ORIGINAL ARTICLE

Modeling the effect of fire on the demography of *Dicerandra frutescens* ssp. *frutescens* (Lamiaceae), an endangered plant endemic to Florida scrub

Margaret E. K. Evans · Kent E. Holsinger · Eric S. Menges

Abstract Managing populations, either for conservation, harvesting, or control, requires a mechanistic or semi-mechanistic understanding of population dynamics. Here, we investigate how time-since-fire affects demographic transitions in an endangered plant, *Dicerandra frutescens* ssp. *frutescens* (Lamiaceae), which is specialized to gaps created by fire. We used a hierarchical Bayesian model to estimate transition probabilities (i.e., the elements of population projection matrices) as a function of time-since-fire and random effects, from 13 years of data on marked individuals in five populations. Using a standard Bayesian criterion to compare models, we find that death becomes increasingly probable and progression increasingly improbable with time-since-fire. The magnitude of some of the time-since-fire effects is substantial: death is 3–5 times more likely for flowering plants >6 years versus 3–6 years post-fire, 3-step progression is almost 7 times less likely, and large flowering plants are more than 6 times more likely to stop flowering. These insights inspire new hypotheses about the underlying cause of decline with time-since-fire, and how it can be managed. Our approach can be used by others who wish to model the effect of an exogenous factor on demography, while rigorously accounting for uncertainty and variability.

Keywords Hierarchical Bayesian analysis · Florida scrub · Model comparison · Model uncertainty · Population projection · Time-since-fire

M. E. K. Evans (✉)
Unit of Mathematical Eco-Evolutionary Biology,
Laboratoire d'Ecologie, Ecole Normale Supérieure,
46 rue d'Ulm, 75230 Paris Cedex 05, France
e-mail: margaret.evans@yale.edu

M. E. K. Evans
Department of Ecology and Evolutionary Biology,
Yale University, New Haven, CT 06520-8106, USA

K. E. Holsinger
Department of Ecology and Evolutionary Biology,
University of Connecticut, U-3043, Storrs, CT 06269-3043, USA
e-mail: kent@darwin.eeb.uconn.edu

E. S. Menges
Archbold Biological Station, P.O. Box 2057, Lake Placid,
FL 33862, USA
e-mail: emenges@archbold-station.org

Introduction

Accurate modeling of population dynamics is essential for management of rare species [i.e., population viability analysis (PVA); Boyce 1992; Menges 2000; Beissinger and McCullough 2002; Morris and Doak 2002], sustainable harvest of economically important species, and control of pests, weeds, or invasive species (Shea et al. 1998; Ticktin et al. 2001; Mertens et al. 2002; Freckleton 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 (van Mantgem et al. 2004; Maschinski et al. 2006; Morris et al. 2006). Fieberg and Ellner (2001) suggest that incorporating such factors into models can improve prediction of population dynamics. Further, models relating environmental covariates to population growth allow managers to identify the manipulations most likely to have desired effects.

Here, we examine how an exogenous factor, time-since-fire, affects the demography of an endangered perennial herb, *Dicerandra frutescens* Shinners ssp. *frutescens* Huck (Lamiaceae), which is endemic to the Lake Wales Ridge in central Florida, USA. This plant is found in Florida scrub communities, particularly in oak-hickory 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. Most perennials in the community resprout vigorously after fire (e.g., *Quercus myrtifolia* and other oaks), re-establishing the canopy. Others, like *D. frutescens* ssp. *frutescens*, are killed by fire. For populations of such a species to persist, individuals must regenerate from seeds that persist in the soil (Menges et al. 2006) or from seeds produced by surviving individuals if the fire is patchy. Like several other endangered plants endemic to Florida scrub, *D. frutescens* ssp. *frutescens* depends on canopy openings (Menges et al. 1999). Reproductive success and survivorship decline with time-since-fire in other "gap-specialists" of Florida scrub (Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004). A PVA of *D. frutescens* ssp. *frutescens* (Menges et al. 2006) indicated that the asymptotic growth rate, λ, declines below the replacement level of 1.0 (on average) in populations that remain unburned more than 6 years.

A limitation of many PVAs is that they are largely phenomenological (Boyce 1992; Beissinger and Westphal 1998; Fieberg and Ellner 2001). In the case of *D. frutescens* ssp. *frutescens*, for example, we still know little about what changes in demography are associated with increasing time-since-fire and a corresponding decline in the asymptotic growth rate. As a result, we have little indication of what mechanisms may be involved. Here, we dissect the negative effect of time-since-fire on the demography of *D. frutescens* ssp. *frutescens* by exploring its effect on demographic transitions. We use a hierarchical Bayesian model to estimate transition probabilities (i.e., the elements of the population projection matrices used in the PVA) as a function of time-since-fire and random effects. The Bayesian approach allows us to make quantitative, probabilistic statements about the effects of time-since-fire; i.e., statements of how much time-since-fire affects the odds of death, or other demographic transitions, rather than simply rejecting or failing to reject the null hypothesis of no effect (as discussed by Wade 2000; Ludwig et al. 2001; Marin et al. 2003; Ellison 2004). Further, the hierarchical Bayesian approach allows us to rigorously account for both parameter uncertainty and process variability, as discussed by Goodman (2002), Clark (2003, 2005), Harwood and Stokes (2003), and Maunder (2004).

