

POPULATION VIABILITY WITH FIRE IN *ERYNGIUM CUNEIFOLIUM*: DECIPHERING A DECADE OF DEMOGRAPHIC DATA

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Abstract. We analyzed and modeled the demography of *Eryngium cuneifolium*, an herbaceous species endemic to the fire-prone Florida scrub, using 10 annual censuses (1990–1999) of 11 populations at Archbold Biological Station. Nearly every aspect of the demography of this plant is affected by time since fire. Year, time since fire, life history stage, and plant age affected survival, growth, and fecundity of *E. cuneifolium*, but time since fire and life history stage had the most consistent effects. Survival, flowering stem production, and early seedling survival were highest in recently burned sites. Long-term survival, growth, and fecundity were highest for yearling cohorts recruiting recently after fire, with the largest contrast between plants recruiting two years postfire and those recruiting more than a decade postfire. Prior (historical) stage also affected individual plant fates. For example, plants with prior stasis or regression in stage subsequently died in greater numbers than plants with prior advancement in stage. Historical analyses did not suggest any cost associated with the initiation of flowering.

We used a matrix selection approach to explicitly model *Eryngium cuneifolium* population viability in relation to fire. This simulation strategy included preserving observed data and variances within projection matrices formed for individual combinations of population and year. We built 54 of these matrices, each with six stages (seed bank, yearlings, vegetative plants, and three reproductive stages). Each of these matrices also represented a specific time since fire. In building matrices, we minimized the use of pooled data while retaining specific matrices whenever possible. In this way, we preserved both the correlation structure within individual matrices (populations, years) and protected patterns among matrices across the time-since-fire gradient.

To deal with less-detailed data on recruitment processes, we evaluated 13 fertility and seed bank scenarios that bracketed a range of outcomes. All scenarios were similar in showing the positive effects of fire on the demography of *E. cuneifolium*. The scenario with high seed bank survival (0.5) and low germination rates (0–0.005) was the best predictor of observed postfire years of peak aboveground population size (~8 yr) and aboveground population disappearance (30–34 yr), and also did a good job of reproducing observed population trajectories.

Finite rates of increase (λ) were >1 only during the first decade postfire but then declined beyond a decade postfire. Although prior (historical) stage affected most individual demographic parameters, it did not significantly influence finite rates of increase. Elasticities were highest for stasis and germination from the seed bank. Elasticities for survival increased with time since fire, while growth and fertility elasticities decreased. In historical models (those with information on stage from the second-to-last year), the elasticities for stasis were higher and the elasticities for growth lower, compared to models without this history. Bootstrapping suggested small standard errors for several types of model output. Most matrix elements were positively correlated, suggesting that favorable conditions affect many life history stages similarly, and that simulations using element selection would provide a less conservative risk assessment than the matrix selection technique used.

We used a stochastic simulation program to simulate changing demography with time since fire, with various fire-return intervals, and for various initial population sizes. We obtained estimates of extinction risk and probability of population decline. Even populations as large as thousands of individuals will become extinct in the absence of fire. Fire-return intervals of 15 yr or less are necessary for *E. cuneifolium* persistence at individual sites. Fires at intervals longer than 20 yr create substantial extinction risks, and intervals longer than 12 yr produce declining populations. Cycles of widely divergent, alternating short and long fire-return intervals caused slightly higher chances of extinction compared to regular fire-return intervals.

Although shrub regrowth is implicated in the decreased viability of *E. cuneifolium* populations under regimes of infrequent fire, aboveground fuel increases are often too slow

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to allow frequent burning in Florida rosemary scrub. If *E. cuneifolium*'s rosemary scrub habitat burns less often than every 20 yr, local extinctions and metapopulation dynamics may be the norm. Other rosemary scrub specialists (e.g., *Hypericum cumulicola*) thrive with less frequent fires and persist in smaller gaps among the regrowing shrubs. Therefore, we suggest that temporal variation in fire-return intervals and spatial variation in fire intensity and patchiness (pyrodiversity) will allow coexistence of all Florida scrub species and hedge against local extinctions of specialists like *E. cuneifolium*.

Key words: disturbance; elasticity; *Eryngium cuneifolium*; fire; Florida rosemary scrub; Lake Wales Ridge; matrix models.

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INTRODUCTION

Population viability analyses (PVAs) are commonly used for projecting extinction risks, contrasting management tactics, and evaluating the sensitivity of life history stages (Groom and Pascual 1997, Beissinger and Westphal 1998, Menges 2000, Reed et al. 2002). However, exact predictions are hazardous since they are sensitive to small differences in parameter estimation, correlation structure, and model formulation (Fieberg and Ellner 2001, McCarthy et al. 2001). Compounding these modeling problems are studies based on insufficient data. Most PVAs for plant species, for example, are based on only a few populations and a few years of data (Menges 2000). Since demographic parameters vary markedly among populations and microhabitats (e.g., Albert et al. 2001, Hunt 2001) and over time (e.g., Horvitz and Schemske 1995, Bierzychudek 1999), PVAs using data from many populations and years will be more dependable than short-term studies from few populations.

Variation in the environment and consequent variation in demographic rates pose extinction risks (Menges 1998) and alter predictions made from unvarying environments. Many analyses, most commercial models, and much demographic theory deal with more or less randomly varying stochastic environments. However, stochastic environments may often vary in complex yet somewhat predictable ways. For example, disturbance and recovery cycles have strong effects on the demography of many plants (Menges and Quintana-Ascencio 2003).

Fire is the ecological disturbance that has been most often integrated into plant PVAs (e.g., Bradstock and O'Connell 1988, Silva et al. 1991, Burgman and Lamont 1992, Canales et al. 1994, Gross et al. 1998, Hoffmann 1999, Caswell and Kaye 2001, Kaye et al. 2001, Satterthwaite et al. 2002, Menges and Quintana-Ascencio 2003, Quintana-Ascencio et al. 2003). For example, straightforward comparisons of burned and unburned plots show how individual species are affected by fire (Canales et al. 1994, Garnier and Dajoz 2001). Burning was the most important of several variables affecting population growth and extinction risk in a perennial prairie forb (Menges and Dolan 1998). More dynamic modeling of fire cycles has been used

to assess the demographic effects of fire frequency (Silva et al. 1991, Canales et al. 1994, Hoffmann 1999, Brewer 2001), different fire regimes (Caswell and Kaye 2001, Kaye et al. 2001), the interacting effects of fire and rainfall (Enright et al. 1998a, b, Quintana-Ascencio et al. 2003), the interactions of fire with other disturbances (trampling, Gross et al. 1998; herbivory, Pfab and Witkowski 2000), and combinations of rainfall, demographic stochasticity, and inbreeding effects (Burgman and Lamont 1992). These more realistic studies often have more complex results. For example, intermediate levels of serotiny may have evolved in response to variation in fire-return intervals (Enright et al. 1998a). The fire frequency that maximized population size of *Banksia cuneata* (15–25-yr fire-return interval) did not minimize its extinction risk (Burgman and Lamont 1992).

Models predicting population viability generally consider demographic transitions to be determined by the individual's stage at the start of the transition. In perennial plants, individual fate can also be influenced by the individual's prior status or demographic history (Primack and Hall 1990, Bullock et al. 1993, Geber et al. 1997, Ehrlén 2000). The presence of storage organs providing critical resources during reproductive events or unfavorable conditions may explain some carry-over effects (Chapin et al. 1990). Organ differentiation may precede organ expression by months or years in many species (Watson et al. 1995). In addition to determining resource storage and organ preformation, past environmental conditions can also affect current plant morphology and habitat characteristics (Primack and Hall 1990, Geber et al. 1997). Most models assume plant fate depends only on current stage, and analyses of these historical effects on population dynamics are scarce. Higher-order matrices, where each plant fate depends upon both current stage and prior stage, allow the assessment of plant history effects on population dynamics. Incorporation of historical effects in matrix models of *Lathyrus vernus* population dynamics decreased the projected finite rate of increase (λ), and indicated that stasis was more important and recruitment less important for population growth than suggested by models ignoring history (Ehrlén 2000).

This paper provides a detailed population viability analysis of *Eryngium cuneifolium*, a perennial forb

found exclusively in Florida rosemary scrub. This short-lived species is most often found in areas that have been recently burned, and some individual demographic parameters are sensitive to time since fire and to the size of gaps among the dominant shrubs (Menges and Kimmich 1996). We ask whether fire is necessary for population persistence and under what fire regime *E. cuneifolium* populations will be viable. We model population viability with explicit reference to fire, using 10 yr of data from 11 populations to formulate 54 projection matrices. Given data showing stage-related demography and correlation among demographic parameters, we chose stage-based modeling and whole matrix selection, with matrices defined by time since fire. We also consider different scenarios for the seed bank parameters for which we have fewer data. To choose and verify the best scenario, we compare projections under each scenario with empirically observed patterns of peak population size, aboveground disappearance of populations, and population size trajectories. The resulting base scenario is used to examine finite rates of increase (λ) and elasticities for individual times since fire and to discern fire-related demographic patterns. We also evaluate the effects of age and of prior life history stage (history) on demographic parameters. Finally, we model stochastically the effects of fire frequency and regularity on extinction risk, and identify the range of fire-return intervals that will promote viable populations of *E. cuneifolium*. We compare these fire regimes to fire regimes recognized for Florida scrub, and consider the likelihood of periodic extinctions of *E. cuneifolium* populations in this landscape.

METHODS

Study species and community

Eryngium cuneifolium is a perennial herb restricted to Florida rosemary scrub and has one of the most restricted distributions of the many Lake Wales Ridge endemic plants (Christman and Judd 1990). It also has relatively limited genetic variation (Dolan et al. 1999, Menges et al. 1999). Within its range, *E. cuneifolium* is most abundant and has the strongest demographic performance in large gaps and recently burned patches of Florida rosemary scrub and along nearby firelanes (Menges and Kimmich 1996). Most plants are killed by fire (resprouting occurs very rarely in lightly burned patches) and postfire recovery is via seeds (Menges and Kohfeldt 1995). The recruitment of seedlings following a fire in an isolated gap after 7 yr without having flowering plants indicated the presence of a persistent seed bank. Its restriction to gaps may reflect poor germination in the presence of allelochemicals produced by Florida rosemary (Hunter and Menges 2002). Transplants had poorer growth in the neighborhood of Florida rosemary than two other co-occurring species (Quintana-Ascencio and Menges 2000). *E. cuneifolium*

is highly dependent upon insects for fruit and seed production, and is self-compatible (Evans et al. 2003).

Florida rosemary scrub is a shrub-dominated ecosystem found on xeric white sands on ridges and knolls in Florida and neighboring states. This vegetation supports many of the narrowly distributed endemics of xeric uplands in Florida (Christman and Judd 1990). Because the dominant Florida rosemary (*Ceratiola ericoides*) is killed by fire and recovers slowly from a soil seed bank (Johnson 1982), the community remains fairly open for many years after fire (Menges and Hawkes 1998). In these openings, many herbaceous and small woody species, including *Eryngium cuneifolium* and *Hypericum cumulicola*, can occur at high densities (Johnson and Abrahamson 1990, Hawkes and Menges 1996, Quintana-Ascencio et al. 1998). Most of these species are generally killed by fire but recruit seedlings from a soil seedbank postfire (Menges and Kohfeldt 1995). The fire-return interval for rosemary scrub is relatively long, on the order of 15–100 yr (Menges 1999). Fires that burn into rosemary scrub often leave unburned patches.

