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Fire management strategies to maintain species population processes in a fragmented landscape of fire-interval extremes

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Abstract. Changed fire regimes have led to declines of fire-regime-adapted species and loss of biodiversity globally. Fire affects population processes of growth, reproduction, and dispersal in different ways, but there is little guidance about the best fire regime(s) to maintain species population processes in fire-prone ecosystems. We use a process-based approach to determine the best range of fire intervals for keystone plant species in a highly modified Mediterranean ecosystem in southwestern Australia where current fire regimes vary. In highly fragmented areas, fires are few due to limited ignitions and active suppression of wildfire on private land, while in highly connected protected areas fires are frequent and extensive. Using matrix population models, we predict population growth of seven *Banksia* species under different environmental conditions and patch connectivity, and evaluate the sensitivity of species survival to different fire management strategies and burning intervals. We discover that contrasting, complementary patterns of species life-histories with time since fire result in no single best fire regime. All strategies result in the local patch extinction of at least one species. A small number of burning strategies secure complementary species sets depending on connectivity and post-fire growing conditions. A strategy of no fire always leads to fewer species persisting than prescribed fire or random wildfire, while too-frequent or too-rare burning regimes lead to the possible local extinction of all species. In low landscape connectivity, we find a smaller range of suitable fire intervals, and strategies of prescribed or random burning result in a lower number of species with positive growth rates after 100 years on average compared with burning high connectivity patches. Prescribed fire may reduce or increase extinction risk when applied in combination with wildfire depending on patch connectivity. Poor growing conditions result in a significantly reduced number of species exhibiting positive growth rates after 100 years of management. By exploring the consequences of managing fire, we are able to identify which species are likely to disappear under a given fire regime. Identifying the appropriate complementarity of fire intervals, and their species-specific as well as community-level consequences, is crucial to reduce local extinctions of species in fragmented fire-prone landscapes.

Key words: Banksia; *decision-making; ecological fire management; fragmentation; matrix population model; Mediterranean-type ecosystem; obligate seeder; senescence; serotiny; southwestern Australia; wildfire.*

INTRODUCTION

Fire regimes across the globe have changed due to human interventions (Archibald et al. 2012). Some areas, for example, now burn too frequently, such as 70% of the world's fire-sensitive tropical habitats (Shlisky et al. 2009) and many peri-urban areas (Keeley et al. 1999). Too-frequent burning leads to declines of species that rely on long intervals between fires, either for maturation in plants or for shelter and food resources to recover sufficiently for animals (Bradstock et al. 1996). Other areas are burning too infrequently, for example some boreal forests (Wallenius et al. 2011) and agricultural landscapes where fires are excluded and suppressed to avoid loss of crops and pasture (Parsons and Gosper 2011, Salis et al. 2014). Too-infrequent fire can lead to declines of plant species due to senescence in species with a relatively short lifespan and seed longevity or via displacement by competitive but more fire-sensitive species, and consequently, loss of keystone resources for animals (Bradstock et al. 1996, Bird et al. 2013, Shackelford et al. 2015). To counter these threats to biodiversity, strategies to manage fire including prescribed burning or fire

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suppression have been recommended (e.g., Richards et al. 1999, Fuhlendorf et al. 2006).

The range in responses of species and communities to fire means that identifying an appropriate fire regime is crucial to avoid local species extinctions (Bradstock et al. 1996, Watson et al. 2012). Retrospective methods for converting ecological information into fire-interval recommendations are, however, poorly defined. This is primarily because empirical data on historic burning regimes are rarely available, as collecting these data requires intensive field studies to evaluate and date fire scars (O'Donnell et al. 2011). Consequently, a diversity of approaches has been used to identify appropriate fire regimes, ranging from estimating ecosystem-level responses to fire (e.g., Richards et al. 1999), to vital attribute and demographic model approaches based on data directly measuring biodiversity response to fire (e.g., Noble and Slatyer 1980).

Attributes of the fire regime itself have been used to circumscribe appropriate fire regimes for conservation of different vegetation types. For example, one assumption for managing fire-prone environments is that pyrodiversity begets biodiversity, which suggests that varying a wide range of fire regime parameters will maintain biodiversity in fire-prone landscapes (Parr and Andersen 2006). The pyrodiversity begets biodiversity paradigm has gained very little support from the empirical literature (Parr and Andersen 2006). Instead, another approach attempts to identify the optimal fire strategy for vegetation types by estimating the current and ideal distributions of successional stages (Richards et al. 1999), based on the assumption that a specified fire age distribution is appropriate for all species within the landscape. However, many recent studies suggest that the focus for managing fire should shift from maximizing the diversity of fire regimes or rigid adherence to theoretical age-class distributions to a strategic approach that ensures an optimum mix of vegetation age classes across the landscape informed by a foundation of measured responses of biodiversity to fire (Davies et al. 2012, Kelly et al. 2012, Nimmo et al. 2013, Enright et al. 2014).

Studies are now attempting to apply the knowledge that different fire regimes are appropriate for different species to find appropriate fire management strategies for multiple species (Di Stefano et al. 2013, Gosper et al. 2013, Kelly et al. 2015). Some focus on quantifying the abundance and diversity of entire taxonomic groups in relation to different vegetation age classes (years since fire) to find an age-class distribution that might maximize abundance across a fire-prone landscape (Di Stefano et al. 2013). Alternatively, the responses of individual species to fire parameters (or time since fire) are predicted using correlative statistical models, and these are used to determine the ideal allocation of successional states based on the geometric mean of species occurrence or relative abundance in any given area (Kelly et al. 2015). By arbitrarily defining age-class thresholds (Di Stefano et al. 2013, Kelly et al. 2015) and relying on a correlative approach to describe responses of biota to aspects of fire regimes (e.g., Davies et al. 2012, Nimmo et al. 2013), these studies fail to account for demographic processes such as reproduction, growth, and dispersal, processes that are fundamental for maintaining and generating viable populations (Balmford et al. 1999). There is an urgent need to synthesize available information on species' population processes to determine species sensitivity to inappropriate fire regimes and to explore how a process-based approach might be used to maximize the survival of species with diverging fire tolerances in fire-prone environments.

The responses of biota to fire are a result of the direct effects of the fire regime itself on demographic processes and complex interactions among fire, vegetation, coexisting species, topography, climate, and landscape connectivity (Turner and Romme 1994, Bond and van Wilgen 1996, O'Donnell et al. 2011, Parsons and Gosper 2011). Fire can affect demographic processes of growth, reproduction, or mortality of different species in different ways, demonstrating the importance of species-level data for informing fire management decisions (Gosper et al. 2012*a,b*). For example, studies have shown significant differences between and within species in post-fire seedling recruitment (and associated population growth) depending on post-fire growing conditions, such as the season of fire (Bond et al. 1984, Bond and van Wilgen 1996). Incorporating vital attributes with a model underlain by demographic data would allow variability in these processes to be accounted for in decisions about which fire strategy to take (Noble and Slatyer 1980). However, in studies that attempt to synthesize and evaluate the range of fire tolerances within a plant community at a species level using vital attributes, minimum fire intervals are typically defined through estimates of the reproductive potential of the slowest maturing species in the community (Bradstock and Kenny 2003, Burrows et al. 2008). The fecundity of species is rarely known, and it is equivocal as to when a population has reached a reproductive threshold, what the potential for population replacement is between fires (i.e., inter-fire recruitment), and how reproductive capacity should be measured to estimate acceptable lower fire interval bounds (Bradstock and Kenny 2003, Burrows et al. 2008). Methods for estimating maximum fire intervals are even more poorly quantified (Gosper et al. 2013). Survival rates are difficult to predict and are generally estimated based on expert knowledge (e.g., the LANDFIRE approach in the USA; Low et al. 2010) or a small sample of species (Bradstock and Kenny 2003, Kenny et al. 2004). All of this uncertainty means that although vital attribute approaches allow researchers to explore variability within a community in relation to the current fire regime, without an explicit model of demographic processes, they cannot predict the response of a population to alternative future regimes.

Studies that have attempted to incorporate population dynamics have been limited usually to only a single species because of a lack of detailed community data with which to populate population viability analyses (Bradstock et al. 1996, Enright et al. 1996, McCarthy et al. 2001). Empirical studies incorporating demographic processes of multiple species in response to fire are urgently required. Clearly we cannot learn about the likely response of every species to threats and their mitigating actions, especially for highly diverse disturbance-prone regions such as Mediterranean ecosystems that can have hundreds of species in a single patch (Myers et al. 2000). However, management decisions should be made as accurately as possible for a representative sample of species important for maintaining ecosystem function (Pressey et al. 1993). When we want to manage a large number of species but have few species-specific data, we can try to estimate a range of functional responses to management to ensure that in the least the variability of demographic rates is captured in the decision-making process (Gitay and Noble 1997, Sternberg et al. 2000, Watson et al. 2012).

In this paper we ask, how can we strategically maximize species diversity by managing for fire? We estimate the range of functional responses to alternative regimes of fire interval and type for a highly diverse target genus of fire-dependent Proteaceae (*Banksia* spp.), which are a dominant structural component of the vegetation and provide keystone flower and seed resources for fauna (Saunders et al. 1987, Lamont et al. 2007). Our study landscape is in the biodiversity hotspot of southwestern Australia. Current fire frequencies across this landscape are highly polarized, with fires exceedingly rare in native vegetation remnants in the agricultural parts of the landscape, while being frequent and extensive in contiguous vegetation in protected areas (Parsons and Gosper 2011). If left unmanaged, the long-term consequence of this pattern of fire is that the majority of the landscape will experience extremes in fire interval (Appendix S1: Fig. S1). There is a risk of biodiversity decline in long-unburned fire-dependent communities due to senescence and in frequently burned areas due to species being killed before reaching maturity (Lamont et al. 2007, Parsons and Gosper 2011, Gosper et al. 2012*b*). A critical consideration of the fire intervals needed to maintain biodiversity is urgently required (Di Stefano et al. 2013, Kelly et al. 2015). Our specific objective was to maximize *Banksia* diversity (in terms of the number of species with a positive growth rate after 100 yr) in a given patch through fire management, and we explored this in four ways:

1) predict the population-level responses of a representative group of *Banksia* species to alternative managed and wildfire regimes using matrix population models;
2) evaluate how the landscape context affects fire management outcomes by altering population parameters of colonization (reflecting connectivity) and stochastic fire event risk in the population models;
3) explore the impact of post-fire environmental attributes on management outcomes by altering recruitment parameters (germination and seedling survival, impacts of poor growing conditions, such as low post-fire rainfall) in the population models; and
4) recommend the fire interval strategies that maximize the number of *Banksia* species with a positive growth rate after 100 yr.

METHODS

Study area and fire history

The South Coast Natural Resource Management region (SCNRM) is part of the southwest Australian biodiversity hotspot, characterized by high endemism and high threat (Myers et al. 2000). The importance of this region for agriculture (predominantly cereal cropping and sheep grazing in the 210,000 km^2 wheatbelt region) has led to clearing of up to 90% of the extent of some native vegetation types in the hotspot, resulting in subsequent extinctions of flora and fauna species (Saunders et al. 1991), and the creation of a fragmented landscape dominated by small patches (Tulloch et al. 2015*b*). The current scale and frequency of fires in the small fragmented remnant vegetation patches of the wheatbelt is low, with a modelled recent fire interval of 178–339 yr (Parsons and Gosper 2011). This is because many patches have not been burnt since before the time of clearing activities, due to a combination of low ignition probability in poorly connected landscapes (O'Donnell et al. 2011, Gill et al. 2014) and fire suppression activities by landholders. In our study region, the mean fire interval of poorly connected small patches (mean patch area <2 km^2, mean distance to nearest patch 0.2 km ± 0.2 SD, maximum = 8.1 km; Appendix S1: Table S1) is once every 42 yr, with >60% of these patches unburnt over the time covered by the fire record. However, in highly connected parts of the region (defined here as large patches with mean patch area 15 km^2; mean distance to nearest patch 0.03 km ± 0.09 SD, max = 0.8 km; Appendix S1: Table S1), predominantly the public land reserves, fires burn at frequencies of once every 8 yr on average (Fig. 1; Appendix S1). This rate is considerably higher than the estimated acceptable minimum fire interval for many constituent plant species (Gosper et al. 2013).

Within the SCNRM region, we focused on the vegetation community of Proteaceae Dominated Kwongkan Shrublands of the southeast coastal floristic province of Western Australia, also known as proteaceous-rich mallee-heath (PRMH), which has been listed as a threatened ecological community (TEC) under the Environmental Protection and Biodiversity Act (EPBC Act 1999) in Australia. It occurs across the southwest coast of Australia (Fig. 1) and consists of proteaceous shrubland and heath (kwongkan) and mallee-heath (Comer et al. 2001*a,b*). Proteaceous-rich mallee-heath has among the lowest proportions of resprouting taxa

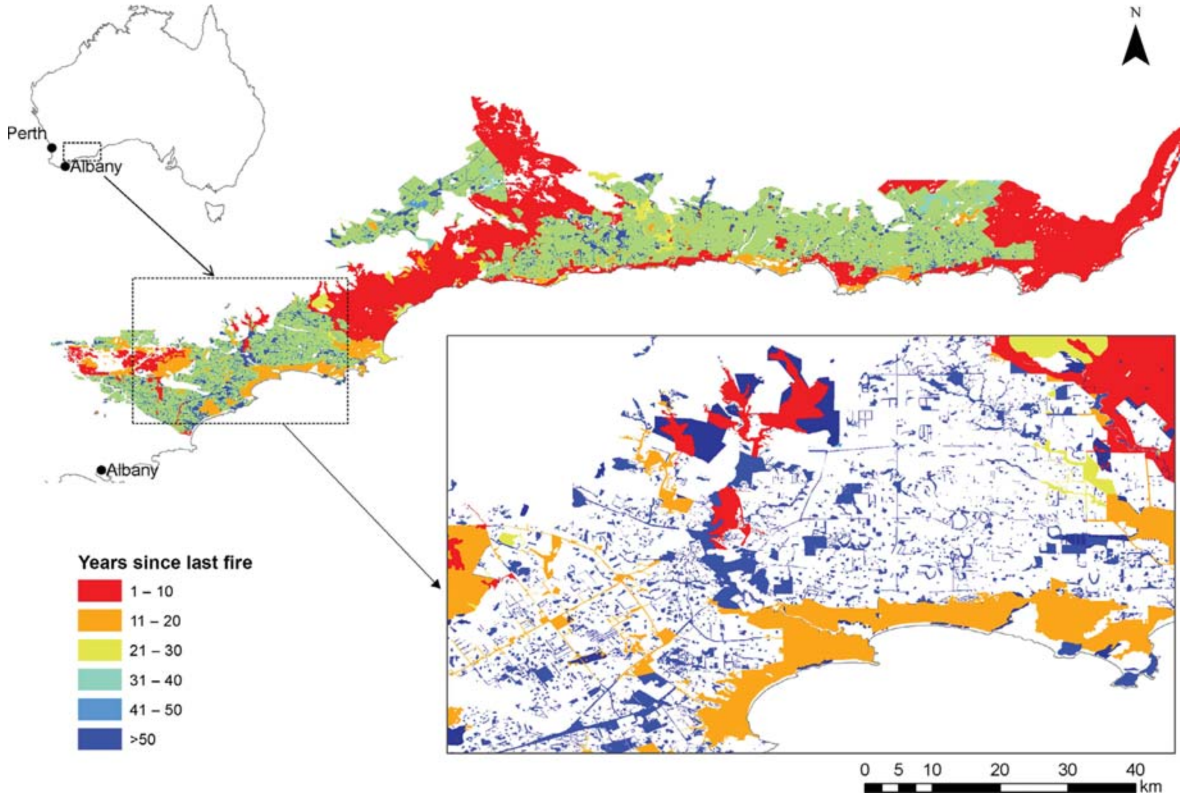

FIG. 1. Current distribution of obligate-seeding, Proteaceae-dominated shrublands and kwongkan (proteaceous-rich mallee-heath, PRMH) in the South Coast Natural Resource Management region, showing time since fire of remnants classified into 10-yr groupings overlaid on pre-cleared extent (light green). We assume that areas with obvious fire scars in the oldest satellite (1972) image have burnt over the 14 yr prior. The insert shows a more detailed view of an example of the fragmented part of the study area.

and the highest proportions of post-fire seeding taxa of all Australian vegetation types (Gosper et al. 2012*a*, Clarke et al. 2015), indicating a high potential sensitivity to variation in fire interval (Gosper et al. 2013). Little is known of the range of ideal fire regimes for species in this community, but in other parts of southwestern Australia dominated by proteaceous species, fire intervals of once every 30–60 or 30–90 yr have been suggested as appropriate (Wooller et al. 2002, Gosper et al. 2013).

Study species and attributes

Banksia species were chosen for this study due to their high diversity, abundance, and endemism in southwestern Australia (Lamont et al. 2007). Diversity patterns of *Banksia* are representative of diversity patterns of other plants in southwestern Australia (Fitzpatrick et al. 2008). Non-resprouters, also known as obligate seeders (50–60% of all *Banksia* species), are killed when their crowns burn and rely on seedlings for replacement in post-fire vegetation (Clarke et al. 2015). A few *Banksia* species release their seeds once mature, but most are serotinous, retaining seeds in their cones to varying extents until the woody follicles are stimulated to open by fire, with very little evidence of soil-stored seed (Cowling et al. 1987, Lamont and Connell 1996). This arguably risky life history of non-overlapping generations in fire-prone landscapes makes non-resprouting *Banksias* important target species for fire management, as they require fire to finish their reproductive cycle, but also need an absence of fire for a period after germination to mature and set seed. *Banksias* are ecosystem provisioners and represent a key structural and floristic component of PRMH, providing a crucial food resource for pollinators and granivores, including the nationally endangered Carnaby's Black-Cockatoo (Saunders et al. 1987, Lamont et al. 2007). Finally, in comparison with many other species, *Banksias* have relatively poor seed dispersal capabilities: seeds generally drop next to the parent (Lamont et al. 1993), with limited dispersal further than 40 m away from adults even with wind taken into account (Hammill et al. 1998), although long distance dispersal of particular species has been noted (He et al. 2004). Poor dispersal in a species leads to potentially greater impact from fragmentation, making *Banksia* a particularly important genus to consider in the heavily disturbed study area.

We compiled a dataset of all published and unpublished literature on functional traits, demographics, and responses to fire of *Banksia* species in southwestern Australia, with the aim of collecting enough information to develop matrix population models. Seven non-resprouting *Banksia* species (*B. baueri, B. baxteri, B. coccinea, B. nutans, B. violacea, B. speciosa, B. sessilis*) were determined to occur within PRMH and have enough life-history information to proceed with modelling population-level responses to fire (Appendix S1). All seven species are woody perennials ranging in size from low shrubs to small trees growing to a height of ~8 m, and, depending on the location of the patch, six of the seven are expected to regularly co-occur.

For our seven study species, fire kills all individuals, and recruitment following fire is solely from seeds. Seed production typically commences when plants are 3–10 yr old (e.g., Richardson et al. 1990, Witkowski et al. 1991, Enright et al. 1998, Gosper et al. 2013; Appendix S1: Table S2). Most species have two seeds per follicle with multiple follicles in an inflorescence that varies in size and abundance on the plant, so the species vary in fecundity, with as little as 60 viable seeds at maturity on *B. coccinea* to more than 1400 per plant reported for *B. speciosa* (Witkowski et al. 1991, Lamont and Witkowski 1995). For five of the seven species, few seeds are released except when fire causes follicles on cones to open. The two exceptions to this in our study are *B. coccinea* and *B. sessilis*, which have been classified as either serotinous (i.e., not releasing seeds between fires), weakly serotinous, or non-serotinous (i.e., releasing seeds between fires), most likely depending on environmental conditions (Lamont et al. 2007). Once released, seeds of most *Banksias* either germinate, if rainfall occurs, or perish, with very little evidence of a soil-stored seed bank (Enright and Lamont 1989). Longevity in the absence of fire varies (when it has been reported), with senescence having been recorded for at least three of the species: *B. baxteri*, *B. coccinea*, and *B. nutans* (Appendix S5; Fig. 2).

Demographic transition matrices at different fire succession phases

We constructed deterministic time-varying transition matrices (hereafter called **D**) that describe the life cycle and population dynamics of the seven non-resprouting *Banksia* species at a patch scale, subject to disturbance by fire. The models were adapted from Enright et al. (1998). Details of the matrix structure, calculations, and Matlab code to produce the results can be found in Appendix S4.

One difficulty when constructing the transition matrices **D** was to account for the periodicity and differences in the time scales of the sequence of demographic events in response to fire. Between fire events, adult vital rates (survival and reproduction) were mostly available at decadal age-classes for *Banksia*, whereas germination, seedling survival, and recruitment occur immediately after fire and need to be studied at an annual time scale. To account for the time-scale differences, and the populations' potential to be burnt every year, we decomposed for each species the corresponding periodic transition matrix **D** into three age-by-stage transition matrices. We first constructed an inter-fire transition matrix **Y** representing a continuous 10-yr demographic succession without fire, a fire transition matrix **F** describing the immediate effect of fire on population demography during the first year post-fire, and a post-fire transition matrix **P** describing the nine subsequent years after the fire transition **F**. Our models therefore integrate matrices representing post-fire population dynamics on annual time-steps with matrices representing inter-fire population dynamics over decadal time steps. The vital rates of these matrices were either estimated directly from available data from the literature (Appendix S1: Table S2), or for seedling survival rates only, predicted indirectly from functional traits using allometric equations (Moles and Westoby 2006). The matrices and associated vital rates are described below in conjunction with Tables S2 and S3 in Appendix S1.

Inter-fire transition matrices.—In the absence of fire, serotinous *Banksias* continuously produce seeds that do not germinate and are stored on the plant (i.e., an aerial seed bank). When a plant dies during the inter-fire period all seeds stored on that plant are lost (Lamont et al. 2007). We constructed a transition matrix observed at a decadal time step to account for the survival and reproduction at a given decadal age *i*. We delimited seven equal age classes of 10 yr for each species, to predict up to the maximum of data availability (70 yr). After 70 yr we assume vital rates do not change. We acknowledge that many *Banksia* species are likely to live for longer than 70 yr (see Appendix S1: Table S2), but we were limited by data availability (see *Methods: Estimation of population statistics and sensitivity analyses* for details of sensitivity analyses examining the role of longevity). The transition matrix Y reflected our partial knowledge of the life-cycle, with individuals in the last age-class of the matrix aging and staying in the same class from decade to decade until they all died (Caswell 2001). For every age-class other than the first-year sapling stage, we estimated adult survival and seed production. To parameterize the transition matrix Y, we first developed a model representing the continuous reproduction process (Caswell 2001):

$$\mathbf{Y}(1,i) \approx \sqrt{S_{[i,i+1]}} f_{[i,i+1]} \sqrt{S_{seeds}{}^{10}} \quad \text{for } i > 1 \tag{1}$$

where $\mathbf{Y}(1,i)$ represents the element of the first row of column i in the matrix (i.e., the age class), $S_{[i,i+1]}$ is adult survival, $f_{[i,i+1]}$ is the decadal seed production, and S_{seeds} is the annual seed survival rate.

Similarly, we modelled adult survival $S_{[i,i+1]}$ between age-class i and $i + 1$ that were positioned in the sub-diagonal of the transition matrix as follows:

$$\mathbf{Y}(2,1) = 0, \mathbf{Y}(i+1,i) = S_{[i,i+1]} \text{ for } 1 < i < a_{max}, \\ \text{and } Y\left(a_{max}, a_{max}\right) = S_{]a_{max}, a_{max}]} \tag{2}$$

where a_{max} represents the maximum age class (≤7).

Fire transition matrices—To start, we assumed that when a fire occurs, all remaining plants are killed and all of their stored seeds in the aerial seed bank of previously live trees are released and either germinate and recruit or perish within a year (Eq. 3). The first-year fire transition matrix **F** describes this annual demographic process following fire. Transition matrix **F** has the same structure as transition matrix **Y**, but this time each stage is observed at an annual time scale (rather than decadal time scale). Because all adults are assumed to die after fire, post-fire survival and new production of seeds were considered null, such that

$$\mathbf{F}(2,1) = S_{seeds}\, Germ\, S_{sg}\, S_{]Sg,1]} \tag{3}$$

where *Germ* is the germination rate, S_{sg} is the average seedling survival rate (determined from the literature, different for each species; Appendix S1: Table S2), and $S_{]Sg,10]}$ is the annual survival of saplings. Germination rate was initially set to 0.1 for all species (and included post-dispersal seed predation and seed emergence).

Finally, to obtain from the transition matrix **F** a 10-yr time step used in **Y**, we also built a post-fire transition matrix **P**, which is equivalent to the transition matrix **Y**, but where the vital rates are estimated at a nine-yr timescale, rather than at a 10-yr time-scale. The product **P** by **Y** creates a new post-fire matrix on a decadal timescale.

Fire regime and landscape connectivity scenarios

We assessed whether all target *Banksia* species could persist in patches across the landscape under different fire regimes, landscape connectivity, and growing conditions by reconstructing global time-varying demographic matrices **D** from the corresponding **F**, **Y,** and **P** matrices (see Appendix S2: Table S1 for more details of scenario data inputs).

Scenario 1: no burning.—We assume no wildfire (due to successful fire suppression) and no management burning. This scenario is most realistic for small poorly connected fragments with low ignition probabilities.

Scenario 2: periodic management burning.—We assume no unplanned fire (wildfire or escapes from management fires) and assess the consequences of management burning by increasing the period between fire events from every 1 yr to every 100 yr, by classes of 10 yr.

Scenario 3: random wildfire only.— We assume wildfire with increasing average frequencies from one every 100 yr to one every 10 yr and no management burning. Here, wildfires are applied randomly subject to the specified average frequency, in comparison with the management fire scenarios in which fires are applied systematically at the specified interval. This means that an average wildfire interval of 20 yr will be derived from a random attribution of five temporal event locations within a 100-yr period (replicated 10,000 times to find the average). For simplicity, this scenario does not account for the effect of fuel age on fire occurrence (i.e., fires can occur in fuels <10 yr post-fire). This is a reasonable assumption given our current knowledge of fire frequency in protected areas (Fig. 1) and experimental evidence (Fontaine et al. 2012).

Scenario 4: current wildfire and periodic managed burning.—We assume regular management burning (scenario 2) plus the addition of natural wildfire events. Current mean wildfire intervals (over an observation period of 55 yr) in the PRMH for the two landscape connectivity classes (calculated from satellite data and fire maps provided by the Western Australian Department of Parks and Wildlife [DPAW]; once every 8 yr for high connectivity and once every 42 yr for low connectivity) were applied as additional events to a management regime of periodic fire intervals. This scenario accounts for the reality of prescribed fires not always excluding wildfires (but does not account for interactions between planned and unplanned fires).

Because parts of the study landscape have been heavily cleared and fragmented, and *Banksia* seed dispersal is low, patch colonization is likely to be restricted to highly connected remnants (except in rare unpredictable cases of long-distance dispersal via avian vectors and uplift mechanisms; see He et al. 2004). We therefore constructed two transition matrices per scenario to account for two extreme alternate possibilities of patches being colonized by *Banksia* seeds from the surrounding landscape. For each scenario, we explored low or high connectivity. We first assumed no colonization due to patches being completely isolated and unable to be colonized in or between fires (representing the low connectivity patches in our landscape). We then adjusted the colonization rate to account for high connectivity patches in which recruitment can occur from nearby concurrently burnt areas (for serotinous species) or from burnt and unburnt areas (for weak or non-serotinous species), adding 100% of seeds (compared to the number of seeds produced locally) to the first age-class of the inter-fire transition matrices **P**.

Weather conditions (especially rainfall) determine germination and seedling survival rates in the first year following fire (Enright and Lamont 1992). Therefore for each scenario, and connected/non-connected landscapes, we also tested two environmental condition scenarios. The first reflected favorable growing conditions (including wet summers) and used the mean reported seedling survival per species (ranging from 5% to 30%), mean juvenile period, and inter-fire recruitment for the two weakly serotinous species that might release seeds without fire (Appendix S1: Table S2a). The second reflected poor growing conditions (to simulate dry post-germination conditions), using the minimum reported seedling survivorship across all species (5%; Appendix S1: Table S2b), zero probability of inter-fire recruitment for released seed, plus the maximum juvenile period (intraspecies variation in juvenile period has been documented for a range of plants in south-western Australia; Burrows et al. 2008, McCaw 2008).

Estimation of population statistics and sensitivity analyses

For each species, the transition matrices **D** were used to estimate the asymptotic population growth rate (i.e., the dominant eigenvalue of the matrices D; Caswell 2001). To facilitate comparisons between scenarios, the asymptotic population growth rates were rescaled at an annual time scale. An asymptotic population growth rate of 1 means a static growth rate, with no predicted change in the long-term population abundance or density. A value higher or lower than 1 means that the population is predicted to increase (and colonize the landscape) or decline (leading to extinction) respectively. We ranked all scenario outcomes and determined which fire strategies (called best fire strategies hereafter) maximized the number of species with an asymptotic population growth rate higher than 1 (i.e., not declining). We ran generalized linear models (GLMs) with a Poisson link in R to explore relationships between the number of *Banksia* species with positive population growth after 100 yr and post-fire conditions, colonization, and the four different management scenarios.

For each of the growing conditions scenarios, we also ran two sensitivity analyses. The first tested the importance of inter-fire recruitment for species survival. For the two species that might release seeds without fire, we started at 1% inter-fire recruitment and increased this value in increments of 1–10%. The second tested the importance of longevity data in informing choice of fire regimes, increasing the longevity of each species. This parameter was the least-reported in the literature, plus *B. coccinea* has been suspected of being affected by disease rather than senescence (Witkowski et al. 1991, Bathgate et al. 1996).

RESULTS

Given favorable growing conditions, allowing no burning to occur for >100 yr resulted in negative growth rates and therefore potential loss of six species (with only *B. sessilis* having positive growth; Fig. 3; Appendix S3). Regardless of landscape connectivity, more species decline and become locally extinct under the wildfire scenario than under managed burning with no wildfire (Fig. 3a, d vs. b, e, respectively; Appendix S3: Tables S2 and S3). Ignoring connectivity, managed burning without wildfire (Fig. 3b, e) resulted in the highest number of species surviving on average for any fire interval compared with all other fire strategies (mean number of species with growth rate >1 after 100 yr under strategy ± SD, good conditions 3.62 ± 1.76, poor conditions 3.17 ± 1.40). The difference in species outcomes between strategies was significant for no burning and random wildfire strategies (Poisson GLM, $P < 0.01$) but not for managed burning with wildfire (Poisson GLM, $P = 0.30$; Appendix S3: Table S1).

Landscape context changed the likely impacts of management scenarios. Poorly connected patches (colonization rate = 0) had lower numbers of species surviving any given patch burning interval on average compared with highly connected patches (Poisson GLM, $P = 0.03$; Appendix S3: Table S1), except for the strategy of managed burning including wildfire, for which the average number of species surviving was higher in poorly connected (mean ± SD, 3.48 ± 1.62) than in highly connected patches (2.50 ± 0.71). In low connectivity patches, where the average fire interval is currently once every 42 yr, five of the seven *Banksia* species are likely to decline and go locally extinct if wildfires occur at this average interval for a 100 yr period, while only one species will maintain a positive population growth rate if wildfires occur at an average interval exceeding 80 yr (Fig. 4a). In highly connected patches, the current rate of wildfire (once every 10 yr on average) is likely to lead to local extinctions of three species (Fig. 4b).

We next explored how post-fire environmental attributes affect *Banksia* persistence, by altering landscape connectivity and likelihood of wildfire occurring under poor growing conditions (such as insufficient rainfall, which reduce seedling survival and germination rates; for detailed results see Appendix S3). As expected, on average significantly more species were predicted to decline and become locally extinct under poor growing conditions (Fig. 4c, d) compared with favorable conditions (Fig. 4a, b; Poisson GLM, $P = 0.02$; Appendix S3: Table S1). Regardless of the connectivity, poor growing conditions led to all seven species declining and becoming locally extinct under a no burning strategy. Only one

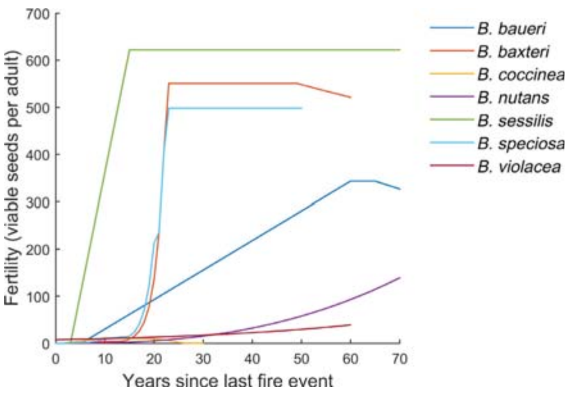

FIG. 2. Contrasting patterns of growth in viable seeds with time since fire for the seven *Banksia* species in our study, showing the total seeds per adult year as a function of time.

Table 1. Sets of top fire management strategies for favorable or poor growing conditions (with an objective of maximizing the number of *Banksia* species with a positive growth rate after 100 yr), showing how often each target species persisted (blank species went locally extinct) (see Appendix S3 for full results).

Strategy	Connectivity	*B. baueri*	*B. baxteri*	*B. coccinea*	*B. nutans*	*B. violacea*	*B. speciosa*	*B. sessilis*
Favorable growing conditions								
Managed fire 1/40–80 yr (no wildfire)	low	✓	✓		✓	✓	✓	✓
Managed fire 1/40 or 80 yr (plus wildfire 1/42 yr)	low	✓	✓		✓	✓	✓	✓
Managed fire 1/90 yr (no wildfire)	low	✓	✓			✓	✓	✓
Managed fire 1/20 yr (with or without wildfire 1/42 yr)	low	✓	✓	✓			✓	✓
Managed fire 1/30–90 yr (no wildfire)	high	✓	✓		✓	✓	✓	✓
Managed fire 1/20 yr (no wildfire)	high	✓	✓	✓		✓	✓	✓
Wildfire 1/50–70 yr	high	✓	✓			✓	✓	✓
Wildfire 1/30–40 yr	high	✓	✓	✓		✓		✓
Managed fire 1/100 yr (no wildfire)	high	✓	✓			✓	✓	✓
Poor growing conditions								
Managed fire 1/70–80 yr (no wildfire)	low	✓	✓		✓	✓	✓	✓
Managed fire 1/90 yr (no wildfire)	low	✓	✓			✓	✓	✓
Managed fire 1/50–60 yr (no wildfire)	low	✓	✓		✓		✓	✓
Managed fire 1/40–80 yr (no wildfire)	high	✓	✓		✓	✓	✓	✓
Managed fire 1/90 yr (no wildfire)	high	✓	✓			✓	✓	✓
Managed fire 1/20 yr (no wildfire)	high	✓	✓	✓			✓	✓

Note: Strategies are ranked in order of the number of species persisting under the strategy after 100 yr.

species persisted under favorable growing conditions in the complete absence of fire, irrespective of landscape connectivity.

To achieve the goal of maximizing *Banksia* species persistence by managing for fire, we found the minimum number of strategies needed to optimize community-level dynamics (in this case the number of species with a positive growth rate after 100 yr). Trade-offs occurred between the scenarios and frequency of burning and the number of likely lost species due to inter-species differences in fire tolerances (Appendix S1: Table S2; Fig. 2). *B. coccinea* and *B. nutans* were the most likely species to be lost under alternative top-ranked strategies. There was no single best management strategy under both high and low connectivity scenarios (Table 1). Instead there were a number of regimes that might be suitable depending on the acceptable final mix of species and the connectivity of the site.

Under most connectivity and growing conditions combinations, a minimum of two different strategies would be needed to maintain all seven target species in the landscape (Table 1). The most complementary strategies under favorable growing conditions were the same for both high and low connectivity patches and depended on no wildfires occurring and either managed fires occurring once every 40–80 yr (six species persisting) or managed fire occurring once every 20 yr (saving a different set of species from the once in 40 to 80 yr burning strategy; Table 1).

In scenario 4 (where prescribed fires do not exclude wildfires), in isolated patches (our low connectivity scenarios) prescribed fire can help to avoid extinctions if applied at certain intervals taking wildfires into account (if and when they occur; Table 1). In large connected areas prone to wildfires (our high connectivity scenarios), however, prescribed fires increase *Banksia* extinction risks and should be avoided. Here the priority is to reduce fire frequency by means other than prescribed fire. As the climate dries (our poor growing conditions scenarios), intervals between burns may need to increase to achieve persistence outcomes due to the increased likelihood of mortality of seedlings and reduced germination. In isolated patches under poor growing conditions, one species (*B. coccinea*) is likely

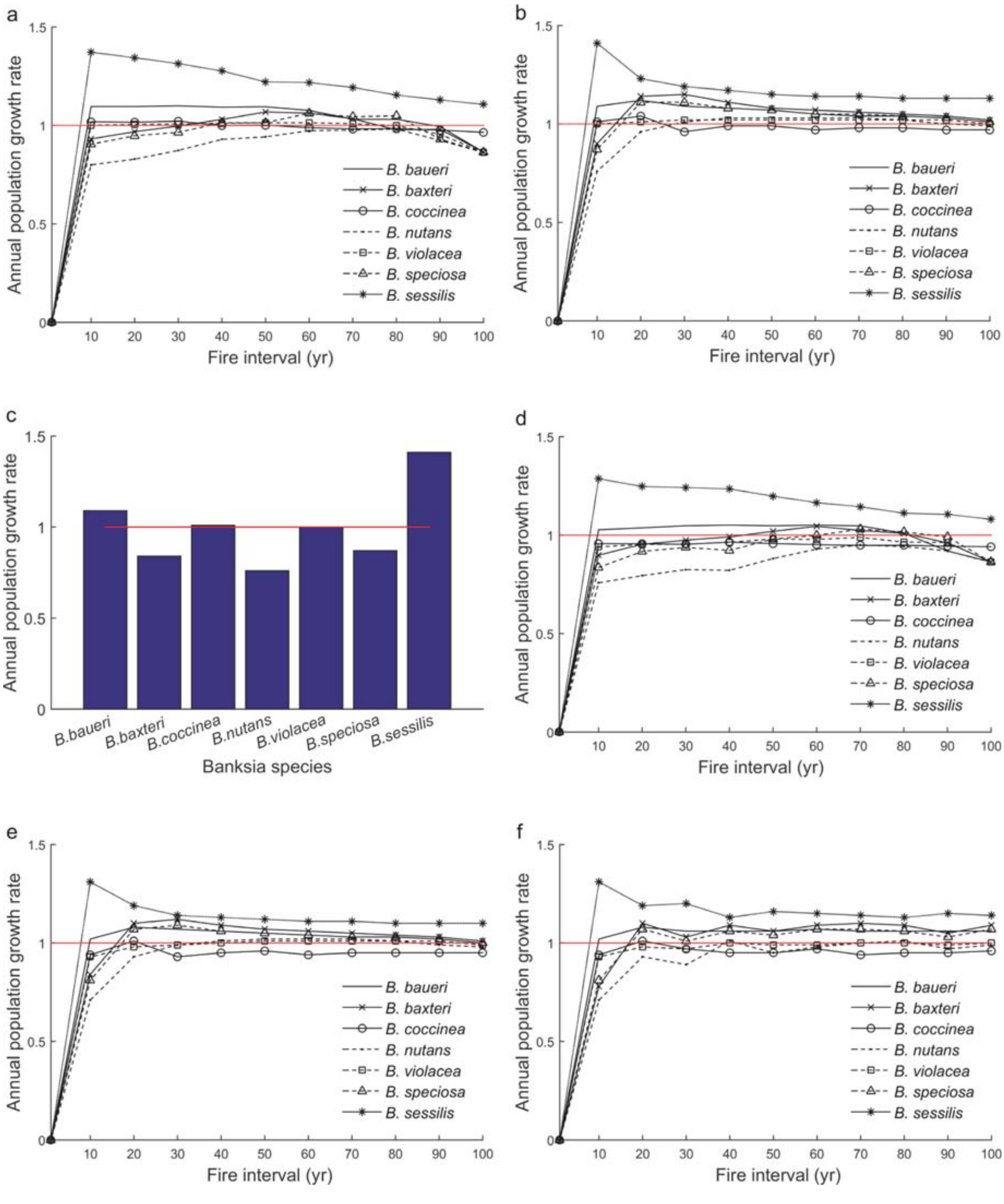

Fig. 3. Annual population growth rates under favorable growing conditions for seven species of *Banksia* under different scenarios of landscape connectivity and fire interval of planned fire and wildfire events (see Appendix S2: Table S1 for details of scenarios): (a) high connectivity landscapes (no fragmentation, colonization rate = 1) and random wildfire events with an average fire interval increasing in 10-yr increments, (b) high connectivity landscapes and managed regular fire intervals from every year (i.e., 1 fire per year) increasing in 10 yr intervals to once every 100 yr, (c) managed burning plus wildfire with high connectivity (presented in a bar graph, as under this scenario fire intervals never exceeded 10 yr), (d) low connectivity landscapes (high fragmentation, colonization rate = 0) and random wildfire events, (e) low connectivity landscapes and planned regular fire intervals, and (f) managed burning plus wildfire for low connectivity patches.

to be lost regardless of the fire management strategy, with managed burning (and no wildfires) once every 70–80 yr maintaining the remaining six species.

Given favorable growing conditions, the worst strategies for low connectivity patches were for wildfires to burn every 1–50 or 90–100 yr or to prescribed burn with

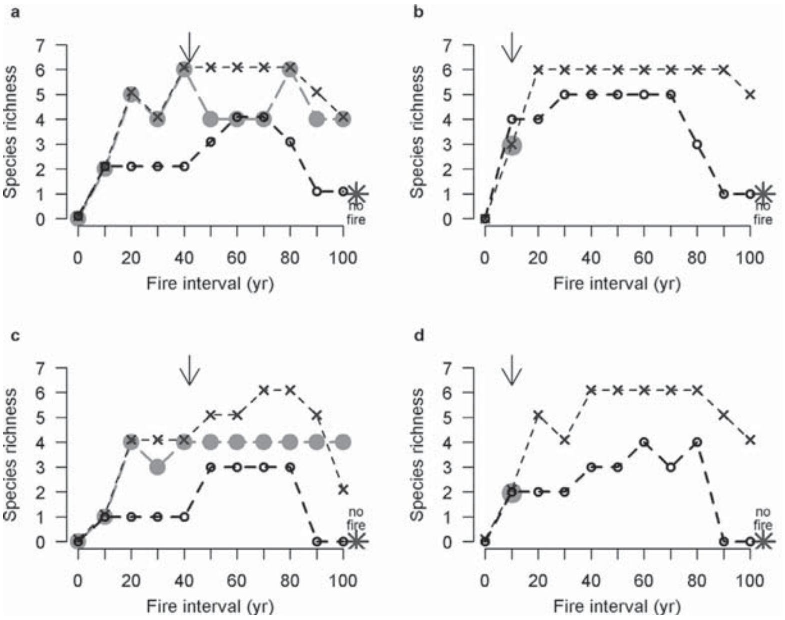

FIG. 4. Outcomes for seven *Banksia* species from alternative management strategies, showing the number of species with a growth rate >1 (i.e. positive) after 100 yr of management under different average fire intervals for (a) favorable growing conditions and no connectivity (colonization rate = 0), (b) favorable growing conditions and high connectivity (colonization rate = 1), (c) poor conditions and no connectivity, (d) poor conditions and high connectivity. Crosses represent the periodic management burning strategy, dark open circles represent the wildfires strategy, light gray filled circles are the periodic burning and wildfires strategy, and gray star at far right shows the no burning strategy. Arrows indicate the current average fire frequency in the PRMH in the study region.

an interval of once every 1–10 yr (Fig. 4a). For high connectivity patches under favorable conditions, the worst strategy is for wildfires to burn once every 90–100 yr (six species lost), followed by prescribed burning with or without wildfires occurring at their current frequency of once every 1–10 yr (Fig. 4b). Under poor growing conditions, wildfire at any interval (with or without prescribed fire) was always a poorer strategy than management fires (and no wildfire) in high connectivity patches (Fig. 4d), and wildfire or managed burning with short (10 yr) or long (90–100 yr) fire intervals was the worst strategy in low connectivity patches (Fig. 4c).

DISCUSSION

Fire is essential for the reproduction and survival of many flora and fauna species in Mediterranean ecosystems globally. There is increasing evidence that indiscriminate burning to maximize heterogeneity of fire-age classes without knowledge of which regimes are optimal for, or detrimental to, biodiversity can have negative outcomes for biodiversity (Parr and Andersen 2006, Taylor et al. 2012). We present the first study that integrates the population dynamics of multiple species with fire regime modelling to investigate how much fire is best to sustain or maximize the species diversity of a keystone genus. Our results suggest that no single fire interval and management strategy will maintain all seven *Banksia* species. Instead, we find that a small set of complementary fire regimes is sufficient to maximize diversity under all the combinations of environmental conditions and patch connectivity investigated (Table 1).

In our case study, managers choosing to implement a single fire regime strategy uniformly across the landscape will always lose at least one *Banksia* species in the next 100 yr from a patch currently containing all the target species (Fig. 4). By exploring the consequences of managing (and not managing) fire, we were able to find a set of fire regimes that maintained all species (but in different patches). For example, excluding wildfire and conducting prescribed burns at a frequency of once every 40–80 yr in some patches, and once every 20 yr in others, was expected to maintain all seven study species in isolated patches under favorable growing conditions (Table 1). However, the first fire regime would lose one species (*B. coccinea*), and the second would likely lose two different species (*B. nutans* and *B. violacea*). Given that no regime maintained growing populations of all species after 100 yr (Table 1) and that at least six of the seven species are expected to co-occur across much of the landscape (Appendix S1), triage allows managers to safeguard patches for different target species and ensures that all species are maintained somewhere in the landscape. Triage has been advocated for managing threats under uncertainty (Hobbs and Kristjanson 2003, Tulloch et al. 2015*a*) or for allocating conservation effort among populations or species (McDonald-Madden et al. 2008). We demonstrate another application of conservation triage:

maintaining multiple fire regimes throughout the landscape that essentially give up on one or more species in some patches to ensure that other species survive there, while giving up on other species in alternative patches to ensure that the first species survive. Human modification and fragmentation of landscapes mean that isolated patches will not recover from fire in the same way as unfragmented landscapes, as important processes such as dispersal, colonization, and recruitment have been altered. Due to this disruption of natural processes, our results suggest that multiple strategies for management of fire in patches in fragmented landscapes will be essential to ensure that populations of particular species can survive.

Studies that assume species can always colonize post-fire through dispersal will overestimate the effectiveness of fire-mediated regeneration and recruitment in many landscapes. Dispersal outcomes in fragmented landscapes depend on isolation distances and seedbank sizes of the source population, dispersal vector (e.g., bird) population sizes and behavior, and post-fire temperature and wind conditions (Hammill et al. 1998). In heavily modified environments such as the southwestern Australian wheatbelt, colonization can be rare. An inappropriate fire regime that kills plants before they can set seed in a patch can cause local extinction if the nearest unburnt patch is further away than the dispersal capabilities of that species. Due to the relatively poor dispersal abilities of *Banksia*, we found that patch connectivity (and the ability of seeds to recolonize a patch from outside) changes the tolerance of species to fire intervals (Figs. 3 and 4). Our results for low connectivity patches rely on the assumption of zero patch colonization and may underestimate patch colonization for some species. For example, He et al. (2004) predicted the possibility of *Banksia* dispersal given particular conditions (the movement of certain species plus suitable uplift winds). Uncertainty in species dispersal ability may be incorporated into future studies by examining varying dispersal scenarios (rather than the extremes of all or nothing in this study). Our results lend conditional support to management burning strategies that ensure that only a proportion of any patch is burnt, ensuring the survival of species unable to colonize from outside that might otherwise be lost due to a burning interval that is too short. However, the interaction between fire patch size and other processes affecting recruitment, such as browsing (Bond and van Wilgen 1996), requires further investigation. Future studies might also model variable fire intensity (i.e., patchiness) within a patch by not assuming 100% mortality from fire (Williams et al. 1999) or perhaps modelling fire occurrence as a function of slope, aspect, and soil, i.e., factors that influence fire intensity and fuel structure (Bradstock et al. 2010).

Knowledge of the variability of responses within a given landscape is important to ensure the optimal range of fire regimes has been identified. We did this by testing species representing a range of traits in best case (favorable growing conditions) and worst case (poor growing conditions) environmental scenarios. In reality, these conditions are not constant year to year, but rather alternate between poor periods and good periods. We were interested in exploring these extreme cases based on evidence that the area is likely to be subjected to an increased drying trend due to climate change (Cary et al. 2006, Steffen and Hughes 2013). In addition to reducing the likelihood of germination and survival of seedling recruits after fire, this drying trend is likely to increase the length of the fire danger periods and increase the likelihood of vegetation burning. Increased wildfire events are likely to have a significant impact on the seven species in this study, even without prescribed fire management, with our models predicting that only one out of the seven species would survive if wildfires burnt more frequently than the current rate of once every 42 yr for poorly connected patches and poor growing conditions, and none would survive if wildfires burnt more frequently than the current rate of once every 10 yr for well-connected patches with poor growing conditions (Fig. 4).

Our results also provide further evidence to support recent experimental findings that poor growing conditions related to lower rainfall, as projected to occur under a drying climate (Schneider et al. 2007), are likely to increase the minimum inter-fire interval required to sustain species (Enright et al. 2014). In poor post-fire growing conditions, connectivity was necessary to maintain populations of *B. coccinea*, which was lost under all fire regimes except for one (burning highly connected patches once every 20 yr). Low connectivity and poor post-fire growing conditions combined with too frequent or too rare fire led to the potential loss of all species. Some species (e.g., *B. nutans, B. coccinea*) were more likely to go extinct than others (Table 1; Appendix S3: Table S2). These generally had low fertility rates (Fig. 2). For *B. nutans*, slow post-fire seed bank accumulation combined with the lowest annual seed survival rate of the seven species (Appendix S1: Table S2) is likely the reason for higher instances of extinction. For *B. coccinea*, slow post-fire seed bank accumulation combined with the shortest estimated longevity of the seven species (Appendix S1: Table S2) could be the reason for extinction under a wider range of scenarios. However, changing the longevity of species did not alter the range of acceptable fire intervals (although it did change the number of species surviving within that best set of intervals; Appendix S3: Figs. S3 and S4), whereas changing inter-fire recruitment allowed species to persist under longer fire intervals. We recommend that future studies of the population dynamics of species in response to fire further explore how connectivity and growing conditions might alter survival, recruitment, and the associated responses of species to alternative fire regimes. This will ensure that the range of potential responses is canvassed, particularly under future changed climates.

Our matrix population models for the seven species in this study considered only a single population at any one time. The deterministic nature of our models and reliance on changes to certain vital rates (germination rate, seedling survival rate, and inter-fire recruitment) to simulate different post-fire and inter-fire interval conditions were necessary simplifications to allow us to incorporate process-based models and fire management strategies for multiple species. Our single-population models would be improved by incorporating spatial considerations, such as through a stochastic metapopulation modelling approach (Bradstock et al. 1996, Westphal et al. 2003, Pichancourt et al. 2012), but this requires a substantial increase in data on patch immigration and emigration (to allow the estimation of patch colonization and extinction probabilities), data that were not available for all the target species in this study. One further limitation was that we did not incorporate inter-species competitive interactions that potentially affect a number of the demographic parameters used (such as seedling survival rate and longevity; Groeneveld et al. 2002). Despite the *Banksias* in this study being the dominant species in the study area, particular fire regimes may result in differing levels of competition, depending on the response of species other than *Banksia* For example, regular short fire intervals may maximize persistence of resprouting species and seed bank size in groups such as *Acacia*, at the expense of serotinous non-resprouters such as these *Banksia* species (Gosper et al. 2012*a*). The derivation of best fire regimes becomes ever more complex if other species or trait groups, such as resprouters, are to be considered simultaneously. Future work could extend our study to optimize a population process (e.g., growth rate) across both flora and fauna to find a complementary set of regimes for multiple taxa.

Our models indicate that under most connectivity and growing condition combinations, a regime of management fires (i.e., prescribed or controlled burning) of some intervals was best in terms of a single regime maximizing the number of *Banksia* species persisting in a patch. However, this scenario explicitly assumes that unplanned fires (either wildfire or escaped management fire) can be excluded. Recent experience suggests that the validity of this assumption is landscape context-specific, with unplanned fires being very rare in the unconnected fragmented landscape, but frequent in the connected larger conservation reserves (Parsons and Gosper 2011). Further, reduced fuel levels after management fires are only likely to reliably exclude unplanned fires for a few years afterwards (Fontaine et al. 2012), although they may at least reduce the intensity of subsequent fires for 5–8 yr post-fire and allow some individuals to survive (McCaw et al. 1992). In situations where our assumption of 100% mortality post-fire is violated, population fecundities (and associated growth rates) are likely to be higher than those predicted in this study (due to the ability of mature plants to continue to produce seed while seedlings are germinating and maturing post-fire).

Overall, prescribed management-only fires appear a viable and low-risk way forward for fire management for *Banksia* in unconnected landscapes (or management fires and wildfires, which performed nearly as well). In connected landscapes, the application of the scenario of management-only fires is likely to be fraught, as the frequent occurrence of unplanned fires has resulted in the recent fire scenario being one of management fires and wildfires, which our analyses indicate has catastrophic consequences for *Banksia* persistence. It would seem that to improve the conservation status of *Banksia* in connected landscapes, the frequency of unplanned fires needs to be reduced, but via methods that do not involve the extensive use of prescribed fire.

There is no single ideal fire regime in our highly modified and fragmented study landscape. The ideal fire management strategy is context specific, driven by the needs, life histories, and diversity of species within a given habitat, as well as the landscape characteristics. Prescribed fire can help to avoid extinctions in isolated patches if applied at certain intervals taking wildfires into account. However, prescribed burning may increase extinction risks in large connected areas, and the prescribed intervals between burns may need to increase as the climate dries. Incorporating the likely effects on population demographics of alternative future growing conditions, patch connectivity, as well as the possibility of wildfire events disturbing a given fire management strategy, should help managers make more realistic predictions of the impacts of a chosen set of burning regimes. Given the scale of global vegetation clearance and modification of fire-prone environments and the reality of patch fragmentation leading to lower post-fire colonization and subsequently reduced ability of some species to survive under a wide range of fire regimes, managers of highly-fragmented fire-prone landscapes in many parts of the world could be forced to diversify and find complementarities between fire regimes through space. Even with this approach managers could face population triage in some cases, such as isolated patches in poor growing conditions where there might be no mix of fire strategies that saves all species. This study demonstrates a way to inform prioritization and triage decisions such as these. Using information on the demographic responses of fire-dependent species to different management actions and exploring the impacts of changing environmental conditions on population responses to fire, we have shown how to find the best complementary sets of fire management strategies necessary for maintaining the persistence of multiple species.

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