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### Understanding the long-term impact of prescribed burning in mediterranean-climate biodiversity hotspots, with a focus on south-western Australia

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**Abstract.** Wildfires are expected to increase worldwide both in frequency and intensity owing to global warming, but are likely to vary geographically. This is of particular concern in the five mediterranean regions of the world that are all biodiversity hotspots with extraordinary plant and animal diversity that may be impacted by deliberately imposed fire. Wildland managers attempt to reduce the impact and mitigate the outcomes of wildfires on human assets and biodiversity by the use of prescribed burning. The response that we must 'fight fire with fire' is understandable, perceived as reducing the flammability of wildlands in fire-prone regions and lessening the impact of wildfires. The long-term impact on biodiversity is, however, less clear. The practice of prescribed burning has been in place and monitored in south-western Australia for 50 years, longer and more intensively than in most other mediterranean ecosystems. The present target is for 200 000 ha burned each year in this biodiversity hotspot. Published studies on the impact of this burning on infrastructure protection and on biodiversity are here used to understand the protective capacity of the practice and to foreshadow its possible long-term ecological impact across all mediterranean ecosystems.

Additional keywords: biodiversity hotspot, fire frequency, fire interval, mosaic burning.

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#### Introduction

Twenty-five global biodiversity hotspots threatened by habitat alienation and degradation were highlighted in a landmark study in 2000 (Myers *et al.* 2000). The number was later increased in 2004 to 34 (Mittermeier *et al.* 2004) and then 35 (Williams *et al.* 2011), with 5 located in ecosystems with mediterranean-type climates (Brooks *et al.* 2002). These are: the Greater Cape Floristic Region (GCFR) known as fynbos; South-west Australian Floristic Region (SWAFR) or kwongkan;<sup>1</sup> Californian Floristic Region (CalFR) or chaparral; Mediterranean Floristic Region (MFR) or maquis and garrigue, and the Chilean Floristic Region (ChilFR) or matorral.

Endemicity in both plants and vertebrate species is exceptionally high in these biodiverse mediterranean ecosystems, ranging, in plants, from 46.8% in the Chilean matorral to 69.5% in the Cape Province fynbos (Table 1). Fire is an integral component of the natural ecological processes of many global biomes (Bond *et al.* 2005), with some of the most fire-prone being in the mediterranean biodiversity hotspots (Di Castri *et al.* 1981; Pignatti *et al.* 2002; Burrows 2008; Underwood *et al.* 2009). However, combustibility of these systems due to their warm, dry summers means that the natural cycle of fires during the dry season often leads to large and, in human terms, catastrophic impacts (Pausas *et al.* 2008; Syphard *et al.* 2009).

Prescribed burning is undertaken in all mediterranean regions, and almost exclusively for the purposes of fire hazard reduction, despite science being available to inform fire management for environmental and biodiversity objectives

<sup>&</sup>lt;sup>1</sup>The preferred spelling of 'kwongan' is now 'kwongkan', following Hopper (2014).

### Table 1. Biodiversity and endemicity in five Mediterranean-climate ecosystems

(adapted from Myers et al. 2000, with other sources as noted)

Ecosystem	Plant species	% Endemic	Vertebrate species	% Endemic
Chilean matorral Californian chaparral Cape Province fynbos	4333 <sup>D</sup> 6143 <sup>B</sup> 8920 <sup>E</sup>	46.8 42.0 <sup>B</sup> 69.5	335 584 562	18.2 12.2 9.4
Mediterranean basin SW Australia	25000 8379 <sup>A</sup>	52.0 47.0 <sup>A</sup>	770 550 <sup>C</sup>	30.5 21.5 <sup>C</sup>

<sup>A</sup>Gioia and Hopper (2017); <sup>B</sup>Burge *et al.* (2016); <sup>C</sup>Rix *et al.* (2015); <sup>D</sup>Moreira-Munoz (2011);

<sup>E</sup>Goldblatt and Manning (2002).

(Van Wilgen *et al.* 1992; Driscoll *et al.* 2010*a*, 2010*b*; Penman *et al.* 2011). Minimising fuel loads in an attempt to reduce the impact of unplanned fires on life, property and forestry assets remains the primary objective of prescribed burning in South African fynbos (Van Wilgen *et al.* 2010), fire-suppressed forests in California (Bagne and Purcell 2011), woodland and forest in south-western Australia (McCaw and Hanstrum 2003; Boer *et al.* 2009; McCaw 2013), and fire-prone ecosystems throughout Mediterranean Europe (Fernandes *et al.* 2013; Sagra *et al.* 2017). Biodiversity management is sometimes a secondary objective (Fernandes *et al.* 2013; Enright and Fontaine 2014).

