The Role of Population Dynamic Models in Biogeographic Studies: An Illustration from a Study of *Lobelia boykinii,* a Rare Species Endemic to the Carolina Bays

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ABSTRACT

Here we submit that mathematical tools used in population viability analysis can be used in conjunction with floristic and faunistic surveys to predict changes in biogeographic range. We illustrate our point by summarizing the results of a demographic study of *Lobelia boykinii*. In this study we used deterministic and stochastic matrix models to estimate the growth rate and to predict the time to extinction for three populations growing in the Carolina bays. The stochastic model better discriminated among the fates of the three populations. It predicted extinction for two populations in the next 25 years but no extinction of the third population for at least 50 years. Probability of extinction is likely correlated with hydrologic regime and fire frequency of the bay in which a population is found. The stochastic model could be combined with information about the geographic distribution of *L. boykinii* habitats to predict short-term biogeographic change.

INTRODUCTION

If one looks at the history of biogeography, one finds that since its inception biogeography has been a historical and mechanistic science. This is reflected both in the definitions of biogeography and in the types of questions that biogeographers ask. For example, textbooks sometimes define biogeography explicitly as the study of past and present distributions (Table 1). Other texts emphasize or discuss only past and present distributions, even though their definition is less explicit. Concomittantly, many biogeographic questions are descriptive and historical in nature, such as: What is the geographic distribution of taxon "x"? How did the taxon come to occupy its present range? What are the taxon's closest relatives and where are they found? Other questions are ecological and mechanistic, such as: What attributes allow a taxon to live where it does? How do abiotic and biotic factors influence a taxon's distribution? What determines species richness? These questions seek to explain why we observe extant distributions.

Recently, however, biogeographers have begun to expand their purview to ask questions about the future of extant distributions. This expansion has come about because of the birth of conservation biology. Conservation biologists seek not only to determine why a taxon, usually a species, is rare but also to predict how the distribution of the rare taxon will change over the next ten, twenty, or fifty years (e.g., Drake et al. 1989, Gubbay 1995, Primack 1995, Meffe and Carroll 1997, Vickery and Herkert 1999). For exotic taxa, the goal is to determine not only how invasive the taxon has become but also to predict the future rate of spread. For a nature preserve of a given size, the goal is to predict how many and what taxa can be preserved. These conservation goals, because they concern geographic distributions, are essentially biogeographic

Table 1. A sample of definitions of biogeography found in biogeography textbooks

1. "Plant geography is that branch of botany that deals with the spatial relationships of plants both in the present and the past." (Good 1964)
2. Biogeography "studies the origin, distribution, adaptation, and association of plants and animals." (Dansereau 1957)
3. Biogeography is the "study of patterns of distribution of organisms in space and time." (Cox et al. 1976)
4. "Biogeography is the study of distributions of organisms, both past and present." (Brown and Gibson 1983)

goals. Conservation biology has added a new and predictive dimension to the field of biogeography, and this new dimension has generally not yet been recognized.

In the past twenty years, plant conservation biologists have begun to use mathematical models to understand the population dynamics of rare species and to estimate a species' extinction risk (e.g., for plants: Menges and Gawler 1986, Menges 1990, Schemske et al. 1994, Byers and Meagher 1997, Floyd and Ranker 1998, Menges and Dolan 1998). From an applied perspective, these models suggest which management program will give an endangered or threatened species the best chance for survival. We believe that these models also could be used in biogeographic studies to suggest how a species' range will change in the future.

To illustrate how this could be achieved, we describe here some of the results of a population dynamic study of *Lobelia boykinii,* a rare plant species endemic to the Carolina Bays. First we describe the species' natural history, which we had to determine before we could construct a population dynamic model. Then we describe deterministic and stochastic models of population growth and their predictions for the longevity of three populations. The complete methodology and results of the population dynamic study will be presented fully in another paper (Royo et al., in prep.). Our goal here is to summarize our results so that we can discuss the relevance of the models and their predictions to the biogeography of *L. boykinii,* and to biogeographic studies generally.

SPECIES' HABITAT AND LIFE HISTORY

Lobelia boykinii (Campanulaceae) is a rhizomatous perennial that grows vegetatively as a small rosette until flowering, when it produces a flowering stalk (Radford et al. 1968). Flowering in the Carolinas occurs from May into July and seed dispersal follows from July to September. Because there are approximately 6–20 extant *L. boykinii* populations worldwide (Weakly 1993), it is under consideration for listing nationally.

One reason for the rarity of *L. boykinii* is that it grows only in Carolina Bays, which are themselves declining in number. Carolina Bays are shallow, elliptical depressions that occur in the coastal plain of the southeastern United States. Underlain by an impervious clay lens, the depressions annually fill with water for different lengths of time, depending on depth of the bay and amount of rainfall (e.g., Schalles et al. 1989, Ewel 1990). The bays are unique in that they have no connection to springs or above-ground stream or river systems and so rely almost entirely on direct precipitation and surface runoff for their water volume (e.g., Sharitz and Gibbons 1982, Schalles et al. 1989, Ewel 1990, Kirkman 1995). They are also unique because of their distinctive plant and animal communities, which include many rare endemics (Sutter and Kral 1994). *Lobelia boykinii* is one such endemic.

There are five known populations of *L. boykinii* in North Carolina (Figure 1). Most are located in bays dominated by a broken canopy of pond cypress. Two populations are adjacent to or in bombing practice sites of military bases. Therefore, these two populations were not available for study. The other three populations, which we did study, are found in bays owned by The Nature Conservancy (TNC): Antioch Church Bay (ACB), Big Cypress Meadow (BCM), and State Line Prairie (SLP). These bays fill with water in winter and dry out during summer (Royo 1998).

We chose to study all three populations because the bays differ in their hydrology, depth of accumulated litter, and degree of openness of vegetation. ACB holds far more water than do
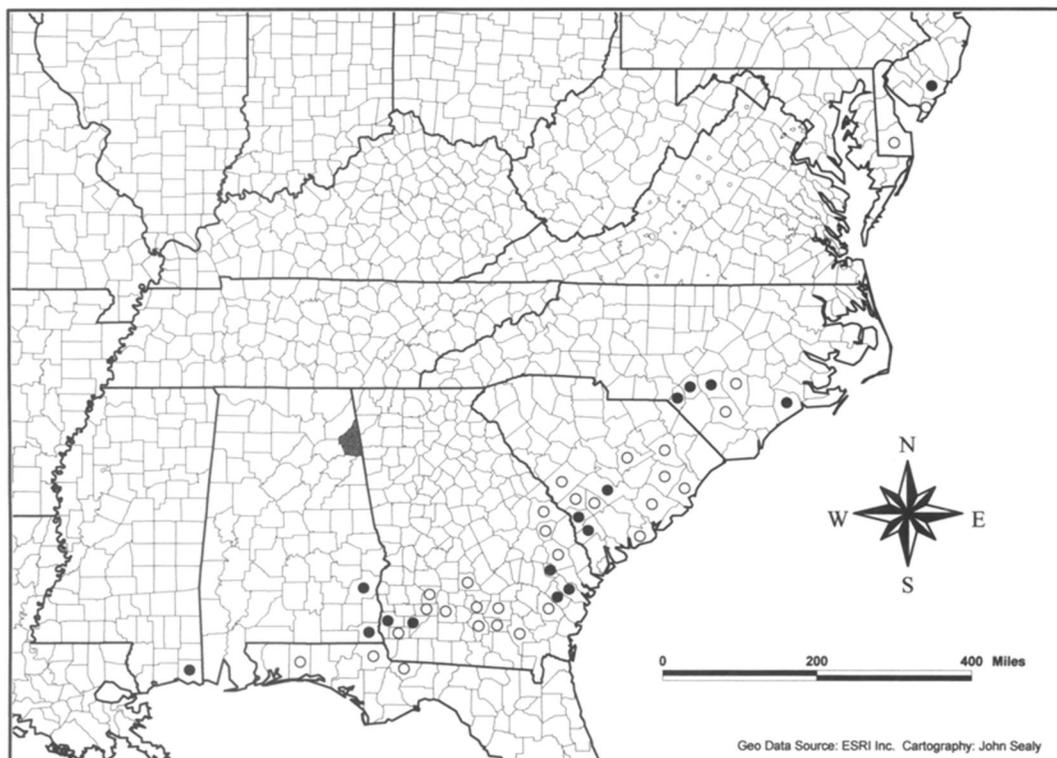
Figure 1. Distribution map of *Lobelia boykinii* (Source: Bruce A. Sorrie, 1999). Symbols represent county records: open circles = historical records, prior to 1980; closed circles = recent records, 1980 to present; hatched county in northern Alabama = literature report.

SLP and BCM, and it is characterized by an open canopy of pond cypress and much bare soil below the cypress (Royo 1998). SLP and BCM are much drier, and one cannot predict which of these two bays will hold less water in any particular winter. Both loblolly pine and pond cypress dominate in the open canopy in BCM, where there are also thick litter and herbaceous layers. There is no tree canopy in SLP, although there were young loblolly pine saplings at the time of our study. SLP has an herbaceous layer but has little accumulated litter.

To determine the species' life history, we conducted a demographic study in each bay from fall 1994 to winter 1996 and from late spring to fall 1997 (Royo 1998, Royo et al., in prep.). Our observations indicate that seeds germinate during late summer and early fall in years when rainfall is sufficient to saturate the soil. Seedlings develop into rosettes during the fall (Figure 2). Rosettes grow during winter, even when covered by low levels of water. In April, rosettes disappear from aboveground view to reappear the next fall, when they recommence above-ground growth, and presumably also belowground growth. These new rosettes develop from meristems in the subterranean rhizomes and can be as much as 3–5 cm away from the previous year's rosettes (Bates 1996). If a rosette survives its first nineteen months of life, it either bolts or again dies back to the rhizome in April. Probability of bolting in April is not correlated with estimated rhizome mass in early winter (Royo 1998). Bolting plants flower in June. Mature capsules dehisce throughout July (Bates 1996). When standing water persists into July, flowering and fruiting can be delayed until July and August, respectively (Royo and Lacey, pers. obs.). If an individual rhizome survives after flowering, it produces one to several new rosettes the following fall. Information about the longevity of a rhizome is not available.

Seeds fall directly under the maternal parent, but the buoyancy of seeds in water suggests that seeds can float for a while to new locations when standing water is present during the
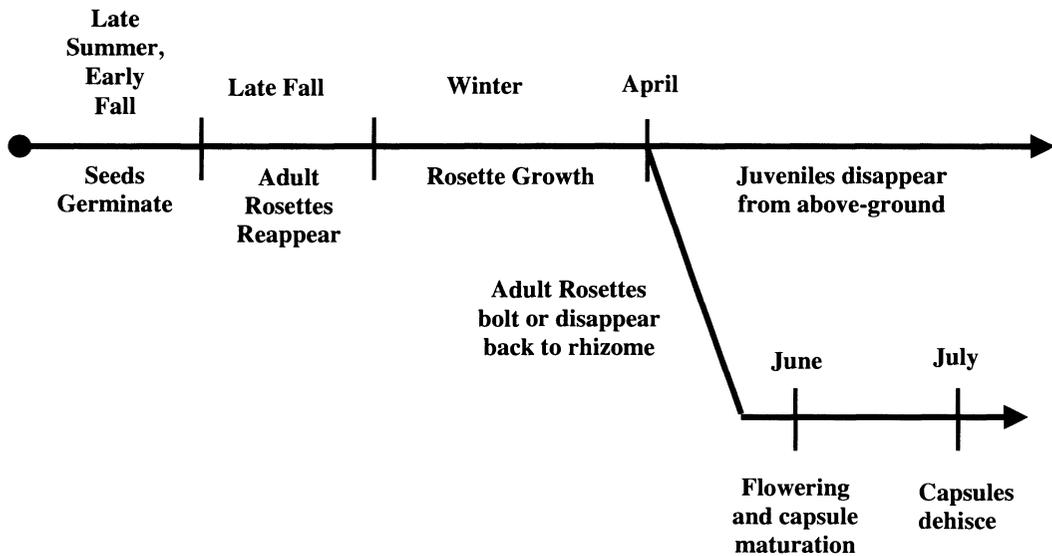
Figure 2. Schematic drawing of life history of *Lobelia boykinii*.

dispersal season (Bates 1996). Rosettes severed from their rhizomes can disperse in the same way during the winter. Seeds appear to require complete saturation for germination, which has been generally poor under controlled conditions thus far (Royo 1998; Bates, unpubl. data). Two seed bank studies (Royo 1998; Sutter, unpubl. data), which detected no seedlings of *L. boykinii* germinating from soil cores of the three bays, and germination tests, in which only freshly collected seeds germinated (Bates, unpubl. data), suggest that seed longevity is short.

POPULATION PROJECTIONS

Methods

A plant's life history can be portrayed in terms of a life-cycle model (Hubbell and Werner 1979) and a population matrix model that is derived from the life-cycle model (Caswell 1989). A life-cycle model is a schematic representation of the ages, sizes, or stages of individuals constituting a population (Figure 3a). It shows the pathways by which an individual at one age/size/stage can move or contribute to another age/size/stage. The matrix model includes a matrix of transition probabilities among the ages/sizes/stages and the vector of numbers of individuals in a population (Figure 3b). When one multiplies the transition matrix by the vector at time t, one can project the number of individuals in the population at time t+1. If the elements of the transition matrix remain constant over time, population growth stabilizes at the finite rate of increase, λ, also called the eigenvalue (Caswell 1989, Burgman et al. 1993). Conservation biologists use these matrix models to calculate λ, i.e., to estimate population growth rate, given constant birth and death rates.

The natural history of *Lobelia boykinii* suggested that we use a combined age-/stage-based demographic model having two stages (Figure 3a, also see Royo 1998): juveniles (rosettes developed directly from seeds, which germinated the previous summer/fall) and adults (rosettes vegetatively produced from rhizomes that are >1 yr old). The model characterizes a ramet rather than a genet population because it is presently impossible to identify genets. Rhizomes are quite fragile relative to root systems of other species in the soil, which makes it difficult both to extract whole genets from the soil and to identify genets nondestructively in the field.

From the demographic model, we constructed a 2 × 2 matrix model to examine the population dynamics (Figure 3b). The matrix elements are: F_{ja}, the per capita contribution of adults at time t to juveniles at time t+1 by means of sexual reproduction; P_{aj}, the per capita vegetative contribution of juveniles at time t to adult rosettes at time t+1; P_{aa}, the per capita vegetative

A.
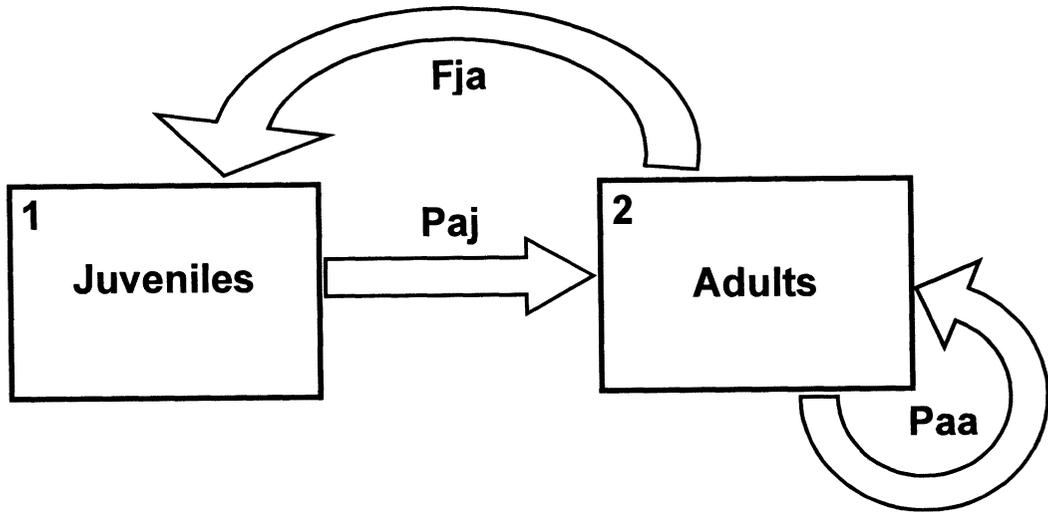
B.

$$\begin{pmatrix} 0 & F_{ja} \\ P_{aj} & P_{aa} \end{pmatrix} \begin{pmatrix} J_t \\ A_t \end{pmatrix} = \begin{pmatrix} J_{t+1} \\ A_{t+1} \end{pmatrix}$$

