A Fire-Explicit Population Viability Analysis of *Hypericum cumulicola* in Florida Rosemary Scrub

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Abstract: *Land managers seeking to reestablish historical fire regimes need guidance on how to apply prescribed fire to promote the population persistence of endangered species. We explored extinction risks of* Hypericum cumulicola, *a fire-dependent plant endemic to the Lake Wales Ridge, Florida (U.S.A). Stochastic and deterministic matrix population models based on six censuses (1994–1999) and data from several germination and seedling survival experiments were used to compare* H. cumulicola *demography and extinction probabilities under different fire regimes. Environmental variation associated with site, year, and winter precipitation was included in these models. We estimated time to extinction of unburned populations of different sizes and the probabilities of extinction under no fire, different regular fire-return intervals, and alternating short and long fire-return intervals. Following an initial fire, even relatively large populations of thousands of individuals may become locally extinct within 300–400 years without additional fires. Extinction probability declined as intervals between fires decreased. Fire intervals of >50 years resulted in an appreciable extinction probability after 200 years. Cycles of highly staggered short and long fire-return intervals caused slightly higher chances of extinction than regular fire-return intervals. The simulations were sensitive to estimates of survival in the seed bank. Active management will be required to restore favorable fire regimes in areas where fire has been suppressed. To maintain biodiversity, managers should consider variable fire regimes to match the requirements of a variety of species with different life histories.*

Análisis de Viabilidad Poblacional con Incendios Explícitos para *Hypericum cumulicola* en Breñal de Romero de Florida

Resumen: *Los administradores de tierras que buscan restablecer regímenes históricos de incendios necesitan dirección sobre la manera de aplicar los incendios prescritos para promover la persistencia poblacional de especies amenazadas. Exploramos los riesgos de extinción de* Hypericum cumulicola, *una planta dependiente de incendios endémica de la cordillera del Lake Wales, Florida (E.U.A.). Usamos modelos de matrices poblacionales estocásticos y determinísticos basados en seis censos (1994–1999) y datos de varios experimentos de germinación y supervivencia de plántulas para comparar la demografía y las probabilidades de extinción de* H. cumulicola *bajo diferentes regímenes de incendios. La variación ambiental asociada con el sitio, el año y la precipitación de invierno se incluyó en estos modelos. Estimamos el tiempo de extinción de poblaciones de diferentes tamaños sin quemas y las probabilidades de extinción bajo regímenes sin incendios, con incendios a intervalos regulares diferentes y a intervalos que alternan entre periodos cortos y largos. Aún las poblaciones relativamente grandes de miles de individuos subsiguientes a un incendio inicial pueden volverse localmente extintas en 300–400 años sin incendios adicionales. La probabilidad de extinción disminuyó cuando los intervalos entre incendios disminuyeron. Los intervalos entre incendios > 50 años resultaron en una extinción considerable después de 200 años. Los ciclos con intervalos altamente escalonados de intervalos cortos y largos de retorno de incendios causaron probabilidades de extinción ligeramente más altas cuando se compararon con intervalos regulares de retorno de incendios. Las simulaciones fueron sensibles a estimaciones de sobrevivencia en los bancos de semilla. Se requerirá una administración activa para restablecer*

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regímenes favorables de incendios en áreas donde los incendios han sido eliminados. Sin embargo, para mantener la biodiversidad, los administradores deben considerar regímenes de incendios variables para satisfacer los requerimientos de una variedad de especies con diferentes historias de vida.

Introduction

The demographic response of plant species to biological and physical changes that occur across fire cycles is determined by a variety of vital attributes (Noble & Slatyer 1980; Menges & Kohfeldt 1995). Suites of vital attributes are associated with species in particular environmental conditions and may provide assurance to cope with only certain fire regimes (Keeley 1981). For example, in many species, aboveground individuals are killed by fire and their populations recover from seeds. These "obligate seeders" are more common where open spaces persist several years after fire (Menges & Kohfeldt 1995). Obligate seeders are particularly sensitive to the length of the interval between fires because of the timing of critical life-history events such as seedling recruitment, reproductive maturation, and senescence (Johnson 1982; Bradstock et al. 1995; Enright et al. 1998*a*, 1998*b*).

Human-imposed fire regimes, including total fire suppression and extremely infrequent but intense fires, often deviate from presumed historical (pre-European settlement) ranges of fire intensity, extent, and frequency (Parsons 1976; Pianka 1992). In addition, remnant natural areas within human-modified landscapes may not include conditions favorable for the spread of naturally ignited fires. Thus, current fire regimes may fail to provide the conditions required for some species to persist, and disruption of fire regimes is commonly cited as a major threat for many species (Flather et al. 1998; Wilcove et al. 1998).

Matrix models of population dynamics take advantage of available autecological information and can offer guidance for better management (van Groenendael et al. 1988; Burgman et al. 1993; Enright et al. 1998*a,b*). These models provide a powerful tool with which to compare population viability under different fire regimes (Bradstock & O'Connell 1988; Silva et al. 1991; Burgman & Lamont 1992; Canales et al. 1994; Bradstock et al. 1995; Gross et al. 1998; Hoffmann 1999). Stochastic demographic modeling, in particular, allows more realistic population projections and better estimates of extinction risks than deterministic approaches because it incorporates the effects of random temporal environmental fluctuations (e.g., Menges 1992; Bastrenta et al. 1995; Oostermeijer et al. 1996; Picó et al. 2002; Menges & Quintana-Ascencio 2003).

The Lake Wales Ridge in south-central Florida (U.S.A.) supports more than a dozen rare and endemic plant species (Harper 1948; Christman & Judd 1990; Estill & Cru-

zan 2001). Several of these species are essentially restricted to open, sandy areas in xeric Florida rosemary scrub (Abrahamson et al. 1984; Menges & Hawkes 1998). Fire plays a major role in shaping community composition and dynamics of Florida rosemary scrub (Abrahamson et al. 1984; Myers 1990; Menges 1999). Agricultural, commercial, and residential development have changed drainage patterns, modified fire regimes, and fragmented Florida scrub (Peroni & Abrahamson 1985; Menges 1999). A better understanding of the effects of fire variation on plant species viability will provide critical information for the management of fire-dependent species in Florida scrub and in the many other fire-dependent ecosystems worldwide.

We evaluated the extinction risk of *Hypericum cumulicola,* a Florida scrub endemic species, under different fire regimes. We used deterministic and stochastic Lefkovich matrix models of demographic variation with time since fire in Florida rosemary scrub to (1) analyze the demographic patterns of this species along time-since-fire gradients and (2) predict its extinction probability under various fire-return intervals. We included environmental variation associated with site, year, and precipitation in these models.

Methods

Study Species, Site, and Community

Hypericum cumulicola (Small) P. Adams, the Highlands scrub hypericum, is endemic to Polk and Highlands Counties in central Florida (Christman & Judd 1990; Estill & Cruzan 2001). This species is listed as endangered by the U.S. Fish and Wildlife Service (1999) and the state of Florida (Coile 2000). Locally, it may occur in relatively large populations of hundreds or thousands of individuals (Menges et al. 1998). This small, short-lived plant is essentially limited to open areas between vegetation patches in xeric Florida rosemary scrub. Most flowering and fruiting takes place between June and September. Flowering branches are many flowered and indeterminate. *H. cumulicola* is self-compatible but requires the services of pollinators to set seed (Evans et al., in press). Fire kills aboveground individuals (Menges & Kohfeldt 1995; Quintana-Ascencio & Morales-Hernández 1997), but seeds in the soil survive fire and form long-lived seed banks (Quintana-Ascencio et al. 1998). Fire suppression and alteration of fire regimes consti-

tute threats to this species because of its dependence on fire to release local populations from competitive exclusion (Quintana-Ascencio & Morales Hernández 1997; Quintana-Ascencio & Menges 2000). *H. cumulicola* populations have a high degree of genetic differentiation (Dolan et al. 1999) and a patchy distribution consistent with metapopulation dynamics (Quintana-Ascencio & Menges 1996).

The study was carried out at Archbold Biological Station, Highlands County, Florida (U.S.A.). Sandy, infertile soils support a diverse array of vegetation associations, including scrub, flatwoods, and seasonal ponds (Abrahamson et al. 1984; Myers 1990). Detailed community descriptions are given by Abrahamson et al. (1984), Menges and Kohfeldt (1995), and Menges (1999). Archbold comprises a complex mosaic of habitats with different fire histories, including areas not burned since the late 1920s (Abrahamson et al. 1984). Historical records document the occurrence of multiple natural, accidental, and prescribed fires since 1967 (Main & Menges 1997). Natural fire-return intervals vary considerably among habitats because of different community structures, chances of ignition, rates of fuel accumulation, and fire propagation (Abrahamson et al. 1984).