FIELD METHODS

We sampled *Eryngium cuneifolium* plants over a period of 12 yr (1988–1999) using annual censuses in late October and early November. Because data from the initial years of demographic studies are often less complete than later years (e.g., some cryptic plants remain unsampled in early years), we decided to analyze only 10 yr of data (1990–1999). We worked in 11 populations at Archbold Biological Station, Lake Placid, Florida representing a time-since-fire gradient (Table 1). A flag with a numbered aluminum tag was placed near each individual found in defined gaps in each site (for most populations, these were complete samples of plants throughout the site). We recorded survival, number of flowering stems, and basal diameter annually. From 1995 to 1999, we followed seedling recruitment and cohort survival in quadrats, from emergence (often January through March) through November, at intervals of 3–6 wk (Table 1). In addition, we subsampled the populations for fecundity.

DEFINING LIFE HISTORY STAGES

We combined morphological criteria and divisions based on size (rosette diameter) to define the life history stages in our matrix models. The two main challenges were defining yearlings (seedlings surviving to November of their first year) and dividing other (adult) plants into stages based on plant size.

In seedling quadrats censused at intervals of 3–6 wk during the winter and spring, true seedlings were readily identified as plants with evident cotyledons. However, in areas censused only annually in October and November, older seedlings (yearlings) could no longer be distinguished from small, but older, vegetative plants (that may have remained unsampled in prior

TABLE 1. Fire history (1967–present), site area, and sample sizes for *Eryngium cuneifolium* populations (Pop) studied throughout 1999.

Pop	Year(s) of last fire(s)	No. plants†	Site area (ha)	No. gaps studied	No. seedling quadrats‡	Seedling area sampled (m ²)
16	1984	307	0.338	1	1	39
45	1984	308	0.249	5	6	30
54	1968	214	3.578	5	8	26
57	1967, 1993	169, 104	0.094	4
59	1968	77	0.366	5
61	1968	124	0.248	3
63	1972	254	0.166	5
70	1972	66	0.250	4
72	1972, 1986	37, 362	0.743	7
85	1986	427	1.981	5	7	27
91	1986	304	0.807	3	6	27

† Total number of plants during study. For populations 57 and 72, we show number of plants before and after 1993 and 1986 fires, respectively.

‡ Checked in winter, spring, and early summer each year at intervals of 3–6 wk. Seedlings were censused throughout all populations in November of each year.

years). Using data from known seedlings, we tested numerous size (rosette diameter) cutoffs for identifying yearlings in annual censuses. We selected a cutoff (rosette diameter = 3 cm), which best correctly identified true yearlings and best avoided misidentifying true adults as yearlings. We then used a cutoff of rosette diameter <3 cm to define newly appearing plants as putative yearlings. To preserve sample sizes, we decided to combine yearlings and putative yearlings into a single yearling stage.

We defined life history stages of flowering individuals by plant size (there were insufficient numbers of vegetative plants in some situations to subdivide). Rosette diameter was a better predictor of *Eryngium cuneifolium* survival and growth rate than stem number (Appendices A and B). Consequently, we used the Moloney algorithm based on rosette diameter to delimit classes (Moloney 1986). We set the smallest rosette diameter as the initial boundary value of the first category and used the maximum size minus one-third of the range as the initial maximum boundary. The final upper boundary of the first category was defined by the minimum sum of the sample and distribution errors. The procedure was repeated for sequentially larger categories. We used different combinations of decreasing steps, minimum number of plants in each class, number of replicates and type of subsample (population or time since fire) for sample error estimation. We identified three stages based on size for reproductive (flowering) plants: small (rosette diameter <6 cm), medium (6.1–10.5 cm), and large (>10.5 cm). Thus, we modeled the life cycle of *Eryngium cuneifolium* with six stages: seed bank, yearlings, vegetative plants, and the three sizes of reproductive plants (Fig. 1).

Fecundity

We counted the number of reproductive stems (scapes) per plant for each adult sampled and summarized these by population, year, and reproductive stage. Heads per stem and full seeds per head were

counted in randomly selected individuals in several populations from 1994 to 1999 (one head per individual in most years, five heads for 1998–1999, three to five populations in each year, seven populations during the study). The product of mean number of reproductive stems of individuals in a given stage, mean number of heads per stem, and mean number of seeds per head was used as an estimate of seeds produced by each stage (raw fecundity). Exact year and site values were used if available; otherwise we used means of sites with the same or the closest time since fire.

Analyses of survival, growth, and flowering

To compare survival of yearling cohorts originating at different times postfire, we used the Kaplan-Meier method (log rank test; SPSS 2000). For these cohorts, we compared half-life and maximum lifespan estimates by fitting linear regressions to survival trajectories and calculating the number of years when the number of plants dropped below one (data was natural-log transformed; $r^2 > 0.81$ in all cases). To evaluate the significance of variation in number of flowering stems in plants from these cohorts, we used Kruskal-Wallis tests to compare plants of the same age. We used analysis of variance to test the significance of variation in annual growth among plants with same age but different time since fire. We also evaluated annual growth (irrespective of age) among current stages and time since fire with an analysis of variance. We performed a *G* test of heterogeneity on a contingency table summarizing frequency of first flowering year among seedling cohorts initiated at different years postfire (data grouped to optimize sample size).

We employed analysis of variance to test the significance of variation in number of flowering heads per plant (natural-log-transformed data) among populations with different time since fire (only individuals sampled for reproductive structures). Because of the presence of many zeroes we used Kruskal-Wallis test to assess the significance of variation in number of

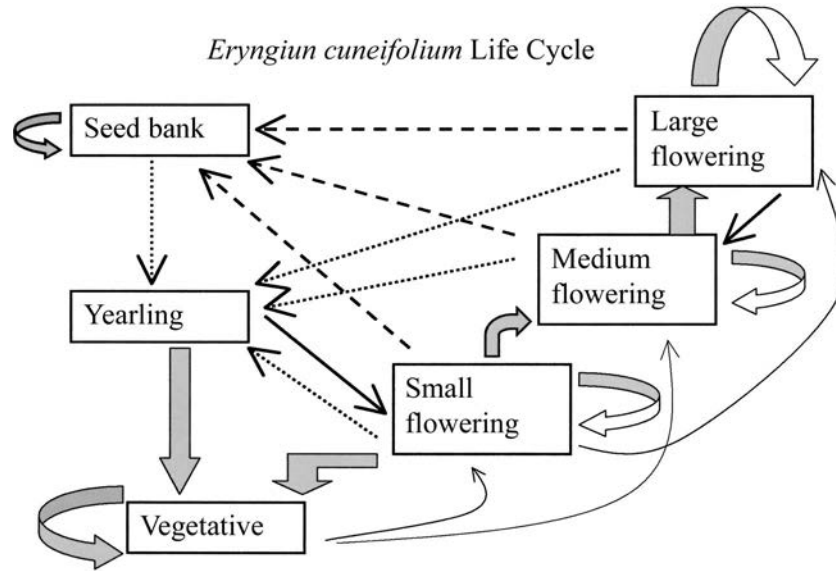


FIG. 1. Life cycle of *Eryngium cuneifolium*. Shown here are six life history stages (persistent seed bank, yearlings, vegetative plants, and three sizes of reproductive plants [with flowering scapes]). Arrows indicate annual transitions (some rare transitions are not shown). Solid and block arrows indicate survival and change of stage of plants, with the width of the arrow indicating the general size of the transition. Dashed arrows show fecundity to the persistent seed bank. Dotted arrows indicate transitions directly to yearlings.

seeds per head (averaged per individual) among populations with different time since fire. For these two analyses, time-since-fire was used as a categorical variable. We used SPSS (2000) version 11 to perform all statistical tests.

Realized fecundity: incorporating seed bank, germination, and early seedling survival

We used the products of seed production, seed germination (Table 2), and seed and seedling survival until the annual census (i.e., to yearlings) to calculate fertility (realized fecundity) per reproductive stage (Fig.

1). Matrix values included six fertility values for three stages with immediate germination (II, III, IV in Table 3) and contribution to a persistent seed bank (V, VI, VII in Table 3).

Available data on estimated germination proportions were 0–0.1 for first year germination, and 0.005–0.04 for second year germination (Table 2). We analyzed the sensitivity of our models to low (0.0) and high (0.1) values of first year germination, and low (0.005) and high (0.04) values of second year germination. We did not have any estimate for *E. cuneifolium* survival in the seed bank. To assess the sensitivity of the matrix

TABLE 2. Germination estimates from various lab and field experiments for *Eryngium cuneifolium*.

Year†	Water‡/ precipitation (mm)†	Germination	Source
Laboratory trials			
First	High	0.04–0.14	Hawkes (2000) (expt. I)
First	High	0.05–0.10§	Quintana-Ascencio and Menges (2000)
First	Low	0.01	Hawkes (2000) (expt. III)
First	High	0.01	Hawkes (2000) (expt. III)
Field trials			
First	122	0.0	Quintana-Ascencio and Menges (2000)
First	547	0.0	Hawkes (2000) (expt. II)
Second	149	0.005–0.04	Quintana-Ascencio and Menges (2000)

† Winter germination season (Dec–Feb). First year refers to germination and precipitation 1–3 mo immediately after seed production (Nov). Second year refers to germination and precipitation 13–15 mo after seed production.

‡ High-water treatments were watered to keep seeds consistently moist. Low-water treatments were allowed to dry between watering.

§ There was also an outlier at 0.2.

TABLE 3. Generalized matrix showing structural zeroes (zero), seeds added to the seed bank (V–VII), seeds germinating and surviving to become yearlings (II–IV), seed bank survival (I), yearlings germinating from the seed bank (VIII), stasis (S), growth (G), and regression (R).

Stage	Seed bank	Yearling	Vegetative	Reproductive		
				Small	Med	Large
Seed bank	I	zero	zero	V	VI	VII
Yearling	VIII	zero	zero	II	III	IV
Vegetative	zero	G	S	R	R	R
Small rep	zero	G	G	S	R	R
Med rep	zero	G	G	G	S	R
Large rep	zero	G	G	G	G	S

Notes: The equations below were used to calculate entries I–VIII. Most terms in these equations are specific to populations and years, or to a time-since-fire class. In equations, SS = seedling survival from germination until the annual census (yearling), SB = annual seed bank survival, G1 = germination in the first year, and G2 = germination in the second or later year. For specific matrices, see Appendix C.

I = SB.

II = no. stems (small reproductive) \times seeds/stem \times G1 \times SS.

III = no. stems (medium reproductive) \times seeds/stem \times G1 \times SS.

