Author/s:
Sitters, H;Di Stefano, J;Wills, T;Swan, M;York, A

Title:
Survey design for precise fire management conservation targets:

Date:
2018-01-01

Citation:
Sitters, H., Di Stefano, J., Wills, T., Swan, M. & York, A. (2018). Survey design for precise fire management conservation targets:. Ecological Applications, 28 (1), pp.35-45. https://doi.org/10.1002/eap.1624.

Persistent Link:
https://hdl.handle.net/11343/294008

Article type : Articles

Running head: Generating precise conservation targets

Survey design for precise fire management conservation targets

Authors: Holly Sitters[1]*

Julian Di Stefano[1]

Timothy Wills[2]

Matthew Swan[1]

Alan York[1]

[1] School of Ecosystem and Forest Sciences, University of Melbourne, 4 Water Street, Creswick, Victoria, Australia

[2] GHD, Level 8, 180 Lonsdale Street, Melbourne, Victoria, Australia

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: 10.1002/eap.1624

* Corresponding author E-mail: holly.sitters@unimelb.edu.au

Abstract

Common goals of ecological fire management are to sustain biodiversity and minimize extinction risk. A novel approach to achieving these goals determines the relative proportions of vegetation growth stages (equivalent to successional stages, which are categorical representations of time since fire) that maximize a biodiversity index. The method combines data describing species abundances in each growth stage with numerical optimization to define an optimal growth-stage structure which provides a conservation-based operational target for managers. However, conservation targets derived from growth-stage optimization are likely to depend critically on choices regarding input data. There is growing interest in use of growth-stage optimization as a basis for fire management, thus understanding of how input data influence the outputs is crucial. Simulated datasets provide a flexible platform for systematically varying aspects of survey design and species inclusions. We used artificial data with known properties, and a case-study dataset from southeastern Australia, to examine the influence of (i) survey design (total number of sites, and their distribution among growth stages) and (ii) species inclusions (total number of species and their level of specialization) on the precision of conservation targets. Based on our findings, we recommend that survey designs for precise estimates would ideally involve at least 80 sites, and include at least 80 species. Greater numbers of sites and species will yield increasingly reliable results, but fewer might be sufficient in some circumstances. An even distribution of sites among growth stages was less important than the total number of sites, and omission of species is unlikely to have a major influence on results as long as several species specialize on each growth stage. We highlight the importance of examining the responses of individual species to growth stage before feeding survey data into the growth-stage optimization black box, and advocate use of a resampling procedure to determine the precision of results. Collectively, our findings form a reproducible guide to designing ecological surveys that yield precise conservation targets through growth-stage optimization, and ultimately help sustain biodiversity in fire-prone systems.

Key words biodiversity conservation, ecological monitoring, fire management, land management, prescribed burning, sampling design, sampling framework, simulation

Introduction

Fire is a natural source of disturbance that drives ecosystem structure and function (Bond and Keeley 2005). It is also used as a management tool in flammable biomes of Africa, Australia, North America and Europe, both to reduce the risk of wildfire and achieve conservation objectives (Penman et al. 2011; Stephens et al. 2012; Fernandes et al. 2013). Common aims of ecological fire management are to sustain biodiversity and minimize extinction risk, but it is rarely clear how best to apply fire to enhance biodiversity.

Ecological fire management is often guided by the notion that variable fire regimes promote biodiversity (Bradstock et al. 2005). Vegetation growth stages (equivalent to successional stages, which are categorical representations of time since fire) can be used as measures of fire-mediated landscape variation. In theory, different species' resource requirements are met by different growth stages, and the responses of individual species to growth stage are reflected in shifts in community composition along successional gradients (Fox 1982; Pons and Clavero 2010). A heterogeneous landscape composed of several growth stages is therefore expected to support more species than a homogeneous landscape (Martin and Sapsis 1992; Parr and Andersen 2006). Some studies have identified positive associations between species diversity and growth stage diversity (Fuhlendorf et al. 2010; Maravalhas and Vasconcelos 2014; Sitters et al. 2014a), while others have highlighted the disproportionate importance of particular growth stages (Davies et al. 2012; Kelly et al. 2012; Taylor et al. 2012; Farnsworth et al. 2014; Robinson et al. 2014; Burgess and Maron 2016; Doherty et al. 2017).

Knowledge gaps regarding appropriate levels of growth-stage diversity can hamper the use of planned fire as a conservation tool (Driscoll et al. 2010). However, a new approach to multispecies conservation defines the relative proportions of different growth stages that maximize a biodiversity index (McCarthy 2012; Di Stefano et al. 2013; Kelly et al. 2015). The method combines data describing species abundances in different growth stages with numerical optimization to determine an optimal growth-stage structure, providing a conservation-based operational target for fire managers. Growth-stage optimization has recently been incorporated into fire-management policy in southeastern Australia because it has a strong theoretical basis (McCarthy et al. 2014), input data can be obtained using standard ecological survey techniques,

and it provides a unified framework for addressing conservation goals associated with multiple species (DELWP 2015).

Growth-stage optimization presents a powerful means of linking real-world operational objectives with desirable conservation outcomes. For a particular set of input data the process generates two outputs; an optimal growth-stage structure and the value of a biodiversity index that is theoretically at its maximum – hereafter we refer to these outputs as "conservation targets" and "optimization results". Both outputs are useful for fire-management planning; the optimal growth-stage structure can be used as an operational target while the maximised value of the biodiversity index can be used as a benchmark to assess the ecological effects of different fire-management scenarios. However, the optimization results for a given ecosystem are likely to depend critically on choices regarding input data, including ecological survey design and the species included in the analysis (Di Stefano et al. 2013; Giljohann et al. 2015; Kelly et al. 2015). For example, species that specialize on particular growth stages should have a greater influence on the optimal growth-stage structure than generalist species, but the sensitivity of results to the inclusion or exclusion of specialists has not been systematically tested. There is growing use of growth-stage optimization as a basis for ecological fire management (Di Stefano et al. 2013; DELWP 2015; Giljohann et al. 2015; Kelly et al. 2015), thus better understanding of the influence of survey choices on optimization results is crucial to ensure that managers are able to make sound investment decisions.