Florida rosemary scrub is an open shrub-dominated community, occasionally with a sand pine (*Pinus clausa*) canopy, occurring on sandy, well-drained soils in ridges and knolls in central and coastal Florida (Abrahamson et al. 1984). In central Florida, stands of uneven-aged Florida rosemary (*Ceratiola ericoides*) often dominate the shrub layer (Johnson & Abrahamson 1990; Gibson & Menges 1994). Other species in this stratum include xeromorphic oaks (*Quercus* spp.) and palmettos (*Serenoa repens* and *Sabal etonia*). The prostrate shrub *Licania michauxii*, ground lichens (*Cladonia* and *Cladina* spp.), spike moss (*Selaginella arenicola*), and several herbaceous species proliferate in the open, sandy areas that characterize this type of scrub. Estimates based on Florida rosemary life span and reproductive maturity suggest that fire-return intervals in this community range between 20 and 100 years (Menges 1999).

Demographic and Environmental Data

We used deterministic and stochastic matrix population models based on six annual censuses (1994–1999) and data from several germination and seedling survival experiments to compare the demography and extinction probabilities of *H. cumulicola* under different fire regimes. We selected 14 *H. cumulicola* populations in rosemary scrub patches representing a gradient of time since fire, patch size, and the north-south range of distribution of rosemary scrub patches within Archbold (Table 1; see also Quintana-Ascencio 1997). Long-term records were used to determine the fire history of each rosemary scrub site (Main & Menges 1997). We obtained monthly precipitation records from Archbold Biological Station (1952-present; Main & Menges 1997) to depict seasonal and annual weather variation.

We estimated the survival and growth of *H. cumulicola* individuals from annual August–September censuses of marked individuals (4029 individuals) conducted for 6 years (1994–1999). All individuals on site were included in populations with <100 plants. We included at least 70 individuals each year in populations with >100 plants, sampled in a stratified random fashion along 1-m-wide belt transects parallel to the longest axes of open sand gaps. We sampled the closest individual, if one was present, for every meter along the center line of each transect. We placed a staked flag with a numbered aluminum tag near each individual. Additional individuals were added throughout the study. We measured maximum plant height each year, the total length of reproductive stalks for every individual in 1995 and 1996, and distance to the nearest conspecific in 1994, 1995, and 1997.

We estimated seed production each year. We counted the number of flowers, fruits, and reproductive buds for each studied individual during their reproductive peak in August–September of each year, except 1997 and 1999. We used linear regressions relating plant height and number of reproductive structures (logarithm-transformed data) to estimate the number of fruits in these 2 years (all $r^2 > 0.75$, $n = 20$ per site). In 1995, 1996, and 1998, we collected the most distal mature fruit of randomly selected individuals in each population. Because *H. cumulicola* has many flowers and is indeterminate, choosing the most distal mature fruit allowed us to evaluate a recently matured fruit, avoiding potential bias for other fruit characteristics. Seeds from these fruits were examined and counted under a microscope. Damaged fruits were eliminated from the sample. We estimated germination rates from seeds experimentally sown in June and December 1995 in recently burned and long-unburned patches (80 seeds per microsite, 10 microsites per site, 2 sites per treatment; Quintana-Ascencio & Menges 2000). We considered *H. cumulicola* seed germination in areas sown with two alternative species as a control (Quintana-Ascencio & Menges 2000).

We studied long-term seed-bank dynamics using *H. cumulicola* seeds in nylon mesh bags buried (5–10 cm depth) for 1 and 2 years in patches with different times since fire (20 seeds per bag, 2 × 2 cm, Applied Extrusion Technologies, hole size 0.8 mm; five bags per year per site, two to three sites per treatment; Quintana-Ascencio et al. 1998). We examined and counted the unearthed seeds under a microscope. Damaged seeds were discarded and undamaged seeds were tested for germination in outdoor conditions for 4 months (Quintana-Ascencio et al. 1998).

We estimated aboveground *H. cumulicola* density and recruitment from 1 × 0.5 m permanent quadrats moni-

Table 1. Rosemary scrub patch-identification number, area (ha), date of last fire, number of gaps sampled and their area, number of 0.5–m² quadrats, and yearly census sample size per site.[a]

Identification number	Area (ha)	Last fire date	Number of gaps (area in m²)	Number of quadrats	n (maximum/minimum) 1994–1999
<6 years after fire					
42	1.69	August 1993	3 (335)	20	110/80
50	0.40	August 1993	1 (180)	20	133/82
57	0.09	August 1993	2 (142)	20	87/61
8–14 years after fire					
29	1.26	January 1985	1 (300)	20	91/44
45	0.25	July 1986	2 (345)	20	80/50
67	0.60	June 1986	6 (220)	20	92/37
87	0.17	June 1986	1 (1260)	50	122/13
88	0.27	June 1986	1 (272)	20	80/45
91	0.81	June 1986	1 (960)	40	87/49
>21 years after fire					
1	1.85	<1967	10 (318)	20	230/57
32[b]	0.17	<1967 and May 1997	1 (183)	20	80/0
59	0.37	1968	7 (189)	20	81/43
62	0.70	<1967	3 (232)	20	113/43
93	0.57	1972	9 (336)	20	139/47

[a] *Patches are grouped by years after fire during this study.*
[b] *Burned in May 1997.*

tored approximately every 6 months from September 1994 through August 1999. At least 20 quadrats were randomly located in open areas between shrubs in each study site. Additional quadrats were located in some patches to sample no less than 2% of the suitable area in these patches (Table 1).

Model Formulation

For each population and year combination, we built a matrix model (Caswell 2001) with the form $\mathbf{n}_{(t+1)} = \mathbf{An}_{(t)}$, where $\mathbf{n}_{(t)}$ and $\mathbf{n}_{(t+1)}$ are vectors whose elements, a_i, are the number of individuals that belong to the ith category at times t and $t+1$, respectively. The element a_{ij} of the population-projection matrix, A, represents the transitions or contributions from individuals in the ith category to the jth category after one time step. To construct projection matrices, we defined six life-history stages by combining morphologically defined stages (e.g., vegetative vs. reproductive plants) with divisions based on size: (1) seeds in the seed bank; (2) a single stage of first-year plants (seedlings) at census time; (3) a single vegetative stage and three reproductive classes; (4) small flowering individuals, 12–33 cm tall; (5) medium flowering individuals, 34–50 cm, and (6) large flowering individuals, >50 cm.

Seedling identification was straightforward in permanent quadrats, in recently burned sites, and for recently germinated plants. Seedling identification was not certain during censuses in sites more than 3 years after fire. We defined putative seedlings as small (<12 cm height, the threshold above which plants present fruits), newly appearing plants with fewer than three stems. This pro-

cedure was consistent with data from recently germinated seedlings followed from May 1995 through November 1997. We combined data for seedlings and putative seedlings to describe a single stage of first-year plants (seedlings) at census time.

Height was the best predictor of *H. cumulicola* growth, fecundity, and survival, compared with other morphological characteristics such as number of stems and total length of reproductive stalks (Quintana-Ascencio & Morales-Hernández 1997). Thus, we used an algorithm based on height variation to delimit adult stage classes (Moloney 1986). This algorithm minimizes sample and distribution errors associated with any classification attempt. Distribution errors occur if categories are so broad that their members do not have the same transition probabilities. Sampling errors result from insufficient sample sizes, which imply inaccurate estimations of transition probabilities (Moloney 1986). The algorithm can also account for differences in transition probabilities among sites, time-since-fire groups, and census periods.

To implement Moloney's (1986) algorithm, we set the smallest size as the initial minimum boundary value of the smallest category and used the maximum size minus one third of the range as the initial maximum boundary. We chose the upper boundary of the first category to yield the minimum sum of sampling and distribution errors, with 100 subsamples and 1-cm increments. The procedure was repeated for sequentially larger categories. Stages were defined from samples of at least 50 plants. Stage boundaries were defined by fire groups rather than by populations because the minima were sharper. We identified three reproductive classes: small

flowering individuals (≤33 cm height), medium flowering individuals (>33–50 cm), and large flowering individuals (>50 cm). Because of small sample sizes, a single vegetative category was employed. We found no evidence of plant dormancy because only 0.3% of plants, originally recorded as dead, were later found alive; these were attributed to sampling error.

Transitions other than fertility (stages 1 and 2) were calculated as the probability that a plant classified in stage i changed to stage j in the subsequent census (a_{ij}). Most annual growth and survival transition probabilities were estimated directly from population-specific demographic data. We used mean values across groups defined by time since fire to estimate transitions when the sample size for a given stage in one population was smaller than six (following Bullock et al. 1994). This procedure avoids the use of estimates from low sample sizes. Overall, 76.5% of these matrix entries had specific data for population and year, and 23.5% had data averaged across a time-since-fire group within a year. Population- and year-specific matrices are available at http://www.archbold-station.org/abs/data/plantdata/hypcumApp1.htm (accessed 2002).