IV = no. stems (large reproductive) \times seeds/stem \times G1 \times SS.

V = no. stems (small reproductive) \times seeds/stem \times (1 – G1) \times SB.

VI = no. stems (medium reproductive) \times seeds/stem \times (1 – G1) \times SB.

VII = no. stems (large reproductive) \times seeds/stem \times (1 – G1) \times SB.

VIII = SB \times G2.

models to the variation of this parameter we initially used three values: low, 0.1; medium, 0.3; and high, 0.5. The combination of values for first year germination, second year germination, and seed bank survival yields $2 \times 2 \times 3 = 12$ fertility scenarios. To better consider the full range of potential variation, we considered an additional scenario with very high seed bank survival (0.8) and low levels for the two other parameters.

We included seedling survival from germination to November (the annual census, at which time the plants are termed yearlings) in the products to provide matrix entries for fertility. If there were no data on site-specific seedling survival through the first annual census, we used a multiple regression inverse function including time since fire and March precipitation to estimate this variable (see *Results: Seedling and cohort dynamics*). This regression had the best fit among other possible regressions including combinations of precipitation during spring and early summer months and alternative relationships with time since fire.

Matrix formulation and analysis

We built matrix models (Caswell 2001) whose elements, a_{ij} , represent the transitions or contributions from individuals in the j th category to the i th category after one time step (one year). A total of 54 matrices for each of the 12 fertility scenarios were built and ordered according with time since fire. Each matrix includes six stages (six by six; Fig. 1). The matrix for the year of burn had only one nonzero entry: seed bank survival, since all *E. cuneifolium* plants in studied burn sites were killed by fire. The matrix for the first year postfire had two entries, seed bank survival and yearling production from seed bank. The matrix for the

second year postfire included entries for seed bank and for the fates of the yearling stage. The other 51 matrices had estimates for every matrix entry except structural zeroes (Table 3, Appendix C).

Data used to fill the nonfertility parts of matrices depended on sample size for the specific years and populations. We used population- and year-specific matrices if three or more stages in the matrix had $n \geq 6$. Within these specific matrices, matrix elements per stage were kept if stage-specific sample size $n \geq 6$. For stages within these specific matrices with smaller sample sizes, we substituted pooled data from populations with the same time since fire. Eighty-one percent of the matrix entries for these specific matrices had population- and year-specific data (170/210). If fewer than three of six stages had $n \geq 6$, we constructed pooled matrices, pooling data among sites and years (Appendix C). Weighted averages reduced the disproportionate effect of single individuals that occurred in some years.

Correlations among matrix elements and analyses of plant fates

We examined Spearman correlations between pairs of matrix elements, including only those elements with specific data for population and year (excluding pooled data). We distinguished between correlations within a matrix column (which will necessarily be related) and between column matrix element correlations that may reflect common responses to environmental variation. Correlations were considered significant at $P < 0.05$, and we tallied the number of significant correlations by sign (positive or negative) and by type of transition (advances, stasis, regression).

We used loglinear analyses to examine temporal variation in plant fates (stage in subsequent year) within populations, and to assess the effects of year and time since fire among populations.

Verification of scenarios

We chose among the 13 fertility scenarios based on their performance in matching three types of partially independent data: postfire year of peak aboveground population size, postfire year of aboveground population disappearance, and observed population trajectories (scaled to the maximum) 5–15 yr postfire. We refer to the best scenario as the base scenario.

Modeling

We used MATLAB (MathWorks 1997) to obtain the eigenvalues (λ) of the matrices of each population and their respective elasticity matrices. The elasticities were summed to calculate the relative contribution of three major life history components: fertility, survival, and growth (as in Silvertown et al. 1996, see also Table 3). We evaluated patterns of the finite rate of increase (λ) as a function of time since fire for all fertility scenarios. Elasticity patterns of the base scenario were evaluated in relation to time since fire. We obtained bootstrapped confidence intervals for λ of the base scenario after 2000 simulations. In each bootstrap run, we kept the correlations between fertility and survival and growth using estimates from the chosen individuals in a given simulation.

We used the stochastic simulation program DISTPROJ (written by the authors) to model extinction probability, using 1000 replicated simulations. Using the base fertility scenario, we estimated extinction probabilities predicted as a function of fire-return intervals. We also used the base scenario to estimate time to extinction of unburned populations having different seed numbers after an initial fire, varying the initial number of seeds by five orders of magnitude from 10 to 100 000. We initially modeled fire as a regular disturbance. During all simulations not evaluating the effect of initial population size, we used 7000 seeds as the initial population size. Using a linear relationship between projected number of seeds and number of plants (projected number of plants = $4.216 + 0.0045 \times$ projected number of seeds; $r^2 = 0.67$, $P < 0.001$), this number of seeds approximately regresses the mean number of plants observed in populations 15 yr after fire ($n = 5$; 35 vs. 33). The length of simulation was 99 yr, and the extinction threshold was 1.

In DISTPROJ simulations, stochasticity was introduced by random choices of matrices (matrix selection) with selection of a year's matrix determined by time since disturbance. We did not use a periodic matrix approach to modeling fire frequency effects because vital rates varied substantially among years and sites and because we lacked data on certain times since fire. Using a periodic matrix approach would have required

creating completely new matrices for time since fire intervals for which we lacked data.

In our matrix selection approach, for a year since fire for which we had matrices, we chose randomly among the appropriate matrices. Across the time-since-fire gradient, two intervals produced limited data. The first four years postfire were described only for one population (three matrices), so those matrices were chosen without stochasticity. We had no data for the interval between 14 to 18 yr postfire. In this interval, DISTPROJ randomly selected matrices between the prior (13) and the next (19) time since fire, but with linearly changing probabilities that increased chances of selecting matrices from 19 yr postfire, and decreased chances of selecting matrices from 13 yr postfire, as fire-return interval increased.

We obtained extinction probabilities for population thresholds of 1 and 100 individuals under regular fire intervals. Standard errors of extinction probabilities were calculated replacing observed matrices with bootstrapped matrices in each step of the simulation algorithm. In bootstrapping, we obtained 200 extinction estimates of 200 simulations each for each fire interval.

We did not vary burn frequencies stochastically. Instead, we examined the effect of two staggered fires with diverging intervals, for mean intervals of 30, 32, 40, 44, and 50 yr, using the same modeling parameters (base scenario, 7000 seeds, 99 yr, and 1000 simulations).

Analyzing the effects of prior stage (historical effects)

The matrix modeling described above is first-order in nature, where the fate of plants during an interval is dependent only upon their beginning stage and its transitions. The effect of stage during prior time intervals (historical effects) can be analyzed by extending the matrix to higher orders, such as a second-order matrix with each plant's fate dependent upon the beginning (current) stage and the stage during the prior year (Ehrlén 2000). To preserve sample sizes, we built only five of these compound historical matrices pooled across years and populations, dividing the data into classes based on time since fire (3–6, 7–8, 9–10, 11–15, and >20 yr postfire). Yearlings were included without reference to history because they do not have a prior nonseed stage. We calculated finite rates of increase and elasticities for these pooled historical matrices, and compared them to first-order matrices (ignoring history) pooled in a similar manner.

RESULTS

Demographic parameters

Fecundity.—The number of flowering *Eryngium cuneifolium* stems increased with plant size, and decreased with time since fire, but only for medium and large reproductive stages (Fig. 2, analysis of covariance

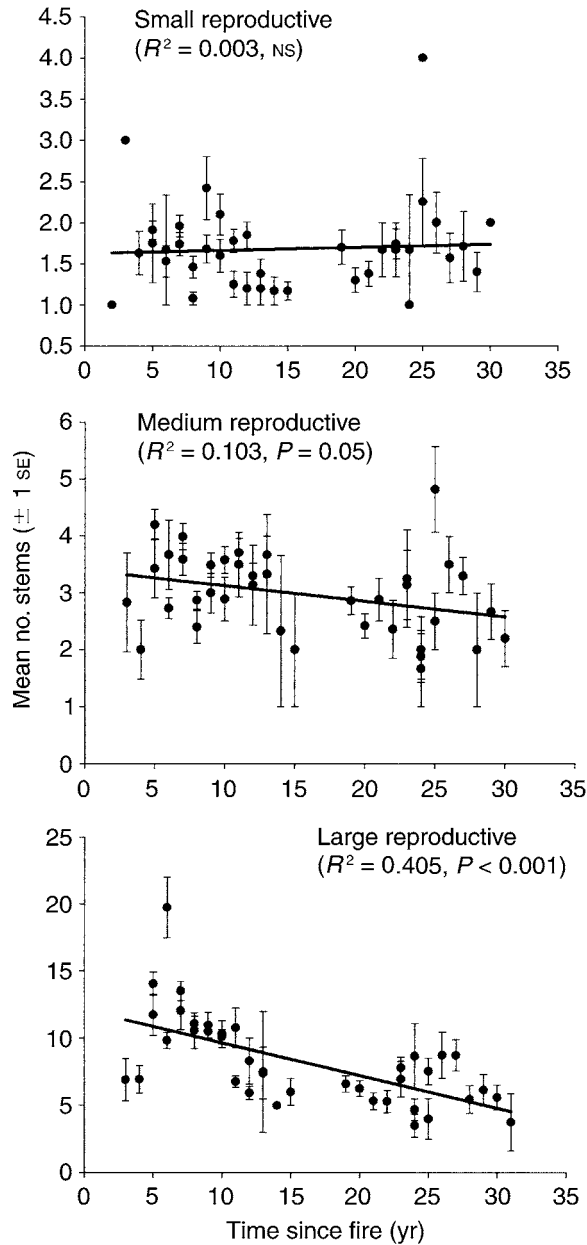


FIG. 2. Mean (± 1 SE) number of flowering stems among small, medium, and large reproductive (flowering) *Eryngium cuneifolium* plants in populations with different times since fire.

of mean values by population and year; time since fire, $F_{1,110} = 25.96$, $P < 0.001$; stage, $F_{2,110} = 111.07$, $P < 0.001$; time since fire \times stage, $F_{2,110} = 20.19$, $P < 0.001$). Previous historical stage also affected the number of flowering stems. Plants with previous larger reproductive outputs had greater number of flowering stems (positive $\rho > 0.299$, $P < 0.05$ for 21 of 24 tests, 1991–1998; Fig. 3).

Time since fire affected *E. cuneifolium* seed production. Number of seeds per head (Kruskal-Wallis test

$\chi^2_{11} = 122.13$, $P < 0.001$, Table 4), heads per stem ($F_{11,520} = 11.60$, $P < 0.001$, Table 4), and seeds per stem (Kruskal-Wallis test $\chi^2_{11} = 94.39$, $P < 0.001$, Table 4) varied with time since fire. Seeds per head peaked 6–7 yr postfire, heads per stem peaked 4–5 yr postfire, and the highest seed production per stem occurred 4 yr postfire (Table 4).

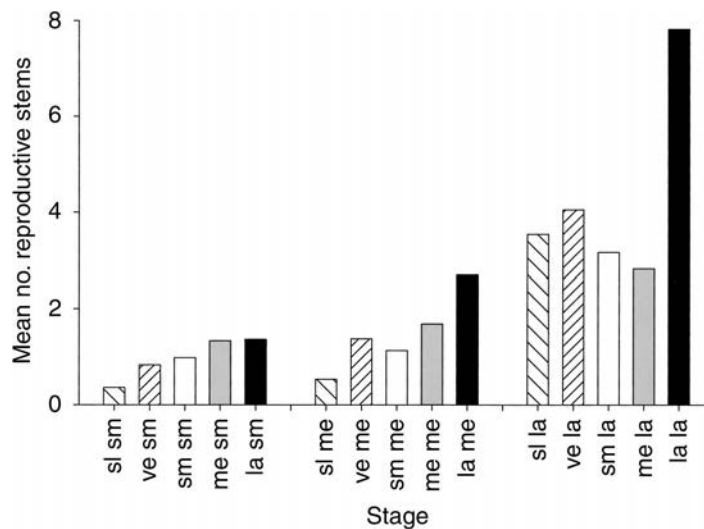
Seedling and cohort dynamics.—Initial seedling survival (from emergence in January through May to annual census in October through November) varied widely among years and populations (Table 5). When March precipitation was included in a multiple regression analysis, we found that early seedling survival was highest in more recently burned areas (years postfire; $y = 0.434 + 0.309[1/\text{years since fire}] - 0.0795[\text{March precipitation}]$; $r^2 = 0.716$).

Time since fire also affected survival, growth, and fecundity (number of reproductive stems) of yearling cohorts (yearling cohorts begin as seedlings that have survived through October and November; Fig. 4). Cumulative survival functions of 2–7-yr postfire cohorts were significantly higher than two 9-yr postfire cohorts, and significantly higher than all >10-yr postfire cohorts (log rank test statistics > 7.68 , $P < 0.006$). However, the cumulative survival function of a cohort initiated 10 yr postfire was not significantly different from 2–7-yr postfire cohorts but was different from cohorts initiated 9, 12, and 21 yr postfire (log rank test statistics > 10.19 , $P < 0.001$). Half-lives were 4 yr for yearlings recruited 2 yr postfire, 3 yr for cohorts recruited 7 yr postfire, and < 2 yr for cohorts recruited > 9 yr postfire. Predicted maximum lifespans were 11–12 yr for yearlings recruited 2–7 yr postfire, 4–8 yr for yearlings recruited 9–12 yr postfire, and 4 yr for those recruited 21 yr postfire. Annual growth rates were significantly different among time-since-fire cohorts for plants younger than 3 yr ($F_{6,161} = 13.4$, $P < 0.001$; and $F_{3,107} = 3.2$, $P = 0.03$, respectively for ages 2 and 3; only cohorts with $n > 5$). Growth rates were noticeably higher for the cohort beginning 2 yr postfire (Fig. 4). Yearling cohorts recruited 2 yr postfire also started flowering earlier ($G_4 = 33.53$, $P < 0.001$, Fig. 5) and produced a markedly higher number of reproductive stems ($P < 0.001$ after Kruskal-Wallis tests for ages 2 and 3, Fig. 4) than plants recruiting later postfire.

Fate, survival, and growth.—Year-to-year variation in plant fate was highly significant for most populations and life history stages (log-linear analyses; Tables 6 and 7). Variation was particularly high for populations 85 and 91, burned in 1986 and studied 4–13 yr postfire. Temporal variation was greatest for vegetative, medium reproductive, and large reproductive plants. Across sites, year-to-year variations were stronger than variation due to time since fire, although both were highly significant (Table 7).

Time since fire and life history stage had more consistent effects on survival than age. For each of eight transitions analyzed, stage had stronger (or equally

FIG. 3. Mean number of reproductive structures by transition (previous to current). Abbreviations on *x*-axis are as follows: sl, seedling; ve, vegetative; sm, small reproductive; me, medium reproductive; la, large reproductive. Bars are grouped by current reproductive stage.



strong) predictive power as age in categorical logistic regressions. Time since fire was as strong or stronger as a predictor than stage. Often mortality was highest for first year plants (~50% long-term average), intermediate for vegetative individuals (~44%), and lowest for reproductive plants (30–35%). Among flowering plants, those in the medium size class frequently had the lowest mortality, and those in the small size class had the most variable mortality rates. Increasing time since fire significantly increased mortality with similar patterns among stages (Fig. 6). Across populations, the prior (historical) stage had significant effects on mortality for medium and large flowering plants. In each case, plants that had a larger prior stage had lower survival than those having a vegetative or smaller reproductive stage.

There were significant effects of history, time since fire, and their interaction on current fate (Fig. 7, Appendix D). Plants that advanced to a higher stage in the prior year tended to have a range of fates. However, plants with prior stasis tended to remain static or die,

and plants that had previously regressed in stage tended to die in greater numbers (note relatively larger striped bars for regressed vs. stasis groups in Fig. 7). Longer times since fire increased the proportion of plants dying, particularly among plants previously regressing. During the first 8 yr postfire, a larger proportion of previously regressing plants advanced than perished (46–50% vs. 23–32%, respectively). In sites with longer time since fire, the proportion of previously regressing plants dying was 41% in sites 9–10 yr postfire and 57–64% in sites more than a decade postfire.

Our analysis including all plants (regardless of age) did not show a significant effect of time since fire on individual growth rate (current/prior rosette diameter; time since fire $F_{1,323} = 0.001$, $P = 0.973$; stage \times tsf $F_{4,323} = 1.14$, $P = 0.338$). Individual growth rate was different among stages (stage $F_{4,323} = 9.96$, $P < 0.001$): highest (Tukey hsd test) for yearlings (2.08, marginal mean), intermediate for small flowering plants (1.63), and lowest for vegetative and medium and large flowering plants (1.13, 1.11, and 0.96, respectively).

TABLE 4. Estimated number of seeds per *E. cuneifolium* stem, mean number of heads per stem, and number of seeds per head.

Years	tsf	Population	Seeds/head			Heads/stem			Seeds/stem		
			<i>N</i>	Mean	1 SE	<i>N</i>	Mean	1 SE	<i>N</i>	Mean	1 SE
2		57	25	4.0	1.3	27	15.0	4.4	23	43.3	78.6
3		57	16	7.6	1.6	19	30.9	5.2	16	142.7	94.3
4		57	28	9.4	1.2	32	56.3	4.0	28	643.6	70.0
5		57	27	5.8	1.3	30	41.1	4.1	27	255.2	72.6
6		57	11	21.6	2.0	13	22.7	6.3	11	420.6	113.7
7		57	4	25.3	3.3	30	25.7	4.1	4	536.9	188.5
9		72, 85, 91	80	4.1	0.7	85	17.0	2.5	79	112.2	42.4
10		72, 85, 91	82	12.1	0.7	90	12.3	2.4	82	173.5	41.6
11		72, 85, 91	86	9.4	0.7	90	9.9	2.4	86	93.7	40.7
12		72, 85, 91	49	6.8	0.9	90	11.3	2.4	49	81.1	53.9
14		16	7	19.8	2.5	15	15.4	5.9	7	247.2	142.5
15		16	10	16.9	2.1	11	24.9	6.8	10	518.8	119.2

Note: Data are summarized by time since fire (years tsf).

TABLE 5. *E. cuneifolium* initial seedling survival from emergence (January–May) until annual census (October–November), by population, year, and time since fire (years tsf).

Popu- lation	Last fire	Year	Years tsf	Seedlings/ m ²	No. seedlings	No. surviving	Proportional survival
85	1986	1995	9	9.48	256	8	0.031
91	1986	1995	9	3.65	113	2	0.018
85	1986	1996	10	1.93	52	1	0.019
91	1986	1996	10	0.39	12	0	0.000
16	1984	1995	11	0.06	216	13	0.060
45	1984	1995	11	15.87	476	13	0.027
16	1984	1996	12	0.02	54	19	0.352
45	1984	1996	12	5.17	155	15	0.097
85	1986	1998	12	9.48	256	11	0.043
91	1986	1998	12	3.32	103	0	0.000
85	1986	1999	13	0.15	4	2	0.500
16	1984	1998	14	0.11	258	20	0.078
45	1984	1998	14	7.47	224	9	0.040
16	1984	1999	15	0.00	12	6	0.500
15	1984	1999	15	0.33	10	2	0.200
70	1972	1995	23	0.01	35	1	0.029
54	1968	1995	27	3.19	83	2	0.024
54	1968	1996	28	0.69	18	1	0.056
54	1968	1998	30	14.92	388	8	0.021
54	1968	1999	31	0.04	1	0	0.000

Note: Not shown are data from 1997, a year with very few seedlings, nor seedlings from the recently burned population 57.

Choosing a fertility scenario

All 13 fertility scenarios produced a pattern of decreasing finite rates of increase (λ) with time since fire, indicating more favorable demographic situations in the first decade postfire than subsequently (Appendix E). Some scenarios were clearly unrealistic based on extreme finite rates of increase. For example, the scenario with low values for all three seed parameters (LLL) had only two of 54 population–year combinations with $\lambda > 1$. At the other end of the spectrum, scenarios with high germination in both years (e.g., MHH and HHH), or very high (V) seed bank viability (VLL) produced $\lambda > 1$ beyond 10 yr, which is inconsistent with sharply declining field populations a decade postfire (Menges and Kimmich 1996).

The best two scenarios for predicting the year of peak aboveground population size, the year of aboveground population extinction, and population trajectories were the HLL and MLL scenarios. The HLL scenario predicted peak aboveground population sizes about 8 yr postfire, a closer match to observed peaks (years 6, 9, and 10) than the MLL scenario, which predicted peaks at year 7 (Fig. 8). The HLL scenario also predicted that aboveground disappearances would often occur between years 30 and 34, while the MLL predicted earlier aboveground disappearances before year 20 (Fig. 8). We have observed four disappearances between years 26 and 30, but there is an extant population (in 2002) that last burned in 1968 (34 yr). Both projected trajectories were similar to observed trajectories between 5 and 15 yr postfire (Fig. 9). Based on these criteria, we chose the HLL scenario as our base scenario.

Correlation among matrix elements

Of all correlations examined (leaving aside correlations within columns of matrices and pooled data), 15% were significant for *Eryngium cuneifolium*. Positive correlations dominated among elements representing advances (four of five), correlations between elements representing advances and stasis (six of six), correlations between elements representing stasis and regression (three of three) and among elements representing regressions (three of three). Matrix elements representing advances tended to be negatively correlated with matrix elements representing regressions (six of seven). In only one case was an element representing stasis significantly correlated with another stasis element (this correlation was negative). Positive correlations were especially prevalent among transitions leading to vegetative plants (many in upper left of Appendix F), and among transitions leading to medium flowering plants (lower right of Appendix F).