Figure 3. Models describing the life history of *Lobelia boykinii*. A) Two-stage life-cycle model: The arrows show the paths by which an individual at one stage at time t (in years) can contribute to number of individuals in the other stage at time t+1. B) Matrix model: Multiplying the transition matrix, whose elements represent the per capita contribution of one stage at time t to the other at t+1, by the vector of juveniles (J) and adults (A) at time t gives rise to the vector of juveniles and adults at time t+1. Transition elements: F_{ja} = the per capita contribution of adults at time t to juveniles at time t+1 by means of sexual reproduction; P_{aj} = the per capita contribution of juveniles at time t to adults at time t+1; P_{aa} = the per capita contribution of adults at time t to adults at time t+1. See text for additional explanation.

contribution of adults at time t to adults at time t+1. From a biological point of view, F_{ja} represents the probability of flowering and seed set of an adult rosette followed by germination of its offspring and offspring survival to the first winter. F_{ja} is the product of the following variables: s = mean seed number per capsule, c = mean capsule number per fruiting plant, f = proportion of marked rosettes in winter that fruited, g = percent seed germination, l = percent seedling survival to the winter census.

P_{aj} represents the survival of the rhizome attached to a juvenile rosette and the clonal production of new rosettes. It is the product of the variables: L_{aj} = probability of juvenile rosette at time t surviving to time t+1, X_{aj} = mean number of rosettes produced by each survivor. By definition, a rosette survives from one year to the next if its rhizome produces at least one new

rosette the next year. Because we observed high juvenile mortality, we assumed that resources in juveniles were not high enough to permit the production of more than one rosette in the following season. Therefore, X_{aj} was assumed to equal 1.

P_{aa} represents the survival of the rhizome attached to an adult rosette and the clonal production of new rosettes by that rhizome. It is the product of the variables: L_{aa} = probability of adult rosette at time t surviving to time t+1, X_{aa} = mean number of rosettes produced by each survivor. A surviving adult rosette may produce from one to several new rosettes in the next year.

We estimated the matrix elements from our demographic data (Royo 1998; Royo et al., in prep.). Briefly, from 1994 to 1996 we monitored the fates of marked rosettes and newly-germinated seedlings in ACB, BCM, and SLP. Naturally germinated seedlings were marked in plots that we haphazardly established where we observed germination in 1994 in ACB and SLP. For each seedling we recorded survival and year of flowering though summer 1996. No seedlings were marked in BCM because we found none. Therefore, we used an indirect measure of seedling survival for that bay (Royo 1998). Adult rosettes were marked in fall 1994 and in winter 1995 in all bays. For each rosette we recorded bolting, flowering, fruiting, survival to the next winter, and asexual production of new rosettes. Capsule number per flowering rosette and seed number per capsule were determined for a sample of flowering plants scattered throughout each population in 1995 (Bates 1996). The product of the means was then used to estimate seed set per flowering rosette. Seed germination rates were obtained from experimental field plots into which we sowed known seed numbers in 1995 and 1997 in all three bays (Royo 1998). Plots were established in the areas of each population.

These data allowed us to develop a unique deterministic matrix model for each population. Because it was impossible to collect data for all variables in the same year, each matrix model, by necessity, represented a composite of several years' data. The important thing is that the data for any particular variable, e.g., seed number per capsule, were collected for all bays in the same year, which allows one to compare population growth, λ, among bays. By solving the characteristic equation for each deterministic matrix (Caswell 1989), we derived the the value of λ for each population. We also examined the distribution of λ and its estimated standard error by writing a computer simulation program with SAS (SAS 1996). The program independently generated 100 λ values by drawing values for each variable contributing to a matrix element from within its respective distribution (Royo 1998).

An important assumption made when using a deterministic matrix model to project population growth is that the demographic rates, e.g., birth and death rates, remain constant over time. Our observations indicated that the population dynamics of *L. boykini* do not satisfy this assumption. Germination and rosette mortality both differed greatly across years.