Most germination of *H. cumulicola* occurs during winter and early spring, and fertility terms in the model represent newly recruited individuals surviving until August or individual contributions to the seed bank. We estimated seedling recruitment from permanent quadrats and partitioned seedling numbers among reproductive stages in proportion to stage-specific abundance and seed production. We estimated stage-specific contributions to the dormant by multiplying the number of ungerminated seeds by their probability of remaining in the seed bank (Quintana-Ascencio et al. 1998). We always assumed recruitment from seed bank, even when there was no evidence of recruitment in permanent quadrats in a given year. Seedling production from the seed bank was estimated on the basis of experimental observed seed survival and germination, seedling survival in the field until August, and annual variation in recruitment.

Analysis of Vital Rates Patterns

We used MATLAB (MathWorks 1997) to obtain population- and year-specific finite rates of increase (eigenvalue[5], λ). We do not include analyses of deterministic asymptotic parameters of matrices from the first and second years after fire because only seeds and seedlings were present. We used SPSS 10.0 (SPSS 2000) to estimate transition probabilities and evaluate regression models for the association between r (ln(λ)) and time since fire and to perform loglinear and analysis of variance (ANOVA) tests on demographic parameters. We used a loglinear analysis to test the significance of time since fire (T), stage (S), and distance (D) to the nearest

conspecific neighbor for plant mortality (M) in the following year (Fienberg 1987; Caswell 2001). Individuals were divided in two classes of distance to the nearest conspecific: <20 cm and ≥20 cm (threshold corresponds to the median value). We declared as "the null model" the model DST, M, which reflects the distribution of the data among stages, time since fire, and distance but assumes that fate is independent of these variables. The change in log-likelihood following the addition or deletion of a term provides its statistical significance (Fienberg 1987; Caswell 2001). We examined the significance of adding terms representing the interaction of mortality with stage, time since fire, distance, and their combinations.

Fire Simulations

We determined times to extinction and extinction probabilities of *H. cumulicola* in Florida rosemary scrub patches under various fire-return intervals from simulations of population trajectories. We used an algorithm that projects random sequences of different matrices while also incorporating changes in their probability of occurrence. By varying matrices rather than individual matrix elements, we preserved life-history correlation structure and obtained a more conservative risk assessment (Greenlee & Kaye 1997; Menges 2000; Fieberg & Ellner 2001). We changed the probability of occurrence of these matrices in relation to time since fire and winter precipitation. Our method expands modeling strategies introduced by Bierzychudek (1982), Silva et al. (1991), and Canales et al. (1994) and later used in other studies (e.g., Beissinger 1995; Damman & Cain 1998; Hoffmann 1999).

Every simulation assumed an initial postfire population that consisted of a vector including only seeds from a seed bank. Matrix choices during the simulation were governed by the following sequence of eight phases (number of matrices in parentheses): (0) fire year ($n = 1$); (1) first year after fire ($n = 1$); (2) second year after fire ($n = 4$); (3) 3–6 years after fire ($n = 12$), (4) 6–8 years after fire, (5) 8–14 years after fire ($n = 12, 12, 6$), (6) 14–20 years after fire, and (7) >20 years after fire ($n = 10, 8, 4$). For phases 1, 2, and 3 we used a random sequence of matrices chosen among those belonging to the reference phase. For phases 5 and 7 we used a random sequence of matrices chosen among those belonging to the reference phase with their probability of occurrence determined by the relative frequency of the winter precipitation of the year sampled (0.37 for precipitation <12.7 cm; 0.59 for 12.7–38.1 cm; and 0.04 for >38.1 cm, based on Archbold weather data, 1952–1999). For phases 4 and 6, for which we had no specific matrices, we interpolated by choosing a random sequence of matrices, with the probability of occurrence of the matrices

in the next lowest phase linearly decreasing and those of the next highest phase increasing. We modeled fires, which eliminate all aboveground individuals, using a matrix with only the probability of seeds remaining in the seed bank (phase 0). In the absence of empirical estimates of fire effects on seeds in the soil, we used an average of seed survival from all populations (Quintana-Ascencio et al. 1998) and evaluated the sensitivity of our extinction estimates to the variation in this parameter.

We used DISTPROJW, a modified version of POPROJ (Menges 1990), written in Pascal (Borland), to run the simulations described above. A version of this algorithm executable in IBM-compatible microcomputers is available from the authors. The model does not consider density dependence, but it constrains projected plant densities after 1 trillion individuals per stage. These numbers occurred only under extremely favorable scenarios and long runs (>600 years). We obtained 1000 replicated simulations to estimate time to extinction. We performed two thousand simulations to estimate extinction probability for each fire regime studied. Preliminary runs indicated that the range of variation of the output of 2000 simulations is <5%.

We estimated (1) time to extinction of unburned populations having different seed numbers after an initial fire, (2) probability of extinction after 99, 199, 399, and 599 years under regular fire-return intervals ranging from zero to three fires every 100 years (no fires and fires every 200, 150, 100, 75, 50, 40, and 30 years), and (3) extinction probabilities after 401 years under alternating short and long fire-return intervals repeating every 200, 100, and 50 years. These fire regimes cover the range of proposed fire-return intervals for rosemary scrub, which will usually not burn before 20 years after fire (Menges 1999).

To examine the effect of population size, we varied the initial number of seeds by five orders of magnitude from 10 to 100,000. For all other simulations not examining the effect of initial size, we used 1000 seeds as the initial vector. This number of seeds in the seed bank is associated with plant numbers in stable stage distributions of *H. cumulicola* within the range estimated for long-unburned populations in 1999 (94–244 plants). We determined the effect of variation in seed viability in the soil by modifying the transition for seed survival in the soil to 50% of the value determined experimentally (Quintana-Ascencio et al. 1998). This change assumes that mortality in the soil could be higher than that estimated in our study.

Populations were considered locally extinct upon the "death" of the last individual (threshold = 1). Because seeds make >90–99% of stable stage distributions, however, we also examined 10 and 100 individuals as alternative quasi-extinction thresholds. These are more conservative thresholds that provide an estimate of the probability of aboveground plant disappearance.

Results

Fire and *H. cumulicola* Demographic Attributes

Demographic vital rates varied among life stages, among years, and across the time-since-fire gradient. Growth (natural logarithm of height change rate) was greatest for seedlings (1-year-old plants) and decreased with size for the other stages (Fig. 1 [ANOVA]: stage, $p < 0.0001$ for all years; time-since-fire [tsf], $p > 0.18$ in 1994, 1995, and 1997, and $p < 0.0001$ in 1996 and 1998; stage*tsf, $p > 0.18$ in 1994 and 1997, and $p < 0.0001$ in 1995, 1996, and 1998). In most conditions, individuals in the largest adult stage showed slightly negative or no change in height (Fig. 1). Number of reproductive structures (buds, flowers, and fruits) increased with plant size and was highest in recently burned sites (Fig. 1 [ANOVA]: stage, tsf, and tsf*stage, $p < 0.0001$ for all years). The most extreme differences in fecundity among stages occurred in recently burned sites (<3 years after fire), where a few large flowering plants had >6000 reproductive structures. Size category and time since fire affected *H. cumulicola* mortality (Fig. 1), but distance to nearest conspecific did not affect this variable (Table 2). Although mortality was variable among years and stages, it was generally lower in recently burned populations (particularly <5 years after fire; Table 2; Fig. 1) than a decade or more after fire.

Population-year specific λs ranged from 0.66–5.53 in recently burned sites (3–6 years after fire; median = 1.34, $n = 12$ matrices), to 0.78–2.30 in sites a decade after fire (8–14 years; median = 0.96, $n = 30$), and 0.59–2.10 in long-unburned sites (>20 years; median = 0.95, $n = 20$). A significant inverse relationship was found between time since fire and ln(λ) (Fig. 2). Inverse function was the best among linear models, including logarithmic and exponential models. This relationship predicts high finite rates of increase during the first years (<5) after fire, followed by a rapid decline, with the fitted line crossing the stable finite rate of increase (ln(λ) = 0) about 17 years after fire.

