

Using ideal distributions of the time since habitat was disturbed to build metrics for evaluating landscape condition

AYESHA I. T. TULLOCH,^{1,2,6} JANE McDONALD,² PETER COSIER,³ CARLA SBROCCHI,^{3,4}
JOHN STEIN,¹ DAVID LINDENMAYER,¹ AND HUGH P. POSSINGHAM^{2,5}

¹*Fenner School of Environment and Society, The Australian National University, Canberra,
Australian Capital Territory 2601 Australia*

²*Centre of Excellence for Environmental Decisions, Centre for Biodiversity and Conservation Science, The University of Queensland,
St Lucia, Queensland 4072 Australia*

³*Wentworth Group of Concerned Scientists, Level 4, Plaza Building, Australia Square, 95 Pitt Street, Sydney,
New South Wales 2000 Australia*

⁴*University of Technology Sydney, 15 Broadway, Ultimo, New South Wales 2007 Australia*

⁵*The Nature Conservancy, South Brisbane Queensland 4101 Australia*

Abstract. Developing a standardized approach to measuring the state of biodiversity in landscapes undergoing disturbance is crucial for evaluating and comparing change across different systems, assessing ecosystem vulnerability and the impacts of destructive activities, and helping direct species recovery actions. Existing ecosystem metrics of condition fail to acknowledge that a particular community could be in multiple states, and the distribution of states could worsen or improve when impacted by a disturbance process, depending on how far the current landscape distribution of states diverges from pre-anthropogenic impact baseline conditions. We propose a way of rapidly assessing regional-scale condition in ecosystems where the distribution of age classes representing increasing time since last disturbance is suspected to have diverged from an ideal benchmark reference distribution. We develop two metrics that (1) compare the observed mean time since last disturbance with an expected mean and (2) quantify the summed shortfall of vegetation age-class frequencies relative to a reference age-class distribution of time since last disturbance. We demonstrate the condition metrics using two case studies: (1) fire in threatened southwestern Australian proteaceous mallee-heath and (2) impacts of disturbance (fire and logging) in the critically endangered southeastern Australian mountain ash *Eucalyptus regnans* forest on the yellow-bellied glider *Petaurus australis*. We explore the effects of uncertainty in benchmark time since last disturbance, and evaluate metric sensitivity using simulated age-class distributions representing alternative ecosystems. By accounting for and penalizing too-frequent and too-rare disturbances, the summed shortfall metric is more sensitive to change than mean time since last disturbance. We find that mountain ash forest is in much poorer condition (summed shortfall 38.5 out of 100 for a 120-yr benchmark disturbance interval) than indicated merely by loss of extent (84% of vegetation remaining). Proteaceous mallee-heath is in worse condition than indicated by loss of extent for an upper benchmark interval of 80 yr, but condition almost doubles for the minimum tolerable time since last disturbance interval of 20 yr. To fully describe ecosystem degradation, we recommend that our summed shortfall metric, focused on habitat quality and informed by biologically meaningful baselines, be added to existing condition measures focused on vegetation extent. This will improve evaluation of change in ecosystem states and enhance management of ecosystems in poor condition.

Key words: *degradation; environmental accounts; fire management; forestry policy; habitat disturbance; IUCN Red List of ecosystems; threatening processes; vegetation condition.*

INTRODUCTION

Landscapes are changing rapidly under the influence of anthropogenic threatening processes (Laurance et al. 2011). Across the globe, one of the most pervasive drivers of landscape change is habitat degradation (Rodríguez et al. 2011). Driven by cumulative impacts of climate

change, vegetation clearing, invasive species, and altered fire regimes, almost all terrestrial ecosystems have experienced extensive modification and decline in condition (Venter et al. 2016). Most attempts to measure the magnitude of ecosystem change at broad scales focus on overall reduction in the extent of vegetation cover (Hansen et al. 2013, Keith et al. 2013). Despite a variety of methods available to map vegetation characteristics (Zerger et al. 2009, Lawley et al. 2016), there is still no widely accepted approach to measure and account for broad-scale changes to vegetation condition that might occur in addition to, or independent of, loss of extent. Furthermore, measures of

Manuscript received 16 May 2017; revised 1 September 2017; accepted 3 November 2017. Corresponding Editor: Dianne Brunton.

⁶E-mail: a.tulloch@uq.edu.au

extent alone can be misleading, reporting high scores where habitat remains over large areas but is severely degraded (Tulloch et al. 2016a). Developing a standardized approach to assessing vegetation condition would allow a more comprehensive understanding of changes in vegetation, and enable land managers and decision makers to simultaneously evaluate and compare change across different systems (such as through environmental accounts; Cosier and McDonald 2010, van Dijk et al. 2014), assess ecosystem vulnerability and likely impacts of destructive activities (Rodríguez et al. 2011), and direct management actions to recover systems in poor condition (Moilanen et al. 2011, Evans et al. 2015).

Ecological condition has been expressed in a variety of ways, ranging from the extent of human modification or disturbance (Stoddard et al. 2006) to suitability as habitat for specific taxa (Johnson 2007). To incorporate ecological condition into effective management of degraded landscapes, we need to understand the current quality or state of the system and how it has changed relative to some reference benchmark (Stoddard et al. 2006). Reliance on a benchmark means that vegetation condition is context-dependent (Zerger et al. 2009). There is a decline in condition when threatening processes or disturbances change the environment so that it no longer provides the same “quality” of habitat for dependent species (Felton et al. 2003). Technological advances (e.g., in remote sensing; Boyd and Foody 2011) have improved our ability to map change in the state of different landscapes relative to different processes such as fire or carbon storage (Yang et al. 2014), but most outputs are rarely useful on their own for informing management. This is because existing metrics for summarizing ecosystem change as a result of degrading processes are either insensitive to incremental changes in condition (e.g., categorical classifications such as the VAST framework; Thackway and Lesslie 2006), or lack a clear link to expected baselines, such as biological requirements of species dependent on those ecosystems (e.g., many fragmentation metrics; Debinski and Holt 2000, Wang et al. 2014). Notably, many standard condition metrics ignore the natural dynamics of habitats following disturbance (McCarthy et al. 2004).

Summarizing condition across an entire ecosystem is challenging because disturbances rarely occur evenly across time and space due to a range of factors including weather, soil, and heterogeneity in anthropogenic impacts. Different species and systems are adapted to persisting under different ranges in ecological conditions and disturbance levels (Gosper et al. 2013, Tulloch et al. 2016b). Using this knowledge, studies such as the U.S. interagency LANDFIRE program have quantified the dissimilarity between an ecological system’s current condition and its natural range of variability with respect to a benchmark (Rollins 2009). However, the spatial grid-based outputs of such approaches do not lend themselves to aggregation of data that might be used to derive a single condition metric that is comparable across landscapes and ecosystem types, a requirement for consistent environmental accounts.

Moreover, existing landscape-assessment approaches fail to spatially differentiate the age classes of remaining vegetation, thereby limiting the utility of such approaches to express ecological departure from historical conditions (Thode et al. 2011, Rogeau et al. 2016). Recent disturbance in one location will cause the system to depart from its natural range of variability if that disturbance is not offset by succession in another location.

Here, we propose a new way of rapidly assessing regional-scale habitat condition where the current distribution of vegetation age classes is suspected to have diverged from an ideal distribution (i.e., a biologically defined benchmark set of age-class frequencies). We provide two new metrics for assessing landscape condition based on (1) change in the mean vegetation age class and (2) the shortfall in ideal vegetation age-class frequencies. To illustrate the calculation of the metrics, we use two examples of threatened ecosystems undergoing common disturbance processes, fire and logging, which are major drivers of species declines globally (Archibald et al. 2012). Although disturbances such as fire are essential for the reproduction and survival of many flora and fauna species, there is increasing evidence that altered fire regimes have negative outcomes for biodiversity (Taylor et al. 2012). Many areas now burn too frequently (Syphard et al. 2007, Shlisky et al. 2009), leading to communities dominated by young vegetation and declines of species that rely on long intervals between fires for resources to recover sufficiently (Lindenmayer et al. 2011). Other areas burn too rarely (Wallenius et al. 2011, Salis et al. 2014), leading to communities dominated by old vegetation, which can lead to plant senescence and the decline of fire-dependent species (Taylor et al. 2013, Tulloch et al. 2016b).

Climate change is predicted to increase the likelihood of catastrophic wildfire (Liu et al. 2010), highlighting the need to understand current ecosystem condition so that future changes can be accurately assessed. Logging also impacts the distribution of age classes in a vegetation community due to removal of mature individuals in a stand (McCarthy and Burgman 1995). This can lead to faunal species declines when communities are cleared before trees have matured to provide key food or shelter resources to the species that depend on them (Lindenmayer et al. 2016). In our examples, we evaluate vegetation condition relative to benchmark tolerable fire intervals informed by the needs of either the dominant species in the system, or particular species of concern (McCarthy et al. 2001, Gosper et al. 2013). We compare our condition metrics with a traditional measure of loss of vegetation community extent to demonstrate the complementarity of our approach to existing environmental accounting metrics, and evaluate the effects of simulated age-class distributions on metric performance. Our approach provides a simple way to evaluate the impact of disturbances that affect vegetation condition, such as degradation of vegetation structure and altered composition as vulnerable species are replaced by species tolerant to, or unaffected by, disturbance (Tulloch et al. 2016b).

MATERIALS AND METHODS

The vegetation condition metrics

We define vegetation condition as the divergence of a community from its natural (and in this case, ideal) state, represented by the amount of time lapsed since the last disturbance event (time since last disturbance, or TSLD). We propose two metrics that compare a component of the observed distribution of TSLD (today usually derived from a spatial grid, e.g., MODIS remote-sensing satellite imagery, and historically derived from aerial imagery or on-ground measurements) against the expected distribution of TSLD (a reference benchmark that may be derived in several ways; see *case studies* for examples). The output of each metric is a measure of how similar observed conditions are to the reference conditions, standardized to a value between 0 and 100 to enable cross-community comparisons and integration with other metrics. A value near 100 indicates that observed and expected values are very similar and the ecosystem is in good condition with respect to that disturbance, and a value near 0 indicates the distribution of TSLD is very different between the ecosystem and the benchmark distribution, i.e., ecosystem condition is poor.

The reference benchmark for both metrics depends on the objectives of the condition assessment. Assessing habitat quality for a species dependent on a particular disturbance interval to allow food or nesting sources to become available may require a different benchmark from assessing vegetation condition for an entire community made up of multiple species that differ in tolerable fire intervals (Richards et al. 1999, Gosper et al. 2013, Tulloch et al. 2016b). Here we set the benchmark as the mean “tolerable” TSLD for the target community or species. Ideally, the benchmark is derived from existing peer-reviewed literature or ecological data sets, such as analysis of fire records prior to anthropogenic impacts, simulation of historical conditions (Rollins 2009), or empirically modelling tolerable fire intervals for target species or communities (Tulloch et al. 2016b).

The first metric, “mean TSLD,” compares the observed mean TSLD to the expected mean TSLD across the entire landscape, and estimates a score between 0 and 100 that indicates how similar they are. An observed TSLD lower than the benchmark TSLD indicates the landscape is disturbed more frequently than expected, and higher indicates it is disturbed less frequently than expected on average. The equation is

$$\text{mean TSLD} = \left(1 - \text{MIN} \left(\frac{|\mu_o - \mu_e|}{\mu_e}, 1 \right) \right) \times 100 \quad (1)$$

where $\text{MIN} \left(\frac{|\mu_o - \mu_e|}{\mu_e}, 1 \right)$ is the smallest of 1 and $|\mu_o - \mu_e|/\mu_e$, μ_e is the expected (benchmark) mean tolerable TSLD, and μ_o is the observed mean TSLD. The input is a table calculating the total area (as a percentage) of the vegetation community in each age class from

1 yr old to the maximum known recorded age class (see Appendix S2: Fig. S3 and Data S1). The remaining area that is older than the maximum recorded age class is assigned to the maximum.

The second metric, “TSLD summed shortfall,” describes spatial heterogeneity in disturbance across the landscape. It compares the current variability (or distribution) of different TSLD classes within the vegetation community against an expected distribution. The expected distribution is derived from the geometric distribution to determine the probability of the community reaching a certain age since disturbance, using

$$A_{te} = ((1 - p)^{t-1} p) \times 100. \quad (2)$$

In Eq. 2, A_{te} is the expected probability density function for the time since last disturbance (a value between 0 and 100), given the current time step t years since disturbance, and an expected rate of disturbance p . Time step t is defined at the grid-cell level, and p is defined at the landscape level. For a rate of disturbance once every 60 yr, p is $1/60$. The geometric distribution is suitable for the majority of fire- and logging-disturbed landscapes with variable disturbance rates (McCarthy and Cary 2002). For systems with very high or very low natural disturbance frequencies (e.g., mangroves that experience infrequent flood events or long-term freshwater inundation), or where disturbances could occur more than once a year, modifications to this distribution may be necessary. Other distribution models of age or stand structure that can be used to inform expected age class frequencies include (but are not restricted to) gamma, beta, normal, lognormal, and Weibull probability distributions (Bailey 1980). Because disturbance is defined as binary at the grid-cell level, for many disturbances, a threshold will need to be set that distinguishes low-impact disturbance that does not reset the landscape (e.g., low-intensity selective logging, classified as no disturbance) from high-impact disturbance, such as clear-cutting, that resets the landscape. Classification of a particular location as “burned” at a level that resets it to age-class zero is dependent on the vegetation type, with some vegetation types resetting to zero under lower intensity fires than others that require a higher intensity fire to reset.

The observed TSLD distribution is derived from a frequency distribution of the currently observed area of the community A_{to} aged t years since last disturbance (percentage of total; Appendix S2: Fig. S2). The equation to calculate TSLD summed shortfall is

$$\text{TSLD shortfall} = 100 - \sum A_{ts} \quad (3)$$

where A_{ts} is the percentage shortfall in the amount of any vegetation age class, calculated as

$$A_{ts} = A_{te} - A_{to} \quad \text{if } A_{to} < A_{te}, \\ \text{and } 0 \text{ otherwise.} \quad (4)$$

We group TSLD age classes into n categories according to geometric scaling to ensure that the length of the disturbance history (and hence number of age classes recorded) does not bias the metric, allowing comparisons to be made across communities with different data series. The first category contains all the information for years 0 to t (e.g., 0–2). The next category contains t to $2t$ (e.g., 2–4), and so on. The expected distribution of age classes (representing time since last disturbance; Appendix S2: Fig. S4) accounts for diversity in the years that different areas have been burned, such that some areas will have been burned recently, whereas some areas have not been burned for a long time. For example, even-aged forest management tends to reduce forest variability by truncating the natural age-class distribution and eliminating mature and old-growth forests from the landscape (Lindenmayer and Franklin 2002). We explain the procedure for calculating the two metrics in the following case studies. Spreadsheets of the calculations are provided in Supporting Information Data S1.