Given a population structured by variables such as age, size, sex, or developmental stage, even a single exogenous

factor (like time-since-fire) can give rise to many alternative models of how that factor affects demography. For example, time-since-fire might affect the survival of seedlings but not established plants. Thus, we take a model comparison approach, following the tradition of zoologists analyzing capture–recapture data (Lebreton et al. 1992; Burnham and Anderson 1998). We begin with a fully parameterized model, with structure informed by the life-history. This model allows different effects of time-since-fire both on different life stages and on different types of demographic transitions (death, progression, etc.). We then compare this model to simpler models, using a Bayesian model comparison criterion. This approach allows us to build a more detailed understanding of the effect of time-since-fire on the demography of *D. frutescens* ssp. *frutescens*.

Methods

The data

We used a subset of the data used by Menges et al. (2006) in their analysis of population viability: we included only the five populations occurring in relatively unmodified Florida scrub habitat. The data come from 13 years of quarterly censuses of marked individuals in 1-m^2 quadrats within each study population; this includes a total of 2,191 unique plants monitored. We used the same five stages of plants established by Menges et al. (2006) by use of the Moloney algorithm (Moloney 1986): seedlings, vegetative plants (i.e., non-seedlings that were not flowering), and reproductive plants of three size categories (small, medium, large; Fig. 1a). In contrast to Menges et al. (2006), we did not pool data when the sample size in a particular stage was small (1–5 plants in a given population in the first year of a pair of years), or when no plants transitioned into the large reproductive stage. However, if there were no plants in a particular stage in a given population in the first year of a pair of years, we pooled data from the same stage in other years or populations (the same habitat type and approximate time-since-fire) until reaching a sample of at least five plants in that stage, as described in Menges et al. (2006). Such pooled data comprised <6% of the data set. Based on the analysis in Menges et al. (2006), we created five categories of time-since-fire: year-of-fire (plants killed by fire), 1 year after fire (seedlings recruit), 2 years after fire (seedlings recruit, seedlings transition to other stages), 3–6 years after fire (all transitions possible), and >6 years after fire (all transitions possible). Ultimately, only the last two categories are of interest here. The available data were unbalanced with respect to these time-since-fire categories: there are only 9 population–year combinations that fall into

the recently burned category (3–6 years since fire), compared to 40 in the last category (>6 years after fire).

The model

We used a multinomial logistic model that is fundamentally similar to the "Alligators" example provided in the software WinBUGS (available freely at http://www.mrc-bsu.cam.ac.uk/bugs). For each of five stages of plants at time t (seedling, vegetative, and small, medium, and large reproductive), the number of plants recorded in five possible fates at time $t + 1$ (vegetative, small, medium, or large reproductive, or dead) is modeled as a stochastic realization of the corresponding set of transition probabilities which we wish to infer (first-stage likelihood; Fig. 1a). The logit transform of these transition probabilities are modeled as the sum of fixed and random effects (multinomial logistic model; Fig. 1b). The fixed effects affect seven different types of demographic transitions (Fig. 1b): death, stasis, progression, retrogression, progression from the vegetative stage to a reproductive stage (Pr), retrogression from a reproductive stage to the vegetative stage (Rv), and "leap-frogging". Leap-frogging (or "leap") refers to a direct transition from the seedling stage to a reproductive stage, a rare event that tends to occur in the few years immediately after fire. The random effects capture variation due to factors that were not included in the model, such as population and year effects. Note, however, that population and year effects were not modeled explicitly; instead, separate random effects were estimated for each transition in each population in each year, one corresponding to each transition probability (1,450 transition probabilities, due to 12 year-pairs of data for 4 populations and 10 year-pairs for one population, with 25 transition probabilities per population and year-pair). For example, the logit of the probability of a seedling becoming a large reproductive plant (π_{41}) is the sum of the effect of leap-frogging, the effect of a 4-step progression, and a random effect (Fig. 1b).

