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ABSTRACT

1. Biodiversity indices are widely used to summarise changes in the distribution and abundance of multiple species and measure progress towards management targets. However, the sensitivity of biodiversity indices to the data, landscape classification and conservation values underpinning them are rarely interrogated. There are limited studies to help scientists and land managers use biodiversity indices in the presence of fire and vegetation succession.

2. The geometric mean of species’ relative abundance or occurrence (G) is a biodiversity index that can be used to determine the mix of post-fire vegetation that maximizes biodiversity. We explored the sensitivity of G to i) type of biodiversity data, ii) representation of ecosystem states, iii) expression of conservation values and iv) uncertainty in species’ response to landscape structure. Our case study is an area of fire-prone woodland in southern Australia where G is used in fire management planning. We analysed three data sets to determine the fire responses of 170 bird, mammal and reptile species.

3. G and fire management targets were sensitive to the species included in the analysis. The optimal mix of vegetation successional states for threatened birds was more narrowly defined than the optimal mix for all species combined. G was less sensitive to successional classification (i.e. number of states); although classifications of increasing complexity provided additional insights into desirable levels of heterogeneity.

4. Weighting species by conservation status or endemism influenced the mix of vegetation states that maximized biodiversity. When a higher value was placed on threatened species the importance of late successional vegetation was emphasized.

5. Representing variation in individual species’ response to vegetation structure made it clearer when a decrease in G was likely to reflect a significant reduction in species occurrences.

6. Synthesis and applications. Data, models and conservation values can be combined using biodiversity indices to make robust environmental decisions. Combining different types of
biodiversity data using composite indices, such as the geometric mean, can improve the coverage and relevance of biodiversity indices. We recommend that evaluation of biodiversity indices for fire management verify how index assumptions align with management objectives, consider the relative merits of different types of biodiversity data, test sensitivity of ecosystem state definitions and incorporate conservation values through species weightings.

Keywords: classification, decision making, fire, geometric mean, indicators, management, optimization, policy, relative abundance, weighting

Introduction

Biodiversity indices are widely used to summarise change in the distribution and abundance of multiple species, and measure progress towards policy and management targets (Nicholson et al. 2012). For example, biodiversity indices are used to assess threatened species (Butchart et al. 2004), design protected areas (Loh et al. 2005), manage land and forest resources (Herrando et al. 2010) and implement fire management (Giljohann et al. 2015). Because of their growing use in environmental decision making there is a need to better understand how biodiversity indices and resulting inferences are influenced by the data, models and conservation values that underpin them.

Using biodiversity indices for environmental decision making involves several key steps: identifying broad management goals and specific objectives, collecting data, defining the system and its biodiversity, choosing an index and modelling biodiversity change, then implementing and monitoring actions (Fig. 1; Nicholson et al. 2012 ‘indicator-policy cycle’). Although significant progress has been made on choosing appropriate biodiversity indices for different management goals (Buckland et al. 2005; van Strien, Soldaat & Gregory 2012) there is little guidance available for scientists and fire managers on how to explore and quantify the sensitivity of biodiversity indices.
The geometric mean of species’ relative abundance is a widely used index of biodiversity. It reflects changes in species richness, abundance and community evenness, and is correlated with extinction risk (McCarthy et al. 2014). It also has the advantage that it can combine data from multiple surveys and different units of measurement (e.g. counts, biomass, percent cover; Buckland et al. 2011). A geometric mean combines values on a multiplicative scale, making it more sensitive to changes in the abundance of less common species than an arithmetic mean (Buckland et al. 2005). Because of these useful properties, the index is used as an indicator in a range of ecological contexts. At global and national scales, the geometric mean of species’ relative abundance underpins the Living Planet Index (Loh et al. 2005) and UK Wildbird Indicator (Gregory & van Strien 2010), which calculate temporal trends in multiple species’ relative abundances. In regional fire management planning, the geometric mean of species’ relative abundance or occurrence (G) is used to determine the mix of vegetation successional states that maximize species diversity (Di Stefano et al. 2013; Kelly et al. 2015).