Case study 1: Fire in threatened proteaceous-rich mallee-heath

First, we demonstrate the concepts and application of our metrics using a simple example: the departure from “natural” fire regimes defined according to the needs of the dominant plant species in a threatened ecosystem. The highly fire-prone “Proteaceae Dominated Kwongan Shrublands of the southeast coastal floristic province of Western Australia,” also known as proteaceous-rich mallee-heath (PRMH), has been listed as a threatened ecological community (TEC) under the Environmental Protection and Biodiversity (EPBC) Act (1999) in Australia (see Appendix S1 for more details). It occurs across 14,891 km² of the southern coastal portion of the wheat-belt in southwestern Australia, and is dominated by fire-dependent proteaceous shrubland and heath species such as *Banksia* (Comer et al. 2001a, b). In relatively intact landscapes, predominantly public reserves, unplanned fires burn large tracts of native vegetation at high frequencies (e.g., every 8 yr; Tulloch et al. 2016b), whereas in isolated remnants in the agricultural zone, fire is prevented or suppressed by farmers to protect crops (O’Donnell et al. 2011, Parsons and Gosper 2011, Gill et al. 2014). We aim to assess vegetation condition for the dominant fire-dependent *Banksia* species. Benchmark burn

intervals are derived from published empirical models of seven *Banksia* species (Gosper et al. 2013, Tulloch et al. 2016b). Because it is unlikely that the system has a single optimal age-class distribution (Gosper et al. 2013, Tulloch et al. 2016b), we determine three reference benchmarks: (1) ideal mean (40 yr, most fire-tolerant and fire-sensitive species), (2) lower (minimum) tolerable level (20 yr, some highly fire-tolerant and short-lived species), and (3) upper (maximum) expected tolerable interval (80 yr, many long-lived species that require long time intervals between fires to maximize reproductive outputs).

Metric 1: Mean time since last disturbance.—The fire history database for proteaceous mallee-heath was built by the Western Australian Department of Parks and Wildlife from existing maps of fire-affected areas predominantly from aerial imagery (Hamilton et al. 2009). The observed mean time since last fire μ_o , is the sum of the products of two arrays: the array of t (0 to the maximum age recorded disturbance, here 55 yr), and the array of A_{t_o} values (i.e., the percent area of the PRMH in each age-class category t). The current μ_o is 13.71 yr, lower than all expected benchmark intervals, 31% shorter than the lower tolerable level and 83% shorter than the upper expected tolerable interval. For an expected mean μ_e of 40 yr since disturbance, we apply Eq. 1 to calculate the mean TSLD metric (Appendix S2: Fig. S3) as

$$\left(1 - \left(\frac{|13.71 - 40|}{40}\right)\right) \times 100 = (1 - 0.6573) \times 100 = 34.26.$$

This score represents the most likely condition given no uncertainty in the ideal benchmark that was determined from the tolerable fire intervals of seven target *Banksia* species (Tulloch et al. 2016b). Repeating the condition score for a minimum μ_e of 20 yr (the shortest tolerable fire interval of the target species, below which all target species are likely to go extinct within 100 yr, Tulloch et al. 2016b) increases the mean TSLD score to 68.53, indicating that the ecosystem is in better condition if we believe a shorter fire interval is the ideal state. Conversely, if we believe a longer fire interval is the ideal state and increase μ_e to 80 yr (the longest tolerable fire interval of the target species), the mean TSLD score is reduced to 17.13 (Table 1).

TABLE 1. Output of condition metrics for southwestern proteaceous-rich mallee-heath (PRMH) condition in relation to time since disturbance in 2013.

Assessment	Benchmark (expected mean TSLD) μ_e (yr)	Observed TSLD μ_o (yr)	Mean TSLD score (Eq. 1)	TSLD summed shortfall (Eq. 3)
Lower tolerable interval	20	13.71	68.53	63.62
Ideal mean tolerable interval	40	13.71	34.26	51.25
Upper tolerable interval	80	13.71	17.13	39.21

Notes: Scores in the last two columns are a value out of 100, with higher values representing higher condition. TSLD, time since last disturbance.

Metric 2: Summed shortfall in time since last disturbance.—A frequency distribution of the observed area of the community A_{t_o} aged t years since last disturbance shows a highly unbalanced distribution of age classes relative to the ideal distribution under each of the three reference benchmarks (Fig. 1a, Table 2). Age classes between 4 and 16 yr are over-represented irrespective of the expected benchmark due to several recent broad-scale fires that increased the extent of younger and reduced the extent of older age classes (Fig. 1b). To calculate the TSLD summed shortfall metric (Appendix 2: Figs. S7 and S8), we sum each of the individual age-class shortfalls A_{t_s} (aggregated into geometric intervals), which are expressed as the difference between the expected percentage of the community’s area in that age class A_{t_e} and the observed area of the community in that age class A_{t_o} (Table 2). Longer expected tolerable intervals result in lower TSLD shortfall scores than short expected intervals (Table 1). The shortfall metric indicates that the proteaceous mallee-heath is in worse

condition than indicated by loss of extent for an upper benchmark interval of 80 yr, with the age-class distribution falling short of a 100% perfect exponential distribution by 61% (TSLD shortfall = 39; Table 1). The shortfall is almost halved to 36% (TSLD shortfall = 64) when the benchmark interval is lowered to 20 yr.

Comparison of disturbance metrics with loss of extent metric.—We can compare our two metrics to a traditional condition metric of loss of vegetation extent, which estimates the percentage of total original extent remaining for a vegetation community since European settlement of Australia (van Dijk et al. 2014, Tulloch et al. 2016a). By calculating the total area (in square kilometers) from maps of pre-1750 and extant vegetation (NVIS 4.1, Australian Government Department of Sustainability, Environment, Water, Population and Communities), we estimate the percentage of the community’s original vegetation that remains, resulting in a value of 100 if there has been no change, and a value of 0 if all vegetation has been lost. As 52.2% of the vegetation remains, the vegetation extent metric of condition for PRMH is 52.2/100. This value is very close to the summed shortfall score of 51.3 for the benchmark distribution of 40-yr intervals between fires (Table 1). This indicates that if we were certain that 40-yr intervals would ensure persistence of all target species, habitat quality is in roughly the same condition (one-half that of pre-European quality) and quantity (one-half of the original extent remaining). However, shortfall metrics based on the lower or upper bounds of uncertainty in baseline conditions yield different scores from the extent metric (20-yr intervals vs. 80-yr intervals between fires; Table 1). If an 80-yr interval between fires were the true baseline, vegetation quality is much poorer than indicated by quantity (a score of 39 compared with 52, respectively). Mean TSLD shows the same trends in relative condition as TSLD summed shortfall compared with vegetation extent, with the exception that it also suggests that for the ideal expected baseline (40-yr intervals), condition is worse than indicated by extent (Table 1).