We considered models that placed different types of constraints on the fixed effects (Fig. 1c). We examined the hypothesis of no effect of time-since-fire by constraining the fixed effects estimated for the different time-since-fire

Fig. 1 Schematic of the statistical model used to investigate fire effects on non-seed demographic transitions in *Dicerandra frutescens* ssp *frutescens*. **a** The data, counts of plants in five stages at time t and time $t + 1$ (x_{ij}'s), are stochastic draws from underlying multinomial probabilities (π_{ij}'s). **b** The multinomial probabilities are the sum of fixed effects and random effects (ε_{ij}'s). Fixed effects affect seven kinds of transitions: stasis (*S*), progression (*P*), retrogression (*R*), death (*D*), leap-frogging (*L*), and transitions into (*Pr*) and out of (*Rv*) reproductive stages. Subscripting within each group of transitions indicates where different parameters were estimated in the "full" version of the effect. **c** Fixed effects on death (like most other fixed effects) can depend on plant category (subscripting) and/or time-since-fire category
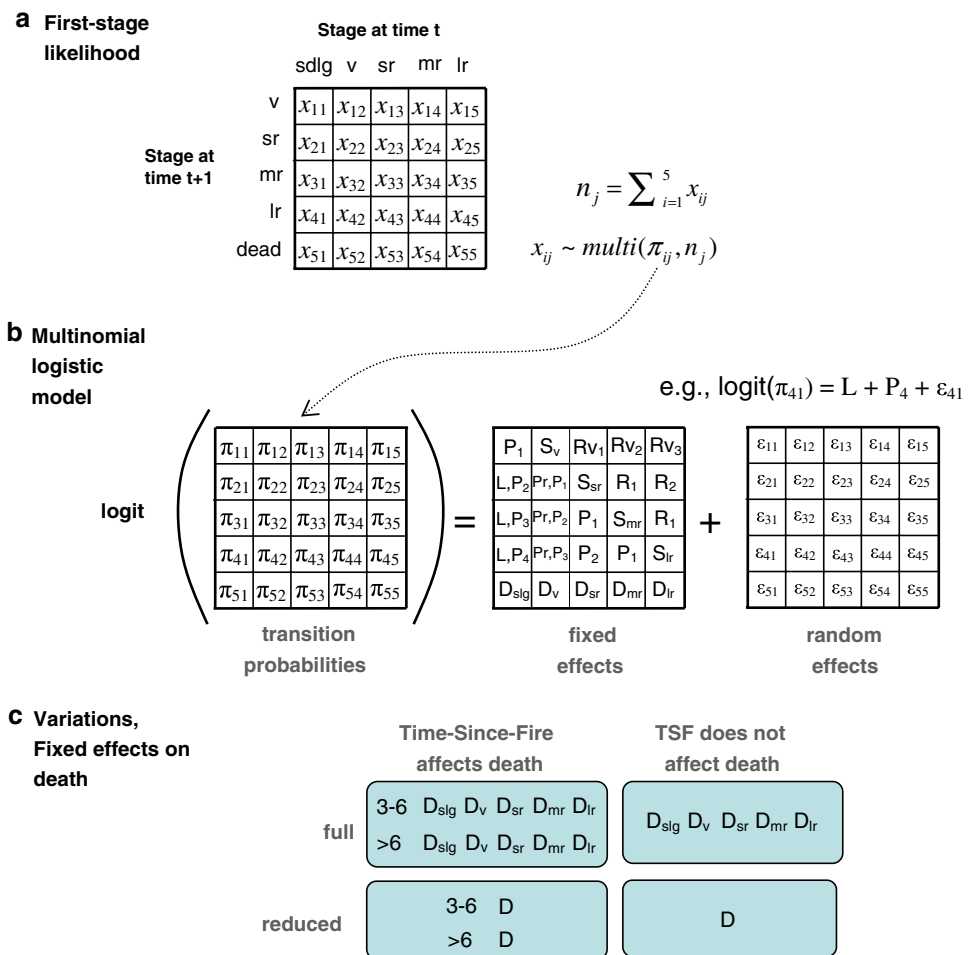
categories to be equal. Alternatively, separate effects were estimated for each time-since-fire category. A second dimension of model variation involved "full" versus "reduced" effects, as delineated by the subscripting in the fixed effects panel of Fig. 1b. For example, the "full" version of death estimates different odds of death (or effect of time-since-fire on the odds of death) for each plant stage ($D_{slg} \neq D_v \neq D_{sr} \neq D_{mr} \neq D_{lr}$), whereas the "reduced" version fits one effect for all types of plants ($D_{slg} = D_v = D_{sr} = D_{mr} = D_{lr}$). Hence most fixed effects (not Pr or Leap) may be parameterized in four different ways: full or reduced, with or without an effect of time-since-fire (Fig. 1c). We systematically explored these alternative models. Table 1 shows the number of parameters estimated for each fixed effect model that we considered (7–42). These, added to the 1,450 random effects and 1,450 transition probabilities, make the total number of parameters large. Finding the maximum likelihood estimates (MLE's) of such a large number of parameters would be essentially impossible. Taking a Bayesian approach avoids this problem: MCMC (Markov chain Monte Carlo) methods allow the posterior distribution to be explored efficiently, generating posterior distributions for each parameter.

The prior distributions for both random and fixed effects were centered on zero. We found that the ranking of alternative models was somewhat sensitive to the choice of the variance of these prior distributions, so we constructed the model to estimate the variance of the random and fixed effects. We chose a uniform distribution (bounded from zero to four) for the prior distribution of the logit of the standard deviation of the random and fixed effects (i.e., "hyperpriors"). A value of one for this standard deviation corresponds roughly to a 5D uniform distribution for the

multinomial probabilities in each column of the transition matrix, hence this choice for hyperpriors induces a vague prior on the multinomial probabilities, one in which all combinations of probabilities are about equally likely.

Implementation

The posterior densities of the fixed and random effects were estimated via MCMC simulations in WinBUGS (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. We used the Gelman–Rubin–Brooks diagnostic to assess convergence. This diagnostic compares the variation within versus among chains; the 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 20,000 iterations by examining traces of the chains. After discarding the burn-in phase, we continued the simulation for another 125,000 iterations. The magnitude of the DIC statistics changed by less than $10^{-4}\%$ when we repeated a MCMC simulation of the same model, suggesting we had obtained a good sample of the posterior. Based on examination of autocorrelation plots of the MCMC output, we retained only every 25th sampled value, leading to a posterior sample of 15,000 (5,000 samples from each of three chains). The WinBUGS code for our analysis is found in the Electronic Supplementary Material (ESM).

Model comparison

Having fit a variety of models, we must then have a way to compare them statistically. Bayes factor, the ratio of posterior to prior odds for two models, has sometimes been used for this purpose, but Han and Carlin (2001) point out that Bayes factor estimates can be unreliable when derived from complex, hierarchical models like the one that we use. Instead, we used the deviance information criterion (DIC) for model comparison. DIC is a generalization of the more familiar Akaike Information Criterion (AIC; Akaike 1973), but based on the posterior distribution of the deviance (Spiegelhalter et al. 2002; Carlin et al. 2006; where deviance is defined as –2 times the log of the likelihood of the data, given the model). The DIC statistic summarizes the fit of the model to the data (Dhat, the deviance at the posterior mean of the parameters) penalized by the effective number of parameters (p_D = Dbar-Dhat, where Dbar is the posterior mean of the deviance). In a hierarchical model (like ours) the effective number of parameters (p_D) is typically not the same as the number of parameters in the model. Like AIC, a lower value of DIC indicates a better fit of the

Table 1 The number of parameters estimated per variation of each fixed effect, considering only the last two time-since-fire categories (3–6 years after fire, >6 years after fire)

	Full		Reduced	
	tsf	nef	tsf	nef
Death	10	5	2	1
Stasis	8	4	2	1
Progression	8	4	2	1
Retrogression	6	3	2	1
Ret to vegetative (Rv)	6	3	2	1
Leap	2	1	–	–
Pro to reproductive (Pr)	2	1	–	–

tsf time-since-fire; *nef* no effect of time-since-fire

Most of the fixed effects (not Leap and Pr) can be full or reduced, with or without an effect of time-since-fire ("tsf" vs "nef", respectively). Compare the numbers shown here for death to Fig. 1c

model to the data, taking into account a penalty for model complexity. DIC differences greater than five are regarded as moderately strong evidence and those greater than ten are regarded as very strong evidence in favor of the model with the smaller DIC. Differences less than two are regarded as negligible (Spiegelhalter et al. 2002).

Results

Model comparison (DIC)

We considered a total of 26 models that varied in DIC (listed as increasingly poor models in Table 2). By scanning each column of Table 2, one can see the important variation among models (highlighted with grey shading). For example, the addition of random effects improved the model dramatically (DIC is reduced; model 10 vs model 26, Table 2), in spite of increased model complexity (pD), because the fit of the model to the data is improved greatly (Dhat). Adding time-since-fire effects also improved the model tremendously (DIC is reduced by ~242 units; model 10 vs 25, Table 2), which reflects a reduction in the effective number of parameters, since the fit to the data actually suffers. Thus there is overwhelming evidence that both time-since-fire and additional unmeasured factors influence the transition probabilities.

Using the most parameter-rich model (model 10) as a point of reference, we discuss models with "reduced" versus "full" versions of the time-since-fire effects. Treating the effect of time-since-fire on stasis as homogeneous across the five plant stages improves the model by almost 3 DIC units (model 2 vs model 10, Table 2). Thus, stage-specific effects of time-since-fire on stasis are not supported (Fig. 2a). A model that treats the effect of time-since-fire on cessation of flowering (Rv) as homogeneous across the three reproductive stages is indistinguishable from model 10 (model 7 vs model 10, Table 2; see Fig. 2g), indicating that stage-specific effects of time-since-fire on cessation of flowering may or may not occur. In contrast, models with reduced versions of time-since-fire effects on death, retrogression, and progression are 4, 20, and 32 DIC units worse than model 10, respectively (models 16, 21, and 23, Table 2). Thus, there is evidence that the effect of time-since-fire on progression, retrogression, and death depends on the magnitude of the change (i.e., 1-step vs 2-step vs 3-step progression, etc.; Fig. 2b, c) or on plant stage (i.e., death of seedlings vs small flowering plants, etc.; Fig. 2d).

Finally, we compare the best model, those statistically indistinguishable from it (within 2 DIC units), and others without time-since-fire effects. Models with the hypothesis of no effect of time-since-fire on stasis, retrogression, and

progression to a reproductive stage are among the best models (models 1, 4, and 5, respectively, Table 2). In addition, models with no effect of time-since-fire on leap-frogging, retrogression to the vegetative stage, and progression are within five DIC units of the best model (models 6, 12, and 14, respectively, Table 2). A model with no effect of time-since-fire on death is 5.09 DIC units worse than the best model (model 15, Table 2). Hence there is some uncertainty about whether time-since-fire affects each of these types of demographic fates.

Time-since-fire effects

In spite of this model uncertainty (above), we report here the best estimates of the direction and magnitude of time-since-fire effects (from model 10, which contains all such possible effects). Consistent with the analysis of Menges et al. (2006), time-since-fire had negative effects on demography; that is, increased time-since-fire modified transition probabilities in a manner that should lead to population decline. Time-since-fire increases the probability of death, particularly death of the reproductive stages (Fig. 2d): the posterior odds of death are 5.30, 5.49, and 3.20 times greater for small, medium, and large flowering plants more than 6 years after fire, compared to 3–6 years after fire (Table 3). Time-since-fire reduces the probability of progression (including leap-frogging and progression to a reproductive stage; Fig. 2b, e, f) and increases the probability of retrogression (including cessation of flowering; Fig. 2c, g). Time-since-fire particularly suppresses the probability of larger increases in size or developmental stage (Fig. 2b); 3-step and 4-step progression are 6.82 and 4.51 times less likely to occur to plants more than 6 years after fire, compared to 3–6 years after fire (posterior means, model 10, Table 3). Leap-frogging is 3.06 times less likely to occur to seedlings more than 6 years after fire, compared to 3–6 years after fire (Fig. 2e; Table 3). Large flowering plants are 6.25 times more likely to regress to the vegetative stage (stop flowering) more than 6 years after fire, compared to 3–6 years after fire (Fig. 2g; Table 3).

Transition probabilities

We obtained good estimates of the transition probabilities from our models, in the sense that the posterior means closely resemble the observed transition frequencies (Fig. 3). The 95% credible intervals of the posteriors illustrate that there is considerable uncertainty about transition probabilities (due to the finite sample size of plants involved), which is ignored when only a point estimate

Table 2 Parameterization and DIC statistics of all the models that we ran, in order of increasing DIC

Model	Death	Stasis	Pro	Ret	Rv	Leap	Pr	ε	Dbar	Dhat	pD	DIC	ΔDIC	
1	F	red, nef	F	F	F	+	+	+	2037.83	1656.35	381.48	2419.31	2.98	
2	F	red	F	F	F	+	+	+	2037.82	1656.16	381.66	2419.47	2.82	
3	F	red, nef	F	F	red	+	---	+	2028.62	1637.69	390.93	2419.55	2.74	within 2
4	F	F	F	F, nef	F	+	+	+	2040.98	1661.53	379.46	2420.44	1.85	DIC
5	F	red, nef	F	F	red	+	nef	+	2032.55	1643.95	388.60	2421.15	1.14	
6	F	F	F	F	F	nef	+	+	2040.80	1659.74	381.06	2421.86	0.43	
7	F	F	F	F	red	+	+	+	2038.18	1654.49	383.69	2421.87	0.42	
8	F	F	F	F	F	+	nef	+	2041.22	1660.36	380.86	2422.08	0.21	
9	F	red, nef	F	F	red	nef	+	+	2032.82	1643.56	389.26	2422.08	0.21	
10	**F**	**F**	**F**	**F**	**F**	**+**	**+**	**+**	**2041.2**	**1660.1**	**381.09**	**2422.29**	**0**	
11	F	F	F	F	F	---	+	+	2039.43	1656.36	383.07	2422.5	-0.21	
12	F	F	F	F	red, nef	+	+	+	2039.7	1656.53	383.17	2422.87	-0.58	within 5
13	F	---	F	F	F	+	+	+	2041.83	1660.71	381.12	2422.94	-0.65	DIC
14	F	F	F, nef	F	F	+	+	+	2039.8	1655.81	383.99	2423.78	-1.49	
15	F, nef	F	F	F	F	+	+	+	2039.35	1654.3	385.05	2424.4	-2.11	
16	red	F	F	F	F	+	+	+	2041.61	1657	384.60	2426.21	-3.92	within 10
17	---	F	F	F	F	+	+	+	2041.74	1656.77	384.97	2426.7	-4.41	DIC
18	F	red, nef	F	F	red, nef	+	nef	+	2034.94	1641.36	393.58	2428.52	-6.23	
19	F	red, nef	F	F	red, nef	+	---	+	2034.97	1640.71	394.27	2429.24	-6.95	
20	F	F	F	F	F	---	+	+	2028.7	1615.56	413.14	2441.83	-19.54	
21	F	F	F	red	F	+	+	+	2051.7	1661.27	390.43	2442.12	-19.83	
22	F	F	F	---	F	+	+	+	2053.99	1664.77	389.21	2443.2	-20.91	
23	F	F	red	F	F	+	+	+	2063.46	1672.61	390.86	2454.32	-32.03	
24	F	F	---	F	F	+	+	+	2063.13	1671.53	391.60	2454.72	-32.43	
25	---	---	---	---	---	---	---	+	2022.41	1380.93	641.48	2663.89	-241.6	
26	F	F	F	F	F	+	+	---	2889.96	2852.78	37.18	2927.14	-504.85	