Analysis of asymptotic parameters

Finite rates of increase.—For the base scenario (HLL), finite rates of increase (λ , lambda) declined with time since fire through about 14 yr, with more variable but low values (most $\lambda < 1$) after 15 yr (Fig. 10). High rates of increase in the first 6 yr postfire are consistent with rapid population increases observed in the field. The range of variation estimated within populations with bootstrapped lambdas was larger among recently burned populations (Fig. 10). There was a negative bias between “observed” and mean bootstrapped λ for 82.3% of the matrices (2.63 mean, and 0.94 median percent difference overall between bootstrapped and

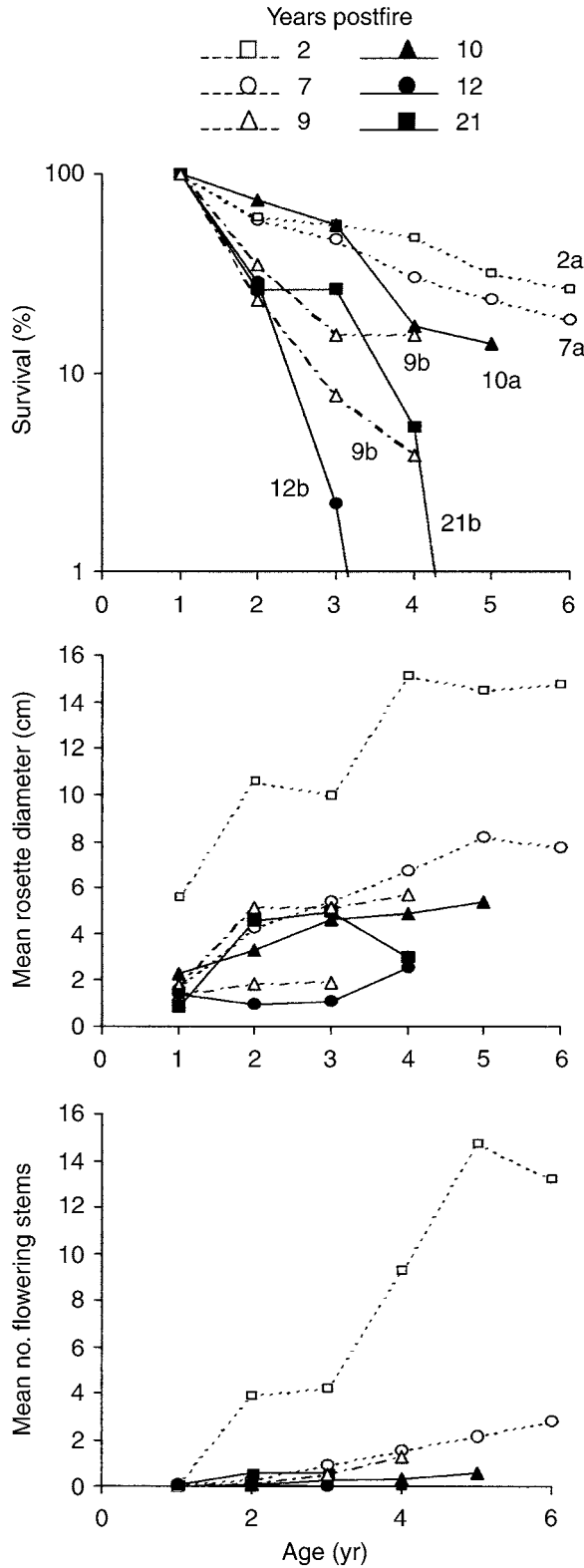


FIG. 4. Survival, mean rosette diameter, and mean number of flowering stems during the first 6 yr of yearling cohorts recruited at different times since fire. The numbers within the top panel refer to the time since fire for each cohort. The letters within the top panel indicate significantly different groups

nonbootstrapped λ). We did not calculate λ for years 1–3, when only seeds or seedlings were present, but populations were also expanding rapidly at that time.

Finite rates of increase from matrices that incorporated the prior stage (historical), using the base scenario, and with data pooled by time since fire class to preserve sample size, also showed a similar decreasing pattern with time since fire. Lambdas were 1.28 for 3–6 yr postfire, 1.18 for 7–8 yr, 0.94 for 9–10 yr, 0.72 for 11–15 yr, and 0.79 for >20 yr postfire. The finite rates of increase obtained when nonhistorical matrices were grouped by time since fire in the same way were similar (1.39, 1.18, 0.97, 0.77, and 0.76, respectively). Both sets of pooled lambdas are within the range of values found on the graph of lambda values with time since fire for individual populations and years under the more complete nonhistorical base scenario (Fig. 10). This suggests that historical effects (for the prior year) did not have large impacts on dynamics at the population level, despite their importance for individual survival, growth, and fecundity.

Elasticity patterns.—Transitions with highest elasticities under the base scenario were survival and germination of individuals in the seed bank, stasis in the vegetative stage and stasis in the largest flowering stage. Several elasticities changed with time since fire. The importance of seed survival, stasis in the vegetative stage and stasis in the largest flowering stage increased with time since fire (8% mean elasticity in populations 3–6 yr postfire to 29% in populations >20

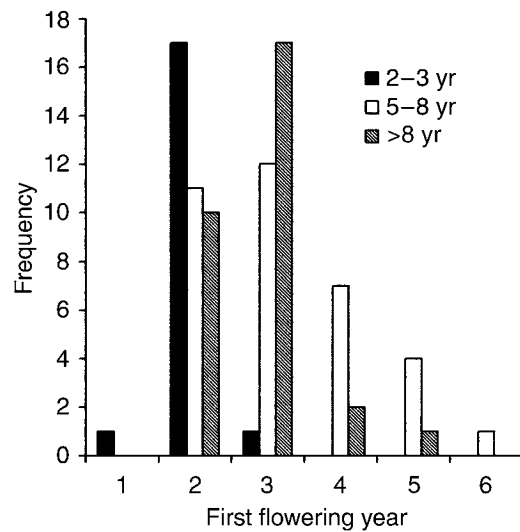


FIG. 5. Frequency distributions of first flowering year for individuals of *Eryngium cuneifolium* recruited at different times since fire (2–3, 5–8, or >8 yr postfire).

←
after a Kaplan-Meier test. Line and symbol types also indicate separate cohorts and are consistent among the three panels.

TABLE 6. Log-linear analysis of temporal variation in fate within populations.

Site	Global	Seedling	Vegetative	Small	Medium	Large
16	198.15† (160)	40.32† (16)	48.76** (24)	26.37 (24)	52.50*** (24)	30.20 (32)
45	161.49 (160)	39.91*** (14)	43.46** (24)	17.8 (12)	29.71* (15)	30.6* (18)
54	254.25*** (160)	5.77 (4)	66.97*** (28)	45.68** (24)	65.23*** (28)	70.58*** (32)
57	165.5** (120)	24.62** (8)	54.83*** (24)	28.84 (24)	28.01* (16)	29.19* (15)
59	67.71 (140)	absent	30.85** (15)	9.04* (3)	13.72* (72)	14.08* (6)
61	103.36 (100)	5.43 (2)	18.34 (20)	31.69** (15)	19.85 (12)	28.04* (16)
63	171.67** (110)	7.63 (12)	41.09* (24)	28.86* (16)	52.84*** (16)	41.25** (20)
70	111.65 (120)	4.16* (1)	25.79 (20)	17.19 (12)	29.25 (20)	35.26** (15)
72	403.65*** (160)	21.96 (18)	47.55* (32)	75.62*** (32)	110.86*** (28)	147.66*** (28)
85	637.68*** (160)	31.95 (28)	117.93*** (32)	106.18*** (32)	190.42*** (32)	191.22*** (32)
91	428.43*** (160)	4.75 (4)	105.56*** (32)	90.35*** (32)	104.7*** (32)	123.06*** (32)

Notes: The obtained log-likelihood ratio G^2 -values for the entire matrices were decomposed into contributions of each stage. The degrees of freedom are given below each statistic parameter in parentheses. "Absent" indicates that there were no individuals available for analysis.
* $P \leq 0.05$; ** $0.01 \leq P < 0.05$; *** $P < 0.01$.

yr postfire, 4 to 11%, and 13 to 15%, respectively, for these three transitions). The importance of seed germination decreased along this gradient (15 to 8%). Summed elasticities for the seedling stage also decreased (18 to 11%) with time since fire.

Individual matrices under the base scenario spread along a line nearly parallel to the survival axis in the summed elasticity triangle (Fig. 11). Most matrices of populations in patches 3–5 yr postfire occupied the upper portion of the graph, where survival elasticities were less important. Matrices of populations in patches 6–10 yr postfire were distributed mostly in the central part of the survival axis. Matrices of populations >10 yr postfire occupied mostly the central and lower right end of the survival axis (Fig. 11). In populations >10 yr postfire, survival was the most important parameter

contributing to λ , and fertility and growth elasticities were low.

These general elasticity patterns of *E. cuneifolium* with time since fire were not altered when the history of individuals was considered (Fig. 12). However, under historical models, the importance of stasis was increased and the proportion of growth was decreased (for populations <20 yr postfire). The largest differences were seen in the elasticities for stasis of small and medium flowering plants.

Stochastic analyses

Stochastic simulations using the base scenario for fertility and varying initial seed numbers indicate that even large populations with thousands of individuals will become extinct without fire for several decades.

TABLE 7. Log-linear analysis of variation with time since fire and year (1993/1994 through 1997/1998).

Variable	Model	Base		Change		AIC
		G^2	df	G^2	df	
Null model	STY, SF	872	280			312
Time since fire	STY, SFT	722	240	151	40	242
Year	STY, SFY	472	200	400	80	72
Conditional (tsf)	STY, SFY, SFT	246	160	226	40	-74
Conditional (year)	STY, SFT, SFY	246	160	476	80	-74
All interactions	SFT, SFY, SFY, STFY	0		246	160	0

Notes: Hypotheses about specific factors and their interactions are tested by comparison of the likelihood ratio of the two models that differ in only those terms (Caswell 2001). Model components: S, stage; T, time since fire (tsf); Y, year; F, fate. AIC is the Akaike information criterion.

