

Fire, vital rates, and population viability: a hierarchical Bayesian analysis of the endangered Florida scrub mint

MARGARET E. K. EVANS,^{1,2,5} KENT E. HOLSINGER,³ AND ERIC S. MENGES⁴

¹Unit of Mathematical Eco-Evolutionary Biology, Laboratoire d'Ecologie et Evolution, CNRS UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05 France

²Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520-8106 USA

³Department of Ecology and Evolutionary Biology, University of Connecticut, U-3043, Storrs, Connecticut 06269-3043 USA

⁴Archbold Biological Station, P.O. Box 2057, Lake Placid, Florida 33862 USA

Abstract. Understanding and predicting changes in the abundance of natural populations is a central goal of ecology. These changes are influenced by a variety of exogenous processes (weather, floods, fire); variation in these processes leads to variation in vital rates (survival, fecundity) that may be positively or negatively correlated across the life cycle. We used 20 years of data and a hierarchical Bayesian model to estimate vital rates and their covariation in an endangered plant, *Dicerandra frutescens* ssp. *frutescens* (Lamiaceae), as a function of time since fire and random year effects. Germination and the number of flowering branches declined with time since fire, and all plants were increasingly likely to become nonreproductive with time since fire. Time since fire had negative effects on survival of seedlings, vegetative plants, and small flowering plants, and positive effects on survival of medium and large flowering plants. Model comparison strongly supported inclusion of time-since-fire effects and weakly supported inclusion of year effects influencing all vital rates (“model-wide” year effects). We used samples from the joint posterior distribution of model parameters to simulate population dynamics as a function of fire regime and year-to-year environmental variation. These simulations suggest that populations of *Dicerandra frutescens* ssp. *frutescens* are least likely to go extinct if the average time between fires is ~24–30 years. The design of the simulations allowed us to distinguish variation in stochastic population growth associated with process variability (fire, year effects, and demographic stochasticity) from variation associated with parameter uncertainty (finite amounts of data). Even with 20 years of data, half or more of the uncertainty in population growth rates was due to parameter uncertainty. This hierarchical Bayesian population viability analysis illustrates a general analytical framework for (1) estimating vital rates as a function of an exogenous environmental factor, (2) accounting for covariation among vital rates, and (3) simulating population dynamics as a function of stochastic environmental processes while taking into account uncertainty about their effects. We discuss future areas of development for this approach.

Key words: *Dicerandra frutescens*; element selection; environmental stochasticity; extinction risk; Florida scrub mint; generalized linear mixed models (GLMM); log pseudomarginal likelihood; matrix selection; population viability analysis.

INTRODUCTION

Understanding and predicting fluctuations in the abundance of natural populations, whether they are harvested populations, pest, invasive or disease populations, or endangered species, is both a central activity of ecology and of importance to society (Boyce 1992, Shea et al. 1998, Menges 2000, Beissinger and McCullough 2002, Morris and Doak 2002, Peres et al. 2003). Many aspects of global change, including altered weather patterns, ocean conditions, disturbance regimes, nutrient loads, and introduced species, compel us to understand how exogenous factors affect population dynamics (Doak and Morris 1999, van Mantgem et al.

2004, Maschinski et al. 2006, Morris et al. 2006, Adler and HilleRisLambers 2008). Incorporating such factors into models can improve the understanding and prediction of population dynamics (Fieberg and Ellner 2001, Ellner 2003, Zabel et al. 2006, Evans et al. 2008, Bakker et al. 2009), and allow managers to identify the manipulations most likely to have desired effects.

Here we introduce an integrative approach to population viability analysis (PVA) that involves (1) estimation of vital rates in relation to exogenous factors, followed by (2) simulation of population dynamics using those estimates of vital rates. In particular, this approach involves simultaneous analysis of all vital rates, including their covariation and random year effects. This allows us to incorporate positive or negative covariation among vital rates that arises both through systematic effects of an exogenous variable and through

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⁵ E-mail: margaret.ekevans@gmail.com

random effects associated with particular years. Further, we incorporate parameter uncertainty into population simulations through direct use of the joint posterior distribution of model parameters, and we distinguish process from parameter uncertainty in population viability simulations. Thus we provide one of few examples (that we have been able to find) to model variation in vital rates as a function of known and unknown factors, simulate population growth as a function of those effects, and rigorously account for covariation among vital rates, parameter uncertainty, and process variability (for similar accomplishments, see Bakker et al. 2009). To further set this model in context, we review the challenges involved in modeling the demography of a population under the influence of exogenous environmental variation and approaches that have been developed thus far.

Modeling stochastic demography.—Changing environmental conditions are pervasive. Exogenous processes (e.g., weather, hurricanes, fire) influence the demography and abundance of natural populations. Typically, such processes vary in intensity and timing in ways unrelated to population size, causing them to be modeled stochastically. Further, vital rates vary among individuals that differ in age, size, or developmental stage (making the population “structured”; Gotelli 1998, Caswell 2001, Clark 2007), and individuals of different age, size, or stage are often affected by an exogenous factor (such as harsh weather) in different ways or to different degrees (Coulson et al. 2001). A structured population calls for the use of transition (projection) matrices (Cohen 1979, Lande and Orzack 1988, Tuljapurkar 1989, 1990, Caswell 2001, Morris and Doak 2002). Historically there have been two approaches to simulating the dynamics of a structured population in response to environmental stochasticity (see Caswell 2001: Chapter 14). We refer to the two approaches as “matrix selection” (e.g., Bierzychudek 1982, Silva et al. 1991, Caswell and Kaye 2001, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004, Smith et al. 2005) and “element selection” (Morris and Doak 2002). In matrix selection, observed matrices are selected at random to perform the projection in each year. The advantage of matrix selection is that it makes linking variation in the environment and variation in vital rates straightforward: one selects matrices from categories of the environment (wet vs. dry years, the number of years since fire or hurricane, etc.) and any correlations between vital rates are preserved in the selected matrices. The disadvantage is that the number of matrices is often limited. In element selection a probability distribution for each vital rate is estimated, given several years of data, and matrices are constructed by random sampling from the appropriate distributions (Morris and Doak 2002). The advantage of element selection is that an arbitrarily large number of matrices can be constructed by sampling. The disadvantage is that a straightforward implementation of the approach ignores covariance

among vital rates (though see the methods in Morris and Doak 2002 to address this problem). Here we focus on modeling vital rates as a function of exogenous factors as a way to preserve both the advantages of matrix selection and element selection. Specifying relationships among exogenous variables and vital rates induces a correlation between them, as in matrix selection, and by estimating distributions through those relationships an arbitrarily large number of matrices can be constructed, as in element selection.

Modeling vital rates.—Two distinct approaches to modeling vital rates have emerged that capture correlations among vital rates. One is to estimate correlations among vital rates via their shared response to an unidentified environmental factor. This method was introduced almost 15 years ago (by Doak et al. 1994) and can be found in key textbooks and methodological review papers (Caswell 2001, Fieberg and Ellner 2001, Morris and Doak 2002; see also Runge and Moen 1998), yet there are few examples where correlations among vital rates are estimated or incorporated into simulations of population dynamics.

A second approach is to model vital rates as a function of a specific (identified) environmental factor, such as climate, nitrification, or disturbance (Anderson et al. 1995, Leirs et al. 1997, Lima et al. 1999, 2001, Coulson et al. 2001, Gotelli and Ellison 2006, Zabel et al. 2006, Bakker et al. 2009, Gillespie and Golightly 2010). For example, Meyer et al. (2006) modeled plant vital rates in three years as a function of precipitation (via regression), then simulated population dynamics as a function of precipitation. Increasing the variance of precipitation decreased the risk of extinction because of seed banking (Meyer et al. 2006). Similarly, Gotelli and Ellison (2006) estimated vital rates of a carnivorous plant under three nitrogen treatments, then used simple linear interpolation to generate a continuous function relating nitrogen and vital rates. Extinction risk increased with the rate of nitrogen deposition. Thus population dynamics can be simulated as a function of an environmental factor by combining models of vital rates and matrix population models.

Here we combine both approaches in one model: we model vital rates as a function of time-since-fire and year variation, the latter capturing unidentified sources of variation among years with a common influence on all vital rates. As a result, we construct vital rates whose pattern of correlation reflects both the effect of a measured exogenous variable, time since fire, and unmeasured environmental variables that affect vital rates in each year. Estimating correlations among different parts of the life cycle caused by year variation calls for a single model that estimates all vital rates simultaneously, thus our statistical model consists of an interconnected set of generalized linear models (regressions estimating vital rates from data). In addition, the model includes two dynamical equations that track soil seed dynamics, which allows us to infer seed bank

TABLE 1. Summary of the demographic data available from five populations of *Dicerandra frutescens* ssp. *frutescens*, including the number of populations and (in parentheses) the total number of individuals sampled per year.

Year	N^{germ}	N^{sdlg}	br	sd	x[1]	x[2]	x[3]	x[4]	x[5]
1989	4 (46)	4 (19)	4 (92)	4 (58)	4 (79)	4 (67)
1990	5 (224)	5 (97)	5 (204)	...	4 (19)	4 (154)	4 (43)	4 (49)	4 (38)
1991	5 (102)	5 (67)	5 (131)	...	5 (97)	5 (125)	5 (46)	5 (44)	5 (50)
1992	5 (187)	5 (84)	5 (143)	...	5 (67)	5 (129)	5 (24)	5 (47)	5 (54)
1993	5 (145)	5 (74)	5 (127)	...	5 (84)	5 (86)	5 (30)	5 (52)	5 (50)
1994	5 (135)	5 (54)	5 (133)	3 (75)	5 (74)	5 (95)	5 (21)	5 (37)	5 (52)
1995	5 (110)	5 (49)	5 (113)	4 (67)	5 (54)	5 (95)	5 (16)	5 (25)	5 (39)
1996	5 (57)	5 (40)	5 (82)	3 (57)	5 (49)	5 (84)	5 (13)	5 (19)	5 (36)
1997	5 (31)	5 (25)	5 (57)	...	5 (40)	5 (64)	5 (16)	5 (12)	5 (14)
1998	5 (111)	5 (51)	5 (42)	2 (59)	5 (25)	5 (69)	5 (6)	5 (10)	5 (10)
1999	5 (109)	5 (76)	5 (21)	3 (90)	5 (51)	5 (36)	5 (15)	5 (15)	5 (17)
2000	5 (97)	5 (27)	5 (41)	...	5 (76)	5 (54)	5 (6)	5 (23)	5 (24)
2001	5 (9)	5 (7)	5 (61)	...	5 (27)	5 (55)	5 (18)	5 (33)	5 (38)
2002	5 (382)	5 (95)	5 (89)	...	5 (7)	5 (29)	5 (23)	5 (21)	5 (21)
2003	5 (121)	5 (85)	5 (66)	...	5 (95)	5 (26)	5 (8)	5 (26)	5 (34)
2004	5 (42)	5 (26)	5 (68)	...	5 (85)	5 (84)	5 (16)	5 (18)	5 (43)
2005	5 (11)	5 (10)	5 (78)	...	5 (26)	5 (110)	5 (14)	5 (20)	5 (44)
2006	5 (45)	5 (13)	5 (78)	...	5 (10)	5 (84)	5 (19)	5 (32)	5 (42)
2007	5 (28)	5 (21)	5 (94)	...	5 (13)	5 (54)	5 (8)	5 (19)	5 (26)

Notes: The five types of data were counts of the number of seedlings observed in census areas (N^{germ}), the number of those seedlings that survived to the September census (N^{sdlg}), the number of flowering branches on each flowering plant in census areas (br), the number of seeds produced per flowering branch on a sample of branches (sd), and the number of plants originating from each of five plant classes in the previous September (x[1]–x[5]), i.e., seedlings, vegetative plants, and small, medium, and large flowering plants, respectively. These data were used in regressions (GLMMs) described in *Methods* (see also Fig. 2). Census areas were constant throughout the study. Missing data are indicated by ellipses (...).

parameters. Because of this complex structure and the large number of parameters (at least 1340 parameters; see Appendix: Table A1), likelihood inference is generally impractical (though penalized likelihood [Maunder et al. 2006], importance sampling [Skaug and Fournier 2006], or data cloning methods [Lele et al. 2007, Ponciano et al. 2009] might allow a solution through development of special-purpose software). We chose to estimate parameters of the model using a Bayesian framework because of the flexibility of this approach, its ability to handle large numbers of random effects, its accuracy, our own familiarity with the methods of implementation, and the availability of “off-the-shelf” software to implement the approach (Bolker et al. 2008, Bolker 2009). In fact, a case for Bayesian population viability analysis has been made on the basis of a number of considerations, ranging from practical to rigor and downstream usability (Ludwig 1996, Foley 2000, Wade 2000, 2002, Ludwig et al. 2001, Calder et al. 2003, Clark 2003, Harwood and Stokes 2003, Marin et al. 2003, Drechsler and Burgman 2004, Maunder 2004). Yet there are few worked examples of Bayesian PVA per se (Clark 2003, Winship and Trites 2006; see *Discussion*). There are many examples of Bayesian analyses of population dynamics in fisheries and marine biology, including the role of exogenous effects and the consequences of alternative management actions (e.g., Punt and Hilborn 1997, Newman et al. 2006, Ruiz et al. 2009). Thus it seems that terrestrial ecologists have lagged behind marine biologists in taking advantage of the power and flexibility of hierarchical Bayesian modeling (reviewed in an April 2009 forum in

Ecological Applications [see Hobbs 2009]). Recently, zoologists analyzing mark-recapture data have taken up the use of hierarchical Bayesian modeling to estimate vital rates and critical parameters describing movement (Morales et al. 2004, King et al. 2008, Schick et al. 2008, Calvert et al. 2009, O’Hara et al. 2009, Schofield et al. 2009), but to our knowledge, this has not been incorporated into simulations of extinction dynamics. Our purpose here is to introduce a particular approach to population viability analysis (combining generalized linear mixed models of vital rates and matrix population modeling) facilitated by hierarchical Bayesian modeling, and illustrate how model output can be used for simulations of population viability.

The species that we model, *Dicerandra frutescens* ssp. *frutescens*, is a plant endemic to the Lake Wales Ridge in central Florida, USA, and is listed as an endangered species both federally and by the state of Florida. The Lake Wales Ridge has gained attention as a global hotspot of biodiversity (Dobson et al. 1997, Estill and Cruzan 2001, Turner et al. 2006); habitat loss, fragmentation, and fire suppression are grave threats to this landscape (Turner et al. 2006, Weekley et al. 2008). However, even before the arrival of Europeans in Florida, the distribution of *D. frutescens* ssp. *frutescens* was probably limited by its narrow geographic range and specific preferences for soil type and fire history (Menges et al. 2006, 2007).

We used 20 years of data from marked individuals in five populations of this species; however, we had relatively few data on seed production (Table 1) and no direct data on the seed bank (a common situation). A

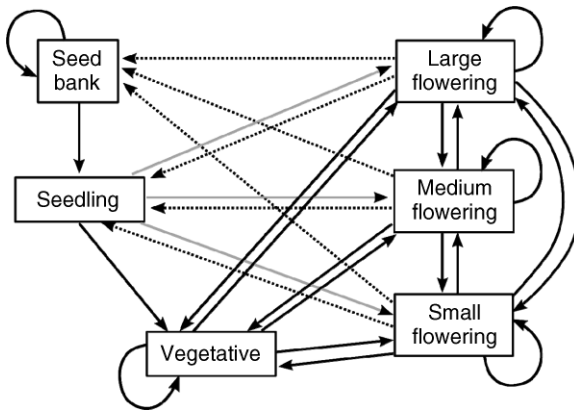


FIG. 1. Life cycle of *Dicerandra frutescens* ssp. *frutescens*. Arrows indicate transitions that can occur within one time step (September–September). Fecundity and seedling recruitment are indicated with dotted arrows. Gray arrows highlight three rare transitions (from the seedling class to a reproductive class, “leap-frogging”).

hierarchical Bayesian approach (like a likelihood approach) allows us to integrate these misaligned data and infer unobserved soil seed parameters (germination fraction, soil seed survival), including the effect of time since fire on germination. Further, it is straightforward in a Bayesian analysis (though not unique to this approach) to explicitly distinguish *uncertainty* about parameter values from *variability* in process outcomes (parameter uncertainty vs. process variability; Mills and Lindberg 2002, Ellner and Fieberg 2003, Harwood and Stokes 2003, Maunder 2004, Clark 2005). Parameter uncertainty can be reduced by the addition of new data. In contrast, process variability, i.e., variation in vital rates due to the influence of stochastic processes (fire, weather) or variation among individuals (arising from genetic differences, plasticity, etc.), cannot be reduced by adding new data. We used samples from the joint posterior distribution of model parameters to simulate population dynamics under alternative fire regimes that managers might apply, exploring the probability of population extinction. We compare our results to a previous PVA in relation to fire, using 13 years of data and a traditional analysis (Menges et al. 2006), and we discuss directions for further development of hierarchical Bayesian population models.

METHODS

Study species, fire ecology, and data

Dicerandra frutescens ssp. *frutescens* is a suffrutescent (partly woody, partly herbaceous) perennial found in Florida scrub communities on the Lake Wales Ridge, particularly in oak–hickory scrub and sand pine scrub on yellow sands (Menges 1999, 2007). These communities are characterized by a dense canopy of oaks, pine, and hickory that is periodically top-killed by fire. Several dominant plants in these communities resprout vigor-

ously after fire (especially *Quercus myrtifolia*), re-establishing the shrub canopy. *Dicerandra frutescens* ssp. *frutescens* is short lived, of short stature, and is killed by fire. Individuals rarely live more than eight years (Evans et al. 2004, Menges et al. 2006). For populations of *D. frutescens* ssp. *frutescens* to persist after fire, individuals must regenerate from seeds that persist in the soil (Menges et al. 2006) or from seeds produced by surviving individuals in unburned patches.

While fire kills individuals of *D. frutescens* ssp. *frutescens*, its populations ultimately depend on fire (or anthropogenic disturbance), because, like several other endangered plants endemic to Florida scrub, it depends on canopy openings (Menges et al. 1999). Fire creates canopy gaps and fire suppression closes those gaps. Population growth rates and many vital rates decline with time since disturbance in the “gap-specialists” of Florida scrub (Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004, Menges et al. 2006, Evans et al. 2008). Because of its sensitivity to time since fire, *D. frutescens* ssp. *frutescens* may be a good indicator of the historical fire frequency in oak–hickory scrub and sand pine scrub (Menges 1999), an approach that can help guide fire management of the community (Menges 2007), in addition to providing guidance on prevention of population extinction.

We included data from five populations of *D. frutescens* ssp. *frutescens* located in relatively unmodified Florida scrub habitat. In these populations, sample areas (1-m² quadrats) were established in patches where plants occur (a total of 84, 37, 12, 13, and 40 quadrats in populations 2, 4, 10, 12, and 19, respectively). All plants in these quadrats were monitored beginning in September 1988. We analyzed data through 2007, thus 20 years of data, yielding 19 transitions. This includes a total of 5144 unique plants monitored, and is the first analysis including post-2000 data. *Dicerandra frutescens* ssp. *frutescens* flowers in September and October and seedlings germinate mainly in winter (approximately January–March). Seedlings were identified by the presence of cotyledons. Quadrats were censused quarterly (in March, June, September, and December) for survival of known plants and the appearance of new plants, whereas size (the number of branch tips) and an indicator of fecundity (the number of flowering branch tips) were recorded in September (the annual census). In addition, seed production was sampled in certain populations between 1994 and 1999: the number of viable seeds per flowering branch was sampled from 8 to 30 branches (mean = 23) per population in two to four populations per year (except 1997; see Table 1).

We model the life cycle of *D. frutescens* ssp. *frutescens* with the same six stages delineated by Menges et al. (2006): seeds, seedlings, non-flowering (vegetative) plants, and flowering plants of three size categories (<12 branches, 12–27 branches, and >27 branches; Fig. 1). The last three categories were decided on the basis of regression analyses and the Moloney (1986) algorithm

TABLE 2. The number of years since fire for five populations (Pop) of *Dicerandra frutescens* ssp. *frutescens* over the course of the study (1988–2007).

Pop	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
2	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
4	61	62	63	64	65	66	67	68	69	70	0	1	2	3	4	5	6	7	8	9
10	4	5	6	7	8	9	10	11	0	1	2	3	4	5	6	7	8	9	10	11
12	48	49	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	0	1
19	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67

(see Menges et al. 2006). We chose to use these stages in order to better compare our results to Menges et al. (2006). The dynamics of a population with these six life stages can be projected with a six by six transition matrix model, or population projection matrix (sensu Caswell 2001), as described in Appendix: Section 1.1.

The fire histories of the study populations are shown in Table 2. Three populations (4, 10, 12) burned at least once during the course of the study. The other two populations have not burned since 1927 (population 2) and approximately 1940 (population 19; this is also the case for population 12 before the 1990 fire). As a result of these fire histories, the distribution of time since fire ranges from 0 to 15 years, followed by a gap from 16 to 48, then values from 49 to 80 years after fire (Table 2).

Estimating vital rates from demographic data

We used a Bayesian hierarchical model to estimate vital rates from the available demographic data. Five submodels estimate vital rates of different parts of the life cycle (Fig. 2). Two submodels estimate components of fecundity (F , per capita seed output) and a third submodel estimates seed germination and soil seed survival (Fig. 2). A fourth submodel estimates seedling survival from the time that a seedling is first detected (at a quarterly census) to the time of the annual census in September (Fig. 2). A fifth submodel estimates the probability of transitions among plant classes (Fig. 2).

In each submodel, we used a generalized linear mixed model to estimate a vital rate as a function of time since fire and two (or three) types of random effects. The first is a year effect (YEAR) shared by all five regressions of vital rates, thus it links them into a single large model (as illustrated in the center of Fig. 2). We refer to this as the “model-wide” YEAR effect. This YEAR effect estimates overall year quality. The biological motivation is that year variation may influence more than one vital rate at once: a good year for seedling survival may also be a good year for flowering branch production. To ensure that the model is well-specified, we arbitrarily assigned a positive correlation of unity between the YEAR effect and the number of flowering branches on large flowering plants (this choice has no effect on the correlation structure, as in Doak et al. 1994). Thus in more concrete terms, the model-wide YEAR effect may be thought of as the effect of year variation on the number of flowering branches on large flowering plants. At the same time, one may suppose that year variation may not

affect all vital rates with the same sign or magnitude. We incorporated two additional parameters to capture this possibility. First are the β_2 parameters, coefficients associated with the YEAR effect (see regression equations below). They were constrained to take on values of either -1 or $+1$, capturing either positive or negative correlation (respectively) between the effect of YEAR variation on the number of flowering branches on large flowering plants and a given vital rate. The other parameter is a second random year effect, one unique to each vital rate (ϵ_{yr} in equations below), modifying the intercept (grand mean) estimated for a vital rate. These year effects (ϵ_{yr}) capture the possibility that a given vital rate responds to variation among years to a different degree than the number of flowering branches on large flowering plants. To summarize, the β_2 and ϵ_{yr} parameters unique to each vital rate allow us to estimate the sign and magnitude (respectively) of the response of that vital rate to year variation compared to the response of the number of flowering branches on large flowering plants. A further point is that these year effects (ϵ_{yr} , YEAR) allow us to calculate correlations among vital rates associated with variation among years (see Appendix: Section 1.2). We also estimated random population effects (ϵ_{pop} in equations below) for flowering branches, seeds per branch, and seedling survival (not germination fraction or transitions among plant classes). We describe each submodel in more detail in the following.

Fecundity regressions.—Two generalized linear models were used to estimate per capita seed production, F (Fig. 2). The data include counts of flowering branches per plant (br; i.e., for each flowering plant in each year in the census areas) and seeds per flowering branch (sd; samples taken in a subset of years and populations; see Table 1). We took these data to be Poisson-distributed:

$$\text{br} \sim \text{Poisson}(\mu_{[p,t,r]}^{\text{br}})$$

$$\text{sd} \sim \text{Poisson}(\mu_{[p,t]}^{\text{sd}})$$

and modeled the mean number of branches per plant ($\mu_{[p,t,r]}^{\text{br}}$) and mean number of seeds per branch ($\mu_{[p,t]}^{\text{sd}}$) in population p , year t , and, in the case of flowering branches, in size class r (small, medium, or large) as a function of time since fire (TSF), year, and population effects using generalized linear models with a log link function:

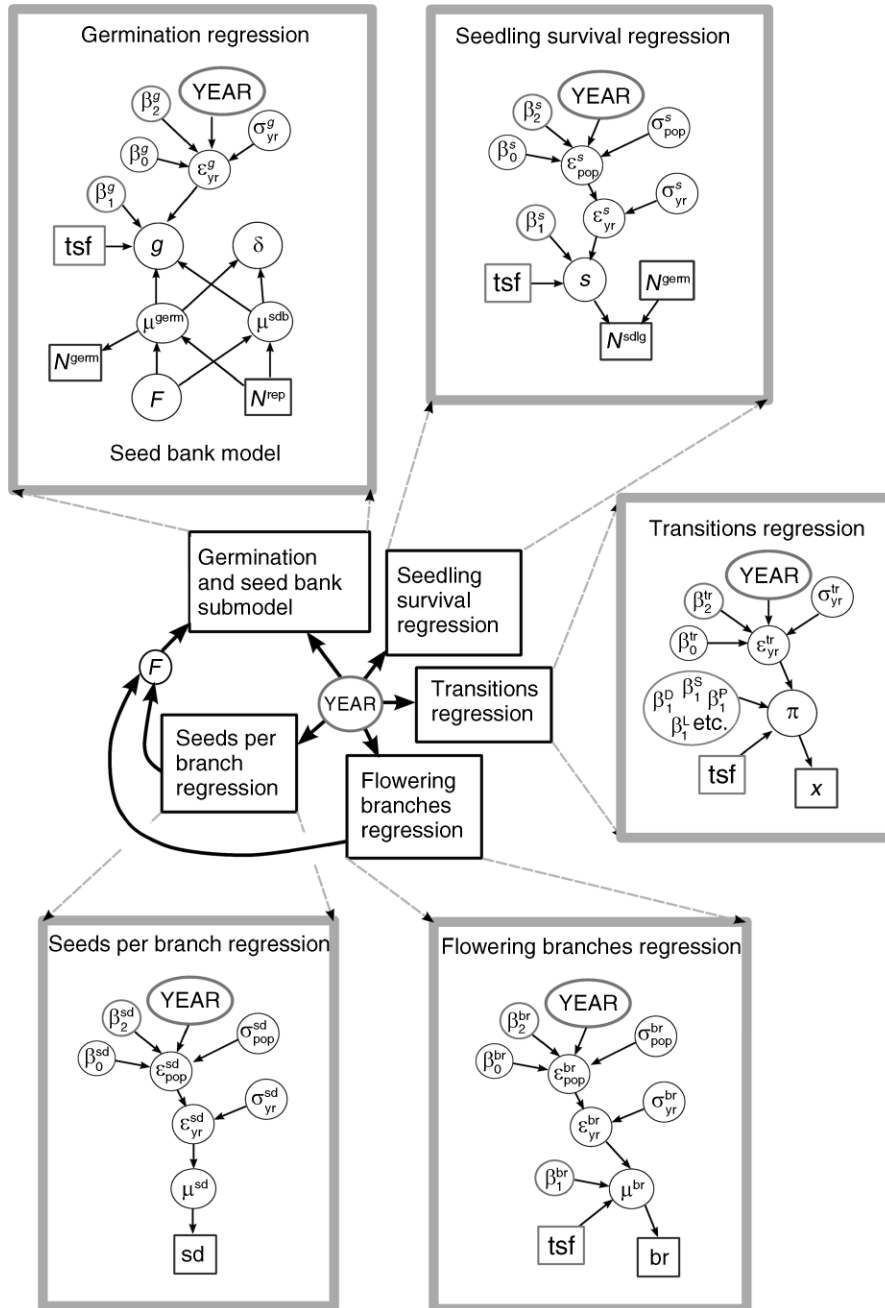


FIG. 2. Graphical representation of the Bayesian hierarchical model used to estimate vital rates. At the center of the figure is a simplified representation of the model, illustrating the five regression submodels linked by a common (model-wide) YEAR effect. Two regressions contribute to estimating seed production per plant (F), which in turn helps estimate germination fraction and seed bank dynamics. Each submodel is additionally shown in an expanded form as a directed acyclic graph (DAG) in a gray box, including all its data (boxes) and parameters (circles). Note that in the DAG of the transitions regression, we do not include a node for each time-since-fire effect (β_1^p , β_1^s , β_1^l , and so on); because there are 20 such parameters (see Fig. 3), it would be difficult to show each as its own node. Note also that the flowering branches DAG and seeds per branch DAG should be connected to F in the seed bank DAG (via μ^{br} and μ^{sd} , respectively), as illustrated in the center of the figure. Parameters are defined in *Methods: Estimating vital rates from demographic data* and in the Appendix.

$$\ln(\mu_{[p,t]}^{\text{br}}) = \beta_{0[t]}^{\text{br}} + \beta_{1[t]}^{\text{br}} \times \ln(\text{TSF}_{[p,t]}) + \beta_{2[t]}^{\text{br}} \times \text{YEAR}_{[t]} \\ + \varepsilon_{\text{yr}[p,t]}^{\text{br}} + \varepsilon_{\text{pop}[p,t]}^{\text{br}}$$

$$\ln(\mu_{[p,t]}^{\text{sd}}) = \beta_0^{\text{sd}} + \beta_1^{\text{sd}} \times \ln(\text{TSF}_{[p,t]}) + \beta_2^{\text{sd}} \times \text{YEAR}_{[t]} \\ + \varepsilon_{\text{yr}[p,t]}^{\text{sd}} + \varepsilon_{\text{pop}[p,t]}^{\text{sd}}$$

The terms β_0^{br} and β_0^{sd} are intercepts describing the mean number of flowering branches per plant and the mean number of seeds per flowering branch, respectively; β_1^{br} and β_1^{sd} are slope coefficients describing how these two components of fecundity respond to time since fire. We chose to model the log of the number of flowering branches and seeds per branch as linear responses to log-transformed time-since-fire data because graphical exploration of the data suggested this gave a reasonable fit. (This was true in all time-since-fire regressions.) We did not evaluate a nonlinear response to log-transformed time since fire (e.g., a quadratic term) because the limited replication with respect to time since fire (see Table 2) would not support inference of a more complex response. These two regressions share a “model-wide” year effect ($\text{YEAR}_{[t]}$), as described above, and each has a random year effect ($\varepsilon_{\text{yr}[p,t]}^{\text{br}}, \varepsilon_{\text{yr}[p,t]}^{\text{sd}}$) and a random population effect ($\varepsilon_{\text{pop}[p,t]}^{\text{br}}, \varepsilon_{\text{pop}[p,t]}^{\text{sd}}$). Because of poor sampling of time since fire among the seeds per branch data, we had little ability to detect an effect of time since fire on the number of seeds per branch, so we set the term β_2^{sd} to zero. We provide a key to all model parameters in Appendix: Table A1.

Seed bank and germination submodel.—We estimated germination fraction (g) and monthly soil seed bank survival ($1 - \delta$), two latent parameters for which we have no direct data, by fitting these parameters to the available time series of data on what goes into the soil seed bank (seed rain) and what comes out (seedlings). The product of flowering branches per plant and seeds per flowering branch yields an estimate of seed production per plant ($\mu^{\text{br}} \times \mu^{\text{sd}} = F$). The product of seed production per plant and the number of reproductive plants in census areas is an estimate of seed rain, the number of seeds entering the soil seed bank in census areas. In these same census areas, we had counts of the number of seedlings that emerged. Difference equations tracking soil seed density (μ^{sdb}) and seedling density (μ^{germ}) allowed us to infer the latent parameters g and δ , given the available data:

$$\mu_{[p,t+1]}^{\text{germ}} = e^{-4\delta} \times g_{[p,t]} [(\mu_{[p,t]}^{\text{sdb}}) + (F_{[p,t]} \times N_{[p,t]}^{\text{rep}})] \\ \mu_{[p,t+1]}^{\text{sdb}} = e^{-4\delta} \times (1 - g_{[p,t]}) \times e^{-8\delta} [(\mu_{[p,t]}^{\text{sdb}}) \\ + (F_{[p,t]} \times N_{[p,t]}^{\text{rep}})].$$

The first equation accounts for the emergence of seedlings (μ_{t+1}^{germ}) from existing seeds in the soil (μ_t^{sdb})

and new seeds produced by reproductive plants ($F_t \times N_t^{\text{rep}}$) in the previous time step. The second equation accounts for the density of seeds in the soil (μ_{t+1}^{sdb}), given soil seed density in the previous time step (μ_t^{sdb}) and new seeds produced by reproductive plants in the previous time step ($F_t \times N_t^{\text{rep}}$). We assumed that soil seed survival can be modeled as a constant decay process. The term $e^{-4\delta}$ describes the decay of seeds in the soil during the (approximately) four-month period from seed production to germination (September to January), and the term $e^{-8\delta}$ describes the decay of seeds in the soil the remaining eight months of the census year (January to September). Further, we modeled the logit transform of g as a function of time since fire and year effects,

$$\text{logit}(g_{[p,t]}) = \beta_0^g + \beta_1^g \times \ln(\text{TSF}_{[p,t]}) + \beta_2^g \times \text{YEAR}_{[t]} + \varepsilon_{\text{yr}[t]}^g$$

following the notation described in *Fecundity regressions* (and see Appendix: Table A1).

Seedling survival regression.—We took the counts of seedlings that survived to the time of the annual census ($N_{[p,t]}^{\text{sdlg}}$) in population p in year t to be draws from a binomial distribution governed by the probability of seedling survival, $s_{[p,t]}$ (specific to that population and year), and the number of seedlings that emerged in that population and year, $N_{[p,t]}^{\text{germ}}$:

$$N_{[p,t]}^{\text{sdlg}} \sim \text{Binomial}(s_{[p,t]}, N_{[p,t]}^{\text{germ}}).$$

We modeled s as a function of time since fire and year effects using a generalized linear model with a logit link function:

$$\text{logit}(s_{[p,t]}) = \beta_0^s + \beta_1^s \times \ln(\text{TSF}_{[p,t]}) + \beta_2^s \times \text{YEAR}_{[t]} \\ + \varepsilon_{\text{yr}[p,t]}^s + \varepsilon_{\text{pop}[p,t]}^s.$$

As before, we estimated two types of year effects: the “model-wide” YEAR effect and a second year effect that affects only seedling survival (plus a random population effect; see Fig. 2 and Table A1).

Transitions regression.—The transitions submodel is an interconnected set of five multinomial logistic regressions, similar to the model described in Evans et al. (2008). For each of five classes of plants at time t (seedling, vegetative, and small, medium, and large flowering), we modeled the counts of plants recorded in five possible fates at time $t + 1$ (vegetative, small, medium, or large flowering, or dead; Fig. 3) as stochastic draws from a multinomial distribution governed by transition probabilities, which we wish to infer, and the number of plants in each stage at time t . The logit transform of each transition probability is modeled as the sum of an intercept, the effect of time since fire, and two year effects (see equations in Appendix: Table A2). Not all of the probabilities in a multinomial model can be freely estimated since together they must sum to one, thus for each class of plants, we standardized the odds of the other fates to the odds of death. In contrast to Menges et al. (2006) and Evans et al. (2008), time since

		Stage at time t				
		sd	v	sf	mf	lf
Stage at time $t + 1$	v	P_1	S_v	Rv_{sf}	Rv_m	Rv_{lf}
	sf	$P_2 + L$	$P_1 + Pr$	S_{sf}	R_1	R_2
	mf	$P_3 + L$	$P_2 + Pr$	P_1	S_{mf}	R_1
	lf	$P_4 + L$	$P_3 + Pr$	P_2	P_1	S_{lf}
	dead	D_{sd}	D_v	D_{sf}	D_{mf}	D_{lf}

FIG. 3. Schematic illustrating the effects of time since fire on transitions, as estimated by the multinomial logistic regression model (transitions regression; see *Methods*). The column indicates the stage of the plant at time t (seedling, vegetative, or small, medium, or large flowering), and the row indicates the stage of the plant at time $t + 1$. The multinomial model estimated the effect of time since fire on seven types of transitions: stasis (S), progression (P), retrogression (R), progression to a reproductive class (Pr), retrogression to a vegetative class (Rv), leap-frogging (L), and death (D). Subscripting indicates unique effects that were estimated; i.e., the model estimated different effects of time since fire on the odds of death of seedlings (D_{sd}) vs. vegetative plants (D_v) vs. small flowering (D_{sf}) vs. medium flowering (D_{mf}) vs. large flowering (D_{lf}). Another example: the model estimated the same effect of time since fire (P_1) on the odds of a seedling becoming a vegetative plant, the odds of a vegetative plant becoming a small flowering plant, the odds of a small flowering plant becoming a medium flowering plant, and the odds of a medium flowering plant becoming a large flowering plant (a one-step progression).

fire was treated as continuous and we did not pool data when the number of plants in a particular class at time t (i.e., sample size) was small or zero.

As in Evans et al. (2008), we estimated the effect of time since fire on the odds of seven biologically distinct types of transitions: death, stasis, progression, retrogression, progression from the vegetative stage to any one of the three flowering classes (Pr), retrogression from any flowering class to the vegetative stage (Rv), and “leap-frogging” (Fig. 3). Leap-frogging (or “leap”) refers to a direct transition from the seedling stage to any one of the three flowering classes, a rare event that tends to occur in the few years immediately after fire. Death is a self-explanatory transition. Stasis occurs when a plant remains in the same stage from one year to the next. Progression and retrogression refer to transitions forward and backward, respectively, in terms of either size or developmental status. Progression into a flowering class and retrogression out of a flowering class are of special interest because flowering starts or stops, respectively. Many of these time-since-fire effects were divided further (e.g., we estimated separate effects of

time since fire on the odds of death of seedlings, vegetative plants and flowering plants of three size classes), as described in the Appendix (Section 1.3, *Transitions regression* and illustrated via subscripting in Fig. 3).

Prior distributions.—Bayesian statistical inference requires that prior distributions are assigned for all model parameters. Of particular interest are the numerical priors assigned to highest-level parameters (Table 3). These prior distributions were broad within a biologically reasonable range. (Defining prior distributions that are too broad leads to instability in the Markov chain Monte Carlo simulation.) For example, in the regression of the number of flowering branches per plant, we assigned normal prior distributions for the intercept terms, $\beta_{0[r]}^{br}$, with mean 0, 1.3, and 3.5, and standard deviation of 1.0, for small, medium, and large flowering plants, respectively (Table 3). Back-transforming these values from the log scale to the original scale, this corresponds to lognormal distributions with mean of 1.7, 5.9, and 54.5 flowering branches, and standard deviation ± 2.2 , 7.3, and 71.7 flowering branches for the three size classes, respectively. These values were assigned based on simple linear mixed effects regressions (using lmer in R; Bates et al. 2008) of the flowering branches data. The slope terms with respect to time since fire, $\beta_{1[r]}^{br}$, were assigned normal prior distributions with mean 0 and standard deviation of 1.0 (Table 4). Back-transforming from the log scale to the original scale, this corresponds to exploring biologically reasonable time-since-fire effects: ranging from -4.4 to $+6.4$ flowering branches per individual with each additional year since fire. As described above, we constrained the prior distributions for $\beta_{2[r]}^{br}$'s to take the values 1 or -1 , with probability $\pi_{b2[r]}^{br}$. This was accomplished by assigning to the intermediate parameter $I_{b2[r]}^{br}$ a sample from a Bernoulli process (coin flip), yielding either the value 0 or 1, then multiplying this sample by 2, and subtracting 1:

$$I_{b2[r]}^{br} \sim \text{Bernoulli}(\pi_{b2[r]}^{br})$$

$$\beta_{b2[r]}^{br} = (2I_{b2[r]}^{br}) - 1.$$

Since $(2 \times 0) - 1 = -1$ and $(2 \times 1) - 1 = 1$, this constrains $\beta_{b2[r]}^{br}$ to take values of 1 or -1 . The Bernoulli process has probability $\pi_{b2[r]}^{br}$ (i.e., the probability of sampling 0 vs. 1), and we assigned uniform prior distributions ranging from 0 to 1 for $\pi_{b2[r]}^{br}$:

$$\pi_{b2[r]}^{br} \sim \text{Uniform}(0, 1)$$

thus allowing the model to estimate the sign of the correlation between the effect of YEAR on a particular vital rate compared to the effect of YEAR on the number of flowering branches in the large flowering class. The model-wide YEAR effect was assigned a normal prior distribution, centered on zero, with a uniform prior distribution (0, 0.5) for the standard

TABLE 3. Prior distributions assigned to highest-level parameters.

Parameter(s)	Submodel	Distribution	Parameter 1	Parameter 2
$\beta_{0[1]}^{br}$	flowering branches	normal	0	1 (std.b0)
$\beta_{0[2]}^{br}$	flowering branches	normal	1.3	1 (std.b0)
$\beta_{0[3]}^{br}$	flowering branches	normal	3.5	1 (std.b0)
$\beta_{1[r]}^{br}$	flowering branches	normal	0	1 (std.b1)
$\tau_{\beta 2[1]}^{br}, \pi_{\beta 2[2]}^{br}$	flowering branches	uniform	0	1
$\sigma_{yr[r]}^{br}$	flowering branches	uniform	0.1	0.9
$\sigma_{pop[r]}^{br}$	flowering branches	uniform	0.05	0.5
β_0^{sd}	seeds per branch	normal	0.15	1.3 (std.b0.sd)
$\tau_{\beta 2}^{sd}$	seeds per branch	uniform	0	1
σ_{yr}^{sd}	seeds per branch	uniform	0.5	1.5
σ_{pop}^{sd}	seeds per branch	uniform	0.5	1.5
$\mu_{[p,1]}^{sdb}$	seed bank	Poisson	1000	
δ	seed bank	gamma	2	20
β_0^g	germination	normal	0	1 (std.b0)
β_1^g	germination	normal	0	1 (std.b1)
$\tau_{\beta 2}^g$	germination	uniform	0	1
σ_{yr}^g	germination	uniform	0	2 (max.sd)
β_0^s	seedling survival	normal	0	1 (std.b0)
β_1^s	seedling survival	normal	0	1 (std.b1)
$\tau_{\beta 2}^s$	seedling survival	uniform	0	1
σ_{yr}^s	seedling survival	uniform	0	2 (max.sd)
σ_{pop}^s	seedling survival	uniform	0	2 (max.sd)
$\beta_{0[i,j]}^{tr}$	transitions	normal	0	1 (std.b0)
$\beta_{1[r]}^{Rv}$	transitions	normal	0	1 (std.b1)
β_1^L	transitions	normal	0	1 (std.b1)
β_1^{Pr}	transitions	normal	0	1 (std.b1)
$\beta_{1[j]}^S$	transitions	normal	0	1 (std.b1)
$\beta_1^{P1}, \beta_1^{P2}, \beta_1^{P3}, \beta_1^{P4}$	transitions	normal	0	1 (std.b1)
$\beta_1^{R1}, \beta_1^{R2}$	transitions	normal	0	1 (std.b1)
$\tau_{\beta 2[i,j]}^{tr}$	transitions	uniform	0	1
$\sigma_{yr[i,j]}^{tr}$	transitions	uniform	0	2 (max.sd)
σ_{YEAR}	shared by all	uniform	0	0.5

Notes: We list the submodel in which the parameter enters and the type of distribution. Parameter 1 and parameter 2 are, for normal distributions, the mean and standard deviation; for uniform distributions, the minimum and maximum; for the Poisson distribution, the mean; and for the gamma distribution, shape and 1/scale. The final column includes (in parentheses) the name given to parameter 2 in the model code (see Supplement 1). Parameters are defined in *Methods: Estimating vital rates from demographic data* and in the Appendix.

deviation (following Gelman et al. 2003) of YEAR effects (σ_{YEAR}). The prior distributions of random population effects ($\epsilon_{pop[p,r]}^{br}$) were centered on the intercept $\beta_{0[r]}^{br}$, and the prior distributions of random

year effects ($\epsilon_{yr[p,r]}^{br}$) were centered on the sum of the intercept, the population effect and the model-wide YEAR effect (see Appendix: Section 1.4, *Hierarchical centering*), with uniform prior distributions for the

TABLE 4. The percentage of variation in the stochastic population growth rate arising from parameter uncertainty in stochastic simulations of population growth with different average intervals between fires (FRI).

Simulation	FRI (years)																				
	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	
Full, 16	64	50	50	52	54	55	55	55	55	55	55	55	55	55	55	54	55	55	55	54	
Full, 64	64	50	50	53	54	55	56	56	56	55	56	55	55	55	55	55	55	55	55	56	55
No year, 16	59	45	45	48	50	51	52	52	53	53	52	52	52	52	53	52	53	52	53	53	53

Notes: Three simulations are compared: two sets of simulations based on the “full” statistical model, and one based on the “no year” statistical model. Simulations were run with the shape parameter of the fire (Weibull) distribution equal either to 16 or 64.

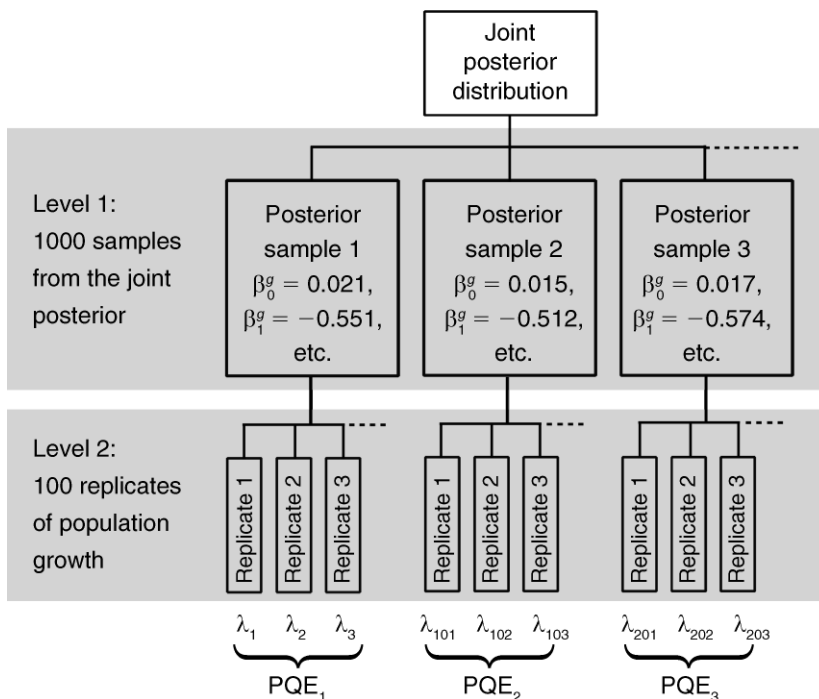


FIG. 4. Nested structure of the stochastic simulations of population growth. A sample from the joint posterior distribution of parameters specifies values for all of the parameters needed to simulate population growth (β_0^g , β_1^g , and so on). These parameter values were used for a set of 100 replicates of population growth. The stochastic population growth rate (λ) was calculated from each replicate of population growth; the probability of quasi-extinction (PQE) was calculated among the replicates of each posterior sample.

standard deviation of population (0.1, 0.9) and year (0.05, 0.5) effects. Prior distributions for other regression parameters follow this pattern (see Table 4). We did not systematically explore the influence of priors on model output (see for example, the method of Millar 2004), thus this paper may be viewed as an introduction to a particular approach, rather than a definitive analysis that management decisions should be based upon (sensu Newman et al. 2006).

Implementation of the statistical model.—The joint posterior density of parameters was estimated via Markov Chain Monte Carlo simulations in OpenBUGS (Version 1.4.1; Spiegelhalter et al. 2003). We ran the simulations with three parallel chains, with initial values for all parameters chosen randomly from the prior distributions. To improve convergence, we used a method of reparameterization known as “hierarchical centering” (detailed in Appendix: Section 1.4). Convergence was assessed using the Gelman-Rubin-Brooks diagnostic, which compares variation within vs. among chains. This comparison is close to unity if the chains are well-mixed (Gelman and Rubin 1992, Carlin et al. 2006). We identified a burn-in phase of 10^5 iterations by examining traces of the chains. The burn-in phase was discarded and we continued the simulation for another 10^5 iterations. Based on examination of autocorrelation plots of the MCMC output, we retained every 100th

sampled value, leading to a posterior sample of 3000 (1000 samples from each of three chains). The BUGS code for our model is found in Supplement 1.

Model comparison.—To explore alternatives to the statistical model described above, we constructed three variations, and compared their fit to the data using an information measure known as the log of the pseudo-marginal likelihood (LPML). The four models were given the following names: full, reduced, no time since fire, and no year. The full model was as described above. The reduced model had no time-since-fire effects on transitions among plant classes (i.e., the multinomial regression). The “no TSF” model had no time-since-fire effects on any vital rates. The “no year” model included time-since-fire effects and year effects unique to each vital rate, but not the model-wide YEAR effect.

The log pseudomarginal likelihood is defined in terms of conditional predictive ordinates (CPO). The CPO for a particular data point is its posterior probability conditional on the remainder of the data (Gelfand et al. 1992, Gelfand and Dey 1994), similar to leave-one-out cross-validation. The LPML is the sum (across all individual data points) of the log of the CPO (Dey et al. 1997), thus it provides a model-wide measure of the fit to all the data (the number of flowering branches and seeds per flowering branch, the number of seedlings germinated, the number of seedlings that survive, and

the number of plants making each of 25 possible transitions among plant classes). Higher values of CPO and LPML indicate a better fit to the data. This criterion does not include an explicit penalty for the number of parameters, but overfitting will cause the model to poorly estimate some data points, reducing the LPML. We did not use DIC (the deviance information criterion, the Bayesian analog of AIC) because it is sensitive to the “focus” chosen during evaluation (i.e., the level of model hierarchy at which likelihoods are evaluated; Spiegelhalter et al. 2002), and in our application a single focus may not be appropriate.

Simulations of population dynamics

We simulated the population dynamics of *D. frutescens* ssp. *frutescens* as a function of fire and year effects using samples from the joint posterior distribution of parameters. The simulation process had two levels of replication, one nested within the other (Fig. 4). The first level of replication involved 1000 different samples from the joint posterior distribution, each specifying a location in n -dimensional parameter space, thus associated with a particular value for each of the parameters estimated by the model. Differences among parameter sets represent parameter uncertainty. For each of these alternative sets of parameter values, we replicated the process of population growth 10^2 times, as described in the following. Differences among simulations for a particular parameter set represent process variability.

Each replicate of population growth began with the year of fire, when the population consisted of 10^6 seeds in the soil. Thereafter, fire occurred stochastically with increasing probability as time since fire increased, according to the cumulative distribution function of the Weibull distribution (see Appendix: Fig. A1.1). The Weibull distribution is often used to model fire (Rupp et al. 2006, Bouchard and Pothier 2008, Moritz et al. 2009) because it is a flexible function that can mimic a variety of other distributions (normal, exponential). In this case we used the Weibull distribution to simulate fire regimes that fire managers might apply, to explore the consequences for population viability (not to infer historical fire frequency). If fire occurred, all plants died and the surviving population consisted of seeds in the soil. If fire did not occur, vital rates were calculated as a function of time since fire and year effects, using the values of regression coefficients (β_0^s , β_1^s , $\beta_{0[1]}^{br}$, $\beta_{1[1]}^{br}$, etc.) and estimates of the standard deviation of year effects (σ_{YEAR} , σ_{yr}^s , $\sigma_{yr[r]}^s$, etc.) sampled for that set of replicates of population growth. Thus year effects were stochastic draws (at each time step) from normal distributions with a mean of zero and standard deviation of σ_{YEAR} (for the model-wide YEAR effect), σ_{yr}^s (variation among years in germination), $\sigma_{yr[1]}^{br}$ (variation among years in the number of flowering branches on small flowering plants), etc. We did not add population random effects, thus we modeled the dynamics of an average population, rather than specific observed populations.

Once vital rates were calculated, plant and seed fates and seed production were sampled from distributions, generating demographic stochasticity. The fates of plants were random draws from multinomial distributions (i.e., their fates were governed by multinomial transition probabilities, calculated as a function of time since fire and year effects). For example, given the transition probabilities 0.40, 0.15, 0.15, 0.10, and 0.20, a total of 10 vegetative plants at time t might become, at time $t + 1$, six vegetative plants, one small flowering plant, zero medium flowering plants, one large flowering plant, and two dead plants, respectively. Similarly, seed fates were random draws from a multinomial composed of three possible fates: seeds might survive and germinate, survive and not germinate, or die (with germination probability a function of time since fire and year effects). Seed production was a random draw from a Poisson distribution (where the mean number of seeds was a function of time since fire and year). This process was repeated at each time step: fire occurred or not, vital rates were calculated as a function of time since fire and year effects, and seed production and the fates of plants and seeds were sampled from appropriate distributions according to those vital rates.

After 75 time steps, we calculated stochastic lambda and determined whether or not the population had fallen below each of four quasi-extinction thresholds (total population size of 1, 10, 100, or 1000 individuals, including plants and seeds). Stochastic lambda was calculated as the mean of the log of all non-zero one time-step population growth rates (population size at time $t + 1$ divided by population size at time t , including plants and seeds), as in Caswell's (2001) Eq. 14.61. In order to evaluate the consequences of different fire management regimes, we performed simulations of population dynamics using a range of mean fire return intervals, from two to 40 years, in increasing increments of two years. Several aspects of the simulations were chosen to match the design in Menges et al. (2006), including the initial population size (10^6 seeds), the duration of replicates (75 years), and the quasi-extinction thresholds (1, 10, 100, and 1000). The simulations of population growth were implemented with original programming in R, provided in Supplement 2.

We performed a nested analysis of variance to evaluate how much of the variability in stochastic lambda arises from parameter uncertainty vs. process variability. Three sources of stochasticity (fire that occurs according to a Weibull distribution, year effects, and demographic stochasticity) generate different trajectories among replicates of the process of population growth (process variability). Because the simulations have a nested structure, with replication of different possible parameter values as well as different stochastic realizations of population growth within each set of parameter values (Fig. 4), we were able to identify variation in the stochastic growth rate due to parameter

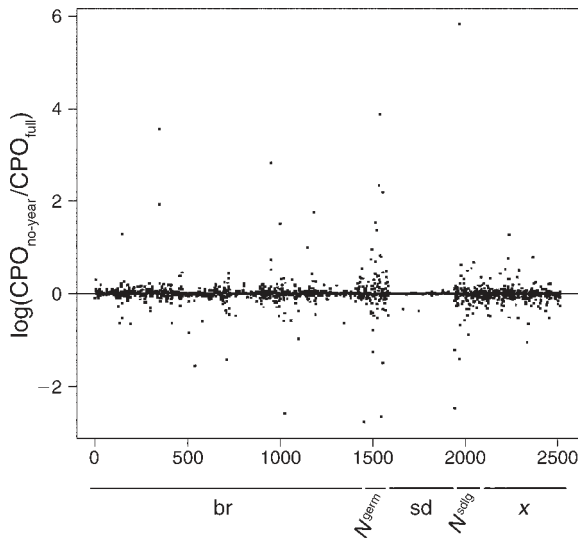


FIG. 5. Comparison of the likelihood of each observed data point given the no-year model vs. the full model (conditional predictive ordinates, CPO). On the y -axis is the log of the ratio of the likelihoods ($\log[\text{CPO}_{\text{no-year}}/\text{CPO}_{\text{full}}]$). On the x -axis are the five types of data analyzed by the model: br (the number of flowering branches per plant), N^{germ} (the number of seedlings observed to germinate), sd (the number of seeds per flowering branch), N^{sdlg} (the number of seedlings that survived to the annual September census), and x (counts of plants in five classes; as in Table 1).

uncertainty vs. process variability. We used a generalized linear mixed model, treating the posterior sample as a random effect modifying the intercept, to analyze variation in stochastic lambda. This model was implemented using the lmer function in the library lme4 in R (Bates et al. 2008).

RESULTS

Model comparison, model fit

Among the four models that we examined, the no-year model and full model were indistinguishable in terms of overall fit to the data (LPML = $-13\,142.45$ and $-13\,142.88$, respectively). The remaining models, reduced and no-TSF, performed much worse (LPML = $-13\,177.98$ and $-13\,387.99$, respectively). Like AIC, differences in the LPML of 2 to 5 units are considered substantial evidence in favor of one model over another (unlike AIC, a larger, less negative value indicates a better fit to the data; see *Methods*).

To more closely examine the fit of the full vs. no-year models to the data, we compared their conditional predictive ordinates. Fig. 5 shows the log of the ratio of the likelihood of each data point under the no-year model (numerator) vs. the full model (denominator). This illustrates that the two models perform equally or close to equally well at predicting much of the data (thus the log likelihood ratio falls close to zero), though slightly more data were better predicted by the full

model than by the no-year model (53% below the zero line, 47% above). Thus the models seem to be indistinguishable by the LPML criterion only as a result of a few data points that were fit better by the no-year model than by the full model (three extreme values above the zero line in Fig. 5).

In Fig. 6, we show the observed data compared to predictions made by the full model, illustrating the fit to the data. The model does very well at predicting seedling survival to the September census (Fig. 6a), as well as the mean number of seeds per branch and the mean number of flowering branches (triangles, Fig. 6b, c). Not surprisingly, there was more variation from the observed data in the multinomial part of the model (Fig. 6d), because the sample size in each category was relatively small (average = 9.6 plants, median = 6 plants). Also, the multinomial regression did not include population random effects, in contrast to the seedling survival, seeds per branch, and flowering branches regressions.

Vital rates and effects of time since fire

Parameter estimates from the full model suggest that time since fire has negative effects on some but not all parts of the life cycle of *Dicerandra frutescens* ssp. *frutescens*. Seed germination per year was low ($\sim 1\text{--}2\%$) and declined with increasing time since fire (x - and z -axes, respectively, Fig. 7a). At the same time, yearly soil seed survival was estimated to be high: $\sim 58\%$ (y -axis, Fig. 7a). Average survival of seedlings from first detection to the time of the annual census in September was estimated to be $\sim 35\%$, and increased with time since fire (Fig. 7b). Time since fire had a positive effect on the number of flowering branches on small flowering plants, but an increasingly negative effect on the number of flowering branches on medium and large flowering plants (Fig. 7c). The average flowering branch produced six seeds.

Fig. 7 also illustrates parameter uncertainty; i.e., we obtained a distribution of possible values for each parameter, rather than a single estimate. Further, particular values for the slope and intercept with respect to germination are associated with one another, and these in turn are associated with particular values of soil seed survival (Fig. 7a). We emphasize this to make it clear that in the simulations of population dynamics, we used samples from the *joint* posterior distribution of parameters; i.e., samples involve non-random combinations of values from the posterior distributions of different parameters estimated by the model (β_0^g , β_1^g , δ , etc.). The non-randomness of those combinations reflects covariation in our uncertainty about them.

Survival of seedlings, vegetative plants, and small flowering plants was negatively affected by time since fire, though only weakly so, whereas survival of medium and large flowering plants was positively affected by time since fire (Fig. 8). All plants were increasingly unlikely to flower with increasing time since fire (Fig. 8). We expected to see this effect for seedlings ("leapfrog-

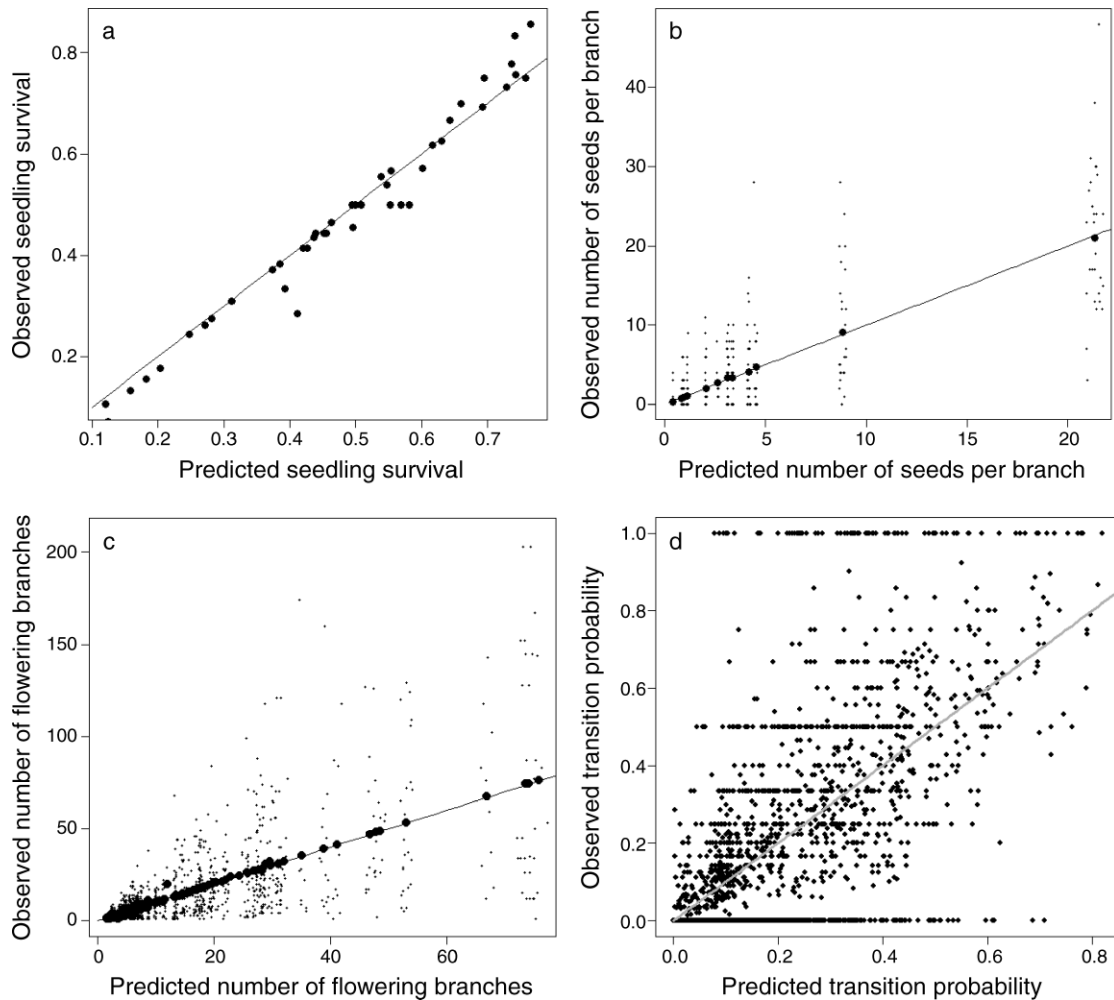


FIG. 6. Comparison of observed data vs. values predicted by the statistical model for (a) seedling survival, (b) the number of seeds per flowering branch, (c) the number of flowering branches per plant, and (d) transition probabilities among plant classes. The 1:1 line indicates perfect match between observed and predicted values in each panel. In panels (a) and (d), each point represents the observed data from a population–year combination; i.e., (a) the fraction of seedlings that survived and (d) the fraction of plants making a transition. In panels (b) and (c), the observed data (counts) for individual plants are the small jittered points, whereas each large point indicates the maximum likelihood vs. Bayesian posterior estimate of the mean of those data (per population–year combination).

ging” is rare other than immediately after fire); the effect is particularly striking for medium and large flowering plants (Fig. 8).

Correlations among vital rates

Posterior distributions of all 325 possible pair-wise correlations between vital rates induced by the model-wide year effect are shown in the Appendix: Fig. A1.2. The 90% credible intervals of all the correlations overlap zero, but some show a clear non-zero trend. For example, variation in the number of flowering branches produced by small flowering plants ($\mu_{[p,t,1]}^{\text{br}}$) was positively correlated with variation in the transition from vegetative to small flowering (posterior mean correlation = 0.34), and negatively correlated with variation in

the number of flowering branches produced by medium flowering plants (posterior mean -0.25 ; Fig. 9). In general, the number of flowering branches on small flowering plants and the odds of a seedling becoming a vegetative plant were positively correlated with transitions “forward” (e.g., progression) and negatively correlated with transitions “backward” (e.g., retrogression; Fig. 9). The number of flowering branches on large flowering plants was correlated with other vital rates in a similar, but weaker pattern, whereas the number of flowering branches on medium flowering plants showed the opposite pattern (Appendix: Fig. A1.2). Several vital rates, including germination fraction, the number of seeds per flowering branch, seedling survival, and the odds of a seedling becoming a flowering plant, showed

no particular correlation with other parts of the life cycle (Appendix: Fig. A1.2).

Stochastic simulations of population dynamics

The probability of total population size falling below the quasi-extinction threshold of 10 individuals (or one individual) was minimized at an average fire return interval of about 24–30 years (Fig. 10). The mean stochastic growth rate increased with the median fire return interval up to about 24 years between fires, after which it changed little (Fig. 11). Figs. 10 and 11 also illustrate that there is a great deal of uncertainty about both the stochastic growth rate and probability of extinction. Uncertainty about the stochastic growth rate includes both parameter uncertainty and process variability (as well as Monte Carlo error; Koehler et al. 2009), whereas uncertainty about the probability of quasi-extinction arises from parameter uncertainty (plus Monte Carlo error). ANOVA indicated that 50–64% of the variation in the stochastic growth rate was due to parameter uncertainty (Table 4). A slightly lower fraction of the variation in the stochastic growth rate was due to parameter uncertainty in simulations based on the “no-year” model compared to the “full” model (Table 4). We found little difference, either in terms of the probability of quasi-extinction or stochastic growth rate, between simulations based on output from the “full” model vs. the “no-year” model (compare Fig. 10 vs. Appendix: Fig. A1.3a and Fig. 11 vs. Appendix: Fig. A1.4a), or between simulations with more vs. less variation around the median time between fires (compare Fig. 10 vs. Appendix: Fig. A1.3b and Fig. 11 vs. Appendix: Fig. A1.4b).

DISCUSSION

*Demography and fire management of *Dicerandra frutescens* ssp. *frutescens**

Modeling vital rates provided estimates of vital rates and how they are affected by time since fire. Germination fraction is predicted to be about 1–2% per year (consistent with germination trials reported in Menges et al. 2006), and to decline with time since fire. Soil seed survival is estimated to be ~60% per year. Production of flowering branches (by medium and large flowering plants) and the odds of becoming reproductive (all plant classes) declined strongly with time since fire, and survival of seedlings, vegetative plants, and small flowering plants declined weakly with time since fire. On the other hand, production of flowering branches on small plants and survival of seedlings up to the time of the annual census increased weakly with time since fire and survival of medium and large flowering plants increased strongly with time since fire. Thus the decline of populations of *Dicerandra frutescens* ssp. *frutescens* with time since fire seems to be a result of negative effects on fecundity and recruitment, rather than survival. In particular, medium and large flowering

plants are predicted to be lost with extended fire suppression.

Negative effects of time since fire on fecundity and recruitment is consistent with the specialization of *D. frutescens* ssp. *frutescens* to gaps (Menges et al. 1999) and the decline of gaps with time since fire. Gaps provide distinct microhabitats compared to the shrub matrix: in gaps, soil water availability is higher (Weekley et al. 2007), light levels are higher, and leaf litter accumulation is lower. Reduced soil moisture as shrubs encroach into gaps may reduce or temporarily end reproduction by mature *D. frutescens* ssp. *frutescens* plants and increased leaf litter may suppress recruitment (germination or seedling survival before the time of seedling detection). Another possible negative effect of time since fire is the decay of a post-fire nutrient pulse (S. Hicks and E. S. Menges, *unpublished manuscript*).

We found positive effects of time since fire on seedling survival from the time of detection to the time of the annual census (Fig. 7b) and survival of medium and large flowering plants (Fig. 8). One possibility is that these plants may survive better in smaller canopy gaps (corresponding to greater time since fire), if small gaps are buffered from extremes of heat or drought. The mechanistic basis of positive and negative effects of time since fire can be explored (confirmed or denied) via experiments with nutrients and canopy removal. In any case, the results from the model have stimulated ideas about the reasons for decline of *D. frutescens* ssp. *frutescens* with time since fire.

Modeling vital rates served a second purpose: it provided the basis for simulations of population-level demography with respect to time since fire. We found that the probability of quasi-extinction (PQE) was minimized with a median fire return interval of ~24–30 years (Fig. 10). The average stochastic growth rate increased up to a median fire return interval of ~24–30 years, but did not decline with longer intervals between fires (Fig. 11). Since this growth rate reflects populations that did not go extinct, we infer that longer intervals between fires increase the probability of extinction, but that the growth rate of persistent populations does not decline.

The overall pattern of PQE with fire that we found is similar to the pattern obtained from a likelihood analysis for parameter estimation and matrix selection for simulations (Menges et al. 2006). However, we found higher extinction probabilities, and the fire return interval corresponding to the minimal probability of quasi-extinction is longer in our analysis (24–30 years, as opposed to 6–21 years reported by Menges et al. 2006). We suggest two possible explanations for these differences.

First, the time-since-fire data may not adequately capture the history of disturbance at one of the two long-unburned sites. One of the long-unburned populations (population 19) declined from a high of 42

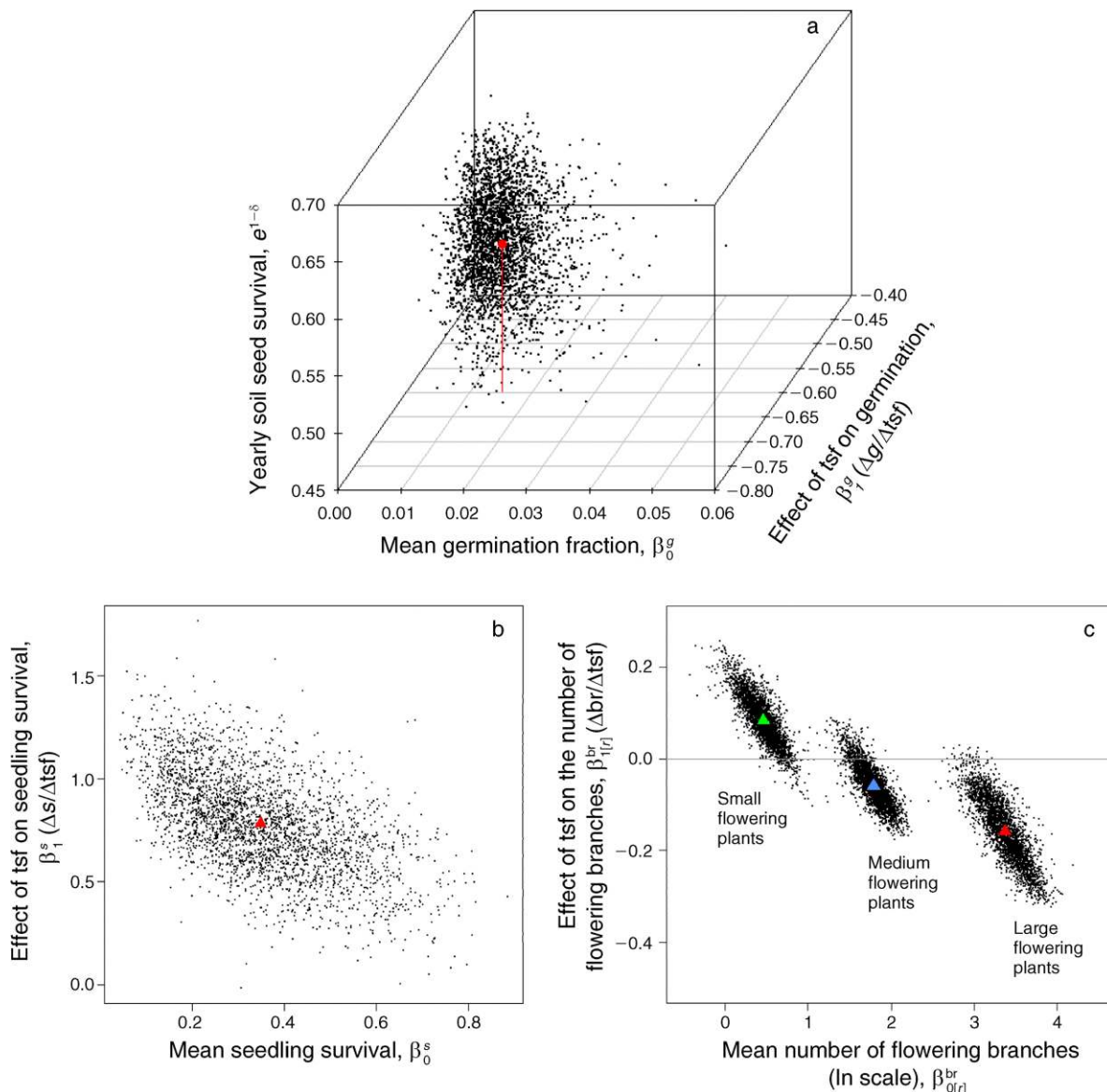


FIG. 7. Joint posterior distributions of parameters estimated by the statistical model. Panel (a) shows parameters relevant to seed dynamics, including average germination fraction (β_0^g , x dimension), the effect of time since fire (tsf) on germination ($\beta_{1[r]}^g$, z dimension), and yearly soil seed survival ($1 - \delta$, y dimension). The posterior mean is identified with a red thermometer. Panel (b) shows average seedling survival (β_0^s , x-axis) and the effect of time since fire on seedling survival ($\beta_{1[r]}^s$, y-axis), with the posterior mean identified with a red triangle. Panel (c) shows the average number of flowering branches per plant ($\beta_{0[r]}^{br}$, x-axis) and the effect of time since fire ($\beta_{1[r]}^{br}$, y-axis) for three classes of flowering plants (small, medium, large), with posterior means identified by green, blue, and red triangles, respectively.

reproductive plants in 1990 to a low of zero reproductive plants in 1997, 1998, and 1999 (with few reproductive plants thereafter). The other, population 2, has not shown such a decline, in spite of the fact that it has not burned in 80 years (as of 2007; Table 2). Population 2 occurs on a trail used for animal surveys (in addition to the quarterly censuses of *Dicerandra*); the plants are found in persistent canopy gaps along this trail. In addition, Hurricane Charlie (in 2004) caused pine mortality at this site, resulting in a progressively more

open canopy. A further point is that zero reproductive plants in 1997–1999 (and other cases of zero plants) in the declining population (population 19) mean that the *only* data available to the model for inferring vital rates and the effect of time since fire on vital rates come from the persistent population (population 2). The result may be the weak increase in PQE seen in Fig. 10 with longer intervals between fires.

A second explanation has to do with the effect of stochasticity in simulations of population growth.

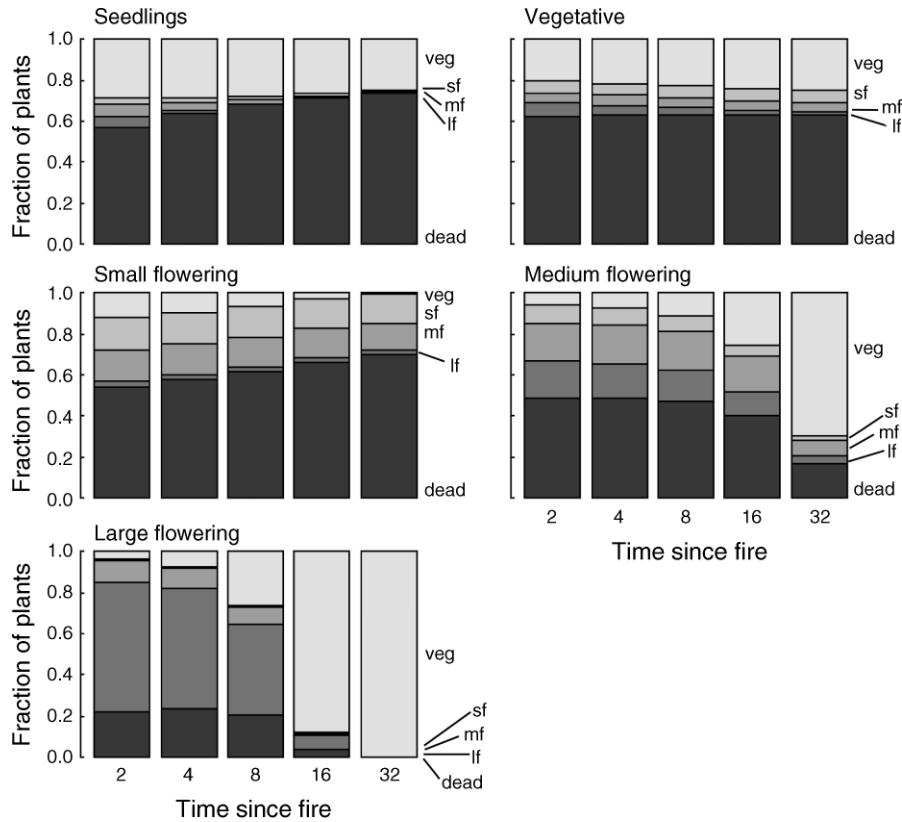


FIG. 8. Predicted fraction of plants experiencing five fates at time $t + 1$ (vegetative, small flowering, medium flowering, large flowering, and dead, in increasingly darker shades of gray within each bar) as a function of increasing time since fire (x-axis in each panel) in populations of *Dicerandra frutescens* ssp. *frutescens*. The five panels show five classes of plants (i.e., the state of the plant at time t): seedling, vegetative plant, and small, medium, and large flowering plant.

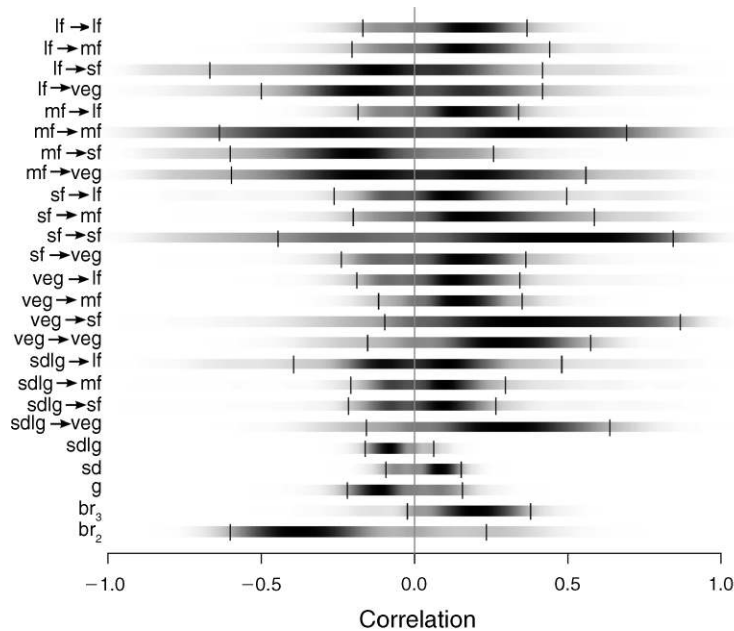


FIG. 9. Posterior densities of the correlation between the number of flowering branches on small flowering plants ($\mu_{br_{pt1}}$) and each of the other (25) vital rates (listed on the y-axis). Tick marks indicate the 90% highest posterior density (or credible interval, CI). Vital rate names are given in model code (see Supplement 1).

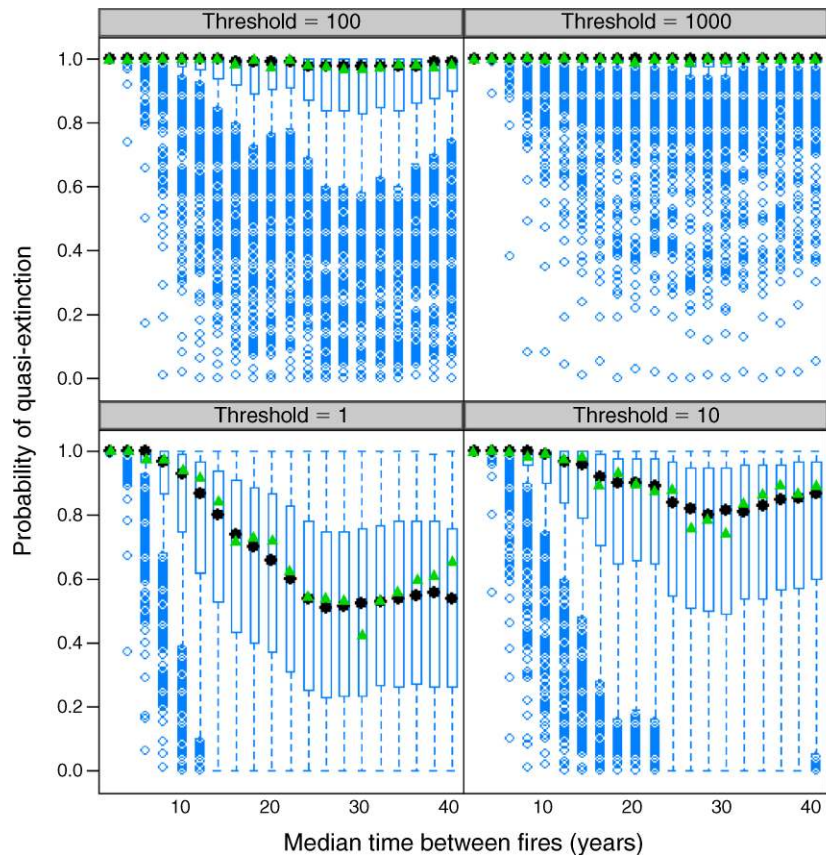


FIG. 10. Box-and-whisker plots of the probability of quasi-extinction (PQE) as a function of fire return interval, given four different thresholds: 1, 10, 100, and 1000 individuals. At each fire return interval, variation among 1000 PQEs is summarized, where each PQE value is derived from 100 simulations of population growth using a different sample from the joint posterior distribution of possible parameter values (see Fig. 4). Box limits fall at the first and third quartiles, whiskers end at 1.5 times the interquartile range, and open circles are outliers. Black dots show the median among 1000 PQEs, whereas green triangles show the PQE based on 100 simulations using the posterior mean values of parameters (i.e., no parameter uncertainty). Parameter estimates are from the “full” model, and simulations used a Weibull shape parameter of 16.