Observed and Predicted Population Density

In observed populations, plant density increased during the first years after fire, reached a peak between the third and fourth year after fire, and subsequently declined (Fig. 3a). Most populations declined at a decade or more after fire (Fig. 3a). Seedlings and small and medium reproductive stages were the most abundant. Relative abundance among stages changed with time since fire, with seedlings making the more variable contributions to total density during the first years after fire. Observed long-unburned populations were denser than observed populations a decade after fire (Fig. 3a).
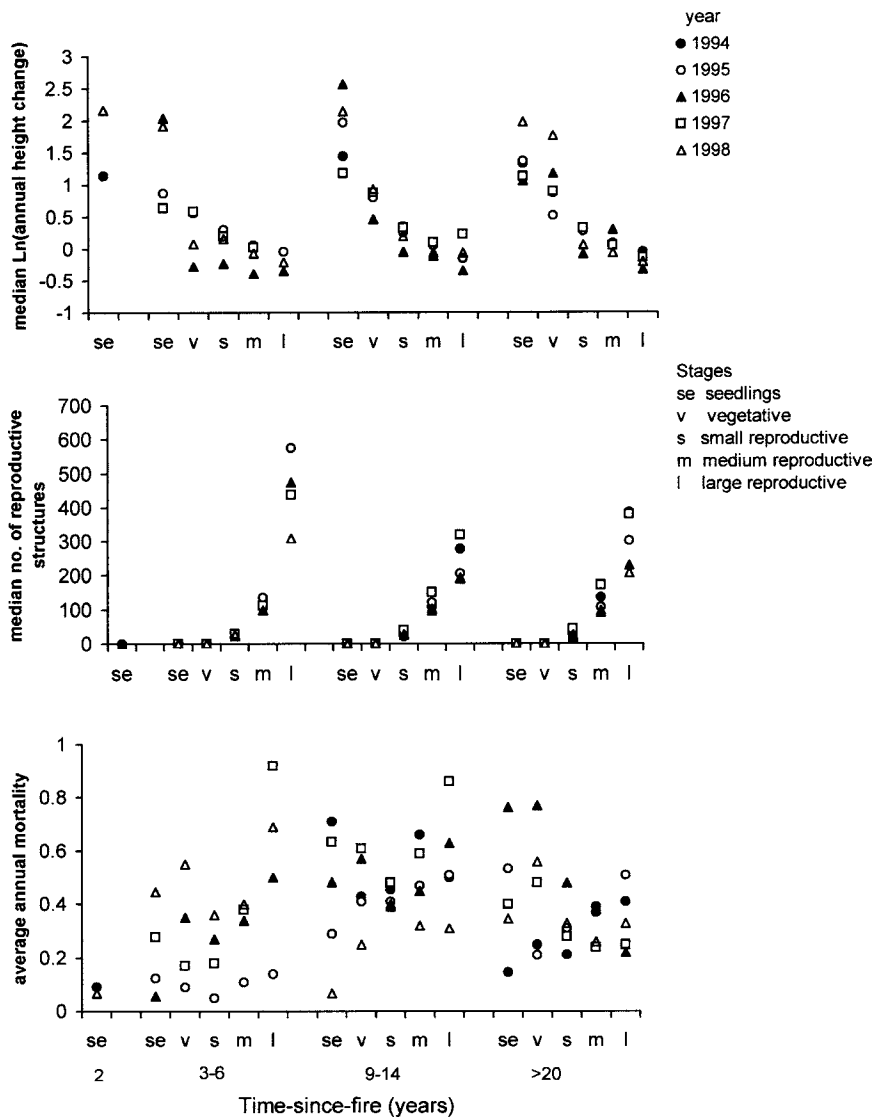
Population trajectories of our model appear to mimic

Figure 1. Demographic parameters per stage of Hypericum cumulicola *and year in Florida rosemary scrub sites with different times since fire: median growth rates [ln(annual height change)], median number of reproductive structures (flowers, fruits, and reproductive buds); and average annual mortality.*

observed density variation and general population trends. Relative to observed dynamics, however, the simulations depicted a larger range of possible outcomes, a slightly delayed median peak population, and slower declines (Fig. 3b). Median predicted densities reached a peak at the fifth year after fire, followed by a steep decrease until the seventh year. Between 10 and 30 years after fire, the model projected relatively stable populations (Fig. 3b). Afterward, the model predicted slow decreases in density.

Extinction Risk and Fire

Our simulations predicted that, in the absence of immigration and without subsequent fires, even populations of thousands of seeds following an initial fire are likely to become locally extinct within 300–400 years. Smaller starting populations may become extinct sooner, often

after <200 years. During simulations, aboveground individuals became rare or absent many years in advance of the "death" of the last seed.

Extinction probability declined as intervals between fires decreased (Fig. 4). Fire intervals longer than 50 years resulted in appreciable extinction risk after 200 years. Extinction probability changed rapidly between fire regimes of 75 and 100 years (Fig. 4). The model was sensitive to estimates of survival in the seed bank. When the survival of seeds in the seed bank was reduced by 50%, extinction probabilities did not change significantly or they increased up to 50%, depending on prediction interval and fire regime (Fig. 4). Cycles of divergent, alternating short and long fire intervals resulted in slightly higher chances of extinction than did regular fire intervals (Fig. 5). This difference was important only when alternating intervals were widely divergent (five-fold or greater).

Table 2.   Loglinear analysis of effects of stage (S), time since fire (T), and distance to nearest conspecific (D) on individual fate.[a]

Factor	Model[b]	df	df	1994–1995 (n = 1130) base	1994–1995 (n = 1130) change	1995–1996 (n = 1121) G base	1995–1996 (n = 1121) change	1997–1998 (n = 1160) base	1997–1998 (n = 1160) change
Null	DST	29		233.8		160.4		116.4	
Stage	DST,S	25	4	103.5	130.3[b]	134.4	26.0[b]	68.4	48.0[b]
Time since fire	DST,T	27	2	53.4	180.4[b]	48.3	112.1[b]	89.9	26.5[b]
Distance	DST,D	28	1	233.7	0.1 ns	158.9	1.5 ns	113.5	2.9 ns
Conditional stage									
	DST,T,S	23	4	28.8	24.6[b]	26.0	22.3[b]	44.5	45.4[b]
	DST,D,S	24	4	100.7	133.0[b]	133.9	25.0[b]	67.2	46.3[b]
Time since fire									
	DST,D,T	26	2	52.0	181.7[b]	48.0	110.9[b]	89.7	23.8[b]
	DST,S,T	23	2	28.8	74.7[b]	26.0	108.4[b]	44.5	23.9[b]
Distance									
	DST,T,D	26	1	52.0	1.4 ns	48.0	0.3 ns	89.7	0.2 ns
	DST,S,D	24	1	100.7	2.8 ns	133.9	0.5 ns	67.2	1.2 ns
Interactions									
	DST,ST	15	8	20.5	8.3 ns	17.2	8.8 ns	14.0	30.5[b]
	DST,DS	20	4	97.0	3.7 ns	129.5	4.4 ns	63.5	3.7 ns
	DST,DT	24	2	49.4	2.6 ns	44.3	3.7 ns	87.3	2.1 ns

[a] *Number of plants per interval in parentheses; ns, not significant.*
[b] $0.001 < p < 0.05.$

Discussion

Population Dynamics and Disturbance of *Hypericum cumulicola*

Environmental changes that occur during disturbance and community recovery affect the availability of essential resources (e.g., water, nutrients, light) and alter species interactions, such as pollination, herbivory, and competition (Bazzaz 1996). Resource pulses associated with disturbances can be essential for population persistence, particularly for species with low tolerance for competition. Most human disturbances in ecological communities deviate from historical ecological disturbance regimes. The modeling of disturbance effects on plant population viability is crucial to understanding the effects of changes in disturbance regimes and to species management and conservation.

After fire in Florida rosemary scrub, *Hypericum cumulicola* had higher fecundity, survival, establishment, and population growth rates than in unburned populations. Several mechanisms may explain these responses. Fire top-kills dominant shrubs, removes lichens (Hawkes & Menges 1996), destroys allelopathic agents affecting seed germination and survival (Hunter & Menges, 2002), and creates unoccupied gaps with higher levels of soil water (Mallik et al. 1984; Gagnon et al., unpublished data). Shrub and lichen dominance increase with time since fire, presumably reducing water and nutrient availability (Abrahamson 1984; Menges & Kohfeldt 1995; Schmalzer & Hinkle 1996). These changes gradually decrease the survival, fecundity, and establishment of *H.*

cumulicola and several other fire-dependent Florida-endemic herbaceous species (Hawkes & Menges 1995; Menges & Kimmich 1996; Quintana Ascencio & Morales-Hernández 1997; Quintana Ascencio & Menges 2000). Population reductions with time since fire may result in the disappearance of aboveground individuals in long-unburned sites (>24 years after fire), as we have seen in gaps within sites for *H. cumulicola* (Quintana-Ascencio 1997) and for entire populations of *Eryngium cuneifolium* (E.S.M. and P.F.Q.-A., unpublished data). With sub-
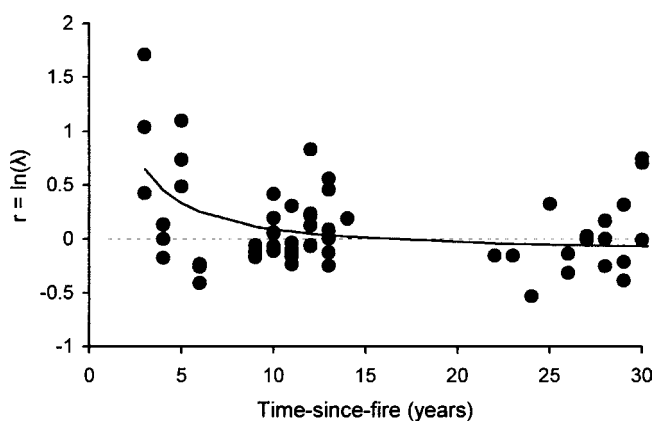