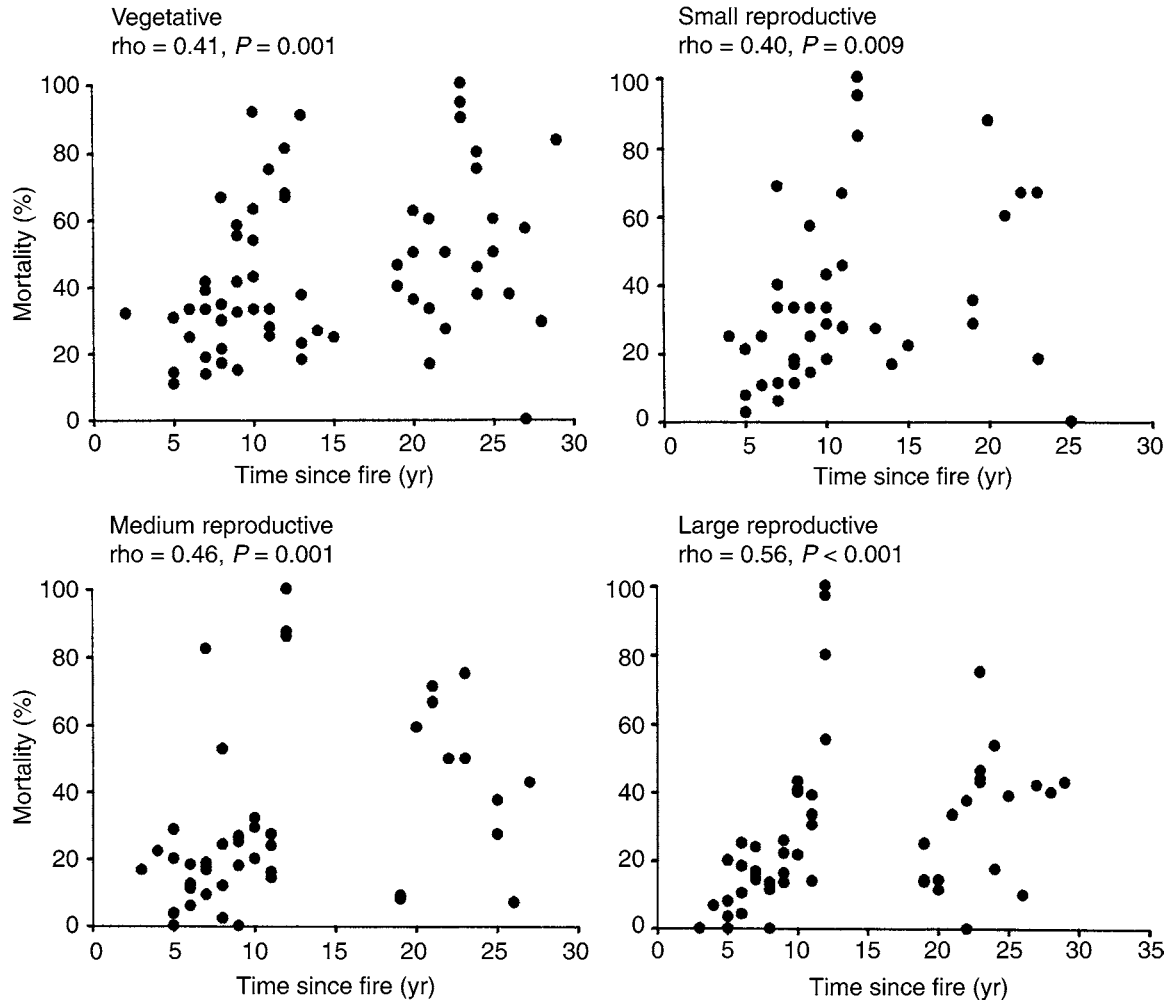


FIG. 6. Annual percentage mortality in *Eryngium cuneifolium* as a function of time since fire for four life history stages. Each point represents a population in a given annual time step. The results of a Spearman correlation are presented for each stage.

Median time to extinction without subsequent fire increased from 20 yr for populations with 10 seeds immediately after an initial fire to 60 yr for populations with 100 000 initial seeds. Using an initial population size of 7000 seeds, the simulations suggest that frequent fires are necessary to avoid extinction risks in *E. cuneifolium*. Fire-return intervals of 14 yr (or more frequently) produce no extinction risk (threshold of one individual) after 99 yr, while fires less frequent than every 20 yr produce high extinction risks (Fig. 13). Shorter fire-return intervals will be necessary to avoid population declines. More than 70% of the simulated populations with fire intervals of 14 yr decreased to 100 individuals or less (including seeds), and 15% of the simulated populations with fire intervals of 12 yr had population declines (<7000 seeds and <35 plants).

Bootstrapped confidence intervals spanned <10% on the extinction probability axis. However, bootstrapped population sizes had wider ranges, higher variances,

and biased (left skewed) distributions of final total and aboveground population sizes, compared to nonbootstrapped projections. This bias is not shown in Fig. 13 because bootstrap standard errors were centered on nonbootstrapped estimates.

Cycles of alternating short and long fire intervals caused slightly higher chances of extinction compared to regular fire intervals when the ratio among the short and the long alternating intervals was lower than 0.4 (Fig. 14). Infrequent fires (at least one fire-return interval >22 yr) promoted extinction no matter how regular or variable the return intervals (Fig. 14).

DISCUSSION

Life history of Eryngium cuneifolium

Our long-term demographic data show that *Eryngium cuneifolium* is a short-lived perennial herb, with few plants surviving as long as a decade. Most plants start

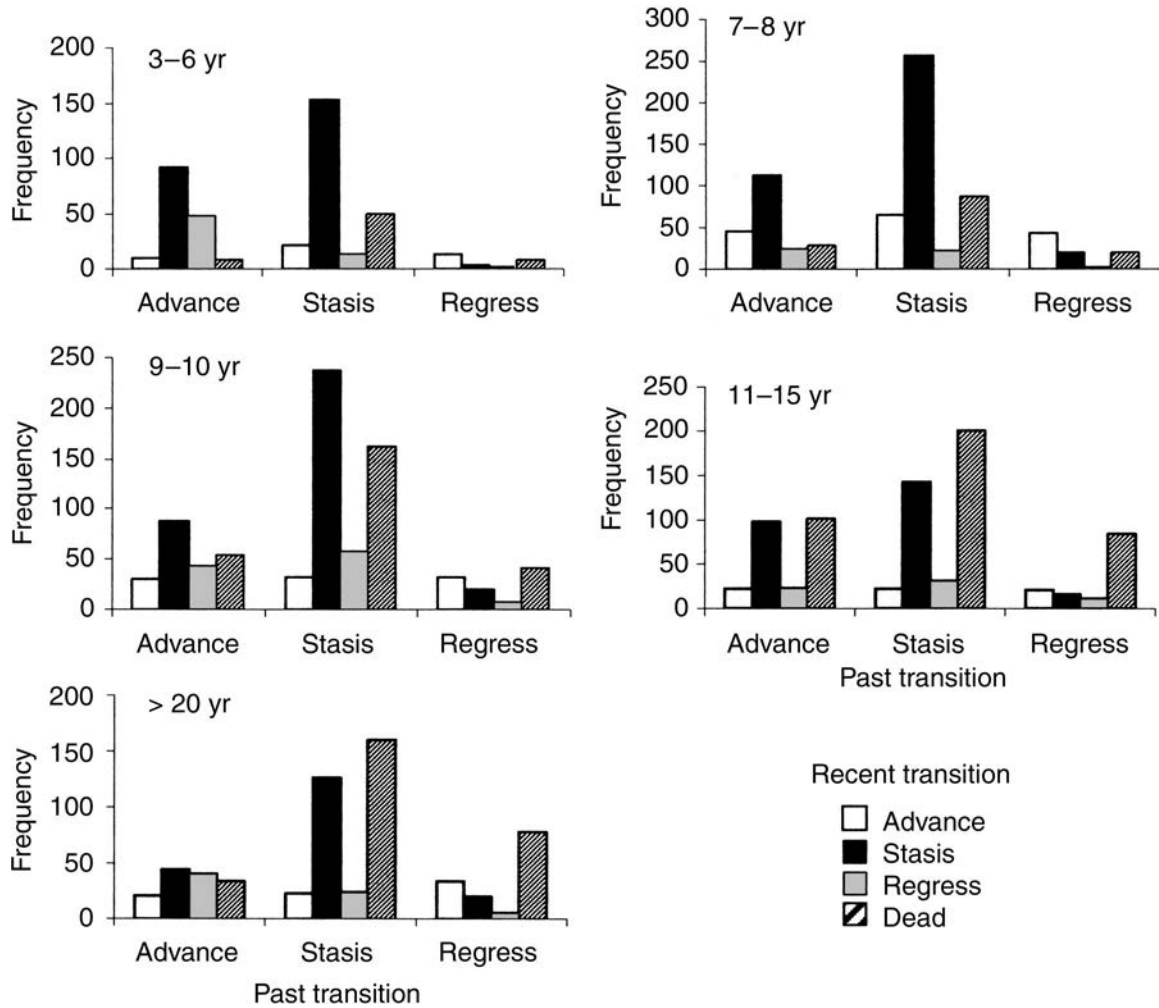


FIG. 7. Frequency of *Eryngium cuneifolium* individuals that advanced in stage, remained in the same stage class (stasis), regressed in stage, or perished during a current census, classified by fate in the past transition, for five different time-since-fire intervals. Data are pooled for vegetative and the three flowering stages. Advances include entering the flowering stages, and regressions include transitions to the vegetative stage after flowering.

flowering at ages 2–3 yr and many continue flowering year after year. However, regression from reproductive to vegetative stages is common and our historical analyses suggest that regression is often a predictor of subsequent mortality. Nearly every aspect of the demography of *E. cuneifolium* is affected by fire. Plants in recently burned areas live longer, survive better, grow faster, and flower earlier than those that germinate in areas that have not been burned recently.

As a result of high survival, growth, and fecundity in the years following fire, *E. cuneifolium* populations explode within the first decade. Large plants with many flowering stems are common beginning the third year postfire. Many of these plants then become rather static in size and fecundity. Increases in mortality through the first decade eventually reverse the population increase by ~9 yr, and the populations subsequently de-

cline. Aboveground disappearances tend to occur between 25 and 35 yr postfire. These patterns are consistent with population trajectories produced by models assuming high seed bank survival and low rates of seed germination. However, the assumed seed bank survival (0.5) is actually lower than the one found in dormancy experiments for *Hypericum cumulicola* (Quintana-Ascencio et al. 1998), which has a similar life history to *E. cuneifolium*. The low (0) rate of first year germination matches all field observations, although we have seen first year germination in laboratory or greenhouse situations with adequate moisture. Additional experiments to quantify the seed bank of *E. cuneifolium* would be useful. The persistence of the seed bank will clearly be important in understanding how long populations can persist after aboveground populations have perished. To date, we have not observed “new” *E.*

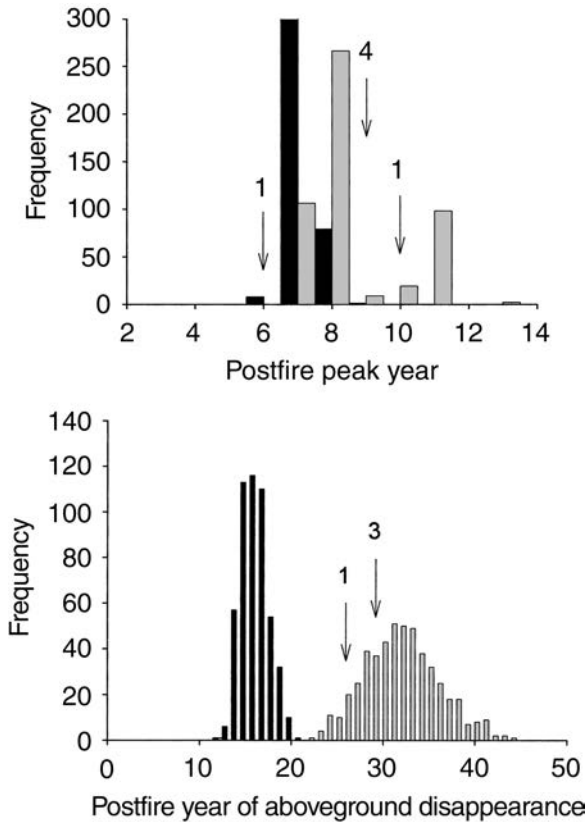


FIG. 8. Histograms of predicted postfire years of peak aboveground population size and aboveground population disappearance for top two scenarios: the base scenario (HLL) in gray, and the second-best scenario (MLL) in black. Arrows and numbers indicate the number of populations observed to peak or disappear in the indicated year.

cuneifolium populations where aboveground populations were not present prefire. However, we have observed postfire seedlings in an annually visited population where there were no plants for a period of 7 yr. Barring long-distance seed dispersal, which is unlikely (Menges et al. 1998), this demonstrates a persistent seed bank that can last at least 7 yr.

