Does intraspecific variation in demography have implications for fire management of an obligate-seeder shrub across its geographic range?

JOHN W. MORGAN,^{1,2,*} MICHAEL A. MCCARTHY,³ AND EMILY WILLOCKS^{1,4}

¹Department of Ecology, Environment and Evolution, La Trobe University, Bundoora 3083, Victoria, Australia (Email: J.Morgan@latrobe.edu.au), ²Research Centre for Future Landscapes, La Trobe University, Bundoora 3083, Victoria, Australia, ³School of BioSciences, The University of Melbourne, Parkville 3010, Victoria, Australia and ⁴Department of Environment, Land, Water and Planning, Nicholson Street, East Melbourne 3002, Victoria, Australia

*Correspondence author

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/AEC.12981](https://doi.org/10.1111/AEC.12981)

This article is protected by copyright. All rights reserved

DR. JOHN MORGAN (Orcid ID : 0000-0003-2003-5983)

Article type : Research Article

Abstract Predicting changes in the abundance of species over time is a central goal of conservation ecology. Typically, demographic data are used to parameterize models which describe population dynamics. Vital rates of plants vary across a species' distribution, yet most demographic estimates are spatially constrained. *Banksia ornata* (Proteaceae), a widespread serotinous obligate-seeding shrub in southern Australia, has previously had a fire management model developed based on demographic data derived from a chronosequence in one part of the species' range. We asked: are demographic data collected from a limited geographic range robust for developing population dynamic models that are applied across the broader species' range? How much variation exists in the demography of species across their range, and does this matter for estimating fire-return intervals necessary for species persistence? We examine site-to-site variation in the pyrodemography of six populations of *B. ornata* encompassing its geographic range. We documented changes in population density, time to first reproduction, and canopy seed bank accumulation in stands varying in age from 0.5 to 55 yrs. We model year of maximum seed production on demographic parameters such as population starting density and survival rate. Density, primary juvenile period, rates of mortality and seed bank accumulation varied across populations. Primary juvenile period varied across populations (from 6 yrs to <20 yrs), while time to maximum seed production was estimated to take 34-39 yrs after fire. Hence, the fire intervals that correspond to minimizing extinction risk (due to variation in primary juvenile periods) diverge more so among populations than the fire intervals that produce (on average) the highest maximum seed production with respect to time-since-fire. Demographic data collected at different locations in a species' range are likely valuable for building realistic species response models to

disturbance, providing underlying assumptions about key transitions, such as mortality rate, are made explicit.

Key words: *Banksia ornata*, chronosequence, fire regime, population dynamics, primary juvenile period, pyrodemography

INTRODUCTION

Plant species vary in their vital rates across their geographic distribution (Kalisz 1991; Svensson *et al.* 1993; Oostermeijer *et al.* 1996; Freville *et al.* 2004), a local adaptation in response to climate gradients (Donohue *et al.* 2010; Messier *et al.* 2010; Cochrane *et al.* 2016). This variation has implications for threatened species management (Menges 1990; Brook *et al.* 2000; Kaye *et al.* 2001; Quintana-Ascencio *et al.* 2003; Liu *et al.* 2005; Nield *et al.* 2009), fire management (Bradstock 1990; Bradstock *et al.* 1996; Drechsler *et al.* 1999; Hoffmann 1999; Beverly & Martell 2004; Menges *et al.* 2006) and invasive species management (Hansen & Wilson 2006; Ramula *et al.* 2008). Many of the plant demographic data that underpin management actions, however, are spatially constrained, i.e. frequently limited to one or few populations (Buckley *et al.* 2010; Franklin *et al.* 2017). Consequently, it is reasonable to ask whether it is valid to scale up from the results obtained from small-scale studies (Cochrane *et al.* 2015). The scales at which we aim to predict the dynamics of ecological systems (i.e. landscape-scale) are usually far larger than those at which we typically observe them (Freckleton 2004), but it is uncertain whether demographic data collected from across a species' range improve models constructed to predict their behavior in response to management actions (Franklin *et al.* 2017). Many models generally assume common among-population environmental similarities and tolerances across a species (Bolnick *et al.* 2011), leading to models that treat species traits as mean values which may be not always be adequate for prediction (as discussed in McGill *et al.* 2006).

Modelling to determine fire management regimes necessary for species persistence has been particularly important in the genus *Banksia*, with several studies documenting fire regime sensitivity for re-sprouting species (Bradstock 1990; Drechsler *et al.* 1999; Bradstock & Bradstock 2017) and obligate-seeding species (Burgman & Lamont 1992; Lamont *et al.* 1994a; Enright *et al.* 1996; McCarthy *et al.* 2001; Muir *et al.* 2014). Fire-return intervals, typically expressed in terms of the time-since-last-fire, are of crucial importance for populations of obligate-seeding species if aiming to minimize their risk of local extinction (Gill & McMahon 1986; Bowman *et al.* 2014). All fire studies of *Banksia* species in Australia have investigated fire regimes based on demographic information that accounted for year of maximum seed production (Enright *et al.* 1996; McCarthy *et al.* 2001; Muir *et al.* 2014), time to maximum population size (Burgman & Lamont 1992; Drechsler *et al.* 1999; Enright *et al.* 1998) and probability of survival (Bradstock *et al.* 1996). Only three studies investigate common, widespread species and these studies have spatially constrained data to parameterize models.