Using a case study on fire management planning for vertebrate conservation in southern Australia, we investigate the sensitivity of G and resulting management inferences to the underlying data, landscape classification and conservation values. Fire profoundly influences ecosystems in southern Australia and a primary objective of fire management is biodiversity conservation (DELWP 2015). One way to quantify this goal is by determining the mix of post-fire vegetation successional states that maximize the G of multiple species (Kelly et al. 2015). Because different birds, mammals and reptiles are associated with different post-fire successional states, changes in vegetation over time are reflected by G. The vegetation structure of a given area that maximizes G varies, depending on the number of species and their relative abundance in the different successional states. Fire managers in southern Australia use G to set management targets and, in turn, implement and monitor fire strategies (DELWP 2014, 2015).
There are several ways that data, landscape classification and values can influence biodiversity indices and management decisions. Biodiversity data are commonly biased towards a small number of taxonomic groups and common species (Baillie et al. 2008). Because fire management strategies are sensitive to taxonomic focus (Giljohann et al. 2015), ensuring species of concern are included in the analysis is crucial. Yet not all types of data are equivalent in the quality of information they provide (e.g. presence-absence, presence-only, expert estimates), so it is important to consider the relative merits and trade-offs of using and collecting different types of data. How ecosystem dynamics are represented can also influence indices (Keane et al. 2008; Branch et al. 2010). For example, indices can be sensitive to the number of classes used to partition a landscape and to the size of the landscape (Keane et al. 2008). Although successional states are often used to guide fire management, sensitivity to how they are defined is rarely tested. Yet, ensuring successional dynamics are represented appropriately is particularly important. If managers seek to prioritize endangered or range-restricted species rather than generalist or wide-ranging species, then weighting species by their conservation value may be appropriate. Yet as conservation value can be measured in multiple ways (e.g. extinction risk or endemism) considering the merits of different approaches and how they influence management targets, such as the landscape-wide mix of vegetation successional states, is important.

Our overarching question was: how do data, landscape classification and conservation values influence biodiversity indices and fire management decisions? Using data on 170 vertebrate species from fire-prone southern Australia we ask four key questions: (i) what are the relative merits of using different types of biodiversity data? (ii) how does the representation of ecosystem states influence evaluation? (iii) how does the value or weighting applied to each species influence management targets? and (iv) how does uncertainty in species’ responses to landscape structure influence management targets?

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MATERIALS AND METHODS

Case study
The Northern Mallee Parks are a connected system of conservation reserves covering 687 770 ha of semi-arid southern Australia. The presence of seven IUCN Red List bird species makes these parks a priority for biodiversity management. Naturally occurring wildfires play a dominant role in shaping system dynamics (Avitabile et al. 2013). As both canopy and understorey are removed by fire, vegetation structural complexity is largely a function of time-since-fire (Haslem et al. 2011). The study area predominantly comprises mallee vegetation; open woodland characterised by resprouting multi-stemmed Eucalyptus trees (<10 m) and an understorey dominated by either the flammable perennial hummock grass Triodia scariosa (hereafter Triodia Mallee) or multiple species of the family Chenopodiaceae (hereafter Chenopod Mallee). Triodia Mallee and Chenopod Mallee cover 60% and 20% of the parks, respectively (Fig. S1 in Supporting Information).

Overview
We modelled the biodiversity data to understand how species occurrence and relative abundance changes as a function of time-since-fire - a proxy for vegetation structure used to delineate successional states. We then determined the proportion of successional states that maximized biodiversity (represented by G) across the landscape. Finally, we explored the sensitivity of the optimal solution to species data, definition of ecosystem states and species weightings.

Defining biodiversity
We used three sources of vertebrate data: presence-only data on threatened birds (hereafter PO), presence-absence data on birds, reptiles and small mammals (hereafter PA), and expert estimates of the relative abundances of birds, reptiles and all-sized mammals (hereafter EE).
The PO data are based on bird surveys at 5091 sites collected from 1999 to 2012 in Triodia Mallee and Chenopod Mallee in the Murray Mallee region (32.8–35.2° S, 139.7–144.1° E; as defined by Haslem et al. 2010) and sourced from Australian government databases, BirdLife Australia and surveys undertaken by La Trobe, Monash and Deakin Universities (Clarke, Boulton & Clarke 2005; Brown, Clarke & Clarke 2009). The data contain records for 11 threatened bird species across a chronosequence of 0–110 years post-fire.