Decreasing demographic performance in the decades following fire is associated with increased cover of shrubs, particularly Florida rosemary (*Ceratiola ericoides*; Johnson 1982). The gaps that support *E. cuneifolium* shrink due to shrub growth (Hawkes and Menges 1996). Within these gaps, lichen and herb growth also occur, decreasing the area of open sand (Hawkes and Menges 1996). Florida rosemary root growth can occur 1–2 m from canopies of large shrubs, effectively closing belowground gaps (Hunter and Menges 2002). Since Florida rosemary is allelopathic (Richardson and Williamson 1988, Williamson et al. 1992, Hunter and Menges 2002), germination and growth of herbs may be suppressed as shrubs close gaps (Petrů 2002). Demographic changes in *E. cuneifolium* with time since fire may be driven by the above pat-

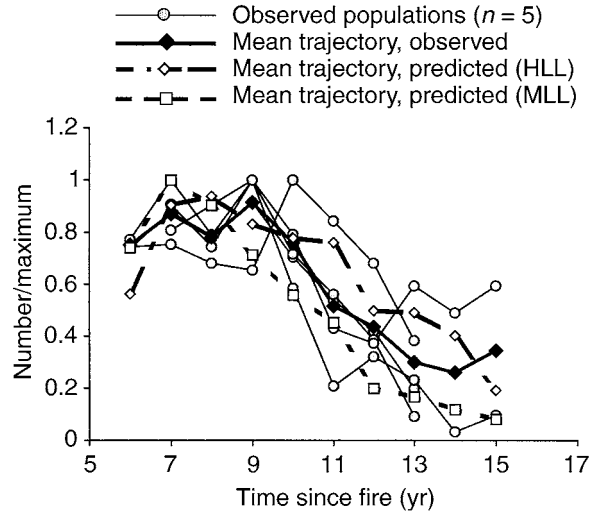


FIG. 9. Observed individual population trajectories ($n = 5$, thin lines), mean observed population trajectory (diamonds, center solid line), and mean predicted population trajectories for HLL (triangles, dotted line) and MLL (squares, dotted line) scenarios between 6 and 15 yr postfire. Numbers are scaled relative to maximum population number per site or simulation.

terns, particularly exploitative and interference competition from Florida rosemary. Survival of *E. cuneifolium* is higher at greater distances from nearby shrubs and when the neighboring shrub is not Florida rosemary (Menges and Kimmich 1996). Transplants of *E. cuneifolium* are particularly sensitive to being planted near Florida rosemary and in long-unburned areas (Quintana-Ascencio and Menges 2000). *E. cuneifolium* was the most sensitive of all species tested to germination suppression in the presence of Florida rosemary leachate (Hunter and Menges 2002).

Since *E. cuneifolium* appears to be specialized for open sites lacking Florida rosemary, it is not surprising

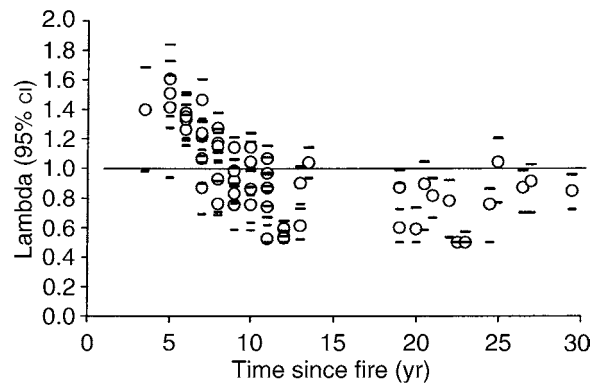


FIG. 10. Finite rates of increase (λ) for *Eryngium cuneifolium* populations in sites with different times since fire under the base scenario (HLL); error bars show 95% bootstrapped confidence intervals (centered on nonbootstrapped λ 's).

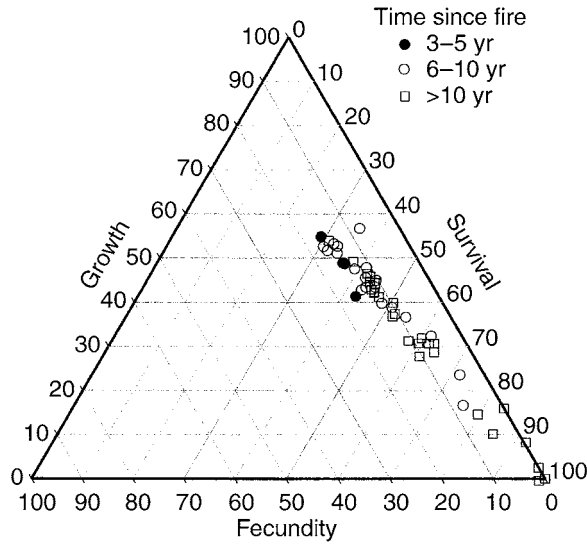


FIG. 11. Triangular chart of growth, survival, and fecundity components of elasticity for *E. cuneifolium*. Symbols represent matrices of populations in patches 3–5 yr after fire, patches 5–10 yr after fire, and long-unburned patches (>10 yr after fire).

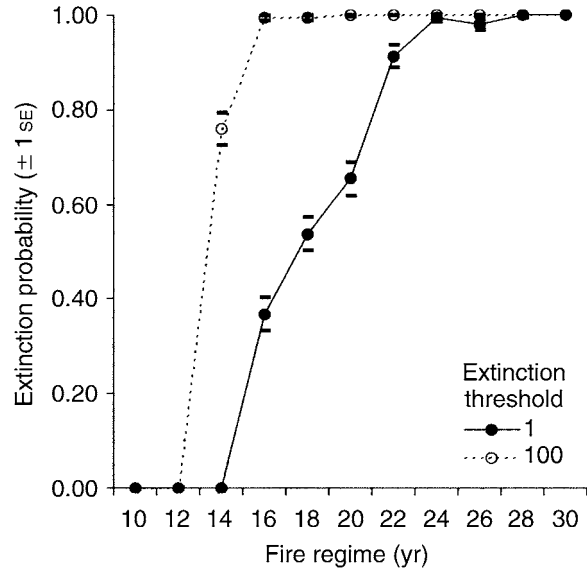


FIG. 13. Extinction probability for *E. cuneifolium* as a function of fire-return interval. Fire is modeled as a regular disturbance. The initial population is 7000 seeds, length of simulation is 99 yr, extinction thresholds are 1 and 100, and the fertility scenario is HLL (base scenario) without historical effects. We used the stochastic simulation program DIST-PROJ to model extinction probability, using 1000 replicate simulations. All matrices were used in the simulation. Standard errors are shown centered on nonbootstrapped means.

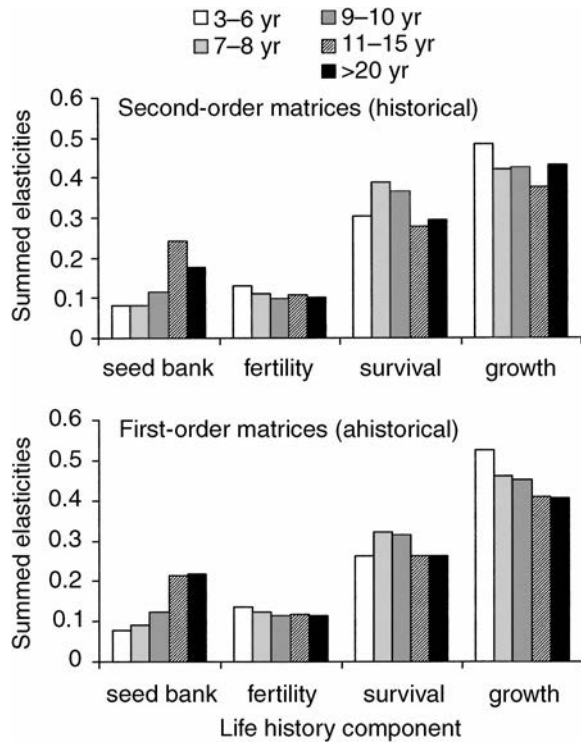


FIG. 12. Summed elasticity values of seed bank, fertility, survival (regression and stasis), and growth for second-order (historical) and first-order (ahistorical) matrices of *E. cuneifolium*. Demographic data used to build projection matrices were pooled among populations within five time-since-fire classes.

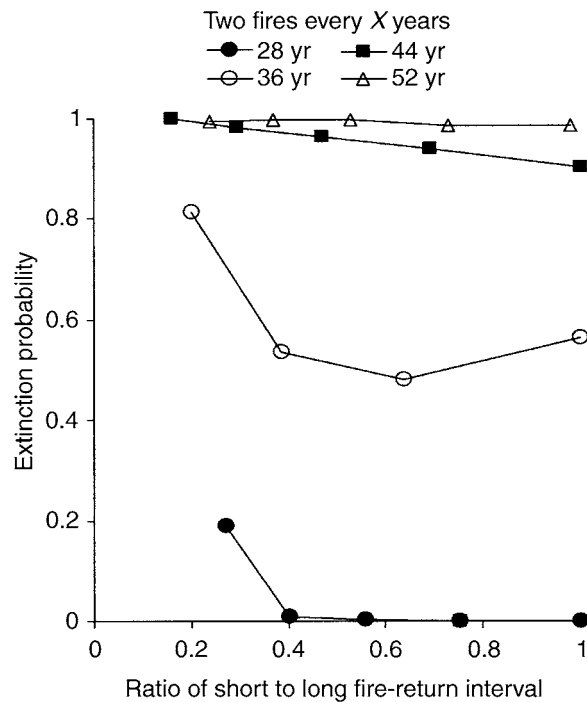


FIG. 14. Extinction probabilities under alternating short and long fire intervals repeating twice every 28, 36, 44, and 52 yr (all other parameters are as in Fig. 13).

that disturbances other than fire can provide suitable conditions for this plant. Indeed, the species is often found in high densities along sand roads and firelanes and in mechanically disturbed areas of xeric white sands. The demography of *E. cuneifolium* in these sites has not yet been studied in any detail.