Simulation provides a flexible means of systematically varying aspects of ecological data sets (Schweiger *et al.* 2016). In this paper we use artificial data with known properties to test the influence of (i) survey design (total number of sites, and the distribution of sites among growth stages) and (ii) species inclusions (total number of species and the influence of removing growth-stage specialists) on optimization results. To enhance our ability to generalize inferences to different ecosystems, we created two artificial communities, each containing 100 species and differing in the proportion of species that responded to time since fire. Community A represented systems in which the majority of species respond to time since fire, such as faunal communities of southwestern USA forests (e.g. Kalies *et al.* 2010). In Community B fewer species responded to time, and older vegetation was of disproportionate importance, as is the case in some southeastern Australian faunal communities (Di Stefano et al. 2013; Kelly et al.

2015). To ensure our simulation study produced realistic results, we also applied our species-inclusion tests to empirical data collected in southeast Australian eucalypt forest. Our results provide a reproducible guide to designing ecological surveys that generate precise conservation targets through growth stage optimization, and improve its utility as a conservation tool.

Methods

The growth-stage optimization procedure involves the following steps (McCarthy 2012; Di Stefano et al. 2013; Kelly et al. 2015) (1) biodiversity surveys at sites of different time since fire, (2) development of statistical models relating individual species to time since fire, (3) converting time since fire to growth-stage categories, and splitting model predictions by growth stage, (4) using numerical optimization to determine the proportional coverage of each growth stage that maximizes a biodiversity index. We sought to follow this process as closely as possible using simulated data, ensuring that the characteristics of our artificial data represented typical faunal community datasets.

Artificial community datasets

We used three response shapes (no response as a null model, linear response, and unimodal response) to capture a diversity of species' responses to time since fire (Fig. 1). We scaled time since fire (x) from 0–100 and species abundances (y) from 0–1. We generated a response function for each species (Table 1, Data S1) by randomly selecting response-shape parameters within a range defined using empirical data (Swan et al. n.d.; Sitters et al. 2014b), ensuring that the slopes of relationships between abundance and time since fire were realistic. Our two communities differed in the proportion of species that responded to time since fire; approximately two thirds of species in Community A responded to time since fire, half of which responded positively and half negatively. In Community B only one third of species responded to time since fire, and most species preferred late-successional vegetation. Response functions corresponding to all species in Communities A and B are provided in Data S1, and summarized in Table 1. We used each species' response function to generate 50 abundance values per growth stage. For each community, this yielded a data matrix comprising 50 observations per species (n = 100) per growth stage (n = 4), which formed input data for all subsequent analyses,

and represented a "best-case" survey design scenario which is probably rarely feasible in real-world contexts. Our four growth stages reflect other optimization studies (Di Stefano et al. 2013; Giljohann et al. 2015; Kelly et al. 2015; Hale et al. 2016), which have defined three or four categories representing major stages in post-fire vegetation growth and development (Cheal 2010) (Fig. 1). We did not systematically vary survey effectiveness or species' detection probabilities, and instead assumed that individuals were detected when present. Artificial data were generated in the R statistical environment (R Core Team 2016) using custom functions modified from Schweiger et al. (2016) and the data manipulation packages plyr (Wickham 2011), dplyr (Wickham and Francois 2015) and reshape2 (Wickham 2007).

Growth-stage optimization

We used numerical optimization to determine the proportions of each growth stage that maximized a biodiversity index, which was the geometric mean of species' abundances (Di Stefano et al. 2013; Giljohann et al. 2015; Kelly et al. 2015). The geometric mean underpins several large-scale biodiversity-monitoring initiatives because of its beneficial mathematical properties (e.g. the Living Planet Index, Loh *et al.* 2005). For example, small differences in the abundance of uncommon species among growth stages represent large relative differences, and have a greater influence on the geometric mean than more common species that may show larger absolute differences in abundance (Buckland et al. 2005, 2011). Further, the geometric mean reflects parallel shifts in the absolute abundance of multiple species; in contrast, popular diversity indices such as Shannon's and Simpson's remain constant when relative abundances are unchanged (Buckland et al. 2005). The optimal growth-stage structure and biodiversity index were calculated using local gradient-based optimization (the NLOPT_LD_MMA algorithm; Svanberg 2002) in the R package nloptr (Johnson 2016), subject to the constraint that the growth-stage proportions sum to 1 (code is provided in Data S2).

We tested the influence of sampling design and species inclusions on: (1) the precision of the biodiversity index, (2) the precision of the optimal growth-stage structure, and (3) the shape of the optimal growth-stage structure. We did this by subsampling our "best-case" artificial datasets under various scenarios, and conducting growth-stage optimization on each subsampled dataset (Fig. 2, Data S2). We used a resampling procedure to generate measures of precision;

species abundance values in each growth stage were resampled with replacement, the mean abundance per species per growth stage was calculated, and the process was repeated 1000 times. Growth-stage optimization was conducted on each resampled dataset, and the mean biodiversity index and optimal growth-stage structure were quantified. We measured the precision of the biodiversity index by calculating the standard deviation of values associated with the 1000 iterations. To yield a single measure of precision corresponding to the optimal growth-stage structure, we calculated the mean of the four standard deviations corresponding to each growth stage. The workflow is illustrated in Fig. 2 and code is available in Data S2; resampling was undertaken in R using the base package and plyr (Wickham 2011; R Core Team 2016).

Survey-design scenarios

We began by examining the influence of two aspects of survey design on the biodiversity index and optimal growth-stage structure: the total number of sites, and the distribution of sites among growth stages. We did this by subsampling the best-case artificial community datasets under various scenarios.

The least exhaustive survey-design scenario we considered was 5 sites per growth stage, and we systematically increased the number of sites per growth stage from 10-50 in increments of 10, such that the maximum number of sites considered was the best-case scenario of 200 (50 sites × 4 growth stages). We were also interested in the extent to which the distribution of sites among growth stages influenced the biodiversity index and optimal growth-stage structure. We therefore limited the number of sites in each growth stage in turn to 10% of the total number of sites, and divided the remaining sites evenly among the other growth stages. In total, we examined 30 survey-design scenarios (Appendix S1: Table S1; six scenarios where the total number of sites varied (20, 40, 80, 120, 160, 200) × five scenarios where the distribution of sites among growth stages varied (evenly distributed among growth stages; sites in each of the four growth stages limited to 10% of the total)).

Species-inclusion scenarios

To examine the influence of species inclusions on optimization results we systematically varied the total number of species included in the optimization routine, while keeping the number of

sites constant at 50 per growth stage (i.e. the best-case survey-design scenario). We began by including 10 species, and increased the number of species in increments of 10 to a maximum of 90. This required a modification to the resampling procedure described above; 100 subsets of *n* species were randomly selected from the full species pool, and resampling was carried out as before, to generate 100 resampled datasets per subset. Growth-stage optimization was carried out on the resulting 10,000 resampled datasets. The precision and shape of optimization results were derived from the 10,000 iterations.

Species that specialize on particular growth stages should have a greater influence on optimization results than generalist species. To establish the influence of growth-stage specialization on optimization results, we used the standardised measure (B_A) of Levins' index of niche breadth (B) to rank species (Levins 1968):

$$B = 1/\Sigma p^2_j$$

$$B_A = \frac{(B-1)}{(n-1)}$$

Where p_j = proportion of the species' total abundance in growth stage j; and n = the total number of growth stages. This produces a single value per species ranging from 0 (if a species occurs in only one growth stage) to 1 (if a species is equally abundant in all growth stages). We selected species that had a Levins index <0.5 (n = 27 in Community A, n = 13 in Community B), and used their mean abundance per growth stage to determine the category on which they specialized.

Next, we excluded a species that specialized on each growth stage in turn, and conducted growth-stage optimization using the remaining species. We considered a total of 45 scenarios (Appendix S1: Table S2; nine scenarios where the total number of species varied × five scenarios where specialist species were excluded (including a scenario where no species were excluded)). Preliminary analysis showed that exclusion of additional specialist species had negligible influence on optimization results provided there were more than two specialists per growth stage. The importance of the number of specialists per growth stage is captured in our 45 scenarios because we limited the number of early-growth-stage specialists to two in Community A and one in Community B. Again, we tested all scenarios on Communities A and B separately, and

examined the precision of the biodiversity index, the precision of the optimal growth-stage structure, and the shape of the optimal growth-stage structure.

Testing species-inclusion scenarios on case-study data

Finally, we sought to confirm that patterns evident in optimization results derived from artificial data were reflected in those derived from empirical data, so we repeated our species-inclusion tests using a case-study dataset collected in a 15,000-ha region of the Otway Ranges, southeastern Australia. We did not test survey-design scenarios using this dataset because the number of sites per growth stage was limited. Testing the species-inclusion scenarios involved (1) surveys of ground-dwelling mammals, birds and vascular plants at sites of different time since fire, (2) development of statistical models relating individual species to time since fire, (3) splitting model predictions by growth stage, and (4) applying growth-stage optimization under different species-inclusion scenarios.

Our study area was dominated by the forby forest Ecological Vegetation Division (EVD; Cheal 2010) and characterized by steep terrain (70-350 m above sea level) and a mild climate (mean annual minimum and maximum temperatures, 10.5 and 18.2°C; mean annual rainfall, 1229 mm) (Bureau of Meteorology 2016). Vegetation was tall-open eucalypt forest supporting *Eucalyptus cypellocarpa*, *E. globulus*, *E. obliqua* and *E. radiata*, and featuring a diverse ground layer of forbs and grasses (Cheal 2010). The midstory shrub layer ranges from sparse to dense, and canopy trees reach 50–60 m in height. Forby forest is flammable during the warmer months, and growth stages are defined as: recently burnt (0-3 years since fire), early (4-10 years), middle (11-40 years), late (>40 years) (Cheal 2010; Cohn et al. 2015).

We used standard field methods to survey ground-dwelling mammals, diurnal birds and vascular plants at 47 sites as part of a larger study examining relationships between fire and biodiversity (see Sitters *et al.* 2014a for a detailed description of the study design). The spread of sites along the time-since-fire gradient, and the corresponding number of sites per growth stage, reflected the spatial coverage of each category at the time of field surveys (10 sites were in the recently-burnt growth stage, 5 early, 11 middle, 21 late). Sites consisted of a 100-m transect positioned along a random bearing, and all were surveyed in both 2010 and 2011. Small mammals (*Rattus* spp. and *Antechinus* spp.) were surveyed at each site with aluminium box traps, and larger

ground-dwelling mammals were surveyed with camera traps (see Swan *et al.* (2015) for details). Diurnal birds were surveyed using 20-minute point counts undertaken at dawn and dusk (Sitters et al. 2014a), and vascular plants were surveyed in 2-m^2 quadrats placed at 3-m intervals along transects (33 quadrats per site). Fauna are often the focus of growth-stage optimization (Kelly et al. 2015; Hale et al. 2016), and our artificial communities were constructed to represent typical faunal datasets. However, data from vertebrates and vascular plants have been used in combination (Di Stefano et al. 2013), and here we use both flora and fauna data to generate a large enough species pool to allow us to test the species-inclusion scenarios. Our case-study dataset contained 107 species; 6 ground-dwelling mammal species, 25 bird species and 76 vascular plant species (Data S3).

We used generalized additive mixed models (GAMMs; Wood 2006) to establish relationships between species' occurrence and time since fire. GAMMs are a flexible, non-parametric form of regression that use smoothing functions to model non-linear relationships. Study sites were spatially clustered in 100-ha landscape sampling units, so landscape and site were specified as random effects to accommodate variance associated with the nestedness of the study design (Zuur et al. 2009). Time since fire was specified as a non-linear smoothed term, and the degree of smoothing was calculated within the model-fitting procedure (Wood 2006). We used species' occurrence (presence-absence) data as the response variable because most species occurred at low prevalence. Models were used to produce predicted probabilities of occurrence for each species at equidistant predictor levels along the time-since-fire gradient, and probabilities of occurrence were then split by growth-stage category. GAMMs were run in R using the package gamm4 (Wood and Scheipl 2014).

Subsequent steps paralleled those applied to the artificial datasets (Fig. 2). First, we systematically varied the total number of species included in the optimization routine (we considered five scenarios: 20 species, 40, 60, 80 and 100); then we used the standardised measure of Levins' index of niche breadth to measure species' growth-stage specialization (Levins 1968) (Data S3). We randomly selected a specialist species per growth stage: shrubby fireweed (*Senecio minimus*; recently burnt specialist (standardised Levins' index (B_A) = 0.28); sword tussock-grass (*Poa ensiformis*; middle specialist (B_A = 0.54 (a relatively high standardised Levin, but the most specialist species in the dataset)); forest starwort (*Stellaria flaccida*; late

specialist (B_A = 0.17)). We did not identify any early specialists, and therefore tested a total of 20 species-inclusion scenarios on the case-study dataset (five scenarios where the total number of species varied × four scenarios where specialist species were excluded (including a scenario where no species were excluded)).

Results

Survey-design scenarios

Reducing the total number of sites relative to the most exhaustive sampling scenario (200 sites) resulted in a decrease in the precision of the biodiversity index, but varying the distribution of sites among growth stages had little influence (Fig. 3). Patterns were consistent in communities A and B; the greatest drop in the precision of the biodiversity index occurred when the total number of sites was 40 or fewer, and when the number of sites in the late growth stage was limited to 10% of the total. Although patterns associated with the two communities were consistent, the precision of biodiversity indices associated with Community A was approximately double the precision associated with Community B under all survey-design scenarios (Fig. 3).

The survey-design scenarios had little influence on the precision and shape of the optimal growth stage structure for either community when the total number of sites was 80 or more (Fig. 3, Appendix S2, Fig. S1 and Fig. S2). Precision associated with the mean proportional coverage of the early growth stage presented an exception; it was low relative to all other growth stages under all scenarios. When the total number of sites was 20, limiting the number of sites in the late growth stage resulted in a small decrease in its proportional coverage, and consequently a change in the shape of the optimal growth-stage structure. Limiting the number of sites in other growth stages had a negligible influence on the shape of the optimal growth-stage structure when there were 20 sites, although precision was generally poor for both communities.

Species-inclusion scenarios

For both communities, the precision of the biodiversity index and optimal growth stage structure was very poor if fewer than 50 species were included, and it steadily improved as the number of

species increased (Fig. 4). The species-inclusion scenarios had little influence on the shape of the optimal growth-stage structure for Community A (Appendix S2, Fig. S3); the mean proportions of each growth stage were approximately equal irrespective of the total number of species and exclusion of specialist species. However, in Community B the shape of the optimal growth-stage structure differed according to the species exclusion tests (Appendix S2, Fig. S4). For example, exclusion of a species that specialized on the early growth stage resulted in a decrease in the proportional coverage of the early category from 0.2 to approximately zero. Changes in the shape of the optimal growth-stage structure arising from the exclusion of species that specialized on other growth stages were less pronounced.

The precision of the biodiversity index and optimal growth-stage structure associated with the case-study dataset also improved markedly as the number of species included increased (Fig. 5). Further, the shape of the optimal growth-stage structure changed when certain specialist species were excluded (Appendix S2, Fig. S5); exclusion of a species that specialized on the middle growth stage (sword tussock-grass) resulted in a reduction in the proportional coverage of both the early and middle growth stages to zero. Exclusion of a recently-burnt specialist (shrubby fireweed) or a late specialist (forest starwort) had a comparatively minor influence on the shape of the optimal growth-stage structure.

Discussion

Growth-stage optimization provides an appealing basis for ecological fire management (Di Stefano et al. 2013; DELWP 2015; Kelly et al. 2015), but the influences of survey design and input data on results are unknown. Our results showed that the precision of the biodiversity index and optimal growth stage structure for a given community increased with the number of sites and the number of species included in input data, but that gains in precision lessened beyond approximately 80 sites and 80 species. The distribution of sites among growth stages and exclusion of specialist species were less influential provided that input data comprised multiple specialists per growth stage. We discuss the insights arising from this work and the implications for ecological fire management.

Unsurprisingly, our results showed that the precision of the biodiversity index and optimal growth stage structure increased with both the total number of sites and the total number of

species. Further, the precision associated with the mean proportional coverage of a particular growth stage reflected the number of species that specialized on that growth stage. Our findings indicate that gains in precision lessen beyond approximately 80 sites, and that fewer sites may be sufficient for reasonably precise optimization results. Importantly, if the precision associated with simulated optimization results is poor, the optimal growth stage structure derived from real data may not represent species' "true" requirements.

While precision increased with the total number of sites, the distribution of sites among growth stages was less important. Limiting the number of sites in a growth stage to 10% of the total had little influence on optimization results except when there were only 20 sites in total, when the shape of the optimal growth stage structure changed slightly. This is reassuring since it is rarely possible to sample growth stages evenly because limited spatial coverage of one or more categories exists at a given time. In general, survey designs comprising unevenly sampled growth stages should yield robust conservation targets as long as the total number of sites is adequate.

Similarly, incomplete sampling of species in a community is unlikely to have a major influence on the shape and precision of the optimal growth stage structure unless an excluded species is the only specialist on a particular growth stage. Rather than feeding biodiversity survey data directly into the black box of growth-stage optimization, we recommend examining relationships between individual species and time since fire as a preliminary step. If two or more specialists are identified per growth stage, optimization results are likely to be fairly insensitive to the addition or removal of a species from input data. We emphasize that specialization spans a continuum and although the stronger the degree of specialization the greater species' influence on results, our case-study data demonstrated that weaker specialists can also be influential.

Although exclusion of specialist species did not have a marked influence on the shape or precision of the optimal growth-stage structure, we identified steady increases in precision with increases in the total number of species included in input data. A high level of uncertainty surrounded optimization results derived from fewer than 50 species, and precision increased quite rapidly until around 80 species were included. These findings underscore the fact that the growth-stage optimization approach was developed as a multispecies conservation solution and will be less appropriate for restricted subsets of species. Our results support the view of Di

Stefano et al. (2013) that as many species from as many taxonomic groups as possible should be used in its application. Ideally, groups such as reptiles, invertebrates and fungi should be incorporated, as well as soil seedbank data, which can show large differences in species composition and fire responses relative to aboveground vascular plant (Wills and Read 2007; Lewis et al. 2012; Di Stefano et al. 2013; Chick et al. 2016).

In capturing the growth-stage requirements of a wide range of species, the needs of rare species may be accommodated. However, growth-stage optimization should not be used as a broad-bush conservation solution in isolation of other methods (Di Stefano et al. 2013), and we highlight the importance of identifying (a) highly specialist species and (b) species of conservation concern. Nevertheless, the capacity of growth stage optimization to accommodate data from multiple taxa presents a major advance over alternative approaches (Clarke 2008; Driscoll et al. 2010; Di Stefano et al. 2013; Kelly et al. 2015).

In general, the influences of species-inclusion scenarios on optimization results were consistent among the artificial communities and case-study data, indicating that our simulations reflected reality. However, optimization results derived from communities comprising a large number of species that respond to growth stage, such as faunal communities typical of forest systems in the southwestern USA (e.g. Kalies *et al.* 2010), are likely to be relatively insensitive to species inclusions. A greater degree of caution should be applied if a smaller proportion of species respond to growth stage. In several southeastern Australian ecosystems, for example, a relatively low proportion of animal species respond to growth stage or time since fire (Watson et al. 2012; Sitters et al. 2014b; Swan et al. 2014). Moreover, species' responses can be idiosyncratic and site-specific (Driscoll and Henderson 2008; Nimmo et al. 2014). The sensitivity of optimization results to species inclusions could be lessened through the inclusion of a wider range of taxonomic groups. If a relatively low proportion of species respond to growth stage, it is essential that underlying survey data are sound because erroneous observations will generate unreliable optimization results. For example, we did not conduct our analyses under scenarios of differing detection probabilities, and instead assumed that species were detected when present; any variation in detection probability among species and growth stages is likely to translate to bias in conservation targets (e.g. MacKenzie et al. 2002). We recommend following general advice regarding design of landscape-scale biodiversity surveys (Buckland et al. 2012) and in

particular, survey design should allow measurement of the detection probability for each species unless it is possible to count all individuals of all species at each site. Additionally, we advocate use of a resampling procedure to provide a measure of the precision associated with optimization results.

A final caveat is that robust conservation targets rely on ecologically meaningful growth-stage delineations that capture major stages of vegetation growth and development after fire (Di Stefano et al. 2013; Kelly et al. 2015). In cases where growth stage delineations are unknown, suitable categories could be identified using a cluster analysis (McGarigal et al. 2000). The appropriate number of growth stages is likely to vary among vegetation types and regions, as well as taxonomic groups. For example, birds have been shown to respond to coarse successional groupings comprising only two growth stages (Taylor et al. 2012; Sitters et al. 2014a). If different taxonomic groups in the same system respond to different numbers of growth stages, we suggest using the largest number of growth stages recognized by a group.

Conclusions

Growth-stage optimization provides a tractable method for linking fire management objectives with multispecies conservation outcomes, but the precision of optimization results depends critically on choices regarding input data. Based on our analysis we recommend that survey designs for precise conservation targets would ideally involve at least 80 sites, and include at least 80 species. More sites and more species will yield increasingly reliable conservation targets, but fewer might be adequate in some cases. The distribution of sites among growth stages is less important, and exclusion of species is unlikely to have a major influence on results, irrespective of their growth-stage specialization, as long as several species specialize on each growth stage. Departures from an ideal survey design are likely to be less critical if a large proportion of the species in a community respond to time since fire. We emphasise the importance of examining responses of individual species to time since fire, and using resampling to define the precision associated with conservation targets. Together, our results form a reproducible guide to designing ecological surveys that yield precise conservation targets through growth-stage optimization, and help to sustain biodiversity in fire-prone environments.

Acknowledgements

426 This work was funded by the Victorian State Department of Environment, Land, Water and
427 Planning. Parks Victoria and the Holsworth Wildfire Research Endowment contributed funding
428 for collection of the case-study data. We thank Fiona Christie, Garry Cheers, Peter Collins and
429 many volunteers for helping with collection of empirical data, and we are grateful to Andreas
430 Schweiger and Graeme Gange for assistance with coding.

Literature cited

Bond, W. J. and J. E. Keeley. 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20:387–394.

Bradstock, R. A., M. Bedward, A. M. Gill and J. S. Cohn. 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. Wildlife Research 32:409–423.

Buckland, S. T., S. R. Baillie, J. M. Dick, D. A. Elston, A. E. Magurran, E. M. Scott, R. I. Smith, P. J. Somerfield, A. C. Studeny and A. Watt. 2012. How should regional biodiversity be monitored? Environmental and Ecological Statistics 19:601–626.

Buckland, S. T., A. E. Magurran, R. E. Green and R. M. Fewster. 2005. Monitoring Change in Biodiversity through Composite Indices. Philosophical Transaction: Biological Sciences 360:243–254.

Buckland, S. T., A. C. Studeny, A. E. Magurran, J. B. Illian and S. E. Newson. 2011. The geometric mean of relative abundance indices: a biodiversity measure with a difference. Ecosphere 2:art100.

Bureau of Meteorology. 2016. Climate Data Online. P. in. Bureau of Meteorolog, Canberra, Australia http://www.bom.gov.au/climate/data.

Burgess, E. E. and M. Maron. 2016. Does the response of bird assemblages to fire mosaic properties vary among spatial scales and foraging guilds? Landscape Ecology 31:687–699.

Cheal, D. 2010. Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Fire and adaptive management. P. in. Victorian Department of Sustainability and Environment, Melbourne, Australia.

Chick, M. P., J. S. Cohn, C. R. Nitschke and A. York. 2016. Lack of soil seedbank change with time since fire: relevance to seed supply after prescribed burns. International Journal of wildland Fire 25:849–860.

Clarke, M. F. 2008. Catering for the needs of fauna in fire management: science or just wishful

thinking? Wildlife Research 35:385–394.

Cohn, J. S. S., J. Di Stefano, F. Christie, G. Cheers and A. York. 2015. How do heterogeneity in vegetation types and post-fire age-classes contribute to plant diversity at the landscape scale? Forest Ecology and Management 346:22–30.

Davies, A. B., P. Eggleton, B. J. van Rensburg and C. L. Parr. 2012. The pyrodiversity-biodiversity hypothesis: a test with savanna termite assemblages. Journal of Applied Ecology 49:422–430.

DELWP. 2015. Policy Position – Measuring ecosystem resilience in strategic bushfire management planning. Victorian Department of Environment, Land, Water and Planning. Melbourne, Australia.

Doherty, T. S., E. J. B. van Etten, R. A. Davis, C. Knuckey, J. Q. Radford and S. A. Dalgleish. 2017. Ecosystem Responses to Fire: Identifying Cross-taxa Contrasts and Complementarities to Inform Management Strategies. Ecosystems 20:1–13.

Driscoll, D. A. and M. K. Henderson. 2008. How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. Biological Conservation 141:460–471.

Driscoll, D. A., D. B. Lindenmayer, A. F. Bennett, M. Bode, R. A. Bradstock, G. J. Cary, M. F. Clarke, N. Dexter, R. Fensham, G. Friend, M. Gill, S. James, G. Kay, D. A. Keith, C. MacGregor, J. Russell-Smith, D. Salt, J. E. M. Watson, R. J. Williams and A. York. 2010. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. Biological Conservation 143:1928–1939.

Farnsworth, L. M., D. G. Nimmo, L. T. Kelly, A. F. Bennett and M. F. Clarke. 2014. Does pyrodiversity beget alpha, beta or gamma diversity? A case study using reptiles from semi-arid Australia. Diversity and Distributions 20:663–673.

Fernandes, P. M., G. M. Davies, D. Ascoli, C. Fernandez, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega, D. Molina, C. Fernández, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega, D. Molina, C. Fernandez, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega, D. Molina, C.

Fernández, F. Moreira, E. Rigolot, C. R. Stoof, J. A. Vega and D. Molina. 2013. Prescribed burning in southern Europe: Developing fire management in a dynamic landscape. Frontiers in Ecology and the Environment 11:e4–e14.

Fox, B. J. 1982. Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63:1332–1341.

Fuhlendorf, S. D., D. E. Townsend, R. D. Elmore and D. M. Engle. 2010. Pyric-Herbivory to Promote Rangeland Heterogeneity: Evidence From Small Mammal Communities. Rangeland Ecology & Management 63:670–678.

Giljohann, K. M., M. A. McCarthy, L. T. Kelly and T. J. Regan. 2015. Choice of biodiversity index drives optimal fire management decisions. Ecological Applications 25:264–277.

Hale, S., D. G. Nimmo, R. Cooke, G. Holland, S. James, M. Stevens, N. De Bondi, R. Woods, M. Castle, K. Campbell, K. Senior, S. Cassidy, R. Duffy, B. Holmes and J. G. White. 2016. Fire and climatic extremes shape mammal distributions in a fire-prone landscape. Diversity and Distributions 22:1127–1138.

Johnson, S. 2016. The NLopt nonlinear-optimization package. <http://ab-initio.mit.edu/nlopt>.

Kalies, E. L., C. L. Chambers and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: A meta-analysis. Forest Ecology and Management 259:333–342.

Kelly, L. T., A. F. Bennett, M. F. Clarke and M. A. McCarthy. 2015. Optimal fire histories for biodiversity conservation. Conservation Biology 29:473–481.

Kelly, L. T., D. G. Nimmo, L. M. Spence-Bailey, R. S. Taylor, S. J. Watson, M. F. Clarke and A. F. Bennett. 2012. Managing fire mosaics for small mammal conservation: a landscape perspective. Journal of Applied Ecology 49:412–421.

Levins, R. 1968. Evolution in changing environments. P. in. Princeton University Press, Princeton, NJ.

Lewis, T., M. Reif, E. Prendergast and C. Tran. 2012. The effect of long-term repeated burning

and fire exclusion on above- and below-ground Blackbutt (Eucalyptus pilularis) forest vegetation assemblages. Austral Ecology 37:767–778.

Loh, J., R. E. Green, T. Ricketts, J. Lamoreux, M. Jenkins, V. Kapos and J. Randers. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 360:289–95.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew, C. A. Langtimm and C. A. Langtimm. 2002. Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One. Ecology 83:2248–2255.

Maravalhas, J. and H. L. Vasconcelos. 2014. Revisiting the pyrodiversity-biodiversity hypothesis: long-term fire regimes and the structure of ant communities in a Neotropical savanna hotspot. Journal of Applied Ecology 51:1661–1668.

Martin, R. and D. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. P. in Proceedings of the Symposium on Biodiversity in Northwestern California. Wildland Resources Centre, University of California, Berkeley, CA.

McCarthy, M. A. 2012. Review of resilience concepts and their measurement for fire management. Department of Sustainability and Environment, Melbourne.

McCarthy, M. A., A. L. Moore, J. Krauss, J. W. Morgan and C. F. Clements. 2014. Linking Indices for Biodiversity Monitoring to Extinction Risk Theory. Conservation Biology 28:1575–1583.

McGarigal, K., S. Cushman and S. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. P. in. Springer-Verlag, New York.

Nimmo, D. G., L. T. Kelly, L. M. Farnsworth, S. J. Watson and A. F. Bennett. 2014. Why do some species have geographically varying responses to fire history? Ecography 37:805–813.

Parr, C. L. and A. N. Andersen. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20:1610–1619.

Penman, T. D., F. J. Christie, A. N. Andersen, R. A. Bradstock, G. J. Cary, M. K. Henderson, O. Price, C. Tran, G. M. Wardle, R. J. Williams and A. York. 2011. Prescribed burning: how can it work to conserve the things we value? International Journal of Wildland Fire 20:721–733.

Pons, P. and M. Clavero. 2010. Bird responses to fire severity and time since fire in managed mountain rangelands. Animal Conservation 13:294–305.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, N. M., S. W. J. Leonard, A. F. Bennett and M. F. Clarke. 2014. Refuges for birds in fire-prone landscapes: The influence of fire severity and fire history on the distribution of forest birds. Forest Ecology and Management 318:110–121.

Schweiger, A. H., S. D. H. Irl, M. J. Steinbauer, J. Dengler and C. Beierkuhnlein. 2016. Optimizing sampling approaches along ecological gradients. Methods in Ecology and Evolution 7:463–471.

Sitters, H., F. J. Christie, J. Di Stefano, M. Swan, T. Penman, P. C. Collins and A. York. 2014a. Avian responses to the diversity and configuration of fire age classes and vegetation types across a rainfall gradient. Forest Ecology and Management 318:13–20.

Sitters, H., F. Christie, J. Di Stefano, M. Swan, P. Collins and A. York. 2014b. Associations between occupancy and habitat structure can predict avian responses to disturbance: Implications for conservation management. Forest Ecology and Management 331:227–236.

Di Stefano, J., M. A. McCarthy, A. York, T. J. Duff, J. Slingo and F. J. Christie. 2013. Defining vegetation age class distributions for multispecies conservation in fire-prone landscapes. Biological Conservation 166:111–117.

Stephens, S. L., J. D. McIver, R. E. J. Boerner, C. J. Fettig, J. B. Fontaine, B. R. Hartsough, P. L. Kennedy and D. W. Schwilk. 2012. The Effects of Forest Fuel-Reduction Treatments in the United States. Bioscience 62:549–560.

Svanberg, K. 2002. A class of globally convergent optimization methods based on conservative

convex separable approximations. SIAM Journal on Optimization 12:555–573.

Swan, M., F. Christie, H. Sitters, A. York and J. Di Stefano. no date. Predicting faunal fire responses in heterogeneous landscapes: the role of habitat structure. Ecological Applications.

Swan, M., J. Di Stefano, F. Christie, E. Steel and A. York. 2014. Detecting mammals in heterogeneous landscapes: implications for biodiversity monitoring and management. Biodiversity and Conservation 23:343–355.

Taylor, R. S., S. J. Watson, D. G. Nimmo, L. T. Kelly, A. F. Bennett and M. F. Clarke. 2012. Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Diversity and Distributions 18:519–529.

Watson, S. J., R. S. Taylor, D. G. Nimmo, L. T. Kelly, A. Haslem, M. F. Clarke and A. F. Bennett. 2012. Effects of time since fire on birds: How informative are generalized fire response curves for conservation management? Ecological Applications 22:685–696.

Wickham, H. 2007. Reshaping Data with the {reshape} Package. Journal of Statistical Software 21:1–20.

Wickham, H. 2011. The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software 40:1–29.

Wickham, H. and R. Francois. 2015. dplyr: A Grammar of Data Manipulation. <https://cran.r-project.org/package=dplyr>.

Wills, T. J. and J. Read. 2007. Soil seed bank dynamics in post-fire heathland succession in south-eastern Australia. Plant Ecology 190:1–12.

Wood, S. N. 2006. Generalized additive models. An introduction with R. P. in. Chapman and Hall, Boca Raton, Florida, USA.

Wood, S. and F. Scheipl. 2014. gamm4: Generalized additive mixed models using mgcv and lme4. <https://cran.r-project.org/package=gamm4>.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed Effects

Models and Extensions in Ecology with R. P. in Statistics for Biology and Health. Springer, New York.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.jd523

Table 1. Frequencies of species in Communities A and B that did not respond to time since fire, or exhibited positive, negative or unimodal responses. Functions and parameter ranges corresponding to each response shape are provided. See Data S1 for a full list of species and their responses.

	No response	Positive linear	Negative linear	Unimodal
Frequency in Community A	30	26	26	16
Frequency in Community B	66	16	8	10
Function	$y = c$	$y = ax + c$	$y = ax + c$	$y = ax^2 + bx$
Range of a	NA	0.0012–0.0053	-0.0060–-0.0013	-0.00130–-0.00009
Range of b	NA	NA	NA	0.005-0.031
Range of c	0.12-0.94	-0.22-0.49	0.03-0.79	NA
Number of parameters	1	2	2	2

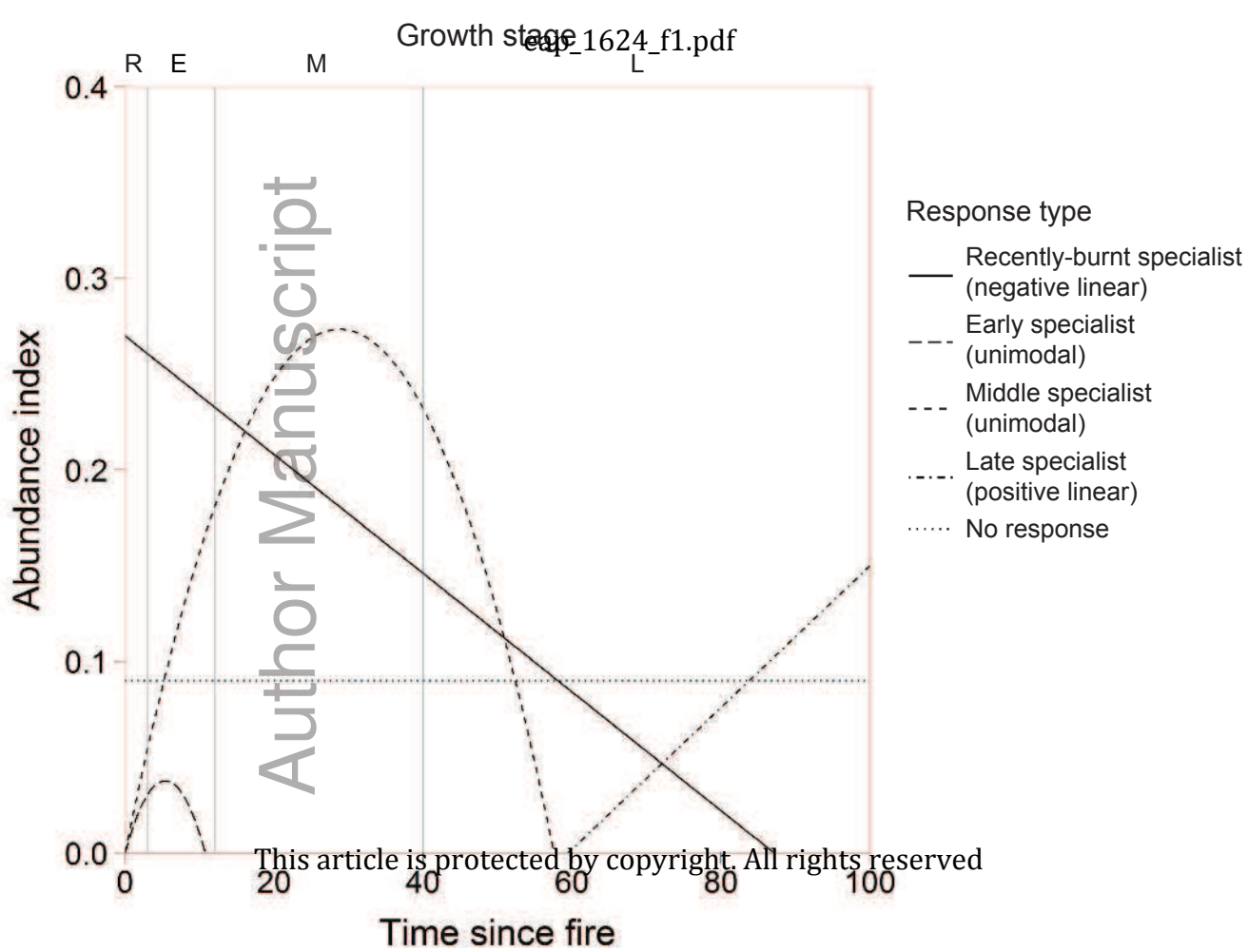
Figure 1. Examples of relationships between the abundance of artificial species and time since fire. Gray vertical lines delineate growth-stage categories: recently burnt (R; 0-3 time-since-fire units), early (E; 3-12 units), middle (M; 12-40 units), late (L; 40-100 units).

Figure 2. Workflow for testing the influence of survey-design or species-inclusion scenarios on (1) the precision of the biodiversity index, (2) the precision of the optimal growth stage structure and (3) the shape of the optimal growth stage structure.

Figure 3. The influence of survey-design scenarios (the total number of sites, and the distribution of sites among growth stages) on the precision of the biodiversity index and optimal growth stage structure for communities A and B. Precision is measured by the standard deviation of results derived from 1,000 iterations. NA indicates that sites were not limited to 10% of the total in any growth stage, and numbers of sites per growth stage were equal.

Figure 4. The influence of species-inclusion scenarios (the total number of species, and the exclusion of specialist species) on the precision of the biodiversity index and optimal growth stage structure for communities A and B. Precision is measured by the standard deviation of results derived from 10,000 iterations (100 resamples per 100 species subsets).

Figure 5. The influence of species-inclusion scenarios (the total number of species, and the exclusion of specialist species) on the precision of the biodiversity index and optimal growth stage structure for ground-dwelling mammals, birds and vascular plants in forby forest. Precision is measured by the standard deviation of results derived from 10,000 iterations (100 resamples per 100 species subsets).



"Best-case" dataset

50 observations per species (n=100) per growth stage (n=4)

↓

Define scenario of interest and subsample

↓

Resample with replacement

↓

Calculate mean abundance per species per growth stage

↓

Conduct growth stage optimisation on resampled dataset

Repeat ×1000

↓

Measure **precision** of the:

- *biodiversity index* (standard deviation of 1000 values)
- *optimal growth stage structure* (mean of standard deviations corresponding to each growth stage)

↓

Determine **shape** of the *optimal growth stage structure* by plotting mean proportions and confidence intervals

↓