Figure 2. Inverse relationship between ln(λ) of H. cumulicola *populations and time since fire of Florida rosemary scrub sites (y = 0.15 + 2.39/x; r^2 = 0.21, F = 15.61; p < 0.001). An inverse relationship remains the best fit even after removal of the highest value at 3 years after fire.*
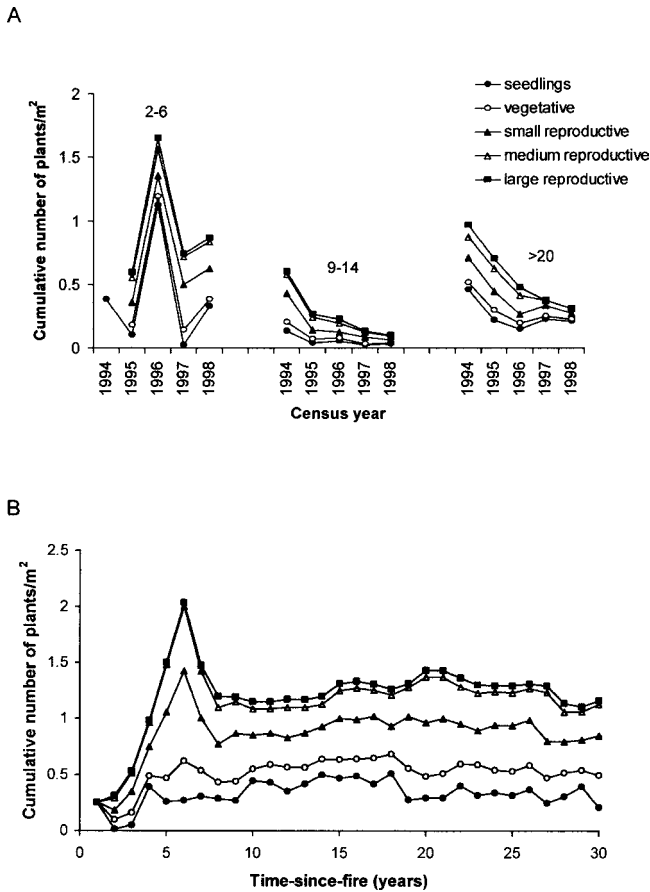
Figure 3. Observed and simulated cumulative above-ground plant densities per stage of H. cumulicola *in each year in sites with different times since fire: (A) median observed plant densities per square meter and (B) median simulated trajectories with time since fire. The initial vector in the model was 1000 seeds.*

sequent mortality in the seed bank, local extinction becomes likely.

Seed and seedling dynamics are critical influences on *H. cumulicola* population dynamics. Although the number of reproductive structures increases exponentially from tens in small individuals to thousands for the largest individuals (see also Quintana-Ascencio & Morales-Hernández 1997), *H. cumulicola* seed germination and seedling survival are extremely low, except in recently burned sites (Quintana-Ascencio & Menges 2000). *H. cumulicola* has a persistent seed bank (Quintana-Ascencio et al. 1998), and survival in the seed bank is an important life-history trait determining finite rates of increase and extinction probability. Simulated 50% reductions of *H. cumulicola* seed survival significantly increased projected extinction risks, confirming the importance of seed banks to its persistence.

Seed dynamics and disturbance can be crucial for species persistence in competitive environments. Species

coexistence can be promoted by a "storage effect" when at least one life history stage is able to survive over periods of poor recruitment, and fluctuating recruitment rates allow competitively inferior species occasionally to increase in population size (Warner & Chesson 1985). Fire provides a mechanism for the storage effect. If recruitment is much higher after fire than between fires, seed storage (as serotiny) may be selected for (Enright et al. 1998*a*, 1998*b*). Among herbaceous species in Florida scrub, the seedling recruitment and survival of *H. cumulicola* and *E. cuneifolium* are highest shortly after fire, and they depend mostly on dormant seeds for recruitment (Menges & Kimmich 1996; Quintana-Ascencio & Menges 2000). In contrast, the performance of *Polygonella basiramia*, another Florida scrub endemic, is less affected by time since fire and it lacks a substantial persistent seed bank, relying instead mainly on recently produced seeds (Hawkes & Menges 1995; Quintana-Ascencio & Menges 2000). Among six shrub species of the fire-prone fynbos shrublands of the Cape Region of South Africa, *Passerina vulgaris* had the largest seed bank and the highest postfire seedling recruitment (Pierce & Cowling 1991).

Seasonal changes in temperature and precipitation also affect plant demographic parameters, and these factors can interact with fire to determine population changes (e.g., Burgman & Lamont 1992; Enright et al. 1998*a*, 1998*b*;). In south-central Florida, winter precipitation is more limited and variable than summer precipitation (Archbold Biological Station, unpublished weather data) and seems to be vital to the survival and recruitment of Florida scrub species (Quintana-Ascencio 1997; E.S.M. and P.F.Q.-A., unpublished data). Levels of precipitation during the winter of 1997, an el Niño year, were seven times above normal, resulting in exceptional levels of germination and recruitment and high population growth rates for *H. cumulicola*. Our model considers the effects of winter precipitation in sites more than a decade after fire by adjusting the probability of matrix selection by the frequency distribution of Archbold rainfall data.

Studies integrating information from many sites with different times since disturbance or different disturbance regimes are necessary to provide estimates of long-term population dynamics and the persistence of disturbance-sensitive species at a landscape level (Menges & Quintana-Ascencio 2003). However, these types of studies present particular challenges. For example, our results indicated that observed long-unburned populations were denser than observed populations a decade after fire. These long-unburned populations may represent different environmental conditions that allowed some *H. cumulicola* to remain relatively large, independent of fire. These idiosyncracies among populations may be a common feature of studies using short-term chronosequences across the disturbance gradient to approximate long-term demographic changes. Because of