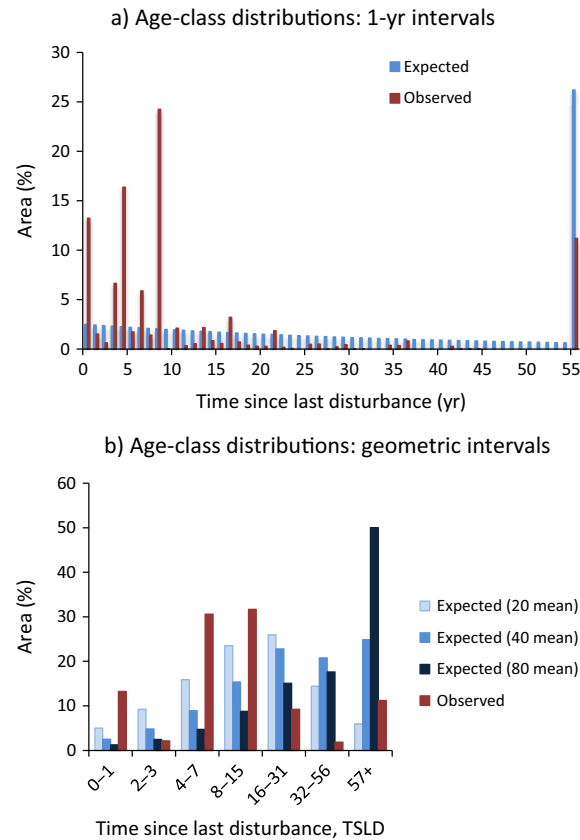


FIG. 1. Comparison of the observed vs. expected percentage of the proteaceous mallee-heath community in different age classes of time since last disturbance (here fire) for (a) age-class intervals of 1 yr and an expected ideal benchmark of 40 yr since fire and (b) geometric age-class intervals for lower (20 yr, light blue), mean (40 yr, medium blue), and upper (80 yr, dark blue) expected benchmarks.

Case study 2: Fire and logging in endangered Victorian mountain ash forest

In the second example, we evaluate departure from disturbance regimes defined according to the needs of a threatened mammal dependent on foraging and denning in the ecosystem. The montane forests of the Central Highlands, Victoria, are dominated by *Eucalyptus regnans* (mountain ash), and managed for multiple uses including biodiversity conservation and timber harvesting (see Appendix S1 for more details). Fires are rare but are of high intensity and severity, usually resulting in death of *E. regnans* and regeneration from seed (Smith et al. 2016). These forests experienced a widespread and devastating wildfire in 2009, destroying much of the old-growth forest, but logging regimes have not been adjusted to account for the likely change in age-class distribution as a result of the

TABLE 2. Expected and observed percentage of vegetation area in each age-class category of PRMH for an ideal mean tolerable fire interval of 40 yr.

Age-class category <i>t</i>	Expected area (%) A_{te}	Observed area (%) A_{to}	Age-class shortfall $A_{ts} = A_{te} - A_{to}$
1–2	2.50	13.23	0
2–4	4.81	2.16	2.66
4–8	8.93	30.62	0
8–16	15.36	31.68	0
16–32	22.78	9.27	13.52
32–56	20.77	1.84	18.94
55+	24.85	11.21	13.64
Sum of shortfalls $\sum A_{ts}$			48.75
TSLD shortfall = $100 - \sum A_{ts}$			51.25

Notes: The shortfall for each age class is the difference between the expected and observed percentages. The TSLD shortfall metric is 100 minus the sum of the age-class shortfalls.

combination of fire and logging (Lindenmayer et al. 2011). Models indicate a >92% chance of ecosystem collapse and therefore led to the listing of mountain ash as a “critically endangered” ecosystem on the IUCN Red List (Burns et al. 2015). Several previous studies have estimated the observed age structure of mountain ash forest (Kuczera 1987, McCarthy et al. 1999, Lindenmayer and Wood 2010), but no studies have evaluated this structure in a way that quantifies the divergence of the current from the benchmark distribution. We show how TSLD metrics may be used to assess vegetation condition for the yellow-bellied glider *Petaurus australis*, which is dependent on old-growth forest for feeding on sap and denning in hollows of mature trees (Lindenmayer et al. 1999). Benchmark disturbance intervals are derived from published literature on yellow-bellied glider resource requirements (Lindenmayer et al. 2011). We again determine three reference benchmarks, this time according to the time needed for either food or denning resources to be produced in mature *E. regnans*: (1) ideal mean (120 yr for tree hollows to develop to a size suitable for use by *P. australis*; Lindenmayer et al. 1991), (2) lower tolerable interval (70 yr required for trees to produce enough sap to meet feeding requirements, but not long enough to produce hollows), and (3) upper interval (trees sometimes need to be up to 190 yr old to produce hollows; Lindenmayer et al. 1990, Incoll et al. 2001, Lindenmayer et al. 2016).

Metric 1: Mean time since last disturbance.—The observed mean time since last fire, μ_o , is 37.26 yr, one-half the expected lower benchmark. To meet denning and food requirements with an expected mean, μ_e , of

120 yr since disturbance, we apply Eq. 1 to calculate mean TSLD as

$$\left(1 - \left(\frac{|37.26 - 120|}{120}\right)\right) \times 100 = (1 - 0.6895) \times 100 = 31.05.$$

Again, mean TSLD declines as the benchmark interval increases, because the observed mean interval since disturbance is lower than all expected tolerable intervals (Table 3).

Metric 2: Summed shortfall in time since last disturbance.—Currently, the frequency distribution of age classes is bimodal and highly skewed toward immature forest (nearly 40% is <6 yr old) and some very old forest (Fig. 2a). Irrespective of the expected benchmark interval, 4–7 yr immature forest is over-represented, and age classes >32 yr are under-represented (including mature forest; Fig. 2b). The distribution of too much area in young age classes means that longer expected tolerable intervals result in only slightly lower TSLD shortfall scores compared with the two other expected interval values, with all scores well under 50/100 indicating that habitat quality is below one-half that of pre-European quality for the yellow-bellied glider regardless of uncertainty in the baseline (Table 3).

Comparison of disturbance metrics with loss of extent metric.—In contrast with the highly cleared proteaceous mallee-heath example, approximately 82% of the original extent of mountain ash remains across 1,567 km², which yields a vegetation extent score of 82 out of 100, indicating

TABLE 3. Output of condition metrics for critically endangered mountain ash forest condition in relation to time since disturbance in 2013.

Assessment	Benchmark (expected mean TSLD) μ_e (yr)	Observed TSLD μ_o (yr)	Mean TSLD score (Eq. 1)	TSLD summed shortfall (Eq. 3)
Lower tolerable interval	70	37.26	53.22	41.71
Ideal mean tolerable interval	120	37.26	31.05	38.54
Upper tolerable interval	190	37.26	19.61	32.05

Note: Scores in the last two columns are a value out of 100, with higher values representing higher condition.

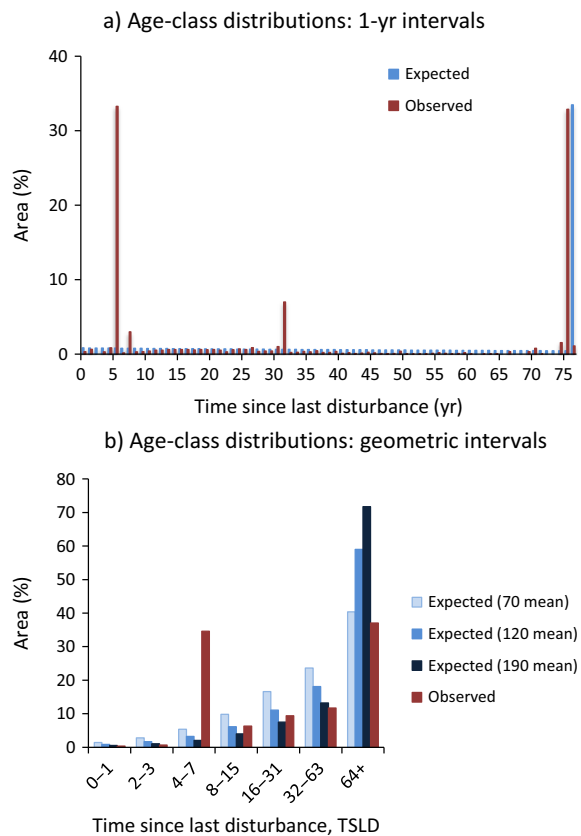


FIG. 2. Comparison of the observed vs. expected percentage of the Victorian mountain ash community in different age classes of time since last disturbance (here fire and tree harvesting of an intensity to kill mature trees) for (a) age-class intervals of 1 yr and an expected ideal benchmark of 120 yr since fire and (b) geometric age-class intervals for lower (70 yr, light blue), mean (120 yr, medium blue), and upper (190 yr, dark blue) expected benchmarks.

relatively good condition. The TSLD age-class distribution (Fig. 2) shows, however, that almost 50% of this extent has been disturbed in the last 30 yr. To ensure resource requirements are met for the yellow-bellied glider, this vegetation would need to be protected from disturbance into the future for 40 yr (for food) and up to 160 yr (for denning). Our disturbance metrics indicate the vegetation community is in much poorer condition (a maximum of 41.7/100 for summed shortfall, and 53.2 for mean TSLD; Table 3) than the metric based on extent alone.