Menges et al. (2006) found that stochastic fire increased the optimal fire return interval for *Dicerandra frutescens* ssp. *frutescens*, from 6–12 years under a deterministic fire regime to 6–21 years, and increased the minimum probability of quasi-extinction. To try to verify this effect of fire stochasticity, we ran simulations of population growth with little variation around the median fire return interval (by specifying a larger value for the Weibull shape parameter), but patterns of PQE changed little (Appendix: Fig. A1.3b compared to Fig. 10). Our simulations included parameter uncertainty, as well as demographic stochasticity, and greater year variation (by estimating and sampling from the distribution of year effects, rather than resampling observed vital rates), compared to Menges et al. (2006). Simulations without parameter uncertainty (green triangles, Fig. 10) follow the trend of simulations with parameter uncertainty (black dots, Fig. 10), indicating that parameter uncertainty is not responsible for the differences between this study and Menges et al. (2006). Thus it may be that demographic stochasticity

and a different approach to modeling year variation resulted in yet higher optimal fire interval, PQE that increases more weakly with time since fire after that optimal range, and higher minimum PQE, compared to Menges et al. (2006). Further dissection of the effects of different sources of variability (sensu Melbourne and Hastings 2008) would be revealing.

In addition to these unresolved issues, the gap in the time-since-fire data between 16 and 48 years (Table 2) means that the response of the probability of quasi-extinction to fire return interval (Fig. 10) is an interpolation in this range of time since fire. For all these reasons, we do not recommend long intervals between fires as a management regime to support populations of *D. frutescens* ssp. *frutescens*, in spite of the weak increase in PQE after 30 years between fires. We recommend fire management with median intervals between fires no more than 30 years.

Mean stochastic growth rates were, for the most part, well below the replacement level of 1.0, regardless of fire return interval (Fig. 11), suggesting populations of

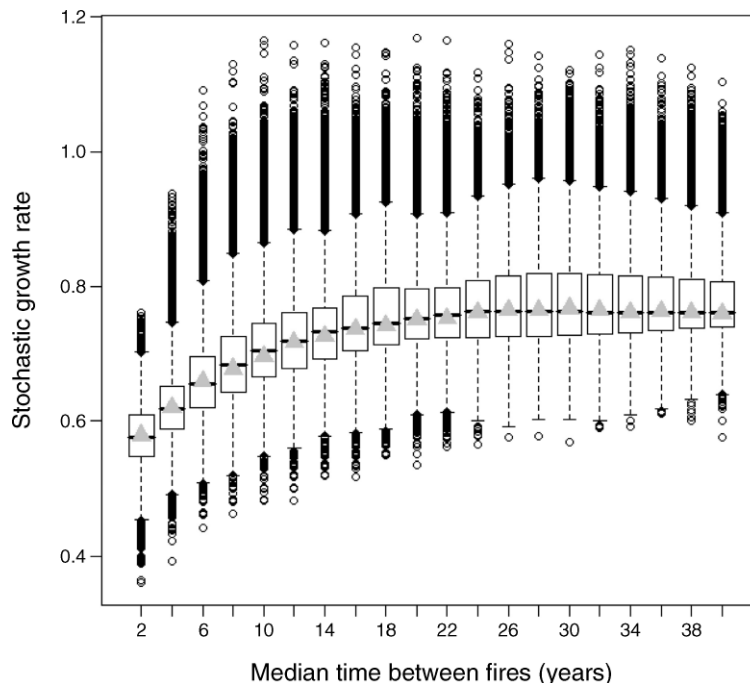


FIG. 11. Box-and-whisker plots of the stochastic growth rate (λ) as a function of fire return interval. At each fire return interval, variation among 100 000 λ 's is summarized, due to 1000 samples from the joint posterior distribution of parameter values and 100 replicates of population growth each (see Fig. 4). The mean among all 100 000 λ 's is indicated with a horizontal black bar, whereas triangles show the mean λ based on 100 simulations using the posterior mean values of parameters (i.e., no parameter uncertainty). Parameter estimates are from the "full" model, and simulations used a Weibull shape parameter of 16.

Dicerandra frutescens ssp. *frutescens* will decline even under the "best" fire management regime. We see several possible interpretations of this result. First, an optimal fire regime really should lead to stochastic growth rates near one and low extinction risks, but we do not yet have enough data to reliably infer the effect of time since fire on vital rates, since we have observed only three fires (Table 2). Second, factors other than fire may have been negatively affecting populations of *Dicerandra frutescens* ssp. *frutescens*. In terms of annual precipitation, 2000 and 2007 were the second and third driest on record since 1934, and 2002 was the fifth wettest. Winter precipitation, which normally supports seedling recruitment, has been low over the period 2000–2007. Explicitly including weather variables in the model and simulating population growth under alternative weather regimes may help better understand the influence of weather on demography and the possible effects of climate change. A third possibility is that the Florida scrub landscape is now missing a source of disturbance (other than fire) that was historically present (for example, megafauna present up until ~10 000 years ago; Koch et al. 1998). Populations of *Dicerandra frutescens* ssp. *frutescens* found in road margins perform very well (Menges et al. 2006), indicating that fire is not the only form of disturbance to which this plant responds.

Parameter uncertainty vs. process variability

Hierarchical Bayesian methods have been noted for their ability to account for both parameter uncertainty and process variability (Wade 2002, Clark 2003, Maunders 2004), though this is not unique to a hierarchical Bayesian approach. The nested design of our simulations (Fig. 4) allowed us to distinguish between them. We found that parameter uncertainty was responsible for 50–64% of variation in the stochastic growth rate (Table 4). This is a sobering result given that the data set that we used is extraordinarily long (20 years) and involved thousands of individuals in multiple populations. On the other hand, we observed only three fires (Table 2), thus the information available for regressions involving time since fire was relatively limited. Another probable source of parameter uncertainty was the choice to split plants into classes and estimate separate parameters for the transitions among classes. We made this choice to better compare our results to Menges et al. (2006). A future analysis may do well to avoid this (parameter-rich) aspect of the model by employing an integral projection model approach (Childs et al. 2004, Ellner and Rees 2006), where plant fates are modeled as a function of continuous (i.e., size) data. Also sobering is the result that much of the variability in the population growth rate resulted from process variability, including stochastic variation in fire history, year variation, and

demographic fates among replicates of population growth, which would not be reduced by additional data. Thus our analysis is useful for choosing a fire management regime, not for predicting the exact fate of populations over a long time span (as discussed by Menges 2000, Reed et al. 2002, Drechsler et al. 2003). We suggest PVA is best used in the framework of ecological forecasting or adaptive management, assimilating new data into the model as they are generated and updating forecasts of population trends using specific scenarios of fire and other factors (Clark et al. 2001, Hui et al. 2008, Bakker and Doak 2009).

Model comparison, model structure

Our current (modest) effort at exploring alternative models found that the full model and no-year model were indistinguishable in terms of their fit to the data (according to the LPML criterion). We used the full model to estimate correlations among vital rates associated with year-to-year variation, and incorporated those correlations into simulations of population growth. This aspect of our model is similar to Doak et al.'s (1994), in that correlations between vital rates (not due to time since fire) were assumed to be caused by their shared dependence on an "unidentified" factor (YEAR). However, Doak et al. (1994) made multiple estimates of the correlation between each vital rate and the environmental variable, based on each of the other vital rates in the life cycle, then calculated the average of these estimates. Here all vital rates, time-since-fire effects, YEAR effects, and the correlations among vital rates arising from their shared dependence on YEAR were estimated simultaneously using a single model. Contemporary Bayesian methods make it possible to create a single complex model that estimates several vital rates as a function of a shared variable (here, YEAR). Correlations between vital rates could also be estimated from the independent year effect estimated by the "no-year" model, however, if those correlations are important, the estimates of other parameters will not be as good as they should be. That is, the full model better reflects the design of the data, thus it should provide better estimates of parameters. The full model structure also offers an avenue for including climate effects: weather variables (precipitation, drought) could be regressed on the YEAR effect to identify specific drivers of variation in demography. On the other hand, it may be that different vital rates are affected by different aspects of weather and to different degrees, such that it is more efficient to regress weather variables on year effects unique to those different vital rates, and do away with the model-wide YEAR effect altogether.

Ultimately, we think further evaluation of alternative models is needed. Simulated data should be used to test the ability of the full model vs. the no-year model to detect exogenous effects on vital rates and correlations among vital rates. Alternative responses of vital rates to time since fire are also worth pursuing.

The threefold challenge of PVA

Population viability analysis is challenging for *at least* three reasons: ideally, one would like to (1) incorporate the effects of covariates, (2) include correlations among vital rates, and (3) account for both parameter uncertainty and process variability. Our model accomplishes these three things. Parameter uncertainty is a familiar problem: the use of a single value (e.g., the maximum likelihood estimate, MLE) for each vital rate in a population model ignores parameter uncertainty, resulting in underestimation of the risk of early population collapse (Ludwig 1996, Wade 2002). Bootstrapping, either parametric or nonparametric, is the usual solution to this problem (Kalisz and McPeck 1993, Caswell 2001, Morris and Doak 2002, Evans et al. 2007, Beissinger et al. 2008), however bootstrapping does not account for process variability. Process variability can be addressed by repeated simulation of the relevant process (here, replication of population growth with respect to stochastic fire and year variation). Yet there are few examples in the literature where bootstrapping has been combined with repeated simulation to address both parameter uncertainty and process variability (but see Restrepo et al. 1992, Bakker et al. 2009). A further point is that without explicit attention to correlations among vital rates, bootstrapping potentially creates unrealistic combinations of vital rates, which alters estimates of population growth rate and extinction risk (Tuljapurkar 1990, Doak et al. 1994, Ferson and Burgman 1995, Fieberg and Ellner 2001). Morris and Doak (2002) explain methods to account for correlations among vital rates. Here we've taken the approach of modeling vital rates as a function of fixed effects (time since fire) and random effects (random year effects) to capture both process variability and correlations among vital rates. Many previous examples that included covariates have ignored uncertainty about their effect (Anderson et al. 1995, Leirs et al. 1997, Lima et al. 1999, 2001, Coulson et al. 2001, Gotelli and Ellison 2006, Meyer et al. 2006); here we account for parameter uncertainty by sampling from the joint posterior distribution of parameters. None of these previous examples with covariates included a shared random effect to account for correlations among vital rates not due to the measured covariate. Thus we provide one of very few examples that model vital rates as a function of known and unknown sources of variation, account for covariation among vital rates, as well as parameter uncertainty and process variability. Bakker et al. 2009 focus on a similar set of issues using likelihood methods. The growing literature using hierarchical Bayesian methods to analyze demography (Sullivan 1992, Ver Hoef and Frost 2003, Wikle 2003, Rivot et al. 2004, Royle and Wikle 2005, Newman et al. 2006, Winship and Trites 2006, Diez 2007, Diez and Pulliam 2007, Hooten and Wikle 2007, 2008, Hooten et al. 2007, LaDeau et al. 2007, McMahon and Diez 2007, Purves et al. 2007, Royle et al. 2007, Adler and HilleRisLambers

2008, Lillegard et al. 2008, Schick et al. 2008, Snall et al. 2008, Gillespie and Golightly 2010) also addresses several of these issues, though not all at once, that we have been able to find. The model presented here, among other emerging analytical approaches to demography, should allow us to make better use of hard-earned data and gain a better understanding of the reasons for changes in the abundance of populations of concern.

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APPENDIX

Additional methodological details about the statistical model (*Ecological Archives* M080-022-A1).

SUPPLEMENT 1

WinBUGS code for the statistical model that estimates vital rates, effects of time since fire, year and population effects (*Ecological Archives* M080-022-S1).

SUPPLEMENT 2

R code that simulates the dynamics of populations of *Dicerandra frutescens* ssp. *frutescens* experiencing alternative fire regimes, using BUGS output (*Ecological Archives* M080-022-S2).