ASSESSING SCRUB BUCKWHEAT POPULATION VIABILITY IN RELATION TO FIRE USING MULTIPLE MODELING TECHNIQUES

WILLIAM H. SATTERTHWAITE,[1] ERIC S. MENGES, AND PEDRO F. QUINTANA-ASCENCIO

Archbold Biological Station, Lake Placid, Florida 33862 USA

Abstract. We used a variety of modeling approaches to assess the effects of fire on the demography and population viability of scrub buckwheat (*Eriogonum longifolium* var. *gnaphalifolium*), a threatened herb endemic to periodically burned xeric uplands in central Florida, USA. We compared the management implications of different approaches. Using demographic data from ten years including five fires, we constructed Lefkovitch matrix models of scrub buckwheat populations in unburned habitats for populations experiencing a burn and for populations one year after burning. Deterministic analysis of the unburned matrices predicted relatively stable populations in unburned habitats using optimistic fertility estimates ($\lambda =$ 1.002, 95% CI 0.975–1.033), but almost certain decline given pessimistic fertility estimates ($\lambda =$ 0.981, 0.962–1.003). Burned populations are always predicted to increase (CI on $\lambda >$ 1.08). Numerical calculations of single-year growth rates based on the expected stable stage distribution of an unburned population yielded positive, but lower, growth rates. The λ's calculated for periodically burned populations had confidence intervals entirely above 1 for fire return intervals shorter than 20 yr (optimistic) or 5 yr (pessimistic). Stochastic simulations yielded highly uncertain estimates of the probability of quasi-extinction over 250 yr, with only fire return intervals shorter than 20 yr (optimistic) or 5 yr (pessimistic) yielding quasi-extinction confidence intervals entirely below 1. Population growth rates in partially burned areas increased linearly with the proportion burned. The results of these density-independent simulations remained virtually unchanged (maximum difference of 5.2%) by introducing plausible population ceilings. Regression and stasis transitions had the highest elasticities for unburned populations, while fecundity elasticities were relatively greater for burn years. Transient elasticity analysis on total population size of simulated single-year post-fire growth and on the population vector five years in the future showed broadly similar patterns to standard elasticities, although the standard analysis assigned higher elasticity values to transitions contributing to future reproductive potential. Fire management is important to encouraging viable populations. Our analysis suggests minimum fire return intervals of 20 yr (optimistic) or 5 yr (pessimistic). These fire return intervals are consistent with those often used in the sandhill and oak–hickory scrub habitats of scrub buckwheat.

Key words: conservation; demography; density dependence; elasticity; Eriogonum longifolium *var.* gnaphalifolium; *fire; Florida scrub; matrix models; population ceilings; population viability; sandhill; scrub buckwheat.*

INTRODUCTION

Fires can have marked effects on plant population dynamics (Bond and van Wilgen 1996). Fires may enhance population growth through physiological mechanisms such as stimulating flowering (e.g., Daubenmire 1968), seed release (e.g., Lamont et al. 1991), or germination (e.g., Keeley 1991). Alternatively, fires may encourage growth of particular plant species through effects on the surrounding ecosystem, such as the removal of competitors (e.g., Magee and Antos 1992) or a temporary increase in nutrient availability (e.g., Anderson and Menges 1997).

Many researchers have sought to determine the effects of fire regimes on population dynamics (e.g.,

Bradstock and O'Connell 1988, Silva et al. 1991, Canales et al. 1994, Bradstock et al. 1996, Gross et al. 1998, Hoffman 1999; Menges and Quintana-Ascencio 2002), often applying a population viability analysis (PVA) approach. PVAs are useful tools for evaluating population persistence and extinction risks (Gilpin and Soule 1986, Beissinger and Westphal 1998, Groom and Pascual 1998, Menges 2000). Although PVAs are often handicapped by limited data and are based on models requiring numerous simplifying assumptions, they are nonetheless useful for comparing alternative management strategies for species of concern (Groom and Pascual 1998, Menges 2000).

Plant PVAs employ a wide variety of approaches (Menges 2000). A common approach is the construction of deterministic models to calculate λ, the finite rate of increase of a population, assuming constant environmental conditions and unchanging demographic rates among individuals. Generally, these models are

structured by age, gender, or (most commonly for plants) stage and size (Lefkovitch matrices, Caswell 2001). These calculations are frequently accompanied by sensitivity and elasticity analyses (Heppell et al. 2000), measures of the effect of each stage transition on λ. Usually these analyses only consider the effect of changing a single transition rate on the asymptotic, long-term growth rate of the population. Asymptotic rates may be misleading as indicators of transient changes in populations not at a stable stage distribution (Fox and Gurevitch 2000).

Alternate approaches employ stochastic models to calculate either stochastic growth rates (e.g., Nakaoka 1996) or the probability of population decline or extinction over a specified time period (e.g., Menges 1998), letting environmental conditions and/or individuals' demographic rates vary over time. A common way to simulate the effects of environmental stochasticity is through the ''element selection model,'' in which each element of a single Lefkovitch matrix is chosen (often independently) from a probabilistic distribution for each step of the simulation (Beissinger 1995). Periodicity can be introduced by covarying the selection of elements with an environmental autocorrelation function. Alternatively, the ''environmental state method'' (also called ''matrix selection''), draws entire matrices from different pools depending on the current environmental state being simulated (Beissinger 1995, Kaye et al. 2001, Menges and Quintana-Ascencio 2002).

The selection of a deterministic vs. stochastic approach requires numerous trade-offs. Environmental stochasticity can lead to significant extinction risks for populations in which deterministic growth rates imply population persistence (Menges 1998). Most stochastic approaches require substantially more data and computing resources than their deterministic counterparts and do not lend themselves as readily to sensitivity analyses, which can provide important guidance for managers (Schemske et al. 1994, but see Mills et al. 1999).

Most PVA models do not incorporate density dependence. In some cases, this is simply because adequate data to construct density-dependent functions are not available. However, it has been argued that incorporating density dependence would tend to make PVAs more optimistic (due to increased demographic performance at small population sizes), underestimating threats to a species' persistence (Ginzburg et al. 1990), or that populations of concern are generally affected more by interspecific interactions (Menges 1998). However, density dependence may substantially alter outcomes of some PVAs (Alvarez-Buylla et al. 1996).

This study used both deterministic and stochastic approaches, with and without density dependence, to evaluate the effects of fire on population viability of scrub buckwheat, *Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gandog. (Polygonaceae), a perennial herb endemic to xeric uplands in central peninsular Florida. *E. l. gnaphalifolium* (also referred to as *E. floridanum* Small) is listed by the United States government as threatened (USFWS 1999) and by the state of Florida as endangered (Coile 2000). Scrub buckwheat is a perennial herb with a basal rosette of leaves and one to several flowering scapes produced sporadically. Each individual plant has a woody taproot that may allow it to remain dormant with no aboveground structures for one or more years. It primarily occurs in xeric upland sandhills, turkey oak barrens, and Florida scrub (USFWS 1999).

Fires are of demonstrated importance to the persistence of many threatened and endangered plants in scrub and sandhill plant communities of central Florida (Menges 1999 and references therein). Although some *E. l. gnaphalifolium* plants can be killed by intense fires (USFWS 1999), Carrington (1999) found a resprouting rate of 92% after a prescribed fire at Archbold Biological Station, and 100% of plants resprouted following another fire in the same area (McConnell and Menges 2002). Flowering of *E. l. gnaphalifolium* plants is also stimulated by fire (Carrington 1999), a response that seems to be due chiefly to the removal of aboveground tissues (McConnell and Menges 2002).

These studies suggest that fire may play an important role in enhancing population growth for *E. l. gnaphalifolium*. However, we know little about the demographic response of *E. l. gnaphalifolium* populations to different fire regimes. This PVA evaluates prescribed fire as a tool in managing populations for persistence. Specifically we considered the effects of fire return intervals and the proportion of the population burned on *E. l. gnaphalifolium* population viability. We assessed population viability in terms of λ, probabilities of population decline (smaller total size 250 yr in the future) and quasi-extinction (total size <10 individuals at any point within 250 yr). We used bootstrapping methods (Caswell 2001) to generate confidence intervals for λ and extinction parameters. We also used simple models incorporating population ceilings to test the sensitivity of these results to the incorporation of density dependence. Lastly, we compared transient elasticities on total population growth, transient elasticities on the population vector (Fox and Gurevitch 2000), and standard elasticities in burned and unburned populations.