Seven types of fixed effects, in addition to random effects (ε), may be present in a model (see Fig. 1b)

Variations on fixed effects include full (*F*), reduced (*red*), and no effect of time-since-fire (*nef*). Presence versus absence of an effect is indicated by + versus −. We use horizontal lines in the table to indicate those models within 2, 5, and 10 DIC units of the best model, and shading to highlight what is discussed in the text. The most highly parameterized model (10), in bold text, is a point of reference; thus, ΔDIC is in relation to model 10

(MLE) is used in simulations of population viability (Fig. 3).

Discussion

Our analysis offers new insights into the process of population decline with time-since-fire in *D. frutescens* ssp. *frutescens*. We found that time-since-fire increases the odds of death, particularly the odds of death for flowering plants (Fig. 2d). Time-since-fire also reduces the odds of progression, particularly those progression terms involving greater increase in size or advances in developmental stage (Fig. 2b). Increased time-since-fire also suppresses flowering, either by increasing the odds of changing from a reproductive stage to the vegetative stage (stronger evidence, based on DIC; Fig. 2g), by decreasing the odds of changing from the seedling or vegetative stages to a reproductive stage (weaker evidence, based on DIC; Fig. 2e, f), or both (as in models 1–4; Table 2). While the Bayesian analysis that we used admits both model uncertainty (Table 2) and parameter uncertainty (the intervals in Fig. 2) in time-since-fire effects, the best estimates of the magnitude of these effects are substantial. For example, the posterior mean of the odds of death is 3–5.5 times greater for flowering plants more than 6 years after fire, compared to 3–6 years after fire (Table 3; Fig. 2d). Similarly, the posterior mean of the odds of a 3-step progression is

reduced more than 6 times and the posterior mean of the odds of a large flowering plant stopping flowering is increased more than 6 times, more than 6 years after fire compared to 3–6 years after fire (Table 3; Fig. 2b, g).

These insights suggest some directions for future research and management. For example, the result that time-since-fire reduces survival of reproductive plants rather than non-reproductive plants is surprising and intriguing. One might have expected seedlings and vegetative plants to be affected more by conditions that develop with increased time-since-fire than older, larger, reproductively mature plants. There are a number of possible mechanisms by which time-since-fire could negatively affect *D. frutescens* ssp. *frutescens*, including belowground competition for water and nutrients from increasingly large post-fire resprouting plants, allelochemicals from those shrubs, reduced light availability as the canopy closes, and microenvironmental effects caused by accumulating leaf litter. The fact that seedling survival appears to be little affected by time-since-fire argues against belowground competition, allelochemicals and leaf litter as factors, since all three would be expected to affect new, small plants disproportionately. A closing canopy on the other hand might have a moderating effect for seedlings (moderating the heat load received at ground level, for example) but a negative effect on flowering plants, which may require high light conditions to recoup the energy costs involved in reproduction. If canopy closure is the main mechanism for