Years for simulation

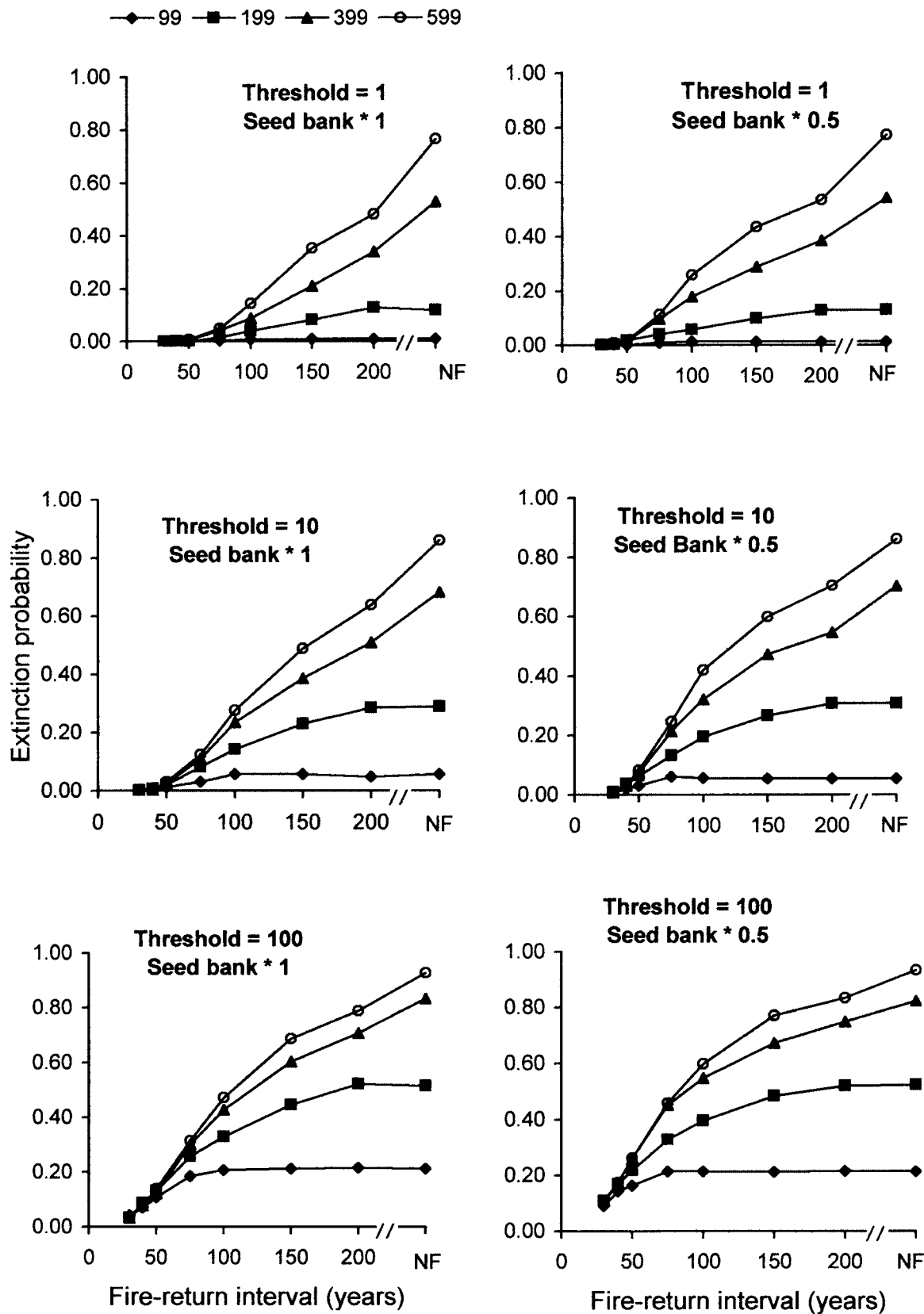◆— 99 ■— 199 ▲— 399 ⊖— 599

Figure 4. Modeled extinction probabilities of H. cumulicola *(initial vector = 1000 seeds) after 99, 199, 399, and 599 years without fire (NF) and under various regular fire-return intervals, three quasi-extinction thresholds (1, 10, and 100 individuals), and no or 50% reductions in the observed rate of seed survival in the soil seed bank.*
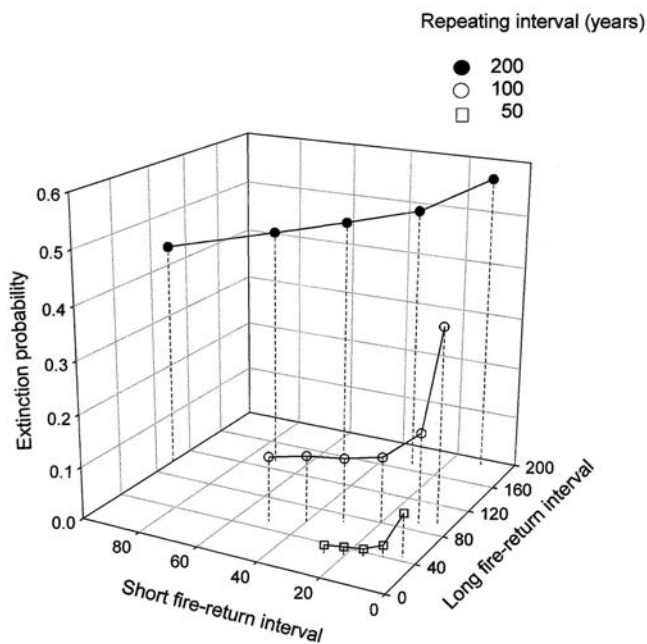
Figure 5. Modeled quasi-extinction probabilities (threshold =100, initial vector = 1000 seeds) of H. cumulicola *populations after 401 years under alternating short and long fire intervals repeating every 200, 100, or 50 years.*

this limitation, our simulations may underestimate population decline and extinction. Longer data sequences and consideration of more factors will be necessary for better estimates.

Conservation and Management of Fire-Sensitive Species

Changes in disturbance regimes associated with human intervention may hinder the population persistence of disturbance-sensitive species. Our population model portrays fundamental aspects of *H. cumulicola* demography and indicates ways to improve its management. Our model suggests that the long-term persistence of *H. cumulicola* in Florida rosemary scrub will require fire. Although some populations of this species can number several thousand plants, most are smaller than 1000 individuals (median 539 in 34 populations; Menges et al. 1998) and may be at risk without fire. Fire intervals shorter than 50 years may imperil the local persistence of most *H. cumulicola* populations, and longer intervals without fire may eliminate even the largest populations.

High risks of population extinction without frequent fires, limited seed dispersal ability (Menges et al. 1998), high population differentiation (Dolan et al. 1999), greater occurrence in large and aggregated patches (Quintana-Ascencio & Menges 1996), and similar demographic responses of transplanted individuals in occupied and un-

occupied Florida rosemary scrub patches (Quintana Ascencio et al. 1998) all indicate the possibility of regional metapopulation dynamics in *H. cumulicola.* Because local extinction is associated with fire frequency, and because variation of fecundity and recruitment along gradients of time since disturbance affects the number of seeds available for dispersal and colonization opportunities (e.g., Valverde & Silvertown 1997), population viability analysis of *H. cumulicola* at a regional level may require greater understanding of the interactive effects of local and regional dynamics.

Optimal fire regimes can be conflicting among co-occurring species. Fire regimes intermediate between the optima of the shrubs *Hudsonia montana* and *Leiophyllum buxifolium* are necessary to allow their coexistence in North Carolina (Gross et al. 1998). An analysis of population-level responses to fire regimes for four woody species in the cerrado savannas of Brazil suggests that changes in fire frequency cause shifts in their relative abundance (Hoffmann 1999). Among Florida scrub species, fire outside of 15–40 year intervals may threaten the local persistence of Florida rosemary (*Ceratiola ericoides*), which requires longer fire cycles to maximize seed storage (Johnson 1982). Similarly, ground lichens in the genera *Cladonia* and *Cladina* reach their highest abundance in long-unburned scrub patches and may be extirpated by frequent fires (R. Yahr, personal communication). On the other hand, rapid declines in *Eryngium cuneifolium* numbers and demographic parameters <15 years after fire suggest that it requires even shorter fire-return intervals than *H. cumulicola* (Menges & Kimmich 1996; E.S.M. and P.F.Q.-A., unpublished data). Our simulations revealed that alternating short and long fire-return intervals only slightly changed the probability of local extinction of *H. cumulicola,* compared with the larger effect of regular fire intervals. Such staggered fire regimes may allow species to coexist, whereas invariant fire-return intervals may be detrimental to some species.

Acknowledgments

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Appendix 1. Projection matrices of *H. cumulicola* at Archbold Biological Station.*

Population (year), years after fire

Matrix entry	32(97) 1-2	32(98) 2-3	42(94) 2-3	50(94) 2-3	57(94) 2-3
1,1	0.6281	0.6281	0.6281	0.6504	0.6504
1,2	0.00731	0.00005	0.00044	0.00067	0.00064
2,1		0.000	15.864	11.71	12.67
2,2		0.000	1.463	0.507	0.000
2,3		0.409	0.138	0.058	0.313
2,4		0.318	0.563	0.315	0.094
2,5		0.205	0.250	0.426	0.405
2,6		0.000	0.038	0.080	0.108

Matrix entry	42(95) 3-4	42(96) 4-5	42(97) 5-6	42(98) 6-7
1,1	0.6281	0.6281	0.6281	0.6281
2,1	0.0033	0.00079	0.01301	0.00009
3,2	0.175	0.250	0.000	0.000
4,2	0.775	0.417	0.472	0.714
5,2	0.050	0.278	0.250	0.000
6,2	0.000	0.000	0.000	0.000
3,3	0.273	0.500	0.091	0.192
4,3	0.545	0.400	0.636	0.154
5,3	0.091	0.000	0.091	0.108
6,3	0.000	0.000	0.000	0.000
1,4	55.047	53.91	70.86	54.67
2,4	0.108	0.011	0.157	0.009
3,4	0.022	0.085	0.045	0.071
4,4	0.533	0.745	0.591	0.514
5,4	0.378	0.043	0.182	0.129
6,4	0.067	0.000	0.000	0.000
1,5	252.82	229.42	262.50	270.78
2,5	0.496	0.045	0.580	0.044
3,5	0.000	0.065	0.067	0.115
4,5	0.200	0.645	0.200	0.269
5,5	0.500	0.161	0.333	0.462
6,5	0.200	0.000	0.067	0.038
1,6	570.64	691.50	1013.57	298.49
2,6	1.865	0.136	41.47	0.048
3,6	0.042	0.000	0.000	0.000
4,6	0.042	0.250	0.000	0.033
5,6	0.353	0.500	0.000	0.278
6,6	0.426	0.000	0.084	0.000