Hydrologic variability most likely caused the observed yearly demographic fluctuations. Standing water levels in our study bays fluctuated greatly across years, particularly in ACB, and high water levels were accompanied by high rosette mortality and a great reduction in water clarity (Royo 1998; Royo et al., in prep.). For example, in winter 1996/97, when standing water reached 70–80 cm in ACB, visibility was reduced to a few centimeters, far less than was needed for sunlight to penetrate to rosettes at the bottom of the bay and for us to see the rosettes. Rosette mortality was very high between winter 1996 and winter 1998. When water levels were lower in neighboring years, winter rosettes were clearly visible through the water, and mortality was much lower. With respect to germination, only in years when soil was saturated in late August and early September did we observe germination. It appeared that regional and local precipitation patterns, as reflected in standing water levels in the bays, change unpredictably from one year to the next. Also, these precipitation patterns affect population size in two critical ways. First, if late summer and early fall rains do not at least saturate the soil, seed germination and seedling establishment do not occur. Second, increasing the depth and duration of winter/spring water levels increases rosette/rhizome mortality.

Failure to incorporate the stochastic nature of the environment, which can produce demographic fluctuations, may lead to overestimates of population growth rates generally (Tuljapurkar 1989, Damman and Cain 1998). Therefore, stochastic rather than deterministic modeling may be a more realistic way to assess population growth (Kalisz and McPeek 1992, Menges and Dolan 1998). Our goal was to incorporate the stochastic effects of annual hydrologic

ACB	BCM	SLP

Good fall , good winter

$$\begin{pmatrix} 0 & 2.42 \\ .33 & .82 \end{pmatrix} \qquad \begin{pmatrix} 0 & .52 \\ .207 & .99 \end{pmatrix} \qquad \begin{pmatrix} 0 & .16 \\ .58 & 1.23 \end{pmatrix}$$

Good fall, bad winter

$$\begin{pmatrix} 0 & 2.42 \\ 0 & .267 \end{pmatrix} \qquad \begin{pmatrix} 0 & .52 \\ 0 & .435 \end{pmatrix} \qquad \begin{pmatrix} 0 & .16 \\ 0 & .435 \end{pmatrix}$$

Bad fall, bad winter

$$\begin{pmatrix} 0 & 0 \\ 0 & .267 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ 0 & .435 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ 0 & .435 \end{pmatrix}$$

Bad fall, good winter

$$\begin{pmatrix} 0 & 0 \\ .33 & .82 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ .207 & .99 \end{pmatrix} \qquad \begin{pmatrix} 0 & 0 \\ .58 & 1.23 \end{pmatrix}$$

Figure 4. Alternative transition matrices representing all possible combinations of good/bad falls and good/bad winters for Antioch Church Bay (ACB), Big Cypress Meadow (BCM), and State Line Prairie (SLP). See text for additional explanation.

change into our matrix models. We did this by constructing four alternative matrices for each population (Figure 4). Each matrix represented a qualitatively different year, defined in terms of good/bad fall for germination and good/bad winter for rosette survival. For the qualitatively best year, i.e., the good fall/good winter alternative, we used our deterministic model (Figure 4). In a bad fall, germination, and therefore also F_{ja}, equaled 0. In a bad winter, prolonged high standing water levels caused higher adult rosette mortality than in a good winter. Juvenile mortality, and therefore also P_{aj}, were assumed to equal 100% in a bad winter.

After constructing the matrices, we then estimated the frequency of occurrence of each qualitatively different year for each bay from water level data available from spring 1994 to fall 1998 (Royo et al., in prep). Finally, using SAS (SAS 1996), we wrote a computer simulation program to project the number of juveniles and adults in each population over time. The simulation randomly selected one of the alternative matrices based on its frequency of occurrence

to calculate the vector at time t+1 for 50 iterations (years). If the sum of both stage classes in the vector fell below 1.0 after an iteration, the population was considered extinct. The simulation to year 50 was replicated 1000 times to determine the mean time to extinction. Our estimates of juveniles and adults in winter 1997/98 were used for our initial vector at time t. Due to the ephemeral nature of rosettes and flowering shoots, population size can be estimated only in the winter, when both newly-germinated rosettes ("juveniles") and rosettes connected to established rhizomes ("adults") are visible above ground.