Fig. 2 Posterior distributions of the effect of time-since-fire category on seven different types of demographic transitions: **a** stasis, **b** progression, **c** retrogression, **d** death, **e** leap-frogging, **f** progression to reproductive from vegetative, **g** retrogression from reproductive to vegetative. The *y*-axis of each panel is the odds ratio (relative to a model without that effect) on a $\log_{10}$ scale. The posterior means (*thick horizontal bars*), 50% quantiles (*boxes*), and 95% credible intervals (*whiskers*) are shown, as well as extreme values (*dots*). These posteriors were obtained from model 10
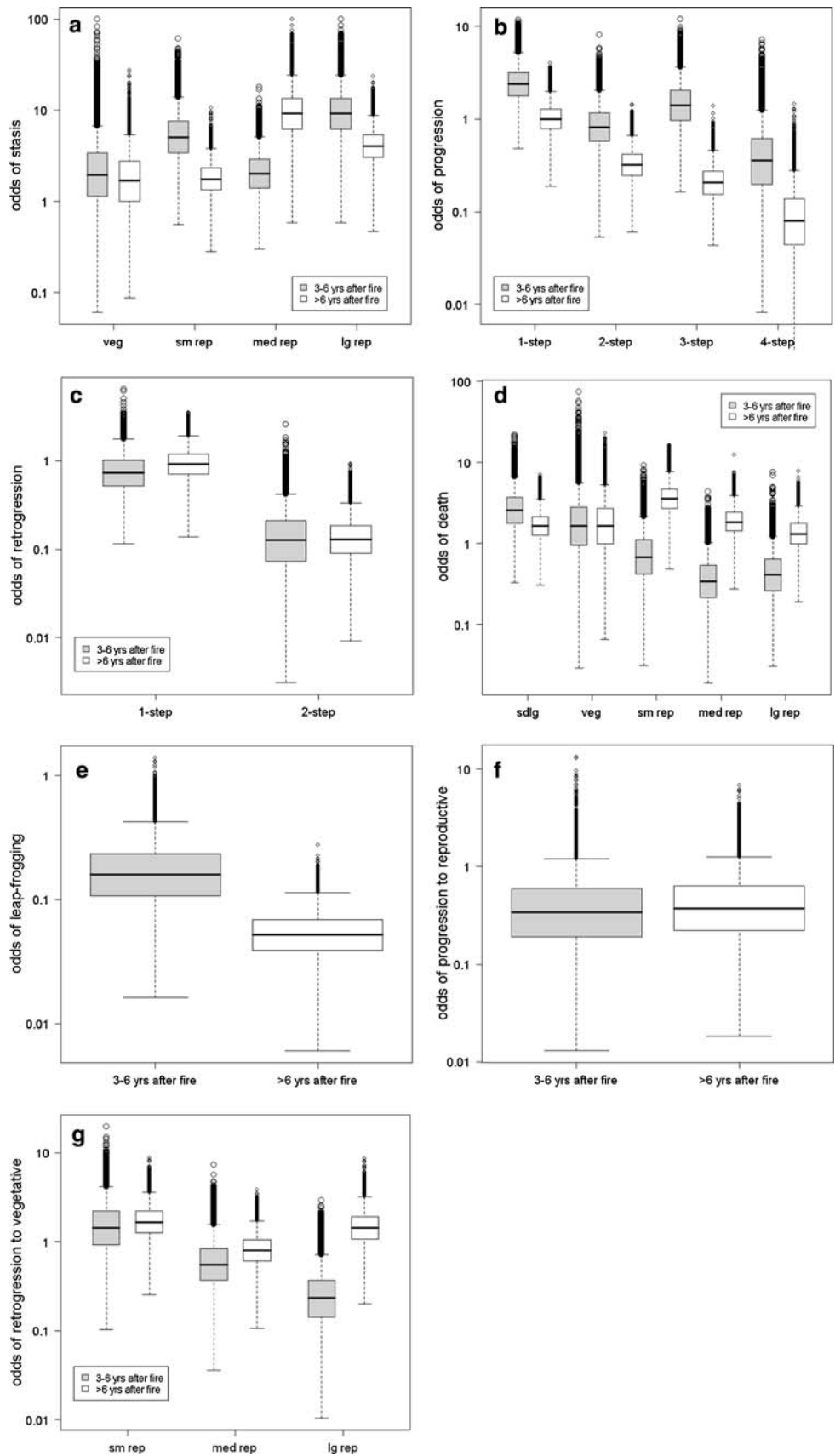
Table 3 Odds of each type of demographic transition, more than 6 years after fire, compared to 3–6 years after fire, from the posterior means of model 10 (shown in Fig. 2)

Death		Progression		Retrogression		Stasis		Retro to veg		Leap	Prog
sdlg	−1.56	1-step	−2.38	1-step	1.27	veg	−1.17	sr	1.17	−3.06	1.09
veg	1.00	2-step	−2.57	2-step	1.05	sr	−2.93	mr	1.45		
sr	5.30	3-step	−6.82			mr	1.36	lr	6.25		
mr	5.49	4-step	−4.51			lr	−2.26				
lr	3.20										

sdlg seedling; *veg* vegetative stage; *sr* small, *mr* medium, *lr* large flowering plants

A value of 1.00 indicates equal odds in the two time-since-fire categories. For example, seedlings are 1.56 times less likely to die >6 years after fire, compared to 3–6 years after fire