The PA data were collected from 2006 to 2008 as part of a large-scale natural experiment. The data are based on surveys of birds, reptiles and small mammals in 28 study landscapes at sites across a chronosequence of 0–110 years post-fire within the same region as the PO data (see Kelly et al. 2011; Watson et al. 2012; Nimmo et al. 2012 for survey details). The PA data record the presence or absence of species at each site in Triodia Mallee (61 bird, 54 reptile and 6 small mammal species) and Chenopod Mallee (60 bird, 47 reptile and 5 small mammal species).

The EE data are predominantly expert estimates of species’ relative abundance in post-fire vegetation successional states combined with published empirical fire responses for a small number of species (MacHunter, Menkhorst & Loyn 2009). The EE take one of four integer values (0–3) with higher values representing an increase in relative abundance in a given state and zero indicating absence in Triodia Mallee (85 species) and Chenopod Mallee (83 species; Table S1). Definitions of vegetation state follow Cheal (2010; Appendix S1).

Establishing species time-since-fire relationships

The different data types required multiple approaches to establish time-since-fire relationships. For the PO and PA data we used species distribution models. We used MaxEnt (Phillips, Dudík & Schapire 2004) to model the response of PO species to time-since-fire and an interaction with vegetation type. The MaxEnt output is the relative likelihood of species occurrence, which in this
case provides a measure of relative habitat suitability as the vegetation changes post-fire.

Generalised additive mixed models (GAMMs) were used to model PA fauna responses to time-since-fire and an interaction with vegetation type. The GAMM output is a probability of occurrence, which is highly correlated with relative abundance when species are at low prevalence; as is the case in the PA data set. Detailed description of modelling methods and results are provided in Appendix S2. The EE estimates were rescaled to the unit interval (0–1) such that values of 1 represent the highest abundance and 0 represents absence. Rescaling put the estimates on the same range as outputs from the species distribution models. Hereafter, we use the term ‘relative occurrence’ to describe the outputs from presence-absence and presence-only models, and ‘relative abundance’ for the expert estimates.

**Defining ecosystem states: vegetation structural classifications**

Vegetation successional states define the availability of key structural habitat features and their occurrence along a time-since-fire gradient. For each vegetation type we had three alternative models of successional dynamics that differed in the number and breadth of states: a simple three-state model, a four-state model with an additional older category, and a more complex model of six/seven states.

The three-state model in Triodia Mallee had: Early (0–10 years), characterised by bare ground, small coppicing *Eucalyptus* species and post-fire ephemerals, Mid (11–35 years), characterised by high cover of *T. scariosa* and Late (36+ years), characterised by larger trees with decorticiating bark and progressive development of tree hollows. Chenopod Mallee was classified as Early (0–10 years), Mid (11–30 years) and Late (31+ years) and differs from Triodia Mallee in that the Mid state is characterised by medium cover of Chenopodiaceae shrubs and generally sparser vegetation.
The four-state model used updated mapping of longer-unburnt vegetation. This classification is of specific interest to park managers. Triodia Mallee was classified as Early (0–10 years), Mid (11–35 years), Late 1 (36–80 years) and Late 2 (80+ years) and Chenopod Mallee as Early (0–10 years), Mid (11–30 years), Late 1 (31–60 years) and Late 2 (60+ years).

The third model had six or seven states depending on vegetation type. This classification used structure plus floral composition and maturation rates to define the states (based on Cheal 2010). We used seven states in Triodia Mallee: renewal, juvenility, adolescence, vigorous maturity, early stasis, late stasis and early senescence, and six states in Chenopod Mallee: renewal, juvenility, adolescence, early maturity, mid maturity and late maturity (Appendix S1).

**Modelling biodiversity change: calculating G**

Based on species responses to vegetation succession, we determined the optimal combination of vegetation states for biodiversity conservation in Triodia Mallee and Chenopod Mallee. We calculated the geometric mean of species’ relative occurrence or abundance (G) for each dataset separately (PO, PA and EE) and for two combinations of data (PO & PA and All data) in each vegetation type. For the PO and PA data, only those species that showed a clear response to time-since-fire in each vegetation type were included in the optimizations (Appendix S2).

For the PO and PA data, we calculated species’ relative occurrence in each vegetation state by averaging model predictions over the period defined by each state (e.g. 11–35 years). For the EE, we averaged the estimates of relative abundance to align with the three and four-state models. The three data sets each provide information on species’ relative habitat use (scaled 0–1) therefore we considered them to be proportional and that combining them was reasonable. The ability to combine data sets from different surveys is a major benefit of using G (Loh et al. 2005; Buckland et al. 2011). Combined data sets were created by merging individual data sets. When species were
present in multiple data sets we retained the entry that maximized information (PA>PO>EE). New estimates using data from multiple data sets were not created as data sets were not always independent.

The average relative occurrence or abundance of species in a given vegetation type was dependant on the proportion of area in each successional state and is given by

\[
P_i = q_{C_j,i}a_{C_j} + q_{C_2,i}a_{C_2} + \ldots + q_{C_S,i}a_{C_S},
\]

where \(q\) is the relative occurrence or abundance of species \(i\) in successional state \(C\), \(a\) is the proportion of area in successional state \(C\) and \(C\) takes values from \(j\) to \(S\) the total number of states. As \(P_i\) averages across all successional states, even if a species does not occur in one or more successional states (e.g. \(q_{C_1,i} = 0\)), its relative occurrence or abundance across the landscape will always be greater than 0.

The geometric mean of the \(N\) total number of species is then

\[
G = \exp\left(\frac{1}{N}\sum_{i=1}^{N} \log(P_i)\right).
\]

Exploring alternative ways of valuing species

To explore how species weights can be used to incorporate conservation values, we use three examples. In the first two, species were weighted by their relative risk of extinction and in the third, species were weighted on the basis of endemism. To weight species by their relative risk of extinction, we used the IUCN Red List Australia threat categories (Cogger 1993; Garnett & Crowley 2000; Burbidge 2014). Threat categories were weighted using two methods presented in Butchart et al. (2004), i) geometric scaling, reflecting the change in relative extinction risk between categories and ii) the ‘equal-steps’ approach, which indicates at least one measure of extinction risk has become worse with each step. The weights were: Least Concern (0), Near Threatened (0.0005), ...
Vulnerable (0.005), Endangered (0.05) and Critically Endangered (0.5) for the geometric scale, and 0–5 respectively for the ‘equal-steps’.

To prioritize endemic species, we calculated the proportion of each species’ global range falling within the parks. Species occurrence records from 1999 to 2015 were sourced from the Atlas of Living Australia (ALA 2015); the restricted timeframe minimized the chance of including extirpated populations. Species range was defined using a minimum convex polygon and the resulting area clipped by extant native vegetation (DSEWPaC 2012). Calculations were undertaken in ArcMap 10.2 (ESRI 2013).

We used only the combined PO and PA data to calculate a weighted G by weighting the log of each species’ average relative occurrence as

\[ G = \exp \left( \frac{1}{w} \sum_{i=1}^{N} (w_i \log(P_i)) \right), \]

where \( w_i \) is the weight given to species \( i \), \( N \) is the total number of species, \( w \) is the sum of all \( w_i \) from \( i \) to \( N \), and \( P_i \) is from equation 1. If all species weights equal one, the formula reduces to the standard geometric mean.

**Optimization procedure**

We used numerical optimization to determine the proportion of area in each vegetation state that maximized \( G \), averaging across species in the community. By maximizing \( G \) we identify the optimal vegetation successional structure for the species in the analysis. We follow the optimization procedure presented in Kelly et al. (2015) and maximize \( G \) as

\[ G_{opt} = \max [G], \]

subject to \( \sum_{j=1}^{S} a_j = 1, \)

where \( a_j \) is the proportional area in state \( j \) and \( S \) is the number of states.
In summary, the vegetation structure that maximized G was calculated for 36 combinations of data, state classifications and vegetation types. Optimizations were completed using RStudio version 3.2.2 with the package Rsolnp version 1.15 (Ghalanos & Theussl 2015).

**Assessing change**

For each vegetation type and successional state combination, we compared the optimal vegetation structure to the current vegetation structure (i.e. October 2015). We calculated the current proportion of the parks in each vegetation type and successional state using digitised spatial vegetation (DELWP 2016; Fig. S1) and fire history data. Fire history data were a combination of fire scars converted from satellite imagery, 1972–2011 by Avitabile et al. (2013) and 2012–2015 by the land management agency. For sites burned prior to 1972 we used predictive mapping by Callister et al. (2016; Fig. S2). Calculations were undertaken in ArcMap version 10.2 (ESRI 2013). To compare the current structure to the optimal we calculated percent difference in G, and quantified precision in the estimate using 95% confidence intervals. We also calculated G for each species individually using both the optimized and current successional state proportions for each vegetation type.

**Results**

Here we show how data source, vegetation type, representation of successional states and species weightings influence G and the optimized mix of successional vegetation. Species responses to fire are included as Appendix S2.

**Sensitivity to biodiversity data**

The optimal mix of successional vegetation was sensitive to the species included in the analysis. In Triodia Mallee, the structure that maximized G for each separate Triodia Mallee data set was weighted towards vegetation ≥10 years (Fig. 2a–e & S3–S4). For example, the optimal structure for PA data with four states was a combination of Mid (11–35 years; 0.54) and Late 2 (80+ years; 0.46).
vegetation (Fig. 2a). For the PO data, the optimal structure was entirely Mid vegetation, reflecting the time when the majority of threatened birds attain maximum relative occurrence (Fig. 2b). When combining all data sets for Triodia Mallee (PO, PA, EE), the structure that maximized G using four states was a combination of Early (0–10 years; 0.09), Mid (0.31), Late 1 (36–80 years; 0.26) and Late 2 (0.34) vegetation (Fig. 2e). This solution was midway between the optimal solution for PO and EE. The requirement for Early vegetation reflects the contribution of some EE species, which are thought to be most abundant in the first ten years after fire and are not present in the other data sets (Fig. 2c).

The successional structure that maximized G for each separate Chenopod Mallee data set was weighted towards vegetation >31 years, except for the PO data where the optimal structure was entirely Mid (11–30 years; Fig. 2f–j & S5–S6). For all Chenopod data combined (PO, PA, EE) the structure that maximized G was also strongly weighted towards vegetation ≥31 years (Fig. 2j).

**Sensitivity to vegetation model**

Although the two modelled vegetation types co-occur in geographic space, their differing temporal dynamics and species assemblages led to distinct optimal structures. The G optimization based on alternative classifications of Triodia Mallee vegetation states yielded broadly similar results. The main differences between the Triodia Mallee solutions were due to refinement of the older vegetation states. The additional complexity of the four- and seven-state models of system dynamics revealed species’ distinct preference for vegetation greater than 80 years post-fire (Fig. 3b–c & S3–S4), which was not observable from the three-state model (Fig. 3a).

G optimization based on alternative classifications of Chenopod Mallee successional states again yielded broadly similar results. As for Triodia Mallee, the main differences between the Chenopod Mallee solutions were due to refinement of older vegetation dynamics. Using four states, the

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optimal structure for all birds, mammals and reptiles was maximized by a combination of Early (0–10 years; 0.03) and Late 1 (31–60 years; 0.97) vegetation (Fig. 2j & S6). The additional complexity in the four- and six-state models of system dynamics clarified a distinct preference for vegetation 31–60 years post-fire (Fig. S6b–c).

**Sensitivity to species weightings**

G and the optimal vegetation structures were sensitive to species weightings. In Chenopod Mallee the most range-restricted species (MCP) have maximum relative occurrence in Late 1 vegetation, thus the optimal vegetation structure was comparable with the equal weighting scenario (Fig. 4b). By contrast, the IUCN ‘equal-steps’ weights shifted the entire allocation to Mid vegetation (Fig. 4d). The IUCN geometric weights shifted only 40% of the allocation to Mid, reflecting the priority given to Endangered and Vulnerable species that have high relative occurrence in Late 1 vegetation (Fig. 4c). This response was midway between equal weighting and the IUCN ‘equal-step’ weights, as the most threatened species are also the most range-restricted. In Triodia Mallee the value-based weights yielded consistent results; shifting the optimal vegetation structure to 100% Mid (Fig. S7). The consistency indicates substantial overlap between threatened and range-restricted species in Triodia Mallee.

**Evaluating change**

The difference between the current state of the parks and the optimal state varied with data set and vegetation type. For Triodia Mallee, the current state of the parks is 18% Early, 31% Mid, 48% Late 1 and 2% Late 2 vegetation. This was similar to the solution that maximized G for all Triodia Mallee data sets combined (Table S2), G decreased by 2.88%, reflecting the small expected change in species occurrence or abundance due to the current landscape composition (Fig. 5a). G decreased approximately 10% for both PA and PO data (Table S2). For PO data the significance of the change
was reflected by minimal overlap of confidence intervals. For PA data the impact of the change was not clear.

The current state of Chenopod Mallee across the parks is 25% Early, 4% Mid, 46% Late 1 and 25% Late 2 vegetation. For three of the five data sets in Chenopod Mallee, the current state of the parks induced a decrease of 10% or more in values of G. The greatest decrease was 17.2% for PO, which is likely to result in a significant reduction in all species occurrences (Fig. 5b). The PA data indicated minimal change, which may partly be because the species have a wider range of habitat preferences, as reflected in the uncertainty around G (Fig. 5b).

Discussion

Using biodiversity indices in the presence of both fire and succession presents unique challenges. We have shown that using biodiversity indices for fire management requires careful consideration of the underpinning biological data, the definition of post-fire successional states, and how species are valued or weighted. Below, we provide guidance on applying biodiversity indices for management of fire-prone ecosystems.

**What are the relative merits of using different types of biodiversity data?**

Choices relating to data type were influential on the mix of successional states that maximized biodiversity. When using presence-only data for threatened birds the optimal vegetation structure in both Triodia and Chenopod Mallee was entirely Mid successional, reflecting the similar habitat
preferences of these species and the restricted taxonomic scope of the sample. The greater
taxonomic breadth and number of species in the presence-absence data and expert estimates
resulted in more diverse optimal vegetation structures.

A benefit of using G as a measure of biodiversity is that different types of data can be combined
(Buckland et al. 2011). By combining presence-absence data, presence-only data and expert
estimates our measure of biodiversity better represented the ecological community. However, this
potential benefit should be assessed based on the quality of the biodiversity data. Data selection for
management decisions involves trade-offs between data quality, data coverage and costs (Wilson et
al. 2005). The largest data set, the presence-absence data, is the result of well-designed systematic
surveys that can discriminate between habitats the species use (presence) and do not use (absence;
Kelly et al. 2011; Watson et al. 2012; Nimmo et al. 2012). The presence-only data set is a valuable
resource, yet as it contains no absence records there is a chance of incorrectly representing species
habitat associations. To minimize this risk we implemented three bias-correcting approaches and
found the results to be robust (Appendix S2). The three presence-only models were able to reliably
rank habitat in terms of the species likelihood of occurrence (AUC >0.8; Pearce, Ferrier & Scotts
2001), demonstrating the potential usefulness of long-term database records for incorporating
habitat requirements of less common species into regional fire management plans. The expert
estimate data set had the least information content, despite consisting of direct estimates of
species’ relative abundance in successional states. Quantifying uncertainty in the point estimates
would increase their value. Ultimately, data should have relevant coverage of the biodiversity being
protected, as an ad hoc selection of a subset of species can bias results. Restricted coverage of
biological data has also been shown to affect other indicators, such as the Mean Trophic Level,
where trends differed considerably when small pelagic fish or Atlantic cod were excluded (Branch et
al. 2010).

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Future research that incorporates spatial measures and other fire regime characteristics into species distribution models, or maps $G$ across the landscape could provide greater understanding of species habitat selection. Such an approach could also minimize the chance of misrepresenting the optimal landscape, which may occur if species adjust their relative habitat usage in proportion to the frequency of those patches in the landscape.

**How does the representation of ecosystem states influence evaluation?**

Models of ecosystem dynamics are a fundamental component in correctly representing biodiversity change over time. Our results demonstrate the importance of exploring how definitions of successional states influence management decisions. Differences in the combinations that optimized $G$ show the importance of identifying the level of complexity appropriate for the species and system under consideration. For Triodia Mallee and Chenopod Mallee increasing the number of vegetation states clarified subtle differences in the mixtures that optimized $G$. We recommend that post-fire successional states are based on demonstrated habitat requirements of the target species and clearly linked to changes in vegetation structure over time.

Sensitivity to the system model is important for other indices, such as Sorenson’s index, which is sensitive to the number of classes (Keane *et al.* 2008) and the Mean Trophic Level indicator which is sensitive to trophic level estimates (Branch *et al.* 2010). Determining the best model to represent the processes of interest may induce a trade-off between simplicity and complexity. The models with over six states provided greatest differentiation but are potentially too detailed to be relevant for on-ground management. What are needed are enough categories to capture the fundamental needs of different taxa. For example, the three-state model for Triodia Mallee clumps all vegetation greater than 30 years in one class. Implementing this on-ground could have an unfavourable effect on species that rely on Triodia Mallee greater than 80 years; for example, bird species such as the Yellow-plumed Honeyeater (*Lichenostomus ornatus*) and Striated Pardalote (*Pardalotus striatus*)
that require large eucalypts to provide food and nesting hollows (Nimmo et al. 2012), and reptile species such as Boulenger’s Skink (*Morethia boulengeri*) that utilize accumulated litter and bark (Nimmo et al. 2012). For late successional specialists, the four-state model has greater relevance.

**How does the value or weighting applied to each species influence management targets?**

Many multi-species indices weight species equally, such as the Living Planet Index (Loh et al. 2005) and Natural Capital Index (ten Brink 2000). However, explicit species weightings provide an opportunity to incorporate societal or conservation values into biodiversity indices. For example, conservation weights are used in global reporting indices such as the Red List Index, which weights species by threat status (Butchart et al. 2004), or the Wild Bird Indicator, which weights by proportion of the European population of that species in each country (Gregory & van Strien 2010).

We have demonstrated how three example weighting schemes influence the optimal vegetation structure in a manner that reflects their underlying priorities. For Chenopod Mallee, the IUCN geometric weights and the weights reflecting endemism (MCP) are similar because three of the four most threatened species that occur in Chenopod Mallee, Regent Parrot (*Polytelis anthopeplus* subsp. *Monarchoides*), Black-eared Miner (*Manorina melanotis*) and Red-lored Whistler (*Pachycephala rufogularis*), have the greatest proportion of their range within the study area. These solutions emphasize the importance of late successional Chenopod Mallee for the species listed as Endangered and Vulnerable. The remaining three species of high conservation concern that occur in Chenopod Mallee have less than 1% of their range in the study area, hence the solution when using the IUCN ‘equal-steps’ weights is predominantly mid successional. The ‘equal-steps’ solution is similar to the solution when equally weighting only the threatened birds (PO). The optimal vegetation structure in Triodia Mallee was similar for all non-equal weights as there was complete overlap between endemic species (MCP) and the species facing highest threat, e.g. Mallee Emu-wren (*Stipiturus mallee*), despite the different approaches to scaling conservation value. Using
weights is a transparent way to incorporate values into the decision-making process and is amenable to updating if weights change (e.g. threat status).

**How does uncertainty in species’ responses to landscape structure influence management targets?**

We used the optimal G to define a reference state aligned to the objective and assessed how far we were from this state by comparing it to the current state of the system. The variation in optimal vegetation structure between the five data combinations emphasizes how a reference state is only as relevant as the data underpinning it. Depending on the data set, the current state ranged from being close to the optimal vegetation structure (e.g. All data in Triodia Mallee) to far from the optimal structure (e.g. only threatened bird (PO) data in Chenopod Mallee), highlighting the importance of ensuring species data accurately reflect the goals set by decision makers.