Simulated age-class distributions

Our case studies both represent communities undergoing extremes of disturbance. To explore the sensitivity of our condition metrics to different distributions of disturbance across the landscape, we test our metrics on five simulated systems with the same extent and mean time since disturbance (40 yr), differing only in the observed distribution of age classes: (1) uniform (equal proportions

of each age class burned across all age classes), (2) two-parameter Weibull approximating that of the geometric distribution, (3) normal, (4) bimodal distribution, and (5) multimodal, subset into two classes of vegetation, large intact continuous vegetation with a homogeneous burning history and small patchily distributed patches with random burning history. This last simulation was designed to mimic burning histories typical of ecosystems such as the western Canadian boreal forests, where continuous tracts of vegetation burn infrequently but relatively homogeneously with high intensity, and small remnant patches burn independently of one another (Stocks et al. 2002). For each simulated system we evaluate mean TSLD and TSLD summed shortfall for reference condition benchmark intervals μ_e of 10–100 yr (incrementing by 10 yr).

The TSLD shortfall metric shows greater sensitivity to change in age-class distributions and behaves in a more logical fashion than mean TSLD. Mean TSLD always shows a similar pattern of increasing as the expected benchmark fire interval μ_e increases up to the mean observed TSLD (40 yr in simulated systems), then declining at benchmark fire intervals longer than the mean observed TSLD (Fig. 3a-e). In contrast, TSLD shortfall shows different patterns of relationship with expected benchmark fire interval μ_e , which depend on the distribution of age classes. For example, a normally distributed disturbed landscape results in a consistently low TSLD shortfall score, particularly for short fire intervals where the expected percentage of area would be much higher than the observed area (Fig. 3c). The simulated bimodal distribution indicates that mean TSLD would increase up to the mean observed fire interval in the community as the expected benchmark increased, despite the age-class distribution having an undesirable form for benchmark intervals around the observed mean observed interval (as indicated by lower TSLD shortfall scores around 40 TSLD; Fig. 3d). Of the simulated age-class distributions, the uniform and Weibull distributions show the strongest correlation between mean TSLD and TSLD shortfall (Pearson's product-moment correlation = 0.92 and 0.90, respectively, $P < 0.01$), with much lower correlation between these two metrics in the bimodal and multimodal landscapes (Pearson's product-moment correlation = 0.65 and 0.81, respectively, $P = 0.01$; Appendix S3: Table S2). This results in a higher correlation between mean metrics for different age-class distributions than correlation between TSLD metrics for different distributions (Appendix S3: Table S2). Importantly, differing condition of landscapes with the same mean disturbance interval may be distinguished using these metrics particularly if the age classes in one of those landscapes are bimodally distributed.

DISCUSSION

Here, we have demonstrated a straightforward way of assessing regional-scale condition of vegetation in ecosystems where the distribution of age classes may have diverged from an ideal or baseline reference distribution.

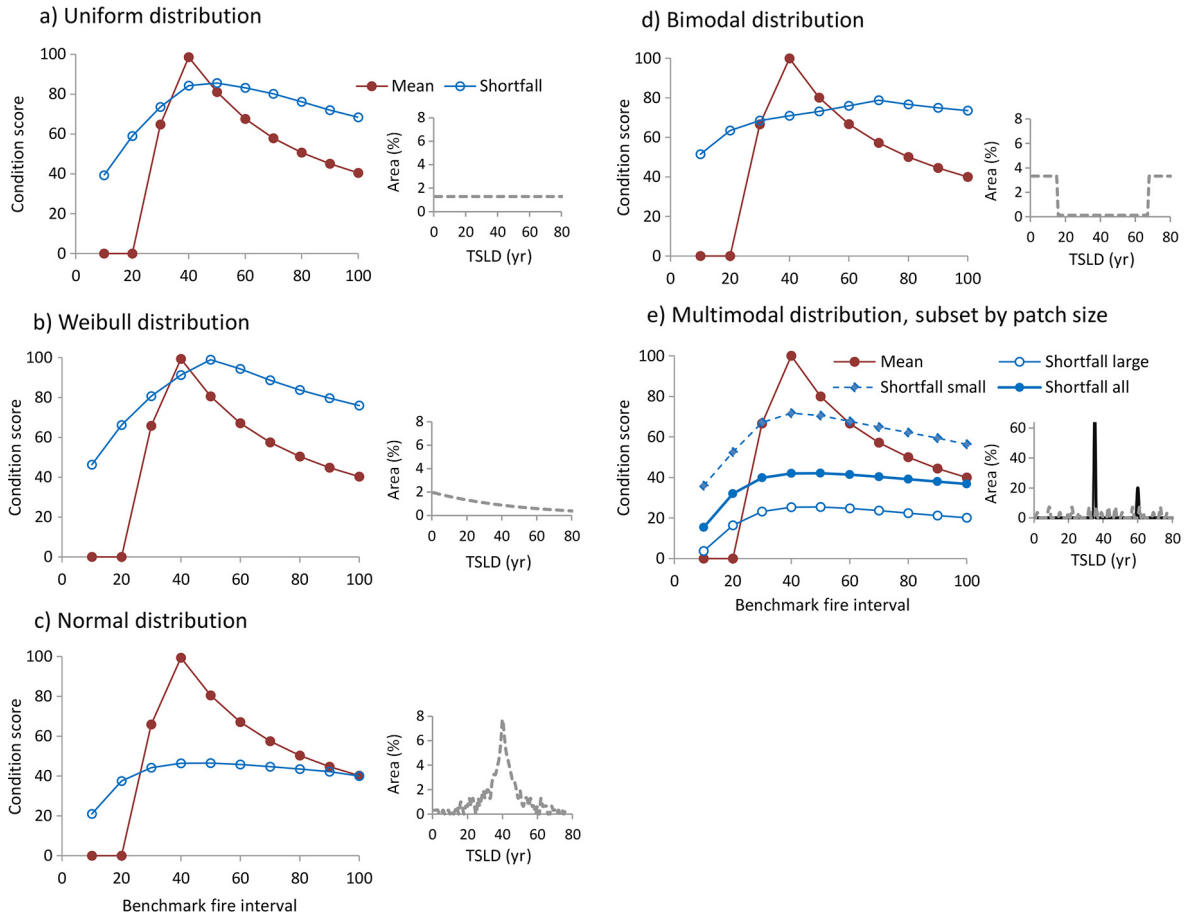


FIG. 3. Metric results for mean time since last disturbance (TSLD; red) and TSLD shortfall (blue) condition of simulation study for observed (a) uniform distribution, (b) Weibull distribution, (c) normal distribution, (d) bimodal distribution, and (e) multimodal distribution of vegetation in each age class with a mean time since disturbance of 40 yr, showing change in each metric as the expected reference benchmark interval increases.