Analysis of the scientific support underpinning prescribed burning practices emphasises this unbalanced focus, with research predominantly concentrated on analyses of ignition patterns, fuel dynamics, fire intensity and fire-return periods from a management perspective (Williams and Bradstock 2008; Fernandes 2018). Additionally, the literature contains an overrepresentative complement of studies from European softwood forests compared with other mediterranean ecosystems. In a recent global review, Fernandes (2018) concluded that prescribed burning has a fragmented and incomplete scientific foundation supported by very few site- or region-specific studies.

The aims of the present review are to understand the impacts of prescribed burning on biodiversity through an analysis of the practice in the highly fire-prone mediterranean biodiversity hotspots, using a two-fold approach: (i) to review current prescribed burning practices in mediterranean-climate ecosystems and recent research on their impact; and (ii) review research over a 50-year period on the impact of prescribed burning on biodiversity in the south-west Australian hotspot as a template for possible impacts in similar regions globally.

# Occurrence of wildfire, timing and frequency of prescribed burning in mediterranean-climate ecosystems

Natural wildfires generally occur in summer throughout mediterranean regions (Van Wilgen *et al.* 2010; Bagne and Purcell 2011; McCaw 2013; Céspedes *et al.* 2014). Typically, managers frequently (and in some instances almost exclusively) burn outside the dry summer, opting for milder seasons when fire intensities are likely to be low and escapes are less likely. Most prescribed burning in South Africa occurs during autumn and winter (April to September) (Van Wilgen *et al.* 2010), in Mediterranean Europe during late winter and early spring (Casals *et al.* 2016; Sagra *et al.* 2017), in California during spring (Bagne and Purcell 2011), and in south-western Australia during autumn, winter and spring (McCaw 2013). There is only one example from the South African fynbos where prescribed burning for protection of biodiversity is emphasised during the 'natural' dry season burn period from November to March (Brown *et al.* 1991; Van Wilgen *et al.* 2010).

Published studies suggest that median fire return intervals for prescribed burning in mediterranean ecosystems, though variable between regions, average between 9 and 15 years (Van Wilgen 1981, 1982; Van Wilgen et al. 2010; McCaw 2013). Duration of the inter-fire period is often ecologically significant. For example, a minimum inter-fire period of 12-15 years is required to minimise changes in life history frequencies and the loss of important overstorey shrubs in fynbos (Van Wilgen et al. 2010). The frequency of prescribed burning in these regions (as frequently as every 2-4 years) is asynchronous with these requirements, and reflects a propensity by land managers to place perceptions of safety before ecological considerations. A global review of the effectiveness of prescribed burning for fire hazard reduction found that these short treatment cycles resulted from the effectiveness of prescribed fire being constrained by high fuel accumulation rates (Fernandes and Botelho 2003). These authors also concluded that 'The operational effectiveness of prescribed fire inferred from case studies is largely anecdotal, and most of the examples of success that are available refer to recently (up to 4 years) treated areas'.

# Impact of prescribed burning in mediterranean-climate ecosystems

Various studies highlight the potentially deleterious effects of high fire frequencies; for example, changes to the chemical and biological properties of soils (Gillon and Rapp 1989; Úbeda *et al.* 2005; Pellegrini *et al.* 2017) and cryptic effects such as increased seedling predation (Sagra *et al.* 2017), indirect mortality due to bark beetle attacks (Fettig *et al.* 2010), changes in the frequency and relative abundance of keystone shrub species (Van Wilgen 1981, 1982; Van Wilgen *et al.* 2010; Céspedes *et al.* 2014), and the invasion of fire-tolerant, fire-enhanced weed species (Van Wilgen 2009; Gomez-Gonzalez *et al.* 2010; Van Wilgen 2013).

More pertinently, the ecological effects of conducting aseasonal prescribed burns remain little studied. Bagne and Purcell (2011) note that low-severity prescribed fires during the spring breeding season in California had a negative impact on groundnesting birds, but generally drove bird communities towