches or quadrats that have the same environmental history. Estimates of the actual past environmental conditions are best derived from stand reconstruction techniques (e.g., Henry and Swan 1974, Oliver and Stephens 1977, Lorimer 1985, Kelty 1986, Larson 1986). Stand reconstruction uses current evidence to infer past environmental events and conditions. For example, fire scars on trees can be used to date and estimate the extent of a past fire and the concomitant changes in light conditions, soil chemistry, and understory competition. To be useful for demographic analysis, stand reconstruction must yield information on the past environment of each sample quadrat. Then the sample quadrats can be placed into groups having identical sequences of past environmental conditions.

The next step requires the translation of environmental conditions into degrees of favorableness (e_j). This conversion must stem from prior studies of the species's mortality response to the environment. For this model, only a few, arbitrary categories of favorableness need to be identified.

The dependent variables in the final model are the series of values representing the number of individuals alive at different ages (the N_x values) that had experienced the same sequence of environmental conditions. These values are obtained by aging and counting individuals occurring in quadrats having the same sequence of environmental conditions.

The values of $F_j(t\text{-}x+i)$ and $N_x(t)$ are then substituted into the series of equations constituting the final demographic model. In the final demographic model, exemplified by equation 7b, there are enough equations to estimate all but one of the parameters. The best solution to this problem is to assume that population birth rates are constant through time: $N_0(t) = N_0$ for all t. This assumption is decidedly poor for most trees if the time intervals are years: mast seeding years in trees are well documented. With longer time intervals, such as 10 years, the assumption of constant population birth rate is much more reasonable. A related characteristic of the model is that birth rates (N_0) cannot be distinguished from first year potential survival rate ($\hat{S}_1$). That is, the method estimates $N_0 \bullet \hat{S}_1$, the number of new seedlings alive at the end of the first age interval under optimal environmental conditions.

The series of equations constituting the final demographic model can be solved by nonlinear regression for the unknown parameters: $N_0 \bullet \hat{S}_1$, the number of new seedlings alive at the end of the first age interval under optimal environmental conditions; $\hat{S}_2, \hat{S}_3, \ldots, \hat{S}_x$, the potential age-specific survival rates; and the β_{ij} values, the coefficients indicating the constraint of environmental factor j on the survival of age class i.

Hypothetical data can help illustrate the method. Consider a tree species with a 90 yr life span growing in a 1 ha forested study area (Table 1). (The short, 90 yr life span was chosen to simplify the hypothetical example. The model can accommodate longer time spans if past environmental conditions can be reconstructed.) In this example, precipitation data are available for the 90 yr time span from 1901 to 1990. Precipitation data coupled with data on soil and topographic affects on water availability allow construction of a quadrat-by-quadrat moisture index for the 30 yr intervals since 1901. Other ecological studies of this hypothetical tree species showed that, in general, abundant water was most favorable for tree survival. That is, drought stress leads to tree death. Stand reconstruction within quadrats revealed past conditions of basal area (the total area of ground covered by trees measured at breast height) during 30 yr intervals from 1901 to 1990. Prior ecological studies of this hypothetical tree showed that the high light environment under sparse canopies associated with low stand basal area was generally favorable for tree survival. Analysis of all quadrats showed six unique sequences of environmental conditions. Tree density (Table 1) ranged between 261.7 individuals/100 m^2 (in the 0 to 30 yr age class undergoing environmental sequence 1) and 1.1 individuals/100 m^2 (in the 60 to 90 yr age class in sequence 4).

Nonlinear regression of population densities against relative favorableness in this hypothetical example produced estimates of the parameters of equation 7b (Table 2). (Details of the solution procedure are presented in the appendix.) This example also shows the types of ecological interpretations possible based on results from the demographic analysis. For example, potential survival rate increased from the second age class (0.46) to the third (0.99), suggesting that adults face fewer hazards than juveniles. Basal area had little effect on survival of the first age class (β_{11} = 0.26). One hypothesis accounting for this result is that, for tree seedlings, the negative effect of reduction in light is compensated for by the positive effect of the reduction in drought stress caused by high canopy cover. In contrast, unfavorable light conditions strongly reduced the survival of age class two (β_{21} = 1.51). Water availability (represented by the moisture index) showed the opposite pattern. The high value of

TABLE 1. Hypothetical field data of the type needed for application of the demographic model. The environmental sequences are six unique temporal patterns of basal area (BA) and a moisture index (MI) over the period 1901-1990. Population density is the number of tree individuals currently alive that have experienced a particular sequence of environmental conditions. This hypothetical example presents densities for three age classes.

Environmental sequence (es)	Relative favorableness						Population density (individuals/100m^2)		
	1901-30		1931-60		1961-90				
	BA	MI	BA	MI	BA	MI	0-30 yr	30-60 yr	60-90 yr
es_1	1	0.6	0.6	1.0	0.5	0.7	261.7	60.6	27.3
es_2	0.8	0.5	0.8	0.8	0.6	0.6	214.8	59.5	27.1
es_3	0.8	0.5	0.5	0.8	0.2	0.6	161.5	10.1	7.7
es_4	0.2	0.3	0.4	0.5	0.2	0.4	96.2	3.9	1.1
es_5	0.8	0.5	0.7	0.8	0.4	0.6	191.1	31.7	18.1
es_6	0.3	0.4	0.3	0.6	0.3	0.4	105.2	8.5	1.6

TABLE 2. Results of nonlinear multiple regression of the hypothetical tree data in Table 1.