Current broad-scale ecosystem metrics of condition fail to acknowledge that a community could be in multiple states, and each state could worsen or improve when impacted by a disturbance process such as fire or selective logging, depending on how far the current state diverges from pre-anthropogenic impact conditions. We evaluate two new metrics based on “time since last disturbance” (TSLD) that compare the mean and shortfall of vegetation age-class frequencies to an expected benchmark state. Our guided examples and simulations of different age-class distributions highlight the three major determinants of vegetation condition that are critical to understanding how the current ecological state of an ecosystem differs from historical conditions: (1) the current distribution of disturbance across the vegetation community, (2) the expected distribution of disturbance age classes associated with a biologically derived mean expected interval, and (3) the deviation of the current frequency of disturbance from expected disturbance frequencies.

Our new condition metrics aim to understand and quantify community change resulting from alternative

disturbance regimes. We describe condition as it relates to the area of disturbance of vegetation age classes, as this is easy to measure and relate to biodiversity responses. Our method relies on accurately mapped vegetation age-class information at broad scales, and clear definition of when an age class “resets” to zero under a given level disturbance in an ecosystem. Remote-sensing products such as MODIS provide excellent fire scar mapping for informing age classes of many fire-dependent ecosystems that reset to zero when the canopy burns, but do not necessarily detect artisanal or selective logging, or low intensity fire in ecosystems such as tropical forests where the canopy frequently obstructs below-canopy degradation (LiDAR products and unmanned aerial vehicles are increasingly useful for this; Paneque-Gálvez et al. 2014). Other elements of disturbance such as the intensity or configuration of one or multiple disturbance events are not assessed here as (1) the intensity (severity of disturbance, for fire often described as “hot” or “cold”) of disturbances such as fire is poorly mapped at a fine scale in comparison with the other elements of

landscape condition (although advances in remote sensing indicate that fine-resolution severity mapping should soon be available; Loschiavo et al. 2017) and (2) measures of vegetation community patchiness, fire seasonality, fragmentation, and landscape configuration already exist (Le Page et al. 2010, Wang et al. 2014, Tulloch et al. 2016a). We suggest future research focus on the most meaningful ways to combine these diverse types of information, thereby providing a nuanced understanding of remaining habitat quality as well as quantity for supporting species and communities.

Our two metrics of vegetation condition rely on an assessment of the expected or “ideal” mean time since disturbance to derive a reference benchmark distribution against which the current state is assessed (here, fire or logging; Stoddard et al. 2006, Thackway and Lesslie 2006, Sutherland and Peel 2010). The extent of anthropogenic change across much of the globe means that benchmark states are difficult to determine with a high degree of accuracy. Our Australian case studies benefitted from multiple empirical studies in each system to inform benchmark intervals (McCarthy et al. 1999, Lindenmayer and Wood 2010, Gosper et al. 2013, Tulloch et al. 2016b). In situations where such data sets are unavailable, a structured expert elicitation process might be used to derive estimates (Stoddard et al. 2006, Martin et al. 2012). Our benchmark disturbance intervals reflected objectives of either preserving the habitat resources for a species of conservation interest (the yellow-bellied glider in mountain ash forest), or maintaining dominant plant species in the community (Table 1). Alternative objectives (e.g., related to hazard reduction or other conservation targets) might lead to different baselines and ideal distributions. We explored the impacts of uncertainty in benchmark tolerable disturbance intervals on our perceptions of ecosystem condition informed by our two TSLD metrics. In both examples, higher benchmark disturbance intervals led to a decline in both metrics due to these vegetation communities having bimodally distributed age classes. In the proteaceous mallee-heath example, this indicates that the condition of the community is substantially worse for long-lived *Bankisia* than for species adapted to short fire intervals. In the mountain ash example, the condition of *E. regnans* is worse for ensuring yellow-bellied glider denning requirements than if we only cared about food requirements. Our results highlight that biologically meaningful benchmark states based on the needs of conservation-dependent flora and fauna are crucial for effective condition assessments that identify how far ecosystems have diverged from their ideal state and their ability to provide for dependent species (Taylor et al. 2013).

By accounting for, and penalizing, too-frequent and too-rare disturbances, our TSLD summed shortfall metric was more sensitive to change in age-class distributions than the mean TSLD metric, which was relatively insensitive to change in the underlying distribution of age classes (Fig. 3). The TSLD summed shortfall was relatively insensitive to the length of the data set used to

inform the condition score, particularly for short benchmark intervals (Appendix S3: Table S1). Our case studies varied in spatial scale, amount and timing of disturbance (fire or logging), the objective for measuring condition, and in benchmark disturbance intervals (Tables 1 and 3). By evaluating highly differing systems as well as a range of hypothetical observed age-class distributions, we ensured that our metrics performed consistently and provided information that in at least some cases is complementary. Our results suggest that the TSLD summed shortfall metric will be more informative than the mean TSLD metric for comparing the condition of ecosystems with different spatial and temporal distributions of disturbance. It should be noted that the age-class distributions that maximize species’ survival and abundance have been shown to vary substantially between taxa in disturbed landscapes (Di Stefano et al. 2009), due to variation in historical disturbance regimes as well as in species-specific needs for food and shelter. We kept the expected (i.e., historical) distribution of age classes constant in this study using a geometric distribution, which suits most systems that undergo regular disturbances (McCarthy and Cary 2002). In ecosystems where the history of disturbances leads to a different age-class distribution (e.g., if disturbances were historically very large and infrequent), the expected distribution of time since fire classes would be multimodal. Because ecosystems around the globe will have age-class distributions different from those evaluated in this study, we encourage managers to test our summed shortfall metric on systems with alternative expected age-class distributions and management scenarios. This will avoid situations where disturbance regimes are manipulated inappropriately due to misspecification of the expected distribution of age classes since disturbance.

The complementarity of our summed shortfall metric to traditional measurements of vegetation loss of extent indicates that a clear understanding of vegetation condition independent of vegetation loss is critical for informing ecosystem management. Numerous factors degrade the condition of a vegetation patch, including the presence and abundance of invasive species, human land management (e.g., livestock grazing), distance from human infrastructure such as urban development or roads, as well as disturbance regimes such as fire. The ability to demonstrate relationships between the location and timing of these processes, and vegetation degradation, represents an important step forward in accurately assessing the current and likely future state of ecosystems.

We ran analyses to determine the sensitivity of our metrics to alternative future disturbance scenarios (Appendix S3: Fig. S1), and results highlighted the usefulness of our summed shortfall metric for decision-makers and the public to comprehend the relative consequences of management alternatives (here, burning younger vegetation, older vegetation, or not at all over the next five years). Analyses such as these could be used by managers to compare proposed fire management

regimes for a portion of the landscape or for the entire ecosystem, and decide on the best option based on which option results in a higher summed shortfall score. Alternatively, managers could use the summed shortfall of an entire ecosystem as a restoration target aimed at elevating vegetation condition (e.g., “by 2030, vegetation type X will reach a TSLD summed shortfall score of 80”), and explore the costs of different strategies that could achieve these targets. As a third example, managers might use the summed shortfall metric to assess alternative subsets of ecosystem patches that differ in their shared characteristics such as ecological attributes or threats or governance (e.g., located within different protected areas, or surrounded by different land uses, or grouped by connectivity; see Tulloch et al. 2016a, b) for their relative condition. The score for each could be used in spatially explicit prioritizations to allocate conservation efforts (Moilanen et al. 2011, Evans et al. 2015). If users apply our proposed summed shortfall metric to different subsets of a vegetation type rather than its entirety, we recommend that (1) clear objectives are set for both habitat quality (measured using our summed shortfall metric) and habitat quantity (measured using a traditional metric such as loss of extent), (2) spatial scale is carefully considered (particularly the minimum mapping unit for defining an ecosystem subset), (3) metrics are updated regularly as new data (e.g., remotely sensed fire scars and vegetation loss) become available (Hansen et al. 2013). This will avoid costly mistakes such as assuming a patch was reset to age zero when in fact it was eliminated due to clearing, or focusing only on habitat quality and prioritizing only small high condition patches.

The state of vegetation continues to decline worldwide due to pressure from increasing human populations and associated resource requirements, as well as altered natural processes such as drought and fire regimes resulting from anthropogenic climate change (Liu et al. 2010, Hansen et al. 2013, Yang et al. 2014). These pressures do not occur homogeneously across the landscape, nor do they universally lead to loss of vegetation extent, and their heterogeneity across time and space creates vegetation communities with highly variable distributions of disturbance. We need more efficient approaches for measuring current vegetation condition to fully describe the extent of degradation of global ecosystems, ensure accurate assessment of change and help effective allocation of scarce land management resources. This paper provides a way forward for managers and policy makers to rapidly assess any landscape for current and future condition under alternative management scenarios, through understanding the landscape’s departure from the ideal distribution of vegetation age classes. Our simple, easily applied and transparent summed shortfall metric evaluates deviance in the distribution of vegetation age classes from an ideal benchmark state, and provides new information on ecosystem condition not currently gleaned from existing measures of ecosystem change based on

extent of vegetation loss or mean time since last fire. The metric can be applied in numerous ways for landscape evaluation or to guide spatially explicit management, from whole-of-ecosystem assessment to comparing the relative condition of ecosystem subsets, and it can be equally applied across large continuous tracts of vegetation or sparsely distributed patches, as long as the ideal benchmark can be estimated. We propose that metrics such as those demonstrated in this paper be applied to existing ecosystem assessments and accounts based on vegetation extent and patchiness (Rodríguez et al. 2011, van Dijk et al. 2014), to better understand the relative condition of different ecosystems and ensure that declines in ecosystem condition are identified before systems cannot be recovered.

ACKNOWLEDGMENTS

We thank the Wentworth Group of Concerned Scientists, particularly the Scientific Standards and Accreditation Committee, the Technical Environmental Accounting Committee, and Steering Committee for feedback on the metric. We are grateful to the regional staff and management of the Regional Environmental Accounts Trial NRM Regions, with particular thanks to Niilo Gobius for numerous discussions and trials of the metrics, and Sarah Comer for providing fire history data for southwestern Australia.

LITERATURE CITED

- Archibald, S., A. C. Staver, and S. A. Levin. 2012. Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences USA* 109:847–852.
- Bailey, R. L. 1980. Individual tree growth derived from diameter distribution models. *Forest Science* 26:626–632.
- Boyd, D. S., and G. M. Foody. 2011. An overview of recent remote sensing and GIS based research in ecological informatics. *Ecological Informatics* 6:25–36.
- Burns, E. L., D. B. Lindenmayer, J. Stein, W. Blanchard, L. McBurney, D. Blair, and S. C. Banks. 2015. Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. *Austral Ecology* 40:386–399.
- Comer, S., S. Gilfillan, S. Barrett, M. Grant, K. Tiedemann, and L. Anderson. 2001a. Esperance 2 (ESP2 – Recherche subregion). A biodiversity audit of Western Australia’s 53 biogeographical subregions in 2002. Department of Conservation and Land Management, Albany, Western Australia, Australia.
- Comer, S., S. Gilfillan, M. Grant, S. Barrett, and L. Anderson. 2001b. Esperance 1 (ESP1 – Fitzgerald subregion). A biodiversity audit of Western Australia’s 53 biogeographical subregions in 2002. Department of Conservation and Land Management, Albany, Western Australia, Australia.
- Cosier, P., and J. McDonald. 2010. A common currency for building environmental (ecosystem) accounts. Prepared for the 16th Meeting of the London Group on Environmental Accounting, on behalf of the Wentworth Group of Concerned Scientists.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342–355.
- Di Stefano, J., A. York, M. Swan, A. Greenfield, and G. Coulson. 2009. Habitat selection by the swamp wallaby (*Wallabia bicolor*) in relation to diel period, food and shelter. *Austral Ecology* 34:143–155.