Fig. 3 Posterior densities of the 25 transition probabilities estimated by model 1 for population 2 in 1988–1989. The posterior means (*thick horizontal bars*), 50% quantiles (*boxes*), and 95% credible intervals (*whiskers*) are shown, along with the observed transition frequencies (*black diamonds*, at *right*). The arrangement of these *panels* corresponds to the 5 × 5 matrix in Fig. 1a
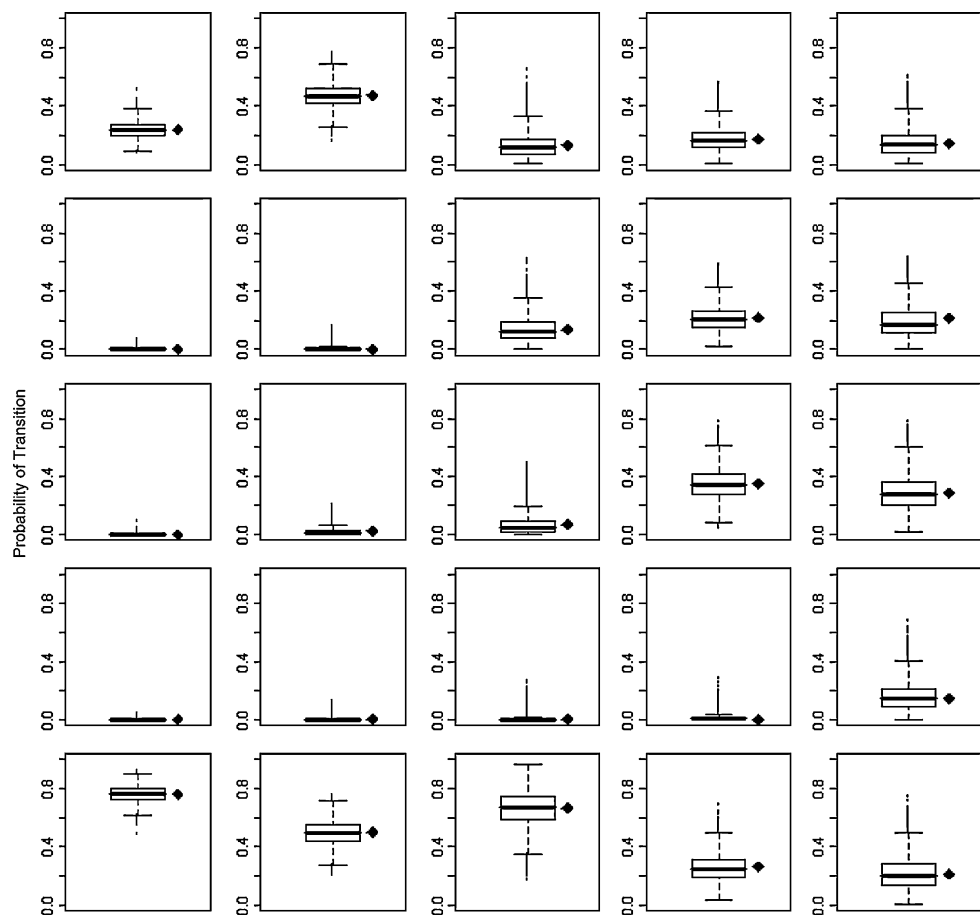
decline in *D. frutescens* ssp. *frutescens* populations with time-since-fire, then mechanical canopy removal may suffice to reverse decline, in situations where prescribed burning is not feasible (e.g., in the proximity of private homes). Future experimentation and analysis can be directed at this next generation of hypotheses and mechanistic understanding.

There are alternatives to the hierarchical Bayesian analysis that we used, but each has several disadvantages. One approach is to treat the MLE's of transition probabilities as known, and analyze their variation as a function of the exogenous factor (e.g., Pfeifer et al. 2006); this approach ignores both parameter uncertainty and process variation due to unknown sources. Another approach is to analyze data from individual plants as a function of the exogenous factor, which provides estimates of the effect of that factor on response variables like survival, growth, flowering, or fecundity, as opposed to transition probabilities (e.g., Kalliovirta et al. 2006). Gross et al. (2006) recently showed how this kind of model can be used

to estimate transition probabilities. Their approach addresses model uncertainty via multimodel averaging (sensu Burnham and Anderson 2002), but does not address parameter uncertainty or process uncertainty due to unknown sources. Another method, life stage simulation analysis (Wisdom et al. 2000), could be used to assess the effect of time-since-fire on population growth, but relies on specifying "plausible or hypothesized" levels of uncertainty and variation in vital rates. In contrast, the Bayesian framework used in this paper allows us to model demographic responses to an exogenous factor and to account for and estimate uncertainty and variation within the context of a single analysis. Moreover, the structure of our model is quite general. It can be easily adapted to examine how any exogenous factor affects demographic transitions. It is a novel and general statistical tool that can be used by others who wish to develop a better understanding of the effect of an exogenous factor on demography, while rigorously accounting for uncertainty and variation.

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