Parameter	Meaning	Estimate	t
$N_0 \cdot \hat{S}_1$	New seedlings alive at the end of the 1st age interval under optimal conditions	504.5/100 m^2	46.0*
$\hat{S}_2$	Potential survival rate during the 2nd age interval under optimal conditions	0.46	5.4*
$\hat{S}_3$	Potential survival rate during the 3rd age interval under optimal conditions	0.99	1.9
β_{11}	Effect of basal area on 1st age interval survival	0.26	13.8*
β_{21}	Effect of basal area on 2nd age interval survival	1.51	9.0*
β_{31}	Effect of basal area on 3rd age interval survival	0.50	1.7
β_{12}	Effect of moisture index on 1st age interval survival	1.39	29.5*
β_{22}	Effect of moisture index on 2nd age interval survival	0.42	1.3
β_{32}	Effect of moisture index on 3rd age interval survival	0.82	0.8

*$P < .05$

β_{12} (1.39) suggests strong reduction of survival because of drought stress in the first age class. The lower and statistically nonsignificant value of β_{22} (0.42) and β_{32} (0.82) suggests that older tree individuals are less susceptible to drought stress, perhaps because of their more extensive roots. Hypotheses stemming from this demographic analysis could be tested by subsequent, more specific studies.

Discussion

The demographic analysis described here uses information derived from stand reconstruction combined with models of population dynamics to derive birth rates and age-specific and environment-specific survival rates. In effect, the method approximates a longitudinal demographic study (such as a cohort life table analysis) by replacing observations through time with the reconstruction of past environmental conditions. The cost for this compression of time is the effort required to collect the data needed to evaluate the many multivariate equations dictated by this technique.

Several assumptions are necessary to apply this demographic approach: (a) Birth rates and intrinsic survival rates ($\hat{S}_i$) are independent of time, (b) the state of each important environmental factor (e_j) can be determined for past conditions, (c) maximum favorableness (max e_j) can be determined independently, (d) the way environmental favorableness affects survival is adequately described by power-function relationships, and (e) the effects of environmental factors on survival are independent of one another. On the other hand, common assumptions of other techniques—such as stationary populations and homogeneous and constant environments—are not required in the analysis presented here.

Other limitations are also intrinsic to this approach. The method cannot address those environmental factors that leave no evidence except their effects on the population. Therefore, successful application will be limited by how well past environmental conditions can be reconstructed. There is no requirement, however, that the entire maximum life span of a population be analyzed. For example, if stand reconstruction can be accomplished only for the past 50 years, this method can still be applied to all individuals of a population less than 50 years old, even though some individuals in the populations might be much older. Such a study would produce estimates of potential survival and environmental constraints on survival over the first 50 years of the species's lifetime. Another limitation is that the independent variables in the final model might, in fact, be related. For example, the hypothetical case in Table 1 considers basal area and moisture index as independent variables. In most ecosystems, water availability will be determined, in part, by the amount of light reaching the understory, which would vary with stand basal area. Such statistical collinearity among the independent variables makes it difficult to interpret the estimated values of the parameters. In practice, however, the magnitude of β_{ij} might not be as important as whether $\beta > 0$ (showing that the factor had a statistically significant effect on survival) or $\beta = 0$ (the factor was irrelevant).

This model is based necessarily on plant age, which allows the description of plant development and environmental conditions with respect to the same temporal scale. Under many circumstances, however, birth and death rates are also strongly linked to organism size (Werner and Caswell 1977, Hughes and Connell 1987). The ability of the model to reveal demographic patterns will be less if size effects outweigh age effects.

Temperate-zone forest tree populations provide special advantages for the application of this demographic approach. Most temperate-zone trees can be aged easily by counting annual growth rings or annual bud scale scars. In addition, stand reconstruction techniques have been best developed in forests. Canopy gaps can be reconstructed from the presence of dead trees and tree fall mounds (Oliver and Stephens 1977) and the growth release date in neighboring trees (Henry and Swan 1974). Local climatic fluctuations (e.g., in temperature and precipitation) can be inferred from dendrochronological evidence (e.g., Graumlich and Brubaker 1986). Fire scars provide evidence of fire history (Barrett and Arno 1988). Historical records chronicle past hurricanes and other severe storms (Oliver and Stephens 1977), fires, and major insect outbreaks. Independent chronosequence or permanent plot studies (Alaback 1982, Agee and Huff 1987) can provide estimates of the past state of less detectable environmental factors, such as the cover of competing herbaceous species. Other factors are more difficult to reconstruct because they do not supply enough evidence of their occurrence. For example, the influence on population dynamics of disease or minor or chronic herbivory would be difficult to assess using the demographic analysis described here.

Few methods have been available for estimating demographic parameters of long-lived species, such as Pacific Northwest trees. If stand reconstruction techniques can supply accurate descriptions of past environments, then the demographic analysis described here should be a useful tool for understanding the population dynamics of long-lived trees. In addition, discovered patterns of survival and environmental constraint can suggest further study. In particular, this type of demographic analysis can suggest specific hypotheses (that can be tested experimentally) about environmental control of population dynamics.

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