Representing variation in species’ responses to vegetation structure provided valuable information on how individual species are expected to respond to vegetation change. Using all species combined in Chenopod Mallee, G for the current state decreased by 10% from the optimal, yet approximately 25% of species would be expected to increase in occurrence or abundance under the current vegetation structure. Exploring the data that underpins indices is important for assessing robustness and understanding how biodiversity is changing (Runge 2011). Whether an index is sensitive to change in the state of the system is also of prime importance. Fisheries have invested significant effort into understanding how well indices respond to changes in system state (Fulton, Smith & Punt 2005). In fire management, further work is needed to identify biologically meaningful system-specific targets, with appropriate levels of confidence, so it is clear when a change should trigger action.
Recommendations for management

We make the following recommendations for applying biodiversity indices to fire management: First, select an index closely aligned to the management objective (Rice & Rochet 2005; McCarthy et al. 2014) and has statistical and theoretical support (Buckland et al. 2005, 2011; van Strien, Soldaat & Gregory 2012). Second, consider the information content of the biodiversity data and account for potential sources of bias. Third, interrogate classifications of ecosystem states, as inappropriate categories may disadvantage certain groups of species. Fourth, species weights provide a transparent means to incorporate societal values into decision making and can be easily updated. And fifth, represent uncertainty in the index as this provides insight into what is a statistically important change.

For example, in the Northern Mallee Parks threatened birds are a priority for managers and multiple species rely on Triodia Mallee greater than 80 years old. Therefore, a relevant indicator would likely incorporate presence-absence and presence-only data, employ the four-state model of vegetation change, and consider how weighting G by species endemism or geometrically-scaled extinction risk influences management targets. A clear understanding of the sensitivity of biodiversity indices should enhance their use in environmental decision making and increase the likelihood of meeting biodiversity objectives.
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Authors’ Contributions

KG, LK, TR and MM conceived the ideas for the paper and designed analyses; MC, RC and LK collected the data; JC collated the threatened bird data; KG analysed the data; KG and LK led the writing of the manuscript. All authors contributed to the development of ideas and drafts and gave final approval for publication.

Data Accessibility

Data are available in the Dryad digital repository. DOI:

doi:10.5061/dryad.2317g (Giljohann et al. 2017)

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**Supporting information**

Additional Supporting Information may be found online in the supporting information tab for this article.
Figure 1. Using biodiversity indices for environmental decision making. Modified from the ‘indicator-policy cycle’ of Nicholson et al. 2012. This study focuses on steps within the dashed lines.

Figure 2. Optimal vegetation structures that maximize the geometric mean of species’ relative occurrence or abundance for three separate data sets and two data combinations in Triodia (dark grey; a-e) and Chenopod Mallee (light grey; f-j) using four vegetation states. The data are: presence-absence (PA), presence-only (PO), expert estimates (EE), combined PA & PO and all data (PA, PO & EE).

Figure 3. Sensitivity of the optimal vegetation structure to successional state representation in Triodia Mallee using a) three, b) four and c) seven states for the combined presence-absence and presence-only data (PA & PO).

Figure 4. Influence of value-based weights on the optimal vegetation structure for combined PA and PO data in Chenopod Mallee using four states. Individual species weights are a) all equal, b) proportion of global habitat in study area (MCP), and extinction risk using IUCN Red List categories with c) geometric scaling or d) ‘equal-steps’.

Figure 5. Comparison between the optimal G (black) and current G (grey) in a) Triodia Mallee and b) Chenopod Mallee using four states and all data combinations. Error bars are 95% confidence intervals. The point data are G calculated for each species individually.
Biodiversity indicator evaluation

Identify broad goals
Define and model the system
Select indicators
Set specific targets
Act and implement

Key questions
Q1. What are the relative merits of using different types of biodiversity data?
Q2. How does the representation of ecosystem states influence evaluation?
Q3. How does the weighting or value applied to each species influence management targets?
Q4. How does uncertainty in species' responses to landscape structure influence management targets?
Author/s:
Giljohann, KM; Kelly, LT; Connell, J; Clarke, MF; Clarke, RH; Regan, TJ; McCarthy, MA

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