Our data suggest that fire will be critical for *E. cuneifolium* persistence, because of its positive effect on seed production, recruitment, and survival. Our elasticity analysis indicates that, in the absence of fire, management strategies directed to increase survival of seeds or standing individuals, especially in unburned sites, may ameliorate population decline and reduce risks of extinction. Success of these management strategies will depend, among other factors, on susceptibility of the vital rates to human intervention, and their actual ranges of variation (Mills et al. 1999). The pattern of increasing survival elasticities with a decrease in finite rates of increase (here with time since fire) is typically found in comparisons across species (Silvertown et al. 1996) and in comparisons of populations within species (Oostermeijer et al. 1996, Silvertown et al. 1996, Quintana-Ascencio 1997, Picó et al. 2003).

The role of history in population projection

Incorporation of historical effects indicates that most *Eryngium cuneifolium* individuals have very low growth rates (change in rosette diameter), tending to remain in the same size class. The elasticity of stasis of established individuals (not seeds) was higher in historical models than in models that did not consider history. This is a similar pattern to the one found for the long-lived herb, *Lathyrus vernus* (Ehrlén 2000). Although historical effects add explanatory power to the fate of individuals or small groups of individuals, finite rates of increase (λ) patterns of *E. cuneifolium* with time since fire were not greatly altered.

Slow growth rates and resource storage can be mechanisms to buffer environmental variation (Chapin et al. 1990, Ehrlén and Van Groenendael 2001). The large taproots of *Eryngium cuneifolium* may help to cope with the limited nutrient and water availability characteristic of the Florida rosemary scrub. Effects of prior stages could also reflect costs of reproduction (i.e., tradeoffs; Ehrlén and Van Groenendael 2001) or some type of senescence or aging (Orive 1995). However, a cost of reproduction in *E. cuneifolium* is not evident from the historical analyses, since a transition to flowering is not associated with a subsequent regression to a vegetative stage. Instead, plants that regress in stage are likely to either further regress or die. This is consistent with some type of senescence or aging. Field observations concur, with visible signs of dieback often proceeding death by months or years.

Evaluating model projections

We used a matrix selection approach to stochastically model *Eryngium cuneifolium* population viability anal-

ysis with fire in an explicit manner. This simulation strategy included preserving observed data and variances within population- and year-specific projection matrices. We minimized the use of pooled data (especially across different times since fire) for individual stages and only in extreme cases built complete matrices from pooled data (mostly for declining populations with few individuals). In this way, we preserved (in nonbootstrapped projections) both the correlation structure within individual matrices (populations, years) and protected patterns among matrices across the time-since-fire gradient. Correlations among matrix elements affect population dynamics and extinction risk. For *Eryngium cuneifolium*, most correlations among growth and stasis (survival components) were positive, suggesting that favorable conditions tend to affect many life history stages in a similar manner. This appears to be a general trend among many species (Horvitz and Schemske 1995, Oostermeijer et al. 1996). Element selection approaches generally assume independent fluctuations of different elements within the matrix, and therefore will break these positive correlations. The result will be a less conservative risk assessment (Greenlee and Kaye 1997, Menges and Quintana-Ascencio 2003), especially for stochastic matrix projections, which are highly sensitive to changes in this correlation structure (Fieberg and Ellner 2001).

Although our simulations were based on many populations and years, population idiosyncrasies could have affected our projections. If studied long-unburned populations are on average more persistent than the rest of the populations, then we may not have sampled many populations that disappeared relatively early in the postfire sequence. If this population sampling bias is important, our results may underestimate population decline and extinction. Long-term study of populations beginning immediately after fire can be used to evaluate this issue.

Bootstrapping underestimated λ and overestimated extinction risk, relative to nonbootstrapped simulations for *E. cuneifolium*. Independence among observational units is an important assumption in bootstrap analysis (Efron and Tibshirani 1998). There are many sources of nonindependence in matrix demographic data. Individual fate within populations may not be independent because exposure to common environmental conditions. Common historical effects may also result in significant autocorrelations along time series. Therefore, bootstrapped estimates of variance should be considered with caution. Due to the inclusion of unrealistic matrices, bootstrapped simulations may overestimate variance and project higher or lower extinction probabilities (depending on the correlation structure).

The use of various fertility scenarios allowed us to bracket a range of conditions for difficult-to-study life history stages. The qualitatively consistent patterns of finite rates of increase with time since fire provides some assurance that the patterns have some reality for

Eryngium cuneifolium. The use of bracketing scenarios to explore a range of outcomes is useful in the real world of incomplete data and recalcitrant study species. We suggest this approach should be used more often and that it would answer some of the criticisms of PVAs that focus on the imprecision of exact estimates (Ellner et al. 2002).

A complete validation would require comparisons matching probability distributions of model outputs with data from alternative populations for which data were not included in the modeling (McCarthy et al. 2001) or projections over a different time interval (e.g., Brook et al. 2000). We have used all data collected on *E. cuneifolium* from Archbold to analyze its population viability. As an alternative, we performed a limited test of the model's ability to predict several demographic results that are not considered during matrix building. This is termed a "verification" as opposed to "validation." The model successfully predicted the timing of peak aboveground population size, the timing of aboveground disappearance, and the trajectories of postfire population dynamics.

Our study does avoid several of the common pitfalls of PVAs (Menges 2000) by including a relatively long time interval combined with many populations. These populations spanned the entire range of time since fire from recently burned to long unburned. Also, we have observations of populations of a given time since fire in different years to provide a fairly independent snapshot of demographic performance. We assert that the essence of *E. cuneifolium* population dynamics in Florida rosemary scrub has been captured. More work needs to be done with this species to assess the role of human-disturbed habitats in its persistence and distribution.

Effects of fire on population viability and management

This population viability analysis for *Eryngium cuneifolium* suggests that frequent fires are necessary for populations to persist. Finite rates of increase decline through the first 14 yr postfire, suggesting that conditions deteriorate early on for this species. Stochastic analyses show that only fire-return intervals of 15–20 yr or less will provide conditions for populations to persist. Intervals longer than 12 yr are predicted to result in an overall decline in population size, although extinction risk in the time period simulated (99 yr) is still small.

Not all species sharing an ecosystem are identical in their responses to fire. *Eryngium cuneifolium*'s pattern of finite rates of increase with time since fire was similar to, but more extreme than, the pattern for *Hypericum cumulicola*, another Florida scrub endemic herb with a similar life history (Quintana-Ascencio et al. 2003). The pattern of finite rates of increase with time-since-fire was best fit by an inverse function for both species. The function had a tighter fit for *E. cuneifolium*

($r^2 = 0.58$ vs. 0.32) with a lower intercept (0.50 vs. 0.74, respectively) and a similar but significantly slower decrease of λ with time since fire (slope = 4.40 and 4.81 respectively, significant interaction with species in analysis of covariance). The fitted line for *E. cuneifolium* shows lower lambda with time since fire, and more consistent negative values after a decade postfire. This is consistent with the notion that *E. cuneifolium* is a more extreme specialist for postfire, open, rosemary-free habitats than is *H. cumulicola* (Menges and Kimmich 1996, Quintana-Ascencio and Morales-Hernández 1998, Menges 1999). At Archbold Biological Station, *E. cuneifolium* occupies fewer patches of rosemary scrub than *H. cumulicola* and is much less likely to be found in patches that have been unburned for more than 20 yr.

The specialization of *E. cuneifolium* for postfire habitats is also more extreme than scrub buckwheat, *Eriogonum longifolium* var. *gnaphalifolium*, an endemic herb of Florida scrub and sandhill habitats. Scrub buckwheat is favored by fire, with a fire-return interval of 5–20 yr indicated by a PVA (Satterthwaite et al. 2002). However, scrub buckwheat differs from *Eryngium cuneifolium* by having high annual survival, less erosion of demographic performance between fires, and a longer life span. This makes it able to tolerate greater variety in fire history.

Although it is well known that Florida scrub, and Florida rosemary scrub, requires fire for maintenance of biodiversity (Abrahamson 1984, Myers 1990, Menges 1999), most authors have suggested that rosemary scrub burns, and should be burned, infrequently. Estimates of fire-return intervals usually are 20–60 yr or 15–100 yr (Menges 1999). Since most rosemary scrub probably has burned (and may continue to be burned) at fire-return intervals less frequent than every 20 yr, local extinctions of *E. cuneifolium* are likely. Several Florida rosemary scrub specialist species, including *E. cuneifolium* and *H. cumulicola*, follow distribution patterns fitting a model of metapopulation dynamics, with greater occupancy in larger and less isolated patches (Quintana-Ascencio and Menges 1996). Fitted parameters suggest that *E. cuneifolium* is particularly limited in its ability to disperse to unoccupied patches. Transplant experiments with *H. cumulicola* show that unoccupied rosemary scrub patches are suitable habitat for population establishment (Quintana-Ascencio et al. 1998) and the same is likely true for *E. cuneifolium*.

At a landscape scale, some spatial and temporal heterogeneity in the fire regime (pyrodiversity) will likely help retain a mixture of species with varying sensitivities to postfire vegetation changes (i.e., Morrison et al. 1995). Of course, radically long or short fire-return intervals, complete fire suppression, or unusually high fire intensities may be beyond the tolerances of certain species. Our simulations suggest that staggered fire-return intervals, in and of themselves, do not create particularly greater extinction risks for *E. cuneifolium*.

Staggered fire-return intervals may allow postfire specialists like *E. cuneifolium* and *H. cumulicola* to coexist with species that require longer fire-free intervals, like Florida rosemary. Patchy burns, which should normally occur even with prescribed fire lighting patterns, may provide refugia for fire-sensitive species. Fire sensitive species without significant persistent seed banks (e.g., *Polygonella basiramia*; S. K. Maliakal, unpublished data; E. S. Menges and C. W. Weekley, unpublished data) may be particularly sensitive to large, complete burns. Burn patchiness is probably also beneficial in promoting diversity and bet-hedging for environmental stochasticity, e.g., droughts following burns. Pyrodiversity should be part of fire management, especially when managing for the needs of multiple species with diversity in life history strategies.

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APPENDIX A

A table showing logistic regression *P* values of *Eryngium cuneifolium* rosette diameter and number of stems on annual survival and samples sizes is available in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A1.

APPENDIX B

A table showing Spearman rank correlations of *E. cuneifolium* rosette diameter and number of stems with annual growth is available in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A2.

APPENDIX C

A summary of matrices for specific populations and years for *Eryngium cuneifolium* is available in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A3.

APPENDIX D

Results of loglinear analysis of the effects of prior transition and time since fire on the current fate of *Eryngium cuneifolium* are presented in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A4.

APPENDIX E

Figures showing finite rates of increase (λ) for *Eryngium cuneifolium* populations in sites with different time since fire under 12 different scenarios are available in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A5

APPENDIX F

A table of Spearman rank correlations among matrix elements for *Eryngium cuneifolium* is available in ESA's Electronic Data Archive: *Ecological Archives* M074-002-A6.