- Evans, M. C., A. I. T. Tulloch, E. A. Law, K. G. Raiter, H. P. Possingham, and K. A. Wilson. 2015. Clear consideration of costs, condition and conservation benefits yields better planning outcomes. *Biological Conservation* 191:716–727.
- Felton, A. M., L. M. Engström, A. Felton, and C. D. Knott. 2003. Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biological Conservation* 114:91–101.
- Gill, A. M., J. Sharples, and G. Johnstone. 2014. Edge effects on between-fire interval in landscape fragments such as fire-prone terrestrial conservation reserves. *Biological Conservation* 169:54–59.
- Gosper, C. R., S. M. Prober, and C. J. Yates. 2013. Estimating fire interval bounds using vital attributes: implications of uncertainty and among-population variability. *Ecological Applications* 23:924–935.
- Hamilton, T., R. S. Wittkuhn, and C. Carpenter. 2009. Creation of a fire history database for southwestern Australia: giving old maps new life in a Geographic Information System. *Conservation Science Western Australia* 7:2.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.
- Incoll, R. D., R. H. Loyn, S. J. Ward, R. B. Cunningham, and C. F. Donnelly. 2001. The occurrence of gliding possums in old-growth forest patches of mountain ash (*Eucalyptus regnans*) in the Central Highlands of Victoria. *Biological Conservation* 98:77–88.
- Johnson, M. D. 2007. Measuring habitat quality: a review. *Condor* 109:489–504.
- Keith, D. A., et al. 2013. Scientific foundations for an IUCN Red List of ecosystems. *PLoS ONE* 8:e62111.
- Kuczera, G. 1987. Prediction of water yield reductions following a bushfire in ash-mixed species eucalypt forest. *Journal of Hydrology* 94:215–236.
- Laurance, W. F., et al. 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biological Conservation* 144: 56–67.
- Lawley, V., M. Lewis, K. Clarke, and B. Ostendorf. 2016. Site-based and remote sensing methods for monitoring indicators of vegetation condition: an Australian review. *Ecological Indicators* 60:1273–1283.
- Le Page, Y., D. Oom, J. M. N. Silva, P. Jönsson, and J. M. C. Pereira. 2010. Seasonality of vegetation fires as modified by human action: observing the deviation from eco-climatic fire regimes. *Global Ecology and Biogeography* 19:575–588.
- Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C., USA.
- Lindenmayer, D. B., and J. T. Wood. 2010. Long-term patterns in the decay, collapse, and abundance of trees with hollows in the mountain ash (*Eucalyptus regnans*) forests of Victoria, southeastern Australia. *Canadian Journal of Forest Research* 40:48–54.
- Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1990. The conservation of arboreal marsupials in the Montane ash forests of the central highlands of Victoria, Southeast Australia: I. Factors influencing the occupancy of trees with hollows. *Biological Conservation* 54:111–131.
- Lindenmayer, D. B., R. B. Cunningham, M. T. Tanton, A. P. Smith, and H. A. Nix. 1991. Characteristics of hollow-bearing trees occupied by arboreal marsupials in the montane ash forests of the Central Highlands of Victoria, south-east Australia. *Forest Ecology and Management* 40:289–308.
- Lindenmayer, D. B., R. B. Cunningham, and M. A. McCarthy. 1999. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-eastern Australia. VIII. Landscape analysis of the occurrence of arboreal marsupials. *Biological Conservation* 89:83–92.
- Lindenmayer, D. B., R. J. Hobbs, G. E. Likens, C. J. Krebs, and S. C. Banks. 2011. Newly discovered landscape traps produce regime shifts in wet forests. *Proceedings of the National Academy of Sciences USA* 108:15887–15891.
- Lindenmayer, D. B., W. Blanchard, D. Blair, L. McBurney, and S. C. Banks. 2016. Environmental and human drivers influencing large old tree abundance in Australian wet forests. *Forest Ecology and Management* 372:226–235.
- Liu, Y., J. Stanturf, and S. Goodrick. 2010. Trends in global wildfire potential in a changing climate. *Forest Ecology and Management* 259:685–697.
- Loschiavo, J., B. Cirulis, Y. Zuo, B. Hradsky, and J. Di Stefano. 2017. Mapping prescribed fire severity in south-east Australian eucalypt forests using modelling and satellite imagery: a case study. *International Journal of Wildland Fire* 26:491–497.
- Martin, T. G., M. A. Burgman, F. Fidler, P. M. Kuhnert, S. Low-Choy, M. McBride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. *Conservation Biology* 26:29–38.
- McCarthy, M. A., and M. A. Burgman. 1995. Coping with uncertainty in forest wildlife planning. *Forest Ecology and Management* 74:23–36.
- McCarthy, M. A., and G. J. Cary. 2002. Fire regimes in landscapes: models and realities. Pages 77–93 in R. A. Bradstock, J. E. Williams and M. A. Gill, editors. *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, Cambridge, UK.
- McCarthy, M. A., A. M. Gill, and D. B. Lindenmayer. 1999. Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. *Forest Ecology and Management* 124:193–203.
- McCarthy, M. A., A. M. Gill, and R. A. Bradstock. 2001. Theoretical fire-interval distributions. *International Journal of Wildland Fire* 10:73–77.
- McCarthy, M. A., et al. 2004. The habitat hectares approach to vegetation assessment: an evaluation and suggestions for improvement. *Ecological Management & Restoration* 5:24–27.
- Moilanen, A., J. R. Leathwick, and J. M. Quinn. 2011. Spatial prioritization of conservation management. *Conservation Letters* 4:383–393.
- O'Donnell, A. J., M. M. Boer, W. L. McCaw, and P. Grierson. 2011. Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. *Journal of Biogeography* 38:112–124.
- Panque-Gálvez, J., M. McCall, B. Napoletano, S. Wich, and L. Koh. 2014. Small drones for community-based forest monitoring: an assessment of their feasibility and potential in tropical areas. *Forests* 5:1481.
- Parsons, B. C., and C. R. Gosper. 2011. Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. *International Journal of Wildland Fire* 20:184–194.
- Richards, S. A., H. P. Possingham, and J. Tizard. 1999. Optimal fire management for maintaining community diversity. *Ecological Applications* 9:880–892.
- Rodríguez, J. P., et al. 2011. Establishing IUCN Red List criteria for threatened ecosystems. *Conservation Biology* 25:21–29.
- Rogeanu, M.-P., M. D. Flannigan, B. C. Hawkes, M.-A. Parisien, and R. Arthur. 2016. Spatial and temporal variations of fire regimes in the Canadian Rocky Mountains and Foothills of southern Alberta. *International Journal of Wildland Fire* 25: 1117–1130.

- Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18:235–249.
- Salis, M., A. A. Ager, M. A. Finney, B. Arca, and D. Spano. 2014. Analyzing spatiotemporal changes in wildfire regime and exposure across a Mediterranean fire-prone area. *Natural Hazards* 71:1389–1418.
- Shlisky, A., A. A. Alencar, M. M. Nolasco, and L. M. Curran. 2009. Overview: global fire regime conditions, threats, and opportunities for fire management in the tropics. Pages 65–83 in M. A. Cochrane, editor. *Tropical fire ecology: Climate change, land use, and ecosystem dynamics*. Springer Praxis, Berlin, Germany.
- Smith, A. L., W. Blanchard, D. P. Blair, L. McBurney, S. C. Banks, D. A. Driscoll, and D. B. Lindenmayer. 2016. The dynamic regeneration niche of a forest following a rare disturbance event. *Diversity and Distributions* 22:457–467.
- Stocks, B. J., et al. 2002. Large forest fires in Canada, 1959–1997. *Journal of Geophysical Research: Atmospheres* 107: FFR 5-1–FFR 5-12.
- Stoddard, J. L., D. P. Larsen, C. P. Hawkins, R. K. Johnson, and R. H. Norris. 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications* 16:1267–1276.
- Sutherland, W. J., and M. J. S. Peel. 2010. Benchmarking as a means to improve conservation practice. *Oryx* 45:56–59.
- Syphard, A., K. Clarke, and J. Franklin. 2007. Simulating fire frequency and urban growth in southern California coastal shrublands, USA. *Landscape Ecology* 22:431–445.
- 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.
- Taylor, R. S., S. J. Watson, A. F. Bennett, and M. F. Clarke. 2013. Which fire management strategies benefit biodiversity? A landscape-perspective case study using birds in mallee ecosystems of south-eastern Australia. *Biological Conservation* 159:248–256.
- Thackway, R., and R. Lesslie. 2006. Reporting vegetation condition using the Vegetation Assets, States and Transitions (VAST) framework. *Ecological Management & Restoration* 7:S53–S62.
- Thode, A. E., J. W. van Wagtenonk, J. D. Miller, and J. F. Quinn. 2011. Quantifying the fire regime distributions for severity in Yosemite National Park, California, USA. *International Journal of Wildland Fire* 20:223–239.
- Tulloch, A. I. T., M. D. Barnes, J. Ringma, R. A. Fuller, and J. E. M. Watson. 2016a. Understanding the importance of small patches of habitat for conservation. *Journal of Applied Ecology* 53:418–429.
- Tulloch, A. I. T., J.-B. Pichancourt, C. R. Gosper, A. Sanders, and I. Chades. 2016b. Fire management strategies to maintain species population processes in a fragmented landscape of fire-interval extremes. *Ecological Applications* 26:2175–2189.
- van Dijk, A., R. Mount, P. Gibbons, M. Vardon, and P. Canadell. 2014. Environmental reporting and accounting in Australia: progress, prospects and research priorities. *Science of The Total Environment* 473–474:338–349.
- Venter, O., et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* 7:12558.
- Wallenius, T. H., J. Pennanen, and P. J. Burton. 2011. Long-term decreasing trend in forest fires in northwestern Canada. *Ecosphere* 2:art53.
- Wang, X. L., F. G. Blanchet, and N. Koper. 2014. Measuring habitat fragmentation: an evaluation of landscape pattern metrics. *Methods in Ecology and Evolution* 5:634–646.
- Yang, J., H. Tian, B. Tao, W. Ren, J. Kush, Y. Liu, and Y. Wang. 2014. Spatial and temporal patterns of global burned area in response to anthropogenic and environmental factors: reconstructing global fire history for the 20th and early 21st centuries. *Journal of Geophysical Research: Biogeosciences* 119:249–263.
- Zerger, A., P. Gibbons, J. Seddon, S. Briggs, and D. Freudenberger. 2009. A method for predicting native vegetation condition at regional scales. *Landscape and Urban Planning* 91:65–77.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1676/full>