Population (year), years after fire

Matrix entry	50(95) 3-4	50(96) 4-5	50(97) 5-6	50(98) 6-7	57(95) 3-4	57(96) 4-5	57(97) 5-6	57(98) 6-7	29(94) 9-10	29(95) 10-11
1,1	0.6504	0.6504	0.6504	0.6504	0.6504	0.6504	0.6504	0.6504	0.8985	0.8985
1,2	0.00495	0.00118	0.01956	0.00014	0.00476	0.00114	0.01879	0.00014	0.00021	0.00159
2,3	0.234	0.250	0.000	0.281	0.121	0.250	0.000	0.107	0.028	0.119
2,4	0.317	0.417	0.167	0.368	0.376	0.417	0.472	0.036	0.119	0.196
2,5	0.317	0.278	0.250	0.158	0.191	0.278	0.250	0.000	0.036	0.262
2,6	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.000	0.107	0.095
3,3	0.333	0.250	0.000	0.192	0.500	0.643	0.500	0.375	0.000	0.107
3,4	0.333	0.000	0.250	0.154	0.100	0.071	0.000	0.063	0.167	0.340
3,5	0.167	0.000	0.750	0.108	0.300	0.071	0.188	0.125	0.167	0.131
3,6	0.000	0.000	0.000	0.000	0.100	0.000	0.000	0.000	0.107	0.009
4,1	65.55	65.50	80.67	55.48	30.90	158.72	107.84	48.09	105.94	83.30
4,2	1.430	0.000	6.626	0.000	3.187	0.009	0.025	0.000	0.017	0.211
4,3	0.063	0.143	0.036	0.033	0.333	0.159	0.231	0.125	0.000	0.000
4,4	0.281	0.190	0.286	0.433	0.000	0.478	0.000	0.125	0.000	0.182
4,5	0.438	0.000	0.357	0.367	0.500	0.014	0.538	0.125	0.087	0.227
4,6	0.063	0.000	0.036	0.000	0.167	0.083	0.154	0.000	0.000	0.045
5,1	592.03	255.97	238.50	201.18	294.77	207.94	456.75	318.30	364.03	403.22
5,2	12.92	0.000	19.59	0.000	30.40	0.011	0.108	0.000	0.056	1.019
5,3	0.093	0.050	0.038	0.050	0.077	0.217	0.192	0.160	0.000	0.000
5,4	0.116	0.100	0.000	0.100	0.038	0.217	0.154	0.080	0.000	0.036
5,5	0.419	0.050	0.346	0.325	0.462	0.435	0.269	0.120	0.000	0.214
5,6	0.140	0.000	0.077	0.050	0.423	0.043	0.115	0.040	0.000	0.107
6,1	913.84	855.90	1013.62	547.09	4247.64	2048.37	1013.51	646.26	874.29	702.50
6,2	14.96	0.000	83.25	0.000	62.58	0.111	0.238	0.000	0.132	1.775
6,3	0.125	0.000	0.000	0.000	0.000	0.053	0.000	0.000	0.029	0.013
6,4	0.125	0.000	0.000	0.033	0.000	0.105	0.000	0.100	0.000	0.000
6,5	0.250	0.000	0.000	0.278	0.143	0.421	0.000	0.000	0.391	0.350
6,6	0.375	0.000	0.084	0.000	0.571	0.158	0.167	0.000	0.086	0.128

Appendix 1. Continued

	Population (year), years after fire									
Matrix entry	29(96) 11-12	29(97) 12-13	29(98) 13-14	45(94) 8-9	45(95) 9-10	45(96) 10-11	45(97) 11-12	45(98) 12-13	67(94) 8-9	67(95) 9-10
1,1	0.8985	0.8985	0.8985	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237
2,1	0.00038	0.00627	0.00005	0.00008	0.0006	0.0002	0.0024	0.00002	0.00013	0.00098
2,3	0.048	0.022	0.192	0.028	0.177	0.375	0.000	0.308	0.028	0.224
2,4	0.238	0.200	0.077	0.119	0.322	0.375	0.000	0.231	0.119	0.240
2,5	0.000	0.144	0.404	0.036	0.171	0.000	0.333	0.385	0.036	0.224
2,6	0.000	0.000	0.135	0.107	0.032	0.000	0.000	0.077	0.107	0.034
3,3	0.149	0.061	0.000	0.250	0.333	0.444	0.125	0.143	0.000	0.107
3,4	0.258	0.247	0.000	0.313	0.278	0.222	0.313	0.714	0.200	0.340
3,5	0.021	0.043	0.444	0.219	0.056	0.000	0.125	0.143	0.100	0.131
3,6	0.000	0.041	0.333	0.031	0.056	0.000	0.063	0.000	0.100	0.009
4,1	110.15	361.51	104.79	95.88	58.24	57.43	102.64	55.41	63.01	72.62
4,2	0.000	0.000	0.178	0.041	0.082	0.038	0.000	0.014	0.000	0.000
4,3	0.100	0.000	0.000	0.147	0.071	0.118	0.133	0.091	0.000	0.231
4,4	0.100	0.240	0.300	0.353	0.250	0.294	0.133	0.273	0.161	0.308
4,5	0.100	0.120	0.100	0.176	0.214	0.059	0.400	0.182	0.129	0.231
4,6	0.100	0.040	0.200	0.088	0.071	0.000	0.033	0.182	0.032	0.077
5,1	360.83	790.99	520.59	271.62	225.57	293.35	453.13	178.17	262.71	371.21
5,2	0.000	0.000	0.887	0.117	0.319	0.193	0.000	0.045	0.000	0.000
5,3	0.043	0.000	0.000	0.000	0.040	0.000	0.048	0.000	0.000	0.000
5,4	0.217	0.000	0.214	0.000	0.200	0.278	0.095	0.143	0.000	0.308
5,5	0.130	0.154	0.286	0.545	0.320	0.444	0.190	0.381	0.115	0.231
5,6	0.043	0.077	0.071	0.273	0.080	0.111	0.333	0.333	0.000	0.077
6,1	1029.99	2370.91	1197.51	708.63	743.47	422.63	576.14	570.86	753.53	767.86
6,2	0.000	0.000	2.040	0.305	1.051	0.278	0.000	0.145	0.000	0.000
6,3	0.000	0.000	0.000	0.029	0.000	0.167	0.000	0.000	0.000	0.013
6,4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.091	0.000	0.000
6,5	0.375	0.000	0.167	0.391	0.375	0.167	0.000	0.273	0.000	0.350
6,6	0.000	0.144	0.167	0.086	0.125	0.000	0.144	0.636	0.000	0.128

	Population (year), years after fire									
Matrix entry	67(96) 10-11	67(97) 11-12	67(98) 12-13	87(94) 8-9	87(95) 9-10	87(96) 10-11	87(97) 11-12	87(98) 12-13	88(94) 8-9	88(95) 9-10
1,1	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237	0.8237
1,2	0.00023	0.00387	0.00003	0.00013	0.00088	0.00021	0.00348	0.00003	0.00012	0.00087
2,3	0.212	0.022	0.235	0.111	0.162	0.212	0.111	0.842	0.000	0.162
2,4	0.306	0.200	0.346	0.333	0.207	0.306	0.833	0.105	0.143	0.564
2,5	0.000	0.144	0.272	0.000	0.058	0.000	0.056	0.000	0.143	0.129
2,6	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.429	0.000
3,3	0.125	0.000	0.072	0.142	0.111	0.149	0.182	0.286	0.142	0.107
3,4	0.125	0.000	0.333	0.255	0.111	0.258	0.636	0.286	0.255	0.340
3,5	0.125	0.000	0.122	0.148	0.000	0.021	0.091	0.143	0.148	0.131
3,6	0.000	0.000	0.222	0.022	0.000	0.000	0.000	0.000	0.022	0.009
4,1	84.38	121.17	81.20	102.77	123.80	41.61	105.71	113.54	128.24	192.84
4,2	0.631	0.000	0.222	0.038	0.000	0.272	2.108	0.292	0.158	0.511
4,3	0.000	0.000	0.034	0.054	0.188	0.000	0.044	0.077	0.000	0.000
4,4	0.091	0.000	0.343	0.108	0.125	0.667	0.441	0.481	0.074	0.278
4,5	0.364	0.174	0.161	0.324	0.030	0.000	0.426	0.327	0.204	0.333
4,6	0.000	0.000	0.076	0.054	0.000	0.000	0.015	0.000	0.000	0.056
5,1	204.22	427.00	339.98	309.60	397.82	123.78	261.41	327.09	586.94	791.94
5,2	1.527	0.000	7.83	0.113	0.000	0.809	5.211	0.840	0.726	2.100
5,3	0.071	0.000	0.000	0.077	0.000	0.027	0.000	0.051	0.000	0.000
5,4	0.071	0.000	0.111	0.077	0.091	0.248	0.000	0.051	0.000	0.000
5,5	0.429	0.048	0.444	0.423	0.030	0.244	0.700	0.590	0.000	0.556
5,6	0.000	0.000	0.000	0.115	0.000	0.035	0.200	0.051	0.000	0.222
6,1	290.09	557.73	691.84	753.78	840.68	706.44	550.58	335.37	753.87	701.37
6,2	2.169	0.000	0.762	0.275	0.000	0.000	10.970	0.861	0.000	0.000
6,3	0.067	0.000	0.000	0.029	0.000	0.067	0.000	0.000	0.029	0.013
6,4	0.033	0.000	0.023	0.000	0.000	0.033	0.000	0.023	0.000	0.000
6,5	0.265	0.000	0.416	0.391	0.125	0.265	0.000	0.416	0.391	0.350
6,6	0.000	0.144	0.256	0.086	0.000	0.000	0.144	0.236	0.086	0.128