Results and Discussion

The eigenvalues for the deterministic models suggest that all populations are increasing in size. All eigenvalues are greater than one (λ_{ACB} = 1.39; λ_{BCM} = 1.08; λ_{SLP} = 1.29). Also, the ACB population appears to be growing most quickly. However, the standard errors associated with the eigenvalues (ACB: 0.34; BCM: 0.54; SLP: 0.45) suggest that the three populations do not significantly differ in growth rate at a 95% confidence level (Royo 1998). Furthermore, given the 95% confidence intervals, the true eigenvalues for all populations could be less than one, indicating that all may be declining in size. Thus, the deterministic models alone are not particularly illuminating, which is not surprising.

More illuminating are the results of the stochastic models. These models predict that two of the three populations would go extinct in the next 50 years. The ACB population had the shortest mean time to extinction (15 years). The mean time to extinction for the BCM population was 24 years. For both bays, all replicated simulations resulted in extinction before 50 years. In contrast, the SLP population did not go extinct within 50 years in any simulation.

Taken together, stochastic and deterministic processes likely explain these differences in predicted outcome. The rapid extinction of the ACB population is best explained by fluctuations in the quality of years and, in particular, by a relatively high frequency of bad winters. While the frequency of a bad winter for ACB was 0.5, it was only 0.1 for the other two bays. Bad winters adversely affect adult rosette survival and new rosette production, element P_{aa} in the transition matrix. Elasticity analysis of the "good fall/good winter" year showed that of all the matrix elements, P_{aa} contributes most to population growth rate in ACB (Royo 1998). Thus, in wet winters when rosette mortality soars, population size crashes. Given the higher probability of a bad winter, ACB is more likely to suffer several wet winters in a row, which greatly increases the probability of extinction.

In contrast, the difference in outcomes between BCM and SLP is not likely explained by temporal hydrologic fluctuations. Both BCM and SLP populations were subjected to similar hydrologic conditions, and their frequencies of good and bad years were identical. Instead, the difference is better explained by the more predictable process of ecological succession in the absence of fire. Data suggest that *L. boykinii* persists in a drier bay only if the bay is periodically burned and thereby returned to an earlier successional stage.

Four lines of demographic and ecological observations support this hypothesis. First, although burns were reported in BCM and SLP in 1988 [Bücher, North Carolina Chapter of The Nature Conservancy (NCTNC), pers. comm.], our observations suggest that the area of the *L. boykinii* population in BCM has not burned for a longer time. The area of the BCM population is characterized by a thick litter layer and an abundance of saplings and trees of various sizes. BCM is many times larger than SLP, and it is possible that the burn occurred elsewhere in the bay. The location of the BCM burn is unknown (Bücher, NCTNC, pers. comm.). In contrast, in SLP the thin litter layer, uniformity of young pine saplings, and absence of older-age trees throughout the bay suggest that the whole bay was burned in 1988.

Second, in summer 1997 all rosettes that we found in BCM were growing through pine litter and were etiolated. This would be expected in a population growing in a bay that had not been burned for a long time. Etiolated rosettes were neglible in SLP.

Third, the size of the BCM population, used for the initial vector in the stochastic simulations, was 2 orders of magnitude smaller than the size of the SLP population (Royo et al., in prep.). A smaller population size would be expected in a declining population. Small population size can, by itself, increase the risk of extinction (e.g., Lande 1993, Groom 1998).

Fourth, P_{aj} and P_{aa} values in SLP exceeded those for BCM in good winters (Figure 4). Over the time interval for which we had data, good winters occurred 90% of the time for these two bays. Thus, the stochastic model predicts that most of the time juveniles will survive better and adults will produce more new rosettes in SLP than in BCM. Of all matrix elements, P_{aa} most strongly affects population growth (Royo 1998; Royo et al., in prep.). Although the contribution of adults to juvenile rosettes via flowering, F_{ja}, is higher in BCM than in SLP in good falls, the frequency of good falls was only 60%. Also, the F_{ja} value for BCM in a good fall is probably inflated. As mentioned before, we never observed seed germination outside our experimental plots in BCM. Thus, we suspect that germination is lower than the value used for a good fall in the BCM model.