METHODS

Study sites

In July of 1989, we began monitoring six populations of *E. l. gnaphalifolium* in four burn units at Archbold Biological Station, located on the Lake Wales Ridge in central Florida, USA (27°11′ N, 81°21′ W). These populations occur in areas characterized as the turkey oak phase or the hickory phase of southern ridge sandhill (Abrahamson et al. 1984). Within each population,

we established between 4 and 14 permanent 10 × 10 m plots. We marked all *E. l. gnaphalifolium* plants within each plot with flags and numbered metal tags and censused them annually. A total of 1114 plants were counted as alive at some point between 1989 and 1999. One population was not burned during this time, three were burned once, and one each were burned three and four times. These burns followed a schedule devised to benefit multiple species of concern at Archbold Biological Station, and the fire return intervals fell within the natural ranges for these habitats (Menges 1999). There were no recorded burns in these areas between 1927 and 1989.

Data collection

At each annual census, we monitored all plants for survival, total basal diameter (summed across all rosettes), and number of flowering scapes. If we did not find a plant adjacent to an old flag, the plant was recorded as dead, but we did not remove the flag, and we checked the area surrounding the flag for scrub buckwheat plants in subsequent years. We searched each plot for new plants every year and every plant found was flagged, tagged, and followed in subsequent censuses.

Seed germination experiment

We collected mature achenes of *E. l. gnaphalifolium* in August 2000. Achenes were observed under a stereoscopic microscope to detect and discard those with any signs of damage or malformation. Visually sound fruits were kept inside aluminum foil until sowing (within 2 wk after collection). We sowed achenes on sand inside PVC tubes (11 cm diameter, 10 cm height) partially buried within gaps in three sandhill sites with different time since fire: recently burned, 5 yr post-fire, and >10 yr without fire. In each site we established 10 replicates of four treatments that tested the effects of litter (presence and absence of litter material from the immediate area), insect predation (edge of PVC coated with tanglefoot or left uncoated), and their interactions. Percentage of canopy cover was also evaluated as the mean of two measurements from the north and south sides of each PVC tube using a spherical densiometer (Lemmon Forest Densiometer, Kenmore, Arlington, Virginia, USA). Six achenes were sown in each PVC tube: three on 21 August and three on 1 September. To evaluate germination and seedling survival, we censused each site every other day between 21 August and 25 September and once per week thereafter until April 2001, marking seedlings with toothpicks of different colors and styles to differentiate germination cohorts. We used an ANCOVA (with percentage of canopy as covariable) in SPSS V.10 (SPSS 2000) to assess significant differences in percentage of germination (after angular transformation of data) among sites with different time since fire and treatments.

Parameter estimation and matrix construction

We represented the *E. l. gnaphalifolium* life cycle with a five-stage model. Stage 1, ''new plants,'' consisted of presumed seedlings: plants with basal diameters <2 cm that had not been found in any previous censuses. Stage 2, ''small plants,'' consisted of all nonseedling vegetative plants with total basal diameters <8 cm. Larger plants that were not flowering were classified as ''vegetative plants'' (stage 3). The 8 cm diameter cutoff was chosen because >95% of all flowering plants found in this study had basal diameters >8 cm. The remaining stages were ''flowering plants'' (stage 4, those with at least one flowering scape) and ''dormant plants'' (stage 5). Dormant plants were present aboveground in the year(s) before and after ''dormant'' years, when they were not observed near their flags and tags.

We calculated separate transition matrices for each year for each of three fire histories: ''burned'' matrices for populations that had been burned between the previous census and the current one, ''after-burn'' matrices for populations that had been burned the year before, and ''unburned'' matrices for all other conditions (Table 1). We did not calculate separate matrices for times since fire >1 yr because the closely spaced fires at some sites left us with inadequate sample sizes. Because of small sample sizes for some stage classes, we pooled across sites for the same year and burn history. If fewer than nine individuals of a given stage were available for a particular year/burn combination even after this pooling, we substituted mean values across all suitable years. For the new plant stage we used data from unburned populations for all burn histories. For each burn history category, we calculated mean matrices as the arithmetic means of each matrix element for all years with adequate data for that element (Table 2). Transitions into all stages other than stage 1 were calculated as the probability that a plant classified in stage *x* was in stage *y* in the subsequent census.

We estimated 95% confidence intervals on these matrix elements using bootstrap percentile intervals (Caswell 2001). Fertility and non-fertility data were drawn independently during bootstrapping. Each of the matrices for each year–burn combination was re-estimated 2000 times by drawing with replacement from the appropriate data set, producing 2000 resampled mean matrices. For stage–year–burn combinations with data sets too small to estimate transition rates, we drew from data pooled across all appropriate sets. For the new plant stage in burn and year-after-burn matrices, we resampled from the pooled unburned data set due to small sample sizes.

Because of small plant size and the presence of substantial litter in some plots, new seedlings were difficult to find. We sometimes found ''presumed 2-yr-olds'': untagged plants >2 cm in diameter, which we judged too large to be first year seedlings. We assumed that

TABLE 1. Transition matrices for each year, split by burn history.

Stage	New	Small	Vegetative	Flowering	Dormant
A) Unburned-year transitions					
1990–1991					
New	0.000†	0.000	0.000	5.084/3.056	0.000†
Small	0.601†	0.091	0.012	0.000	0.136†
Vegetative	0.000†	0.818	0.895	0.900	0.493†
Flowering	0.021†	0.000	0.029	0.100	0.030†
Dormant	0.025†	0.091	0.012	0.000	0.342†
No. sampled	1 (41)	11	171	10	0 (77)
1991–1992					
New	0.000†	0.000†	0.000	1.061/0.665	0.000†
Small	0.601†	0.468†	0.022	0.000	0.136†
Vegetative	0.000†	0.359†	0.846	0.585	0.493†
Flowering	0.021†	0.036†	0.077	0.390	0.030†
Dormant	0.025†	0.037†	0.011	0.000	0.342†
No. sampled	0 (41)	2 (248)	91	41	5 (77)
1992–1993					
New	0.000	0.000	0.000	0.679/0.474	0.000†
Small	0.917	0.500	0.020	0.027	0.136†
Vegetative	0.000	0.300	0.786	0.680	0.493†
Flowering	0.083	0.150	0.134	0.253	0.030†
Dormant	0.000	0.050	0.017	0.013	0.342†
No. sampled	12	20	299	75	6 (77)
1993–1994					
New	0.000	0.000	0.000	1.209/0.740	0.000
Small	0.444	0.591	0.042	0.043	0.167
Vegetative	0.000	0.182	0.787	0.729	0.250
Flowering	0.000	0.068	0.042	0.171	0.000
Dormant	0.000	0.068	0.038	0.014	0.583
No. sampled	9	44	450	70	12
1994–1995					
New	0.000	0.000	0.000	0.139/0.083	0.000
Small	0.444	0.429	0.029	0.000	0.063
Vegetative	0.000	0.429	0.872	0.643	0.562
Flowering	0.000	0.000	0.058	0.286	0.000
Dormant	0.000	0.000	0.012	0.000	0.375
No. sampled	9	42	243	14	16
1995–1996					
New	0.000†	0.000	0.000	1.040/0.625	0.000
Small	0.601†	0.552	0.035	0.063	0.200
Vegetative	0.000†	0.172	0.857	0.688	0.300
Flowering	0.021†	0.034	0.039	0.25	0.100
Dormant	0.025†	0.000	0.008	0.000	0.400
No. sampled	0 (41)	29	258	16	10
1996–1997					
New	0.000	0.000	0.000	1.697/1.023	0.000
Small	0.600	0.613	0.095	0.034	0.250
Vegetative	0.000	0.194	0.800	0.391	0.350
Flowering	0.100	0.000	0.029	0.149	0.050
Dormant	0.000	0.048	0.017	0.299	0.350
No. sampled	10	62	409	87	20
1997–1998					
New	0.000†	0.000	0.000	0.832/0.500	0.000
Small	0.601†	0.500	0.017	0.024†	0.000
Vegetative	0.000†	0.421	0.897	0.659†	1.000
Flowering	0.021†	0.000	0.026	0.229†	0.000
Dormant	0.025†	0.000	0.004	0.047†	0.000
No. sampled	1 (41)	38	232	4 (317)	8
B) Burn-year transitions					
1990–1991					
New	0.000†	0.000†	0.000	10.792/6.486	0.000†
Small	0.601†	0.415†	0.016	0.000	0.057†
Vegetative	0.000†	0.220†	0.047	0.080	0.099†
Flowering	0.021†	0.095†	0.867	0.520	0.537†
Dormant	0.025†	0.063†	0.039	0.040	0.307†
No. sampled	1 (41)	4 (101)	129	26	0 (47)

TABLE 1. Continued.