continued

Appendix 1. Continued

	Population (year), years after fire									
Matrix entry	88(96) 10–11	88(97) 11–12	88(98) 12–13	91(94) 8–9	91(95) 9–10	91(96) 10–11	91(97) 11–12	91(98) 12–13	1(94) >21	1(95) >21
1,1	0.8237	0.8237	0.8237	0.7489	0.7489	0.7489	0.7489	0.7489	0.6721	0.6721
1,2	0.00021	0.00342	0.00002	0.00013	0.00097	0.00023	0.00384	0.00003	0.0001	0.0011
2,3	0.212	0.000	0.259	0.028	0.177	0.212	0.022	0.389	0.619	0.467
2,4	0.306	0.167	0.630	0.119	0.322	0.306	0.200	0.315	0.000	0.133
2,5	0.000	0.000	0.074	0.036	0.171	0.000	0.144	0.189	0.095	0.000
2,6	0.000	0.000	0.000	0.107	0.032	0.000	0.000	0.040	0.000	0.000
3,3	0.149	0.061	0.072	0.142	0.000	0.125	0.000	0.072	0.300	0.452
3,4	0.258	0.247	0.333	0.255	0.167	0.000	0.286	0.333	0.200	0.161
3,5	0.021	0.043	0.122	0.148	0.000	0.000	0.000	0.122	0.100	0.161
3,6	0.000	0.041	0.222	0.022	0.000	0.000	0.143	0.222	0.000	0.000
4,1	87.18	160.27	44.16	168.49	109.82	98.68	147.98	88.09	62.31	81.54
4,2	0.000	0.000	0.625	0.048	0.088	0.019	0.000	0.000	0.214	0.090
4,3	0.077	0.000	0.034	0.069	0.130	0.286	0.034	0.000	0.154	0.091
4,4	0.538	0.136	0.340	0.379	0.217	0.571	0.345	0.161	0.385	0.273
4,5	0.154	0.000	0.161	0.345	0.217	0.000	0.345	0.194	0.385	0.364
4,6	0.000	0.000	0.076	0.000	0.087	0.000	0.034	0.000	0.000	0.000
5,1	676.23	932.97	330.93	384.47	308.87	286.64	400.98	288.80	364.51	201.93
5,2	0.000	0.000	1.92	0.109	0.249	0.054	0.000	0.000	1.254	0.222
5,3	0.000	0.000	0.025	0.000	0.114	0.048	0.000	0.075	0.143	0.000
5,4	0.278	0.000	0.154	0.059	0.029	0.143	0.088	0.250	0.071	0.000
5,5	0.222	0.000	0.390	0.206	0.343	0.238	0.471	0.250	0.286	0.500
5,6	0.056	0.000	0.106	0.176	0.171	0.000	0.059	0.075	0.071	0.083
6,1	1258.89	884.28	691.84	680.42	460.79	557.23	508.40	663.60	1856.77	1013.82
6,2	0.000	0.000	0.762	0.193	0.372	0.105	0.000	0.000	4.325	1.115
6,3	0.067	0.000	0.000	0.143	0.067	0.167	0.000	0.000	0.125	0.000
6,4	0.033	0.000	0.023	0.000	0.000	0.167	0.000	0.000	0.000	0.000
6,5	0.265	0.000	0.416	0.286	0.333	0.333	0.000	0.222	0.000	0.286
6,6	0.000	0.144	0.256	0.429	0.267	0.000	0.144	0.222	0.500	0.286

	Population (year), years after fire									
Matrix entry	1(96) >21	1(97) >21	1(98) >21	32(94) >21	32(95) >21	59(94) >21	59(95) >21	59(96) >21	59(97) >21	59(98) >21
1,1	0.6721	0.6721	0.6721	0.6721	0.6721	0.7732	0.7732	0.7732	0.7732	0.7732
1,2	0.00026	0.0043	0.00003	0.00025	0.00185	0.00012	0.00086	0.00021	0.00341	0.00002
2,3	0.375	0.412	0.536	0.333	0.372	0.204	0.399	0.236	0.162	0.500
2,4	0.000	0.294	0.119	0.500	0.106	0.504	0.193	0.000	0.312	0.167
2,5	0.000	0.088	0.000	0.167	0.170	0.146	0.112	0.000	0.100	0.000
2,6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000
3,3	0.273	0.244	0.000	0.147	0.000	0.182	0.143	0.131	0.088	0.000
3,4	0.409	0.200	0.778	0.186	0.143	0.182	0.286	0.102	0.388	0.236
3,5	0.000	0.044	0.222	0.365	0.571	0.182	0.000	0.000	0.038	0.201
3,6	0.000	0.000	0.000	0.052	0.286	0.000	0.000	0.000	0.000	0.000
4,1	26.78	137.27	72.22	100.62	63.56	84.78	91.63	80.21	120.17	134.22
4,2	0.007	3.113	0.000	0.000	0.018	0.000	0.021	0.046	0.000	0.316
4,3	0.000	0.083	0.000	0.000	0.000	0.041	0.051	0.000	0.023	0.034
4,4	0.545	0.300	0.208	0.154	0.167	0.286	0.179	0.545	0.477	0.552
4,5	0.182	0.317	0.625	0.538	0.250	0.184	0.333	0.000	0.273	0.172
4,6	0.000	0.017	0.125	0.000	0.333	0.061	0.000	0.000	0.000	0.000
5,1	208.15	391.16	277.29	670.73	361.65	451.06	425.98	342.31	474.06	482.94
5,2	0.052	8.871	0.000	0.000	0.103	0.000	0.096	0.196	0.000	1.135
5,3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.048	0.033
5,4	0.294	0.091	0.125	0.065	0.107	0.071	0.037	0.333	0.048	0.333
5,5	0.471	0.636	0.594	0.387	0.429	0.214	0.333	0.333	0.619	0.433
5,6	0.000	0.136	0.219	0.194	0.321	0.143	0.148	0.000	0.048	0.000
6,1	1067.29	1036.50	411.05	1430.38	927.76	1025.53	582.72	712.87	831.90	710.63
6,2	0.265	23.500	0.000	0.000	0.265	0.000	0.131	0.408	0.000	1.671
6,3	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000
6,4	0.271	0.000	0.104	0.000	0.000	0.008	0.008	0.271	0.000	0.104
6,5	0.281	0.250	0.375	0.080	0.222	0.254	0.251	0.281	0.250	0.375
6,6	0.229	0.500	0.188	0.400	0.278	0.298	0.227	0.229	0.500	0.188

Appendix 1. Continued

Matrix entry	*Population (year), years after fire*									
	62(94) >21	62(95) >21	62(96) >21	62(97) >21	62(98) >21	93(94) >21	93(95) >21	93(96) >21	93(97) >21	93(98) >21
1,1	0.6721	0.6721	0.6721	0.6721	0.6721	0.5710	0.5710	0.5710	0.5710	0.5710
1,2	0.00024	0.00177	0.00042	0.00699	0.00005	0.00015	0.00111	0.00026	0.00437	0.00003
2,3	0.204	0.445	0.236	0.000	0.476	0.204	0.334	0.236	0.300	0.167
2,4	0.504	0.310	0.000	0.400	0.143	0.504	0.174	0.000	0.400	0.167
2,5	0.146	0.082	0.000	0.300	0.000	0.146	0.116	0.000	0.000	0.000
2,6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000
3,3	0.000	0.174	0.131	0.088	0.000	0.147	0.000	0.077	0.111	0.000
3,4	0.333	0.278	0.102	0.388	0.361	0.186	0.429	0.462	0.222	0.167
3,5	0.444	0.286	0.000	0.038	0.076	0.365	0.286	0.000	0.111	0.083
3,6	0.111	0.048	0.000	0.000	0.000	0.052	0.000	0.000	0.000	0.000
4,1	95.73	92.10	56.63	137.36	119.57	99.11	60.10	63.56	90.11	39.50
4,2	0.016	0.154	0.122	0.888	0.000	0.010	0.000	0.000	0.000	0.331
4,3	0.033	0.000	0.071	0.000	0.070	0.083	0.042	0.181	0.066	0.015
4,4	0.167	0.182	0.143	0.316	0.326	0.389	0.375	0.102	0.316	0.379
4,5	0.433	0.318	0.071	0.404	0.070	0.417	0.250	0.000	0.237	0.091
4,6	0.100	0.045	0.000	0.018	0.000	0.000	0.000	0.000	0.026	0.000
5,1	557.18	335.97	210.74	397.58	303.10	375.72	125.49	172.67	210.70	116.46
5,2	0.092	0.560	0.453	2.570	0.000	0.037	0.000	0.000	0.000	0.977
5,3	0.063	0.000	0.000	0.000	0.073	0.000	0.000	0.040	0.000	0.021
5,4	0.125	0.118	0.182	0.095	0.293	0.118	0.026	0.480	0.043	0.191
5,5	0.375	0.353	0.136	0.571	0.122	0.294	0.333	0.120	0.522	0.468
5,6	0.063	0.059	0.045	0.095	0.000	0.235	0.103	0.000	0.087	0.043
6,1	1235.5	478.38	522.51	1291.66	1186.92	726.54	276.06	405.30	1179.53	244.93
6,2	0.000	0.797	1.124	8.350	0.000	0.072	0.000	0.000	0.000	2.054
6,3	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6,4	0.008	0.000	0.271	0.000	0.104	0.000	0.000	0.000	0.000	0.167
6,5	0.254	0.167	0.281	0.250	0.375	0.067	0.333	0.375	0.250	0.333
6,6	0.298	0.167	0.229	0.500	0.188	0.133	0.333	0.000	0.500	0.000

The first five matrices represent populations 1–2 years after fire, with only seedlings present; entries 2,1 and 2,2 represent seedling fecundity that occurred only in these years.