Our collective observations suggest that *L. boykinii* population growth is strongly influenced by standing water depth and duration and by litter depth, which is influenced by both standing water and fire frequency. *Lobelia boykinii* can survive in "wetter" bays whose soil is sufficiently saturated to promote germination and seedling establishment in some years and whose winter water levels are sufficiently deep in some years to restrict the growth of water-intolerant species, which produce an abundance of litter. However, if standing water is too deep for too long, the growth of *L. boykinii* is also restricted. Our stochastic model suggests that ACB represents a bay whose standing water levels exceed this limit, which is why the population is predicted to go extinct. *Lobelia boykinii* can also survive in "drier" bays if fire occurs with enough regularity and intensity to remove the litter layer, i.e., the barrier to seed germination, seedling establishment, and rosette production. In SLP, fire appears to have occurred frequently enough to maintain a healthy population. In BCM, it has not. The BCM population appears to be on the verge of extinction.

THE APPLICATION OF POPULATION DYNAMIC MODELS TO BIOGEOGRAPHY

Biogeographic maps, such as that shown for *Lobelia boykinii* (Figure 1), show the geographic locations of extant populations of a taxon. These maps can also indicate how the geographic range has changed in the past (Figure 1). We feel that when maps are coupled with population dynamic studies, the combination becomes a powerful tool for predicting future geographic change. The reason is that population dynamic studies allow one to predict, at least in the short term, the probability of population survival. Studies of multiple populations can estimate survival probabilities over a range of habitats. Given information about the proportional representation and location of different habitat types within and just outside the species' range, one should theoretically be able to predict future change in geographic distribution at least in the short term.

For example, floristic records indicate that *L. boykinii* populations are scattered along the coastal plain from Alabama and the Florida panhandle to New Jersey (Figure 1). One county record for Mississippi (B. Sorrie, pers. comm.) is not shown on the map. If one were able to categorize each population as growing in one of the three habitat types that we have studied in North Carolina (wet bay, periodically burned drier bay, and unburned drier bay), one could use our three transition matrices to explore how the geographic distribution of the species is likely to change in the next several decades. Refinements of the predictions could be made by developing matrix models for habitats located in each of the Midatlantic, Southatlantic, and Gulf Coastal Plain ecoregions (Bailey 1997) of the coastal plain.

In the above course of action for *L. boykinii*, we have made two assumptions, that individuals do not move between populations and that individuals do not move to empty sites suitable for colonization. In other words, we have assumed that migration is zero. Given that human disturbance over the last century has reduced the number of sites suitable for colonization and the number of isolated extant populations in North Carolina, and given that this activity will probably continue, we presently feel that our assumptions for *L. boykinii* are reasonable. These assumptions, however, are likely to be inappropriate for other species.

For such species, one could incorporate a metapopulation-level analysis (e.g., Menges and Gawler 1986, Carter and Prince 1988, Menges 1990, Kalisz and McPeek 1992, Byers and Meagher 1997, Damman and Cain 1998, Floyd and Ranker 1998, Husband and Barrett 1998,

Menges and Dolan 1998) into the course of action described above. A metapopulation is a set of local breeding populations within a larger area, where some migration from one local population to at least some other colonizable patches is possible (Hanski and Gilpin 1997). Migration is necessary for the persistence of the metapopulation because it offsets the periodic extinction of local populations. Hanski and Gilpin (1991) identified three hierarchical spatial scales of distribution for a species. The local scale defines a population in which individuals interact and can potentially interbreed. The next larger scale defines a metapopulation, which is composed of both local populations that occasionally exchange individuals and local empty colonizable sites to which individuals in local populations occasionally disperse. The largest scale, the geographic scale, includes the entire species' range. Biogeographic changes may be determined solely by events occurring on the local scale or on the metapopulation scale. For many species, we suspect that distribution on the geographic scale is determined by processes on both local and metapopulation scales.

Predicting geographic change for a plant species may seem as precarious as reading tea leaves, and it is certainly scarier than making guesses about a past distribution because one's prediction will be tested by direct observation. On the other hand, mathematical tools now exist to assist one in making these predictions. Studies have used these tools to explore local population or metapopulation dynamics of plant species. However, the motivation for many studies has been to determine how a rare species should be managed to prevent its extinction. Only Carter and Prince (1988) have used a metapopulation analysis to try to understand an extant geographic distribution, and no plant study has used mathematical tools (e.g., Lande 1988, Verboom et al. 1991) that incorporate information from both local and metapopulation scales to predict change on the geographic scale. We suggest that these tools could be more fully exploited by plant biologists to address questions about species' distributions generally.

ACKNOWLEDGMENTS

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