In this study, we examine variation in the demography of six populations of the obligate-seeder shrub *Banksia ornata* across its geographic range in southern Australia, in relation to time-since-fire. This species has previously had detailed demographic data collected from one site (Gill & McMahon 1986) that was then used by McCarthy *et al.* (2001) to develop a model to inform fire management. We quantify how variation in the demography across populations dispersed in space affects outcomes for modelling population dynamics. We ask: how much variation is there in the demography of *B. ornata* across its range? And, does this variation lead to different outcomes when considering fire management strategies that are implemented to manage the habitat of the species, i.e. does collecting 'more' demographic data improve our understanding of fire management for this obligate-seeding species?

MATERIALS AND METHODS

Study species

Banksia ornata F.Muell. ex Meisn. (Proteaceae) is a serotinous obligate-seeding shrub of southern Australia, typically dominating in heathland on deep, low-nutrient sands (Specht *et al.* 1958; Beadle 1981; Groves *et al.* 1986). It is fire-sensitive, recovering from canopy stored seed (Gill & McMahon 1986); thus, stands are even-aged. Individuals do not begin to produce seed until >5 years of age, and they survive for ~50 years (Specht *et al.* 1958; Gill & McMahon 1986). Inappropriate fire regimes – too frequent fire, or long-term fire suppression - will lead to local extirpation (Gill & McMahon 1986). *Banksia ornata* is an abundant species, ecologically important and is likely to be indicative of fire management issues for numerous other obligate-seeding species (Gill & Bradstock 1995). Gill & McMahon (1986) regarded *B. ornata* as a potentially useful indicator species for fire managers because it is easily identified, dominant, fire-sensitive and its source of regeneration (seeds) are visible on the plant. A model of population dynamics after fire was developed by McCarthy *et al.* (2001), using the single population demographic data of Gill & McMahon (1986), in conjunction with stochastic dynamic programming to determine optimal fire management strategies for the species' persistence in fire-prone environments. The probability of persistence was maximized when burning occurred at approximately 28 yrs of age, with population state (i.e. age) rather than abundance the most important determinant of extinction risk.

Study sites

To quantify how the demography of *Banksia ornata* varies with time-since-fire across its distribution, chronosequence study areas were selected in six widely spaced regions across the species' range (Fig. 1, Table 1). Study regions spanned a climatic gradient (~5 °C difference in mean annual temperature and ~600 mm difference in mean annual rainfall) which likely affects productivity and fire frequency (Pausas & Bradstock 2007). Fire is relatively common in the region, with lightning ignitions and, increasingly, fuel reduction burning by management agencies the predominant sources of fire (Pausas & Bradstock 2007). To qualify for sampling in each region, five to seven age classes spanning decadal timescales, based on time-since-last-

fire, were located as close as possible to each other (<25 km) on similar land form (typically sand dunes of variable depth; Groves *et al.* 1986) in heathland vegetation, with sites identified primarily by using fire history mapping provided by land management agencies. These sites - within each study region - represent a range of stand responses to individual (i.e. different) fires – some of which occurred up to 55 yrs previously - and which then developed post-fire in a range of climatic conditions. Such differences likely affect stand structure in ways that cannot be easily determined, and this suggests some caution is necessary when interpreting the results. More broadly, space-for-time chronosequence comparisons should be treated with caution (Buckley *et al.* 2010). They risk attributing population differences to the chronological variable (here, time-since-fire) when site differences (such as soils, rainfall variability) or differences in fire type may be causing the patterns (Menges 2007). Indeed, because each site is defined by having been burnt, each site represents responses to different fires (season, intensity, extent), each with different post-fire environmental conditions (i.e. temperature, rainfall, drought). While we tried to minimize spurious patterns by careful choice of study sites within regions that were comparable in soil characteristics and land use history, the temporal variation introduced by differences in fire type and post-fire environment must be acknowledged.

Demography of *Banksia ornata*

The density of *B. ornata* with time-since-fire was estimated at every site by recording the number of individuals in a 6 x 50 m belt transect. This estimate was then converted to density per hectare. At all sites, we use the number of plants in the youngest age-class sampled (either 0.5 yr or 1 yr time-since-last-fire) to estimate the 'starting density of plants per hectare'. We use this estimate as an indicative starting density in each region given seedlings are the most numerous life-history stage in this species and stand thinning occurs thereafter (Gill & McMahon 1986). The absolute number of plants in the earliest age-class we sampled at each site will be influenced by the history of fire before each were last burnt (i.e. the 'invisible mosaic'; Parr & Andersen 2006).

At each time-since-fire site in the chronosequence in each region, 30 plants were then sampled along a variable length transect placed through a visually homogenous population. On each plant, the total number of cones was counted and for each cone, the number of closed, open and damaged follicles was recorded.

Modelling population dynamics

For each chronosequence region, we fitted a linear regression of the number of plants per hectare (log transformed) versus time-since-last-fire to determine how population density changes with time (log-density model, $N_x(t)$). Equations 1, 2 and 3 then provide the basis for the model of *B. ornata* seed production. The structure of the model follows McCarthy *et al.* (2001). The changes in seed production per plant with time-since-fire were non-linear so we fitted a quadratic regression of the average number of seeds per plant (log-transformed based on cone number and closed follicle number per cone derived from field observations across all sites) versus time-since-last-fire to determine how seed production changes per plant with time (log-seed production model, $Y_x(t)$). Plants aged 5 yrs or less were omitted from the regression analysis given *B. ornata* do not start producing seeds until at least six years after fire (Gill & McMahon 1986). The logarithm of average number of seeds per plant with stand age was found to be equal to:

$Y_x(t) = -0.0038t^2 + 0.3005t - 0.6480 + d_x$ [Eqn 1], where d_x is a site effect that accounts for site to site variation in maximum seed production per plant (Table 2).

We then express the average number of seeds per plant with stand age as being equal to:

$$R_x(t) = [\exp(Y_x(t))] - 1 \text{ [Eqn 2]}$$

The state of the system (number of seeds per hectare in each population in each region) was described by the density of plants per hectare and their age ($S_x(t)$; Equation 3) and was equal to:

$S_x(t) = [D_x(0) * R_x(t) * \exp(-m_x t)] - 1$, where $D_x(0)$ is starting abundance of plants per hectare in each region, and $m_x t$ is survival (%) per annum in each region [Eqn 3]

We use field-derived starting population size ($D_x(0)$) to define the initial population size. The equation $N_x(0)$ was used to define the survival rate per annum at each population (m_x ; Table 2), necessary because the model describes the seed production over time. Equation 3 is implemented with annual time steps (up to $n = 60$ yrs). The effects of dispersal from other areas were assumed to be minimal (Gill & McMahon 1986); consequently, no dispersal related addition or loss of seeds was included in the modelling.

Results

Banksia ornata population density (plants ha⁻¹) varied substantially both between regions and with time-since-last-fire (Supplementary Fig. 1). The relationship between log(population density) and time-since-last-fire varied from weak to moderate ($r^2 = 0.06-0.60$; Supplementary Fig. 1), with mortality varying between <1% to 4.3% per annum (Table 2). There was no evidence of inter-fire recruitment at any of the sites.

There was a moderate to strong positive relationship ($r^2 = 0.45-0.98$) between average number of canopy-stored cones per plant and time-since-last-fire at all populations (Supplementary Fig. 2, Table 3). Seed-bearing cones first occurred on plants at 6-7 yrs after fire at two populations (Little Desert, Wyperfeld), later at Ngarkat, Messent and Grampians (>6 yrs but <13, <18 and <13 yrs, respectively) and, for one population (Kangaroo Island), there were insufficient data in the first two decades after fire to clearly define this age (Supplementary Fig. 2). The number of

follicles per plant decreased with plant age at all populations, other than Kangaroo Island (Supplementary Fig. 3), particularly after 20 yrs; the proportion of damaged follicles per cone was low but increased with age in all populations (except Kangaroo Island) and the degree of serotiny observed was very high (Supplementary Fig. 4).

Using the demographic data collected at each population to model year of maximum seed production ($S_x(t)$, using starting density and mortality rate obtained from Table 2), we found that across the populations studied, the maximum seed production occurred between 34 yrs (Little Desert) and 39 yrs (Grampians; Fig. 2). Starting density determines the modelled number of seeds per hectare, with enormous variability (100-fold differences) in seed production across populations (Fig. 2).

Discussion

The demography of the heathland species *Banksia ornata* has been quantified by Gill & McMahon (1986), from which McCarthy *et al.* (2001) determined an optimal fire management strategy for the species, but this was based on data derived from near the eastern edge of the species' range. In our study system, there is a precipitation and temperature gradient which affects productivity and fire regimes (Pausas & Bradstock 2007) and hence, may also affect the population dynamics of this obligate-seeder shrub. We found there was variation in the demography of *B. ornata* across its geographic range (e.g. mortality rates, cone production, time to first reproduction, number of years to maximum seed production), likely a result of populations experiencing differences in climate and prior fire history.

One obvious difference we observed in the demography of *B. ornata* across the regions was how population density varied with time-since-fire (Fig. S1). In Gill & McMahon (1986), the population dynamic model fit was 86% but we had poorer fits (6-60%). Because we have not followed a population through time but rather, have inferred its dynamic in space, this hints

that part of the response we observed may be due to the type of fires that stands have previously experienced and how this affects recruitment. The frequency and timing of burning affects seedling recruitment (Céspedes *et al.* 2014), as does post-fire drought (Moreno *et al.* 2011). As a consequence, we also estimated that the rate of mortality across the study region was lower (at 0.5–4.3% per annum) than that observed by Gill & McMahon (at 8% per annum), but this may be a function of different fires producing different post-fire populations that thin at different rates. Indeed, at Ngarkat and Messent, there was very little difference in density of plants with time-since-fire; whether this is a true reflection of thinning versus an outcome of different fire history responses (i.e. the ‘invisible mosaic’; Parr & Andersen 2006) is not known.

The time-since-fire chronosequences we sampled across six regions within the geographic range of *B. ornata*, which subsequently showed low population model fit with time-since fire at most sites (particularly Messent and Ngarkat), highlights a hitherto poorly recognised outcome of fire on population recovery in this species. For obligate seeders like *B. ornata*, every fire might be a potential ‘demographic bottleneck’ for that population, one that may be exacerbated in populations where modelled seed production (per hectare) was very low (e.g. Messent or Wyperfeld, compared to Grampians). Because fire kills all standing plants, seed germination and survival of seedlings are necessary to recover the population, but these life-history stages can be vulnerable to the post-fire climatic conditions. Limited seedling recruitment, for instance, might occur under extreme drought conditions (e.g. Gazol *et al.* 2018; Young *et al.* 2019) and low numbers of seedlings, due to low post-fire seed rain, could limit opportunities to buffer such losses. One might postulate that minimising the number of times a population is exposed to such risks (i.e. the number of fires from which it needs to recover and hence, the chance of encountering a year with high risk of recruitment failure) may be more important than maximising the seedbank to maximise population growth, as long as there is a minimum number of seeds to achieve population replacement. In other words, once a seedbank exceeds a threshold size, it is no longer the most limiting factor on population persistence. While it is not clear what that threshold seedbank size may be, our population

modelling hints that ~50% of seedbanks persist for at least 10-15 yrs after maximum seed production has been achieved (Fig. 2). There is a clear knowledge gap about early seedling survival after fire in this species that needs to be better understood, linking the likelihood of risk of recruitment failure to post-fire climatic conditions.

The time to first reproduction, where populations started producing cones (with follicles), varied substantially. Some sites appear to produce cones <10 yrs after fire (Little Desert, Wyperfeld), while others take longer (10-20 yrs; Grampians; Messent, Ngarkat). Data for Kangaroo Island are too sparse to adequately determine this critical transition. It would be worthwhile to elucidate the basis of this variation. Age to first reproduction represents the primary juvenile period, or 'immaturity risk' of Keeley *et al.* (2005), the minimum number of years after fire for an obligate seeder to reach reproductive age. The estimates of primary juvenile period we observed for *B. ornata* are similar to those observed in *Banksia* elsewhere (e.g. Muir *et al.* 2014) and Australian and South African Proteaceae more generally (e.g. Enright & Goldblum 1999; Kraaij *et al.* 2013). Local populations are destined for extinction if fire occurs during the primary juvenile period (Gill & Bradstock 1995; Bowman *et al.* 2014) and our study highlights that the minimum fire-return intervals necessary to reduce extinction risk across *B. ornata* populations diverge more so (by potentially >10 yrs) than the fire interval variation (i.e. ~5 yrs) that produce (on average) the highest maximum seed production with respect to time-since-fire. The primary juvenile period is, of course, not the minimum tolerable fire interval of the species given plants are only just starting to become reproductive. The time necessary (in years) to maintain a stable population after time to first flowering has been reached remains uncertain. We did find that maximum seed production occurs at least ~20 yrs after first flowering, but even this parameter varied substantially across populations in this study (i.e. from ~20 to 30 yrs). Substantial time lags between first flowering and maximum seed production have also been seen in other *Banksia* (e.g. Enright *et al.* 1996), but in some species, this lag is much shorter. For *Banksia spinulosa* var. *cunninghamii*, for example, a species of wet

forests, the minimum time to first flowering is ~13 yrs and time to maximum seed production is ~20 yrs (Muir *et al.* 2014).

A key challenge for fire management is to tailor fire regimes for conservation. We took the approach of modelling the time taken for *B. ornata* to reach maximum seed production, the age at which full replacement can be achieved from seed after a fire event, as has been previously done (e.g. McCarthy *et al.* 2001). The modelled times to maximum seed production varied across the distribution of the species (i.e. 34-39 yrs). Environmental gradients therefore created modest variation in demography among populations, a finding echoed in a recent meta-analysis about among-population variation in traits related to plant recruitment (Cochrane *et al.* 2015). McCarthy *et al.* (2001) suggested the optimal fire regime for population persistence was when plants were 34-39 yrs of age and found that prescribed fire at an age of <30 yrs was only optimal when the density of seedlings after a fire was low. The age of the population (time-since-last-fire) and the survival rate were the demographic parameters that had the most influence on their model outcomes. Gill & McMahon (1986) found maximum seed production occurred at 38 yrs of age in the Little Desert; we found maximum seed production occurred at 34 yrs after fire at a similar location.

Currently, fire as a management tool for managing dune heathland habitat, which encompasses much of the range of *Banksia ornata*, varies across management jurisdictions. In the state of Victoria (which includes the eastern populations), a minimum fire interval of 29 yrs has previously been recommended (DSE 2009), which is near our estimates of time to maximum seed production. In the state of South Australia, capturing the westerly populations, no specific fire intervals are recommended; rather there are statements that fire intervals should be between 10 to 50 yrs with no more than two fires within 40 yrs (DEH 2009). The lower bounds of these recommended fire regimes would clearly compromise the long-term ability of *B. ornata* to persist, given the primary juvenile period is >6 yrs and, in some cases, much longer (i.e. closer to 20 yrs). We recommend that to minimize risk of local extinction of *B. ornata*,

more specific guidelines are appropriate. A fire return interval of 30-40 yrs would likely maximise this aim across its entire range, with fires between 25 and 50 yrs apart likely to maintain population stability. Interestingly, Pausas & Bradstock (2007) suggest that the average fire frequency for the shrublands of the Little Desert and Wyperfeld National Parks, two of the areas we studied, is 29.5 to 40.8 yrs. Fire management recommendations for one species must be balanced, however, with the needs of other species in this landscape such as mammals (Kelly *et al.* 2011) and birds (Watson *et al.* 2012) reliant on vegetation as habitat and food. A diversity of fire regimes across the landscape (i.e. pyrodiversity) may be appropriate as a bet-hedging fire management strategy to allow coexistence of species with disparate life histories (Menges 2007), paying particular attention to minimum return intervals.

Conclusions

Many studies show that species vary in their phenology and demography across their range (Kalisz 1991; Bengtsson 1993; Svensson *et al.* 1993; Oostermeijer *et al.* 1996; Freville *et al.* 2004; Buckley *et al.* 2010) leading some to suggest that modelling based on demographic data obtained from temporally or spatially restricted studies should be treated with caution (e.g. Coulson *et al.* 2001; Reed *et al.* 2002; Cochrane *et al.* 2015). We demonstrate that *Banksia ornata* is a species that varies in demography (primary juvenile period, mortality rate per annum, rate of seed accumulation) across its distribution. Consequently, the demographic data obtained from one population of *Banksia ornata* was not sufficient to accurately model population dynamics across the species' range, with variation in primary juvenile period particularly pronounced. This hints that while detailed (but spatially-constrained) demographic data is likely valuable for building realistic species response models to exogenous disturbance, care needs to be taken with respect to its utility across an entire species' range (Warton & Wardle 2003).

ACKNOWLEDGEMENTS

The Department of Environment, Land, Water and Planning, Parks Victoria, and the Department of Primary Industries and Department of Environment and Heritage provided the spatial data from which we selected sites. Curtis Murtagh, Elise King, Alastair Martin and Andy Green assisted with fieldwork. Angela Wong, Peter Arnott, Tim Finger, Bridgid Arnott, Vicky Lam, Sylvia Lim, Laura Fraser, and Charlotte Hehir assisted with lab work. Field sampling was undertaken in accordance with Research Permit #10005096 issued by Department of Environment, Land, Water and Planning (State Government of Victoria) and permit C24793-1 issued by Department of Environment and Heritage (Government of South Australia). We thank Bob Parsons, the editor Prof. Nigel Andrew and two anonymous reviewers for substantially improving early versions of the manuscript. The authors have no conflicts of interest to declare.

Author Contributions

John Morgan: Conceptualization (lead); data curation (supporting); formal analysis (supporting); investigation (lead); methodology (equal); project administration (equal); writing-original draft (lead); writing-review & editing (lead). **Michael McCarthy:** Conceptualization (supporting); formal analysis (lead); writing-original draft (supporting). **Emily Willocks:** Conceptualization (supporting); data curation (lead); formal analysis (supporting); investigation (supporting); methodology (equal); project administration (equal); writing-original draft (supporting).

REFERENCES

- Beadle N.C.W. (1981) *The Vegetation of Australia*. Cambridge University Press, Sydney.
- Bengtsson K. (1993) *Fumana procumbens* on Öland - population dynamics of a disjunct species at the northern limit of its range. *J. Ecol.* **81**, 745-758.
- Beverly J.L. & Martell D.L. (2004) Modeling prescribed surface-fire regimes for *Pinus strobus* conservation. *Cons. Biol.* **18**, 1541-1552.
- Bolnick D.I., Amarasekare P., Araujo M.S., Burger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C. & Vasseur D.A. (2011) Why intraspecific trait variation matters in community ecology. *TREE* **26**, 183-192.
- Bowman D.M.J.S., Murphy B.P., Neyland D.L.J., Williamson G.J. & Prior L.D. (2014) Abrupt fire regime change may cause landscape-wide loss of mature obligate seeder forests. *Glob. Change Biol.* **20**, 1008-1015.

Bradshaw S.D. & Bradshaw F.J. (2017) Long-term recovery from fire by a population of honey possums (*Tarsipes rostratus*) in the extreme south-west of Western Australia. *Aust. J. Zool* **65**, 1-11.

Bradstock R.A. (1990) Demography of woody plants in relation to fire: *Banksia serrata* Lf. and *Isopogon anemonifolius* (Salisb.) Knight. *Aust. J. Ecol.* **15**, 117-132.

Bradstock R.A., Bedward M., Scott J. & Keith D.A. (1996) Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. *Cons. Biol.* **10**, 76-784.

Brook B.W., O'Grady J.J., Chapman A.P., Burgman M.A., Akcakaya H.R. & Frankham R. (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* **4-4**, 385-387.

Buckley Y.M., Ramula S., Blomberg S.P., Burns J.H., Crone E.E., Ehrlén J., Knight T.M., Pichancourt J-B., Quested H. & Wardle G.M. (2010) Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. *Ecol. Lett.* **13**, 1182-1197.

Burgman M.A. & Lamont B.B. (1992) A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic, and genetic effects. *J. Appl. Ecol.* **29**, 719-727.

Céspedes B., Luna B., Pérez B., Urbieto I.R. & Moreno J.M. (2014) Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland. *Appl. Veg. Sci.* **17**, 86-96.

Cochrane A., Hoyer G.L., Yates C.J., Neeman T. & Nicotra A.B. (2016) Variation in plant functional traits across and within four species of Western Australian *Banksia* (Proteaceae) along a natural climate gradient. *Aust. Ecol.* **41**, 886-896.

Cochrane A., Yates C.J., Hoyle G.L. & Nicotra A.B. (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? *Glob. Ecol. Biog.* **24**, 12-24.

Coulson T., Mace G.M., Hudson E. & Possingham H.P. (2001) The use and abuse of population viability analysis. *TREE* **16**, 219-221.

Donohue K., Rubio De Casas R., Burghardt L., Kovach K. & Willis C. (2010) Germination, postgermination adaptation, and species ecological ranges. *Ann. Rev. Ecol. Evol. Sys.* **41**, 293-319.

Drechsler M., Lamont B.B., Burgman M.A., Akcakaya H.R., Witkowski E.T.F. & Supriyadi (1999) Modelling the persistence of an apparently immortal *Banksia* species after fire and land clearing. *Biol. Cons.* **88**, 249-259.

Enright N.J. & Goldblum D. (1999) Demography of a non-sprouting and resprouting *Hakea* species (Proteaceae) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age, drought and disease. *Plant Ecol.* **144**, 71-82.

Enright N.J., Lamont B.B. & Marsula R. (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *J. Ecol.* **84**, 9-17.

Enright N.J., Marsula R., Lamont B.B. & Wissel C. (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *J. Ecol.* **86**, 946-959.

Franklin J., Serra-Diaz J.M., Syphard A.D. & Regan H.M. (2017) Big data for forecasting the impacts of global change on plant communities. *Glob. Ecol. Biog.* **26**, 6-17.

Freckleton R.P. (2004) The problems of prediction and scale in applied ecology: the example of fire as a management tool. *J. Appl. Ecol.* **41**, 599-603.

Freville H., Colas B., Riba M., Caswell H., Mignot A., Imbert E. & Olivieri I. (2004) Spatial and temporal demographic variation in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology* **85**, 694-703.

Gazol A., Camarero J.J., Sangüesa-Barreda G. & Vicente-Serrano S.M. (2018) Post-drought resilience after forest die-off: shifts in regeneration, composition, growth and productivity. *Frontiers in Plant Science* **9**, 1546.

Gill A.M. & Bradstock R.A. (1995) Extinctions of biota by fires. In: *Conserving Biodiversity: Threats and Solutions* (eds R.A. Bradstock, T.D. Auld, D.A. Keith, R. Kingsford, D. Lunney & D. Sivertsen), pp. 309–322. Surrey Beatty and Sons, Sydney, Australia.

Gill A.M. & McMahon A. (1986) A post-fire chronosequence of cone follicle and seed production in *Banksia ornata*. *Aust. J. Bot.* **34**, 425-434.

Groves R.H., Hocking P.J. & McMahon A. (1986) Distribution of biomass, nitrogen, phosphorus and other nutrients in *Banksia marginata* and *B. ornata* shoots of different ages after fire. *Aust. J. Bot.* **34**, 709-725.

Hansen M.J. & Wilson S.D. (2006) Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? *J. Appl. Ecol.* **43**, 269-280.

Hoffmann W. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* **80**, 1354-1369.

Kalisz S. (1991) Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology* **72**, 575-585.

Kaye T.N., Pendergrass K.L., Finley K. & Kauffman J.B. (2001) The effect of fire on the population viability of an endangered prairie plant. *Ecol. Appl.* **11**, 1366-1380.

Keely J.E., Fotheringham C.J. & Baer-Keeley M. (2005) Determinants of postfire recovery and succession on Mediterranean-climate shrublands of California. *Ecol. Appl.* **15**, 1515-1534.

Kelly L.T., Nimmo D.G., Spence-Bailey L.M., Haslem A., Watson S.J., Clarke M.F. & Bennett A.F. (2011) Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Div. Dist.* **17**, 462-473.

Kraaij T., Cowling R.M., van Wilgen B.W. & Schutte-Vlok A.L. (2013) Proteaceae juvenile periods and post-fire recruitment as indicators of minimum fire return intervals in eastern coastal fynbos. *Appl. Veg. Sci.* **16**, 84-94.

Lamont B.B., Rees R.G., Witkowski E.T.F. & Whitten V.A. (1994) Comparative size, fecundity and ecophysiology of roadside plants of *Banksia hookeriana*. *J. Appl. Ecol.* **31**, 137-144.

Liu H., Menges E.S. & Quintana-Ascencio P.F. (2005) Population viability analyses of *Chamaecrista keyensis*: effects of fire season and frequency. *Ecol. Appl.* **15**, 210-221.

McCarthy M.A., Possingham H.P. & Gill A.M. (2001) Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *J. Appl. Ecol.* **38**, 585-592.

McGill B.J., Enquist B.J., Weiher E. & Westoby M. (2006) Rebuilding community ecology from functional traits. *TREE* **21**, 178-185.

Menges E.S. (1990) Population viability analysis for an endangered plant. *Cons. Biol.* **4**, 52-62.

Menges E.S. (2000) Population viability analyses in plants: challenges and opportunities. *TREE* **15**, 51-56.

Menges E.S. (2007) Integrating demography and fire management: an example from Florida scrub. *Aust. J. Bot.* **55**, 261-272.

Menges E.S., Ascencio P.F.A., Weeklet C.W. & Gaoue O.G. (2006) Population viability analysis and fire return intervals for an endemic Florida scrub mint. *Biol. Cons.* **127**, 115-127.

Messier J., McGill B.J. & Lechowicz M.J. (2010) How do traits vary across ecological scales? A case for trait-base ecology. *Ecol. Lett.* **13**, 838-848.

Moreno J.M., Zuazua E., Perez B., Luna B., Velasco A. & Resco de Dios V. (2011) Rainfall patterns after fire differentially affect the recruitment of three Mediterranean shrubs. *Biogeosciences* **8**, 3721-3732.

Muir A.M., Vesk P.A. & Hepworth G. (2014) Reproductive trajectories over decadal time-spans after fire for eight obligate-seeder shrub species in south-eastern Australia. *Aust. J. Bot.* **62**, 369-378.

Nield A.P., Ladd P.G. & Yates C.J. (2009) Reproductive biology, post-fire succession dynamics and population viability analysis of the critically endangered Western Australian shrub *Calytrix breviseta* subsp *breviseta* (Myrtaceae). *Aust. J. Bot.* **57**, 451-464.

Oostermeijer J.G.B., Brugman M.L., De Boer E.R. & den Nijs J.C.M. (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *J. Ecol.* **84**, 153-166.

Parr C.L. & Andersen A.N. (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Cons. Biol.* **20**, 1610-1619.

Pausas J.G. & Bradstock R.A. (2007) Fire persistence traits of plants along a productivity and disturbance gradient in Mediterranean shrublands of south-east Australia. *Glob. Ecol. Biog.* **16**, 330-340.

Quintana-Ascencio P.F., Menges E.S. & Weekley C.W. (2003) A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Cons. Biol.* **17**, 433-449.

Ramula S., Knight T.M., Burns J.H. & Buckley Y.M. (2008) General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *J. Appl. Ecol.* **45**, 1123-1133.

Reed J.M., Mills L.S., Dunning J.B., Menges E.S., McKelvey K.S., Frye R., Beissinger S.R., Anstett M. & Miller P. (2002) Emerging issues in population viability analysis. *Cons. Biol.* **16**, 7-19.

Specht R.L., Rayson P. & Jackman M.E. (1958) Dark Island Heath (Ninety-mile Plain, South Australia). VI. Pyric succession: changes in composition, coverage, dry weight, and mineral nutrient status. *Aust. J. Bot.* **6**, 59-88.

Svensson B.M., Carlsson B.A., Karlsson P.S. & Nordell K.O. (1993) Comparative long-term demography of three species of *Pinguicula*. *J. Ecol.* **81**, 635-645.

Warton D.I. & Wardle G.M. (2003) Site-to-site variation in the demography of a fire-affected perennial, *Acacia suaveolens*, at Ku-ring-gai Chase National Park, New South Wales, Australia. *Aust. Ecol.* **28**, 38-47.

Watson S.J., Taylor R.S., Nimmo D.G., Kelly L.T., Haslem A., Clarke M.F. & Bennett A.F. (2012) Effects of time since fire on birds: how informative are generalized fire response curves for conservation management? *Ecol. Appl.* **22**, 685-696.

Young D.J.N., Werner C.M., Welch K.R., Young T.P., Safford H. D. & Latimer A M. (2019) Post-fire forest regeneration shows limited climate tracking and potential for drought-induced type conversion. *Ecology* **100**, e02571.

List of Tables

Table 1. Location of study populations, environmental setting, and time-since-fire chronosequence sampled at each study site.

Table 2. Summary of results from linear regression of log-transformed density (N_x) in each region versus time-since-last-fire (t) and resultant estimate of survival per annum (m_x). $D_x(0)$ = starting abundance of plants per hectare (as observed in the field); d_x = site effect relating to variation in seed production per plant.

Table 3. Summary of linear regression examining the relationship between the number of cones (H_x) and time-since-last-fire (t) in populations of *Banksia ornata* across the species' range.

List of Figures

Figure 1: Distribution of *Banksia ornata* in southern Australia and the general location of the six study regions.

Figure 2. Modelled number of *Banksia ornata* seeds produced per hectare with time-since-last-fire (years). Starting density and survival rate were derived from field data (see Table 2). A- Little Desert, B- Wyperfeld, C- Messent, D- Ngarkat, E- Grampians (note: change of scale on y-axis), F- Kangaroo Island.

Supplementary Figures

Figure S1. *Banksia ornata* population density (log-transformed) across the species range with time since last fire (years). A- Little Desert, B- Wyperfeld, C- Messent, D- Ngarkat, E- Grampians, F- Kangaroo Island.

Figure S2. Mean number (± 1 SE) of cones per plant with time since last fire (year) in populations studied across the species' range. A- Little Desert, B- Wyperfeld, C- Messent, D-Ngarkat, E- Grampians, F- Kangaroo Island.

Figure S3. Estimated mean number of follicles per plant with time since last fire (years). A- Little Desert, B- Wyperfeld, C- Messent, D-Ngarkat, E- Grampians, F- Kangaroo Island.

Fig S4. Mean (± 1 SE) intact (normal), open (upon collection), unopened (after heating) and damaged follicles per cone with time since last fire (years). A- Little Desert NP, B- Wyperfeld NP, C- Messent CP, D-Ngarkat CP, E- Grampians NP, F- Kangaroo Island.

Table 1. Location of study populations, environmental setting, and time-since-fire chronosequence sampled at each study site.

Population	Latitude	Longitude	Age classes surveyed (years since fire)	Mean annual rainfall (mm)	Mean maximum temperature (°C)
Little Desert	-36° 30'	142° 00'	0.5, 2, 6, 7, 17, 23, 32	400	21.5
Wyperfeld	-35° 30'	141° 50'	0.5, 2, 6, 10, 28, 55	380	22.3
Messent	-36° 00'	139° 50'	0.5, 2, 7, 20, 31	500	22.2
Ngarkat	-35° 40'	140° 50'	1, 4, 10, 18, 22, 30, 54	460	22.9
Grampians	-37° 15'	143° 15'	0.5, 3, 6, 13, 25, 39	1000	19
Kangaroo Island	-35° 50'	137° 00'	1, 7, 31, 38, 44	670	18

Table 1. Summary of results from linear regression of log-transformed density (N_x) in each region versus time-since-last-fire (t) and resultant estimate of survival per annum (m_x). $D_x(0)$ = starting abundance of plants per hectare (as observed in the field); d_x = site effect relating to variation in seed production per plant.

Population	Log-density model ($N_x(t)$)	Model fit (R^2)	Survival (%) per annum (m_x)	$D_x(0)$	d_x
Little Desert	4.22-0.037t	0.48	95.7	16596	0.557
Wyperfeld	2.722-0.0258t	0.60	97.8	527	2.046
Messent	3.6+0.0095t	0.16	98.1	3981	-0.234
Ngarkat	3.485-0.0093t	0.06	98.2	3054	0
Grampians	5.09-0.027t	0.42	99.5	123027	0.031
Kangaroo Island	4.22-0.023t	0.38	97.5	16596	-0.539

Table 3. Summary of linear regression examining the relationship between the number of cones (H_x) and time-since-last-fire (t) in populations of *Banksia ornata* across the species' range.

Population	Model equation ($H_x(t)$)	Model fit (R^2)	P-value
Little Desert	$0.27t + 0.088$	0.71	0.017
Wyperfeld	$0.71t - 0.92$	0.98	<0.001
Messent	$0.34t - 0.099$	0.45	0.21
Ngarkat	$0.64t - 0.282$	0.74	0.028
Grampians	$0.5t - 0.22$	0.48	0.13
Kangaroo Island	$0.81t - 2.6$	0.58	0.13

aec_12981_f1.png

aec_12981_f2.png

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Morgan, JW;McCarthy, MA;Willocks, E

Title:

Does intraspecific variation in demography have implications for fire management of an obligate-seeder shrub across its geographic range?

Date:

2020-11-25

Citation:

Morgan, J. W., McCarthy, M. A. & Willocks, E. (2020). Does intraspecific variation in demography have implications for fire management of an obligate-seeder shrub across its geographic range?. AUSTRAL ECOLOGY, 46 (2), pp.315-323. <https://doi.org/10.1111/aec.12981>.

Persistent Link:

<http://hdl.handle.net/11343/276648>