Stage	New	Small	Vegetative	Flowering	Dormant
1991–1992					
New	0.000†	0.000†	0.000	2.552/1.667	0.000†
Small	0.601†	0.415†	0.026	0.044†	0.057†
Vegetative	0.000†	0.220†	0.412	0.118†	0.099†
Flowering	0.021†	0.095†	0.451	0.641†	0.537†
Dormant	0.025†	0.063†	0.006	0.031†	0.307†
No. sampled	0 (41)	6 (101)	154	5 (41)	0 (47)
1994–1995					
New	0.000†	0.000	0.000	1.664/1.000	0.000
Small	0.601†	0.360	0.064	0.105	0.000
Vegetative	0.000†	0.000	0.084	0.053	0.083
Flowering	0.021†	0.160	0.554	0.737	0.417
Dormant	0.025†	0.080	0.055	0.526	0.500
No. sampled	0 (41)	25	206	19	12
1997–1998					
New	0.000†	0.000	0.000	2.962/1.789	0.000
Small	0.601†	0.470	0.030	0.044	0.114
Vegetative	0.000†	0.439	0.839	0.222	0.114
Flowering	0.021†	0.030	0.101	0.667	0.657
Dormant	0.025†	0.045	0.000	0.000	0.114
No. sampled	1 (41)	66	172	51	35
C) After-burn transitions					
1990–1991					
New	0.000†	0.000	0.000	0.515/0.309	0.000†
Small	0.601†	0.182	0.000	0.028	0.000†
Vegetative	0.000†	0.636	0.464	0.194	0.400†
Flowering	0.021†	0.091	0.429	0.639	0.000†
Dormant	0.025†	0.091	0.000	0.056	0.600†
No. sampled	0 (41)	11	29	36	0 (28)
1991–1992					
New	0.000†	0.000†	0.000	0.189/0.134	0.000†
Small	0.601†	0.136†	0.125	0.009	0.000†
Vegetative	0.000†	0.636†	0.625	0.722	0.400†
Flowering	0.021†	0.045†	0.167	0.176	0.000†
Dormant	0.025†	0.068†	0.000	0.009	0.600†
No. sampled	0 (41)	6 (49)	24	236	7 (28)
1992–1993					
New	0.000†	0.000†	0.000	0.024/0.014	0.000†
Small	0.601†	0.136†	0.139	0.032	0.000†
Vegetative	0.000†	0.636†	0.875	0.758	0.400†
Flowering	0.021†	0.045†	0.056	0.021	0.000†
Dormant	0.025†	0.068†	0.000	0.021	0.600†
No. sampled	1 (41)	7 (49)	73	96	1 (28)
1995–1996					
New	0.000†	0.000	0.000	0.343/0.231	0.000
Small	0.601†	0.091	0.000	0.019	0.000
Vegetative	0.000†	0.636	0.708	0.767	0.400
Flowering	0.021†	0.091	0.167	0.157	0.000
Dormant	0.025†	0.045	0.000	0.013	0.600
No. sampled	1 (41)	25	26	175	20

Notes: Transition rates from the stage on the horizontal axis (column headings) to the stage on the vertical axis (left-most column) are given. For fecundity (Flowering to New) transitions, the optimistic estimate is given first, followed by the pessimistic estimate. Sample sizes for each stage class are reported in the bottom row (number of individuals sampled), with pooled sample sizes in parentheses where applicable.

† Transition for which the sample size of appropriate stages was too small to estimate a transition rate.

these presumed 2-yr-olds had been seedlings the year before, rather than exceptionally large seedlings that had germinated in the year of the current census. This seems to be a reasonable assumption based on the observed ease with which seedlings could be overlooked during censuses or the possibility that seedlings had germinated just after the annual census concluded (Carrington 1996).

Based on this assumption, we estimated realized fertility (RF_i), the transition rate (for year i) from flowering plants to new plants (based on a July census), as the mean over all plots of the following:

TABLE 2. Single-year projection matrices for *Eriogonum longifolium* var. *gnaphalifolium* models, averaged across all years of a given burn history.

Stage	New	Small	Vegetative	Flowering	Dormant
Unburned					
New	0.000	0.000	0.000	1.424 (0.796–2.212)/ 0.833 (0.480–1.344)	0.000
Small	0.600 (0.525–0.687)	0.468 (0.419–0.530)	0.034 (0.026–0.042)	0.024 (0.010–0.114)	0.136 (0.093–0.198)
Vegetative	0.000 (0.003–0.024)	0.359 (0.297–0.406)	0.842 (0.825–0.859)	0.659 (0.592–0.741)	0.493 (0.405–0.537)
Flowering	0.021 (0.012–0.064)	0.036 (0.013–0.059)	0.054 (0.043–0.066)	0.229 (0.148–0.257)	0.030 (0.018–0.076)
Dormant	0.025 (0.003–0.053)	0.037 (0.014–0.067)	0.015 (0.010–0.021)	0.047 (0.028–0.054)	0.342 (0.274–0.415)
Burned					
New	0.000	0.000	0.000	4.493 (1.391–8.918)/ 2.759 (0.877–5.631)	0.000
Small	0.600 (0.531–0.683)	0.415 (0.341–0.474)	0.034 (0.022–0.048)	0.044 (0.021–0.099)	0.057 (0.036–0.112)
Vegetative	0.000 (0.006–0.049)	0.220 (0.209–0.298)	0.346 (0.318–0.375)	0.118 (0.082–0.183)	0.099 (0.050–0.160)
Flowering	0.021 (0.018–0.085)	0.095 (0.067–0.153)	0.493 (0.460–0.524)	0.641 (0.548–0.711)	0.537 (0.470–0.659)
Dormant	0.025 (0.006–0.049)	0.063 (0.030–0.097)	0.025 (0.014–0.038)	0.031 (0.003–0.068)	0.307 (0.175–0.344)
After burn					
New	0.000	0.000	0.000	0.268 (0.102–0.484)/ 0.194 (0.067–0.308)	0.000
Small	0.600 (0.537–0.677)	0.136 (0.061–0.204)	0.035 (0.003–0.073)	0.022 (0.007–0.041)	0.000
Vegetative	0.000 (0.006–0.049)	0.636 (0.559–0.755)	0.668 (0.579–0.752)	0.610 (0.568–0.657)	0.400 (0.277–0.457)
Flowering	0.021 (0.018–0.085)	0.045 (0.001–0.082)	0.204 (0.134–0.280)	0.248 (0.202–0.291)	0.000 (0.018–0.098)
Dormant	0.025 (0.006–0.049)	0.068 (0.001–0.107)	0.000	0.024 (0.006–0.047)	0.600 (0.484–0.673)

Notes: Transition rates from the stage on the horizontal axis (column headings) to the stage on the vertical axis (left-most column) are given. For fecundity (Flowering to New) transitions, the optimistic estimate is given first, followed by the pessimistic estimate. Values in parentheses are 95% confidence intervals.

$$RF_i = (N_{i+1} + [U_{i+2}/S])/F_i$$

where N = the number of new plants (stage 1) in each plot (subscripts refer to years), U = the number of presumed 2-yr-olds (stage 2), F = the number of flowering plants (stage 4), and S = the average annual survival rate of new plants (July–July).

We deemed this to be an ''optimistic'' estimate of fertility, in part because some presumed 2-yr-olds could have been reactivated long-dormant plants and as such should not be included in calculating fertility. Dividing U by S corrects the fertility estimate to account for mortality between years one and two. We generated a second, ''pessimistic'' estimate of fertility that did not correct for yearling mortality by setting $S = 1$, resulting in a lower estimate of fertility. By constructing and analyzing models based on both fertility estimates we hoped to assess the importance of errors in estimating this highly uncertain transition rate.

We did not include an explicit seed stage or seed bank because Carrington (1997) did not report *E. l. gnaphalifolium* in sand pine scrub seed banks. Our seed germination experiment also suggests the absence of a long-term seed bank (see *Results: Seed germination experiment*).

We tested for significant year-to-year variability in transition rates using loglinear models fit to three-way fate × state × time contingency tables constructed for each burn category, adding 0.5 to each entry in the table (Caswell 2001).

Megamatrix construction

Land managers prescribing fire may not want to burn an entire parcel simultaneously, or fires may be natu-rally patchy. Therefore, we simulated the effects of partial burns to see how such practices would interact with fire frequency in driving *E. l. gnaphalifolium* population dynamics. To simulate partial burning of a population, we constructed a 15 × 15 multiregional type megamatrix model (Horvitz and Schemske 1986, Caswell 2001). This approach essentially uses two nested projection matrix models. The first level of the model projects entire subsets of a population between matrix regions. Population vectors within these regions are then projected forward in time by region-specific projection matrices. In this case, the megamatrix had three regions corresponding to each of the just-burned, after-burn, and unburned states, with transitions within and between states described by the simple 5 × 5 matrices (Tables 1 and 2) modified by the fraction of the population burned (Table 3). This model assumes that the spatial distributions of different life history stages are independent (both with respect to each other and the burn pattern) and that portions of the population that burned in previous years are neither more nor less likely to burn than are previously unburned portions.

Eigenanalysis

For each matrix (including averaged matrices), λ was calculated as the dominant eigenvalue of the matrix, using MATLAB v 5.2.1 (Mathworks 1998). In the case of cyclic burns with a return interval of T time steps, λ was calculated as the Tth root of the dominant eigenvalue of **P**, for

$$\mathbf{P} = \mathbf{B} \times \mathbf{A} \times \mathbf{U}^{T-2}$$

TABLE 3.   Construction of fractional burn matrices.

Transition	Unburned	Burned	After-burn
Unburned	$(1 - f) \times \mathbf{U}$	⋯	$(1 - f) \times \mathbf{U}$
Burned	$f \times \mathbf{B}$	$f \times \mathbf{B}$	$f \times \mathbf{B}$
After-burn	⋯	$(1 - f) \times \mathbf{A}$	⋯

Notes: **U** represents the 5×5 matrix for the unburned transition; **B** represents the 5×5 matrix for burned transitions; **A** represents the 5×5 matrix for after-burn transitions (from Table 2); *f* represents the fraction of the population burned and can range from 0 (to represent a year without fire) to 1 (representing a year in which the entire population burns. The symbol "⋯" represents a 5×5 zero matrix.

where $\mathbf{B}$ = burned matrix, $\mathbf{A}$ = after-burn matrix, and $\mathbf{U}$ = unburned matrix. In essence, $\mathbf{P}$ represents the transition matrix for a time step of *T,* so the average yearly λ for the population would be the *T*th root of the dominant eigenvalue of $\mathbf{P}$, and over time the population would reach a stable stage repeating over a cycle of length *T*. We also calculated stochastic growth rates for long unburned populations as the eighth root of the dominant eigenvalue of the product of the eight unburned year transition matrices. Since matrix multiplication is not commutative, this result may depend on the order in which the matrices are multiplied together. We addressed this possibility by also performing 1000 simulations in which we multiplied together 250 random draws of unburned matrices and took the arithmetic mean of the 250th root of the corresponding dominant eigenvalue. We generated bootstrapped confidence intervals on all calculations of λ using the same methodology as for the averaged matrix elements.

For matrices representing burned populations and populations one year after burns, which by definition each apply for only a single year, traditional calculations of λ may not be appropriate (Fox and Gurevitch 2000). For these matrices, we also calculated single-year growth rates or ''transient λ's'' by starting with a population vector at the stable stage distribution of a long unburned population, projecting one time step, and calculating the change in total population size. Transient λ's for after-burn matrices were calculated similarly, starting from an unburned stable stage distribution that had been projected one step with a burn year matrix.

We calculated elasticities for each averaged matrix using standard techniques (Caswell 2001) and generated bootstrapped confidence intervals using the same methodology as for the averaged matrix elements. For year-of-burn matrices we estimated 1-yr ''transient elasticities'' considering the effects on total population size by calculating the proportional change in transient λ for a 0.01% increase in each matrix element and scaling these values so that transient elasticities for the entire matrix summed to one. We also calculated 5-yr ''transient elasticities'' considering the effects on each stage class in the population vector (Fox and Gurevitch 2000), assuming repeated burns for five years. We also

performed 5-yr transient analysis of the unburned projection matrix assuming no burns for five years. For the transient analysis of the burn matrix, we started with a stage distribution corresponding to the stable stage distribution of an unburned population. For the transient analysis of the unburned matrix, our starting population vector was the expected stage distribution following a burn, obtained by projecting the unburned stable stage distribution once with the burn matrix and once with the after-burn matrix. We present only results for the optimistic fertility estimates because results were consistent between scenarios.

We summed elasticities (or transient elasticities on total population size) for all transitions from each stage and for all transitions from each burn history or time since fire. Separate summed elasticities were also calculated in each case for survival, *L* (plants remaining in the same stage or regressing to a smaller stage or dormancy); growth, *G* (plants moving into a more developed stage, along the sequence new → small → vegetative → flowering, and every transition out of the dormant stage); and fecundity, *F* (follows definitions in Enright et al. 1995 and Silvertown et al. 1996). Since all elasticities of a matrix sum to one, summed elasticities can be compared to assess the relative contribution of each stage, burn history, or transition type to the growth rate of the entire population.

Stochastic projections

To examine extinction probabilities for variable environments with management strategies incorporating different (fixed) fire return times (*T*), we used an algorithm to choose projection matrices based on the time since the last simulated fire event. Every simulation began with a stage vector representing the summed sample population in 1996 (2 new plants, 63 small plants, 406 vegetative plants, 46 flowering plants, and 21 dormant plants). This vector was multiplied by a randomly drawn unburned-year matrix for $T - 1$ iterations, then by a just-burned-year matrix, then a year-after-burn matrix, and then by repeated-unburned-year matrices until the next fire event, where the cycle repeated starting with the just-burned-year projection matrix. Each run lasted for 250 simulated years, with 2000 runs for each simulation. A run was terminated and counted as an extinction if the simulated population ever dropped below the quasi-extinction threshold of 10 plants.

We used a quasi-extinction threshold higher than one as a surrogate for increased extinction risk in small populations due to demographic stochasticity, a factor not included in these models (Groom and Pascual 1998, Menges 1998). We counted a run as a decline if the final population size was smaller than the initial population size. We generated bootstrapped confidence intervals on these calculations using the same methodology as for the averaged matrix elements. For each of the 2000 bootstrap resamples, we estimated extinction

TABLE 4. ANCOVA of *Eriogonum longifolium* var. *gnaphalifolium* germination proportion (angular transformed) in field experiments at the Archbold Biological Station, Lake Placid, Florida, USA, with varying time since fire, litter cover, and exclusion of crawling insects ("Tanglefoot").

Source	SS	df	MS	F	P
Time since fire (Tsf)	0.837	2	0.419	3.908	0.023
Litter (Ltr)	0.184	1	0.184	1.714	0.194
Tanglefoot (Tang)	0.0097	1	0.0097	0.091	0.764
Canopy (Cnpy)	0.454	1	0.454	4.236	0.042
Tsf × Litter	0.059	2	0.029	0.273	0.761
Tsf × Tang	0.178	2	0.089	0.832	0.438
Tsf × Cnpy	0.669	2	0.334	3.121	0.049
Ltr × Tang	0.065	1	0.065	0.609	0.437
Tang × Cnpy	0.239	1	0.239	2.228	0.139
Ltr × Cnpy	0.067	1	0.067	0.627	0.430
Tsf × Ltr × Cnpy	0.0018	2	0.0009	0.008	0.992
Tsf × Tang × Cnpy	0.348	2	0.174	1.626	0.202
Ltr × Tang × Cnpy	0.030	1	0.030	0.280	0.598
Tsf × Ltr × Tang × Cnpy	0.019	2	0.0096	0.090	0.914
Error	10.50	98	0.107		

Note: Canopy cover is included as a covariate.

rates based on 100 runs of the simulation, which may have inflated the resulting confidence intervals slightly since >100 runs would be required to generate precise extinction risk estimates for each set of bootstrapped matrices.

We ran separate simulations for full burns with fixed fire return intervals of 3, 5, 10, 20, 30, 40, 50, 75, 100, and 251 yr (i.e., no fires) using matrices chosen from Table 1A–C. We performed additional simulations of fractional burns using the same series of fire return intervals with the fraction burned = 0.25, 0.5, and 1.0. We present only the non-bootstrapped results without confidence intervals (which are similar in magnitude to the other simulations presented), because we are interested in the relative rankings of risk of extinction under different scenarios using a constant data set rather than a precise quantitative estimate.

We repeated the calculations of quasi-extinction and decline probabilities for the simulations of full burns with the introduction of a simple form of negative density dependence by incorporating a population ceiling. Whenever the simulated population would exceed the ceiling (alternately set to 2000, 10 000, or 100 000 plants), seedlings (stage 1 plants) would be removed until the simulated population was no larger than the ceiling. This simulated hard density dependence resulting from seedling mortality in dense populations, which represents highly asymmetric intraspecific competition, where large adults exclude small recruits.

All simulations were performed using a modified MATLAB implementation of the Borland Turbo Pascal program distprojw (Quintana-Ascencio et al. 2002; see the Supplement).

RESULTS

Temporal variation in vital rates

The effect of time on transition rates between stages was highly significant for unburned ($G^2 = 254.3$, df =

120, $P < 0.0001$), burned ($G^2 = 476.1$, df = 60, $P < 0.0001$), and year after ($G^2 = 116.8$, df = 60, $P < 0.0001$) transition rates. This is evidence that the observed yearly variation in vital rates cannot all be attributed to sampling effects and validates using separate years' matrices in our stochastic analyses.

Seed germination experiment

Germination varied with time since fire (Table 4) and was highest in the long-unburned site (mean proportion germinated per PVC tube = 0.43, SD [angular transformed scale] = 0.42; globally 107 of 240 seeds, 0.45), intermediate in the site 5 yr post-fire (0.22 ± 0.30; global proportion = 0.27), and lowest in the recently burned site (0.10 ± 0.32; global proportion = 0.17). Most germination occurred during the first two weeks after sowing (61–74% of the total for the two cohorts). Presence of litter and protection from small ground predators did not affect germination, but germination increased with percentage of canopy cover in the long-unburned site (time since fire × canopy cover interaction significant, Table 4). No seedlings emerged in the second year (ongoing observations through April 2001). The pattern of high first-year germination and no second-year germination is consistent with prior observations that *E. l.* var. *gnaphalifolium* lacks a persistent seed bank (Carrington 1996). Therefore, modeling proceeded based on this assumption.

Estimates of λ

Using optimistic fertility estimates, we predict unburned *E. l. gnaphalifolium* populations to be very nearly stable. The arithmetic mean unburned projection matrix yielded a λ estimate of 0.999, with 95% CI = 0.975–1.033. Multiplying together the eight unburned-year transition matrices in sequence yielded an estimated λ of 1.007 (95% CI = 0.973–1.054), whereas the mean of 1000 250-yr simulations using randomly
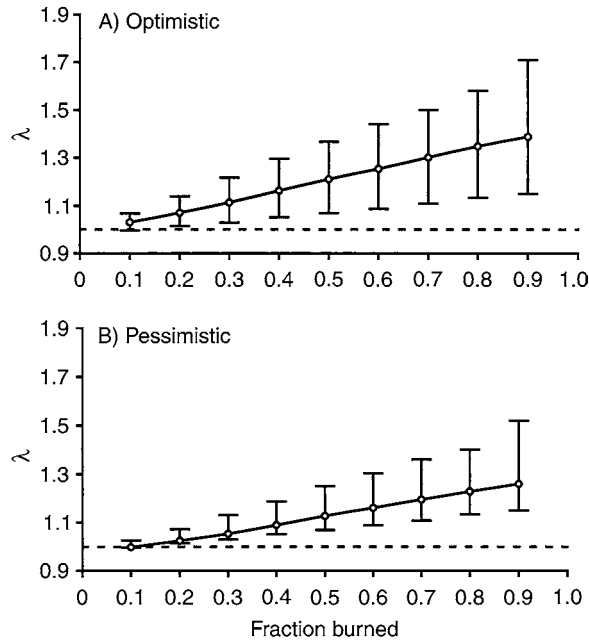
FIG. 1. Population growth rate, λ, increases with the fraction of population burned annually, for (A) optimistic and (B) pessimistic fertility estimates. Error bars are bootstrapped 95% confidence intervals.

selected unburned matrices suggested a λ of 0.995 (95% CI = 0.972–1.031). By contrast, the optimistic burn-year arithmetic mean matrix suggested a rapidly growing population, with λ = 1.359 (95% CI = 1.165–1.689). The transient λ calculated for a single year of growth starting from the unburned stable stage distribution was substantially lower, λ = 1.122, outside the confidence interval for the asymptotic value. Values of λ for the year-after-burn matrix were lower than for unburned or burned populations (95% CI = 0.901–0.995).

Using pessimistic fertility estimates, we predict unburned *E. l. gnaphalifolium* populations are almost certain to decline, although possibly very slowly. The arithmetic mean unburned matrix yielded λ = 0.978 (95% CI = 0.962–1.003), with stochastic estimates of λ = 0.985 (95% CI = 0.960–1.017) using the eight matrices multiplied together in sequence and λ = 0.973 (95% CI = 0.961–1.002) using 1000 replicate series of 250 random draws. As with the optimistic scenario, the averaged pessimistic burn-year matrix predicts a growing population (λ = 1.246; 95% CI = 1.083–1.504) while the transient λ for the same matrix is again lower and outside the confidence interval for the asymptotic value (transient λ = 1.041). Values of λ for the year after burn were lower than for unburned- or burned-year matrices (95% CI = 0.895–0.975).

For annual fractional burns, λ increased linearly with the fraction of the population burned (Fig. 1). Both fertility estimates yield a 95% CI on λ entirely above one if >10% of the population is burned annually.

For cyclic burns, λ decreased as the fire return interval increased (Fig. 2). Using optimistic fertility estimates, 95% CIs on λ were entirely above one for fire return intervals <20 yr (Fig. 2A). Pessimistic fertility estimates yielded confidence intervals on λ entirely above one only if fires occurred at least once every five years (Fig. 2B).

Elasticity analysis

For populations in years without fires, vegetative stages had relatively high elasticities, particularly for stasis of vegetative plants (Table 5). For burn years, survival and fecundity of flowering plants made increasing contributions to λ. For populations a year after burning, transitions from the vegetative state (particularly stasis) had the highest asymptotic elasticities (Table 5).

Five-year transient elasticity analysis on the population vector for the unburned matrix showed stasis in the vegetative stage having the highest transient elasticities for most stages, similar to the importance of this stasis in asymptotic analysis (Table 6A). For burn years, we found substantial differences between asymptotic and transient elasticity analyses on total population size, but the broad pattern of greater contribution by flowering plants was conserved (Table 7). In general, small plants made less contribution to single-year growth while vegetative and flowering plants made more. Transient elasticities on the population vec-
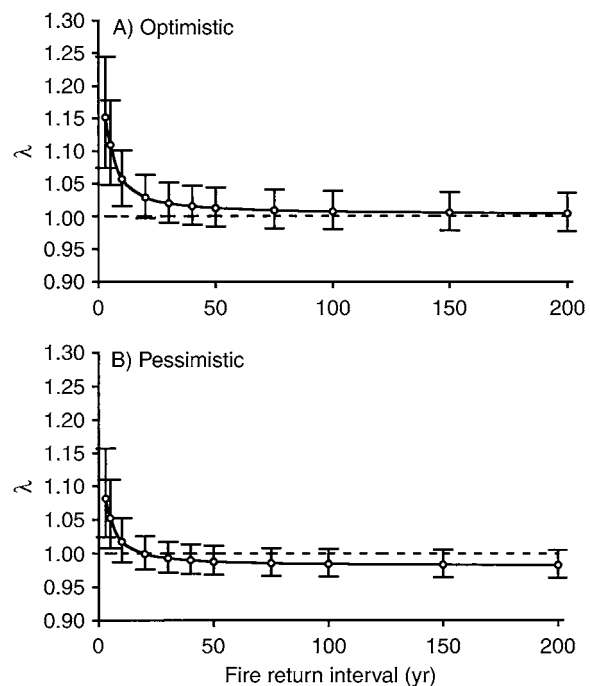

FIG. 2. Population growth rate, λ, increases with the frequency of burning the entire population, for both (A) optimistic and (B) pessimistic fecundity estimates. Error bars are bootstrapped 95% confidence intervals.

TABLE 5. Elasticities of averaged optimistic matrices for three burn-year categories.

Stage	New	Small	Vegetative	Flowering	Dormant
Unburned					
New	0	0	0	0.0492 (0.031–0.076)	0
Small	0.0436 (0.026–0.061)	0.0607 (0.047–0.081)	0.0203 (0.015–0.026)	0.0012 (0.0–0.006)	0.0037 (0.002–0.006)
Vegetative	0 (0–0.002)	0.0524 (0.042–0.063)	0.566 (0.480–0.639)	0.0378 (0.031–0.046)	0.0152 (0.010–0.019)
Flowering	0.0035 (0.002–0.015)	0.0108 (0.004–0.022)	0.0748 (0.061–0.089)	0.0271 (0.016–0.034)	0.0019 (0.001–0.005)
Dormant	0.0021 (0–0.005)	0.0056 (0.002–0.011)	0.0104 (0.007–0.015)	0.0028 (0.002–0.003)	0.0108 (0.007–0.016)
Burned					
New	0	0	0	0.186 (0.131–0.220)	0
Small	0.1515 (0.100–0.152)	0.0693 (0.047–0.085)	0.0016 (0.001–0.004)	0.0034 (0.002–0.015)	0.0011 (0.001–0.003)
Vegetative	0 (0.002–0.019)	0.0726 (0.054–0.082)	0.0322 (0.026–0.056)	0.0178 (0.013–0.044)	0.0038 (0.001–0.006)
Flowering	0.0206 (0.011–0.069)	0.0615 (0.031–0.077)	0.09 (0.081–0.118)	0.1898 (0.161–0.284)	0.0404 (0.020–0.046)
Dormant	0.014 (0.002–0.021)	0.0234 (0.009–0.029)	0.0026 (0.002–0.006)	0.0053 (0–0.017)	0.0132 (0.005–0.017)
After-burn					
New	0	0	0	0.0357 (0.017–0.064)	0
Small	0.0326 (0.014–0.053)	0.0099 (0.004–0.018)	0.0222 (0.004–0.045)	0.0042 (0.001–0.008)	0
Vegetative	0 (0–0.003)	0.0488 (0.028–0.072)	0.4455 (0.338–0.559)	0.1231 (0.093–0.157)	0.0133 (0.005–0.017)
Flowering	0.0014 (0.001–0.008)	0.0041 (0.001–0.008)	0.163 (0.126–0.196)	0.0599 (0.044–0.081)	0 (0–0.004)
Dormant	0.0017 (0–0.004)	0.006 (0.001–0.010)	0	0.0056 (0.002–0.012)	0.0231 (0.008–0.038)

Note: Values in parentheses are 95% confidence intervals.

tor for 5 yr showed largely similar patterns (Table 6B). The major contributions to transient elasticities for most stages were generally made by a few transitions, although elasticities for the dormant stage were affected by many transitions.

A key difference between the 1-yr and 5-yr analyses was the contribution of new and small plants, which had a large contribution in the 5-yr analysis but low transient elasticities for all transitions in the 1-yr analysis. For the dormant stage, transient elasticities were more evenly distributed among transitions.

Summed elasticities for survivorship (L) were highest for unburned and after-burn populations (summed elasticities >0.6 in both cases), while growth (G) and fecundity (F) made relatively greater contributions to population growth in burned populations (combined summed elasticities >0.5; Fig. 3), with non-overlapping confidence intervals in both cases. The summed single-year transient elasticities for the burn-year matrices were all within the corresponding confidence intervals of the asymptotic analysis (Fig. 3).

Density dependence

Imposing a population ceiling as low as 2000 had minimal effects on probabilities of decline or extinction

in any simulations, with a maximum disagreement of 5.2% in the non-bootstrapped point estimates for any scenario. Confidence intervals were very similar across scenarios. We only present the results of density-independent simulations, since the results of the simulations including ceilings are qualitatively indistinguishable.

Extinction probabilities and probability of decline

E. l. gnaphalifolium populations were more likely to decline or go extinct as fires become less frequent. Using optimistic estimates of fertility, confidence intervals on extinction risk always included zero (no risk of extinction), but excluded values >90% only for fire return intervals of 20 yr or shorter (Fig. 4A). Populations were increasingly likely to decline as fires became less frequent (Fig. 4B), with confidence limits excluding a 90% chance of decline only for fire return intervals of 10 yr or shorter. Pessimistic estimates of fertility yielded similar patterns, although only a 3–5-yr fire return interval suggested little chance of assured extinction. Confidence intervals on the probability of decline were >50% for fire return intervals longer than 40 yr.

For intermediate fire return intervals, reducing the

TABLE 6. Five-year transient elasticities for burn-year matrices, using optimistic fecundity estimates (transition- and stage-specific, for individual matrices).

Transition	Code	Component	Transient elasticity on stage†				
			New	Small	Vegetative	Flowering	Dormant
A) Unburned							
Flowering-New	4,1	fertility	0.2378	...	...	...	...
Small-Small	2,2	stasis	...	0.2172	...	...	...
Vegetative-Vegetative	3,3	stasis	0.2753	0.1801	0.5975	0.3824	0.2613
Vegetative-Flowering	3,4	growth	0.1693	...	...	0.1868	...
Partial contribution			0.6824	0.3973	0.5975	0.5692	0.2613
Others <0.15			0.3176	0.6027	0.4025	0.4308	0.7387
B) Burned							
Flowering-New	4,1	fertility	0.2819	0.2128	0.1700	...	0.1849
Flowering-Flowering	4,4	stasis	0.2242	0.1655	...	0.2298	...
Vegetative-Flowering	3,4	growth	0.1723	0.1615	0.1553	0.2039	0.1572
New-Small	1,2	growth	...	0.2029	0.1641	...	...
Small-Vegetative	2,3	growth	...	...	0.1665	...	...
Partial contribution			0.6784	0.7427	0.6559	0.4337	0.3421
Others <0.15			0.3216	0.2573	0.3441	0.5663	0.6579

Note: Shown are individual elasticities >0.15.

† Ellipses (···) indicate transient elasticity <0.15.

fraction of the population burned in each fire led to an increase in the probability of quasi-extinction approximately equal to doubling the fire return interval, although for short fire return intervals doubling the fire frequency increased population risk more than halving the proportion burned (Fig. 5). For fire return intervals >60 yr, there was little effect of fire patchiness on the risk of quasi-extinction.

DISCUSSION

Population dynamics in the absence of fire

Our results suggest a substantial risk of *E. l. gnaphalifolium* population decline in the long-term absence of fire. Optimistic estimates of fertility predict nearly stable population size without fire (λ values close to one), with values possibly as low as 0.97 (halving approximately every 23 yr). Pessimistic estimates of fertility almost always predict declining populations (λ < 1). Stochastic simulations predict that decline is likely in the absence of fire and that decline is nearly certain given pessimistic assumptions of fertility. Extinction is also a possibility without fire, although confidence limits are wide.

If the optimistic estimates of fertilty are appropriate, these *E. l. gnaphalifolium* populations may be stable or decline only very slowly. This suggests the importance of buffering (Doak et al. 2002) or beneficial temporal correlations among vital rates, with stages with high survivorship capable of persisting and storing reproductive potential through relatively unfavorable periods. The apparent capacity for adult plants to remain alive but dormant belowground may also be important in this respect.

Demographic stochasticity may increase extinction risk in declining, fire-suppressed populations of *E. l. gnaphalifolium* (Menges 1998). However, it has also been argued that our method of matrix construction overestimates extinction risks by confounding real year-to-year variation in vital rates (i.e., environmental stochasticity) with apparent variation due to sampling effects independent of any variation in the underlying rates being estimated (Kendall 1998). This is a valid concern, although we do not think it poses a serious problem for our analysis. Our sample sizes for vegetative and flowering plants in unburned populations are generally large, ranging up to 409 and 87, respectively (Table 1A), minimizing such sampling effects. These are the stages with the highest elasticities in unburned populations and are likely to have the largest effects in determining population dynamics when extinction risks are high.
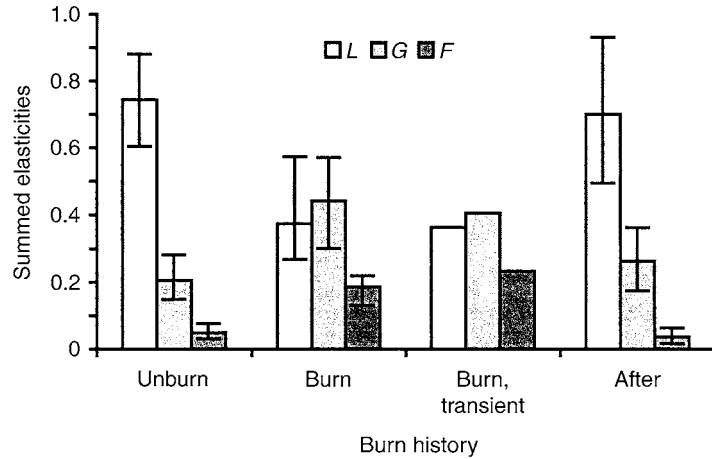
Beneficial effects of fire

Fires benefit *E. l. gnaphalifolium* populations in at least two ways. Reproductive output increases directly as a result of increased flowering (McConnell and Menges 2002). *E. l. gnaphalifolium* seedling establishment also increases in burned areas due to litter removal (McConnell and Menges 2002). However, our germination experiment did not show increased germination

TABLE 7. Single-year transient elasticities of averaged burn-year matrix, using optimistic fecundity estimates.

Transition	New	Small	Vegetative	Flowering	Dormant
New	0	0	0	0.2326†	0
Small	0.0443†	0.0547	0.0206†	0.0023	0.0016
Vegetative	0	0.029	0.2097†	0.0061†	0.0028
Flowering	0.0015	0.0125†	0.2988†	0.0332†	0.0149†
Dormant	0.0018	0.0083†	0.0152†	0.0016	0.0085

† Element outside the 95% confidence intervals of corresponding elements in the asymptotic analysis.

FIG. 3. Summed elasticities (or summed transient elasticities) for stasis and regression (*L*), growth (*G*), and fecundity (*F*) transitions, in populations with different burn histories, using optimistic fecundity estimates. Error bars are bootstrapped 95% confidence intervals. Note that the methodology used to generate confidence intervals could not be applied to the transient analysis.

percentages in recently burned areas and also high-lighted the beneficial effects of partial shading. It is likely that fires favor recruitment, but that post-fire microsite conditions also play a role. Seedling emergence occurred only in shaded and not in unshaded microsites in a prior study of recruitment patterns (Carrington 1996), with shaded, litter-free, watered microsites having the greatest emergence. Complete but moderate fires that remove litter yet allow rapid re-covery of shrub and grass canopies may offer the best opportunities for post-fire recruitment of *E. l. gnaphalifolium*.

In addition, there is a lasting benefit of fires due to their effects on the stage distribution of the population. This results from high transition rates from vegetative to flowering plants whenever a fire occurs and rapid reversion to vegetative plants in years without fire and is evidenced by the (single-year) transient λ for the
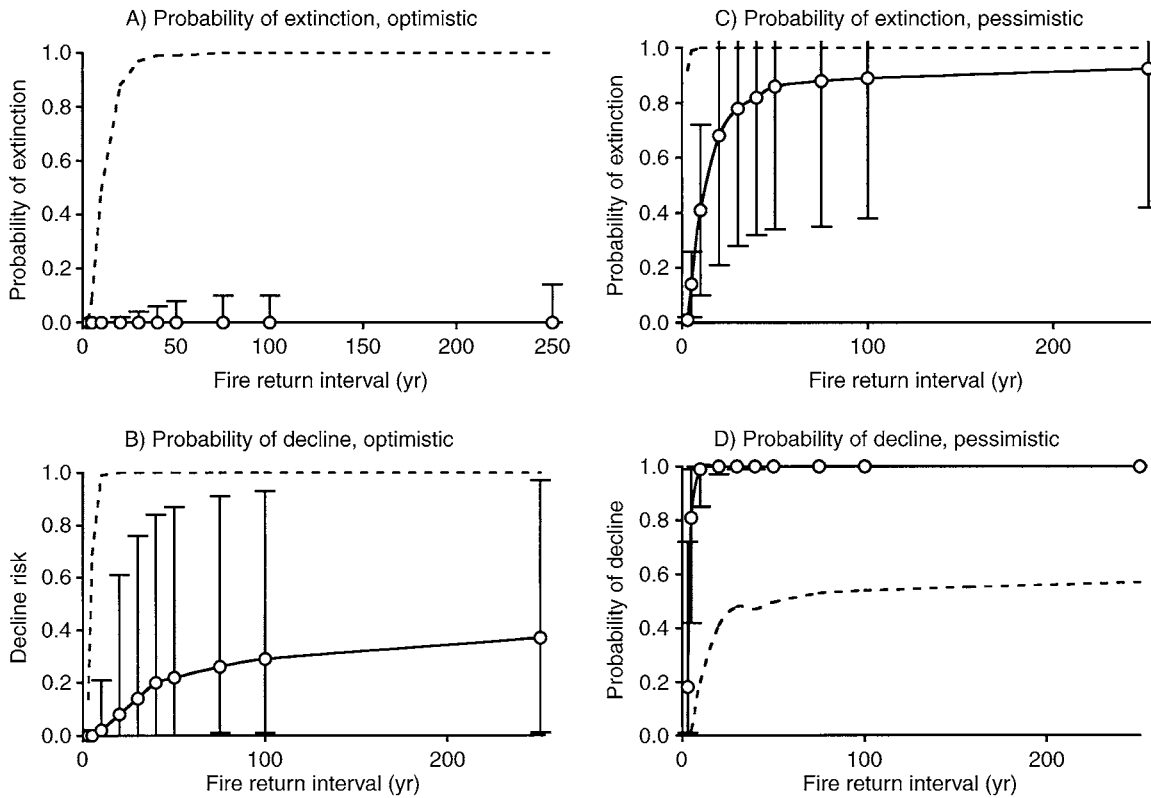
FIG. 4. (A, C) Predicted probability of quasi-extinctions and (B, D) net population declines over 250 yr using the stochastic model. Circles are medians, and error bars are bootstrapped 50% confidence intervals of bootstrapped results. Dashed lines enclose the upper and lower limits of 95% confidence intervals.
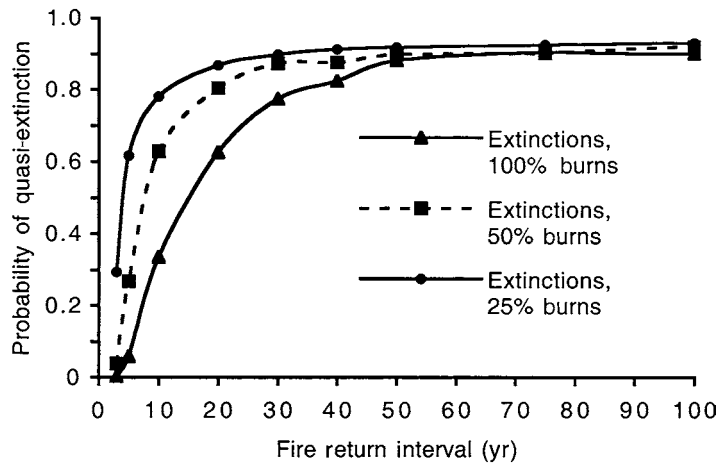
FIG. 5. Predicted probability of quasi-extinction (based on pessimistic fertility estimates, declines certain for fire return intervals >10 yr) over 250 yr using the stochastic model, as a function of the frequency of burning 25%, 50%, or 100% of the population.

after matrix being higher than its asymptotic λ. Similarly, transient λ for an unburned matrix beginning with a post-fire stage distribution is higher than the asymptotic λ. The more often fires occur, the more the population should be skewed away from the unburned stage distribution toward a distribution with more reproductive individuals, so the benefits of fires should increase with increasing frequency. While fire promotes reproduction in *E. l. gnaphalifolium*, it does not hurt survival, which is high after fires due to strong resprouting (McConnell and Menges 2002).

Periodic fires promote population growth in *E. l. gnaphalifolium*. Finite rates of increase for burned years are above one, even given pessimistic assumptions about fertility. With frequent fires, stochastic simulations project low probabilities of decline and very low chances of extinction. Although the after-burn matrices suggested a value of λ below those of the unburned matrices, this possible negative effect was overcome by the positive effects of the burn matrix in all cases we examined.

Life history effects

Vegetative plants make the greatest contribution to population growth in unburned populations, whereas the performance of the flowering stage is of greatest importance in burned populations. Similarly, for fractional burns a stage's "importance" to the population growth rate (sensu Schemske et al. 1994) is relatively higher for the flowering stage when fires are more complete. For burned populations, growth (G) and fecundity (F) combined to make the greatest contributions to population growth, while for unburned populations survival (L) was most important. Since burned populations tended to be increasing, while unburned populations were stable or decreasing, this is consistent with the observation by Silvertown et al. (1996) that fecundity and growth elasticities are more important in growing populations while the importance of survivorship elasticities are higher in declining populations.

Alternative modeling approaches

Our results suggest that stochastic population viability analyses reporting estimated extinction risks should also report probabilities of decline. While the confidence intervals we calculated for extinction risk nearly always included zero (and thus were not particularly informative for determining fire return intervals), for pessimistic estimates of fertility confidence intervals on the probability of decline were >0 for long fire return intervals, meaning population decline is a strong possibility. Extinction risks are sensitive to starting population size, extinction threshold, and model duration, all of which are often chosen somewhat arbitrarily. Using our original criteria for model duration and extinction threshold, we could almost never reject zero threat of extinction. Probabilities of decline had much smaller confidence intervals in the scenarios least favorable to *E. l. gnaphalifolium* populations. By calculating the probability of decline, we were able to see that long-unburned populations were more likely to show net declines than increases (at least in the pessimistic scenario), and further modeling suggests that extinction risks in these scenarios would indeed increase with longer time frames modeled. We also suggest that managers should be concerned with consistent population declines even at rates slow enough to show little risk of short-term extinction. However, this approach carries the caveat that fluctuations around a constant density will also result in some apparent declines.

In the case of *E. l. gnaphalifolium*, neglecting density dependence appears not to substantially affect model outcomes. We chose to model density dependence through imposing a hard population ceiling above which reproduction failed, rather than making per capita fecundity a continuous negative function of population density. As such, we would expect our model to only demonstrate negative impacts of density dependence, since models with continuous negative density dependence would be likely to show a rescue effect

due to increased individual performance at low densities. Very low population ceilings could cause more pessimistic projections. We found increasing effects of incorporating population ceilings below 1000 (with a simulated starting population of 541), but do not believe such low ceilings to be realistic for *E. l. gnaphalifolium*.

We found it informative to consider both traditional elasticities and transient elasticities. Both methods suggested similar broad patterns, with the importance of flowering plants and growth and fecundity transitions increasing for populations that had just burned. However, the two methods disagreed on finer scales of analysis. Both types of transient analyses (1-yr elasticity on total population size and 5-yr elasticity on the population vector) suggested greater importance of fecundity transitions than did traditional elasticity analyses. This is likely because mortality rates were relatively low, so that within a single year, population changes due to mortality were relatively small.

Comparing the two methods of transient elasticity analysis of the burn-year matrix, an interesting difference was the relative contribution of new and small plants, which ranked substantially higher in the 5-yr analysis. This is likely due to the fact that the stable stage distribution feeding into the first burn year has few new or small plants, so their survival has little impact on total population size in one year. By contrast, in the 5-yr analysis continued survival of young plants is important to maintaining the contribution from enhanced reproductive output.

One area in which the disagreement between transient and asymptotic elasticity analyses is particularly large is in the ranking of elasticities. Mills et al. (1999) have demonstrated that elasticity rankings can be affected by changes in a single vital rate, and so many authors recommend a de-emphasis of elasticity rankings (Ehrlen et al. 2001). Our results suggest that elasticity rankings can also change depending on the time frame of analysis. In the case of burn-year transition matrices, only one of the three transitions with the highest ranked asymptotic elasticities is also among the three highest ranking transient elasticities on total population size, with the elements that change ranking in the transient analysis well outside the confidence intervals of the values for the same elements in the asymptotic analysis.

Given a choice between asymptotic and single-year transient elasticity analyses on total population size, we feel that both sets of analysis are informative. Even though asymptotic elasticity analyses of burn-year transition matrices are not strictly appropriate because the transition rates may not apply year after year and the population would never reach the projected stable stage distribution, these analyses do incorporate the positive future effects of even a single burn-year transition on the stage distribution.

Both types of transient elasticity analysis may prove valuable when managers are concerned with maximizing short-term population growth rate. For instance, a population that has recently crashed may be at risk of Allee effects or demographic stochasticity, and a manager may be more concerned with quickly increasing the population above some threshold than with maximizing its long-term growth rate. For extremely short-term effects the single-year transient analysis on total population size may prove easier to interpret, while transient elasticity analysis on the population vector is more informative when stage structure is of substantial interest. Although we applied transient elasticity analyses to the case of fire, we suggest they may prove useful in a variety of scenarios whenever stage distributions of a population do not match the stable stage distribution predicted by their transition rates. Situations in which this mismatch may be expected include reintroduction or restoration of populations, newly established invading species, or invasion fronts.

Management implications

Based on the available data, it appears that the more frequently *E. l. gnaphalifolium* populations can be burned, the better their chances of persistence. The shorter fire return intervals (1–10 yr) are consistent with typical fire return intervals for the turkey oak phase of southern ridge sandhill, while fire return intervals for the hickory phase (also called oak–hickory scrub) are poorly known but may vary widely (Menges 1999). Fire management for *E. l. gnaphalifolium* is therefore broadly consistent with land management objectives in typical habitats.

However, extremely frequent fires might actually be detrimental to *E. l. gnaphalifolium* if the stress of resprouting causes plants to substantially deplete their stored reserves (Bowen and Pate 1993). More data on the effects of numerous, closely spaced fires are needed. In addition, the models used here assumed that the effects of fire were felt for only two years, the year of the fire and one year after, with populations two years after a fire behaving no different from long-unburned populations. However, limited data suggest that populations one year removed from fire did not perform as well as long-unburned populations, implying there may be a recovery period. With the present data set, we were constrained by low sample sizes for intermediate (2+ yr) times since fire, although these data will become available over the next few years in the absence of repeat burns.

Even if extremely high fire frequencies have no detrimental impacts on *E. l. gnaphalifolium* populations, managers often must balance the needs of many species of concern. When managing for multiple species, varying fire regimes (pyrodiversity, Martin and Sapsis 1992) may be advisable so that one suite of species is not repeatedly favored at the expense of others (Howe 1994, Greenberg and Simons 1999). In addition, frequent fires may increase invasions of unwanted exotic

species (Hobbs and Huenneke 1992). At a minimum, however, we can make the recommendation that periodic fires are valuable tools in the reversal of any observed long-term decline in an *E. l. gnaphalifolium* population of concern.

If frequent burning is not practical or desirable, two possible courses of action suggest themselves. For unburned populations, survivorship and the performance of vegetative plants appeared most important to population growth rates, and managers could focus on ways to enhance these aspects of population performance. However such steps are most suitable for the short term only. Ultimately, recruitment is required for population growth. Enhancing survivorship alone usually does more to delay extinction than it does to reverse decline (Silvertown et al. 1996). In addition, traditional elasticity analyses do not indicate what magnitude of changes in the transition rates are actually possible through human intervention, and managers would be wise to target transitions combining high elasticity and ease of manipulation (Caswell 2000). McConnell and Menges (2002) found that clipping *E. l. gnaphalifolium* plants stimulated flowering and that litter removal stimulated recruitment. This suggests that mowing plants and raking litter should stimulate flowering and enhance seedling recruitment. However, the success of recruitment may depend on microsite conditions such as partial shade. In any event, mechanical substitutes for fire are likely to be more expensive than prescribed burns when applied over large areas.

We suggest that prescribed fire is likely to be the most efficient and effective tool for enhancing *E. l. gnaphalifolium* populations over large areas. Based on currently available data, we suggest minimum fire return intervals of 5–20 yr (assuming pessimistic or optimistic fertility estimates). If partial burns are desired or inevitable, more frequent burning will be necessary. For example, halving fire coverage should be accompanied by slightly more than doubling of fire frequency. With partial burns, a 2–20-yr fire return interval that favors *E. l. gnaphalifolium* is consistent with appropriate fire management in Florida's xeric upland ecosystems.

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SUPPLEMENT

MATLAB source code for scrub buckwheat population viability analysis (PVA) is available in ESA's Electronic Data Archive: *Ecological Archives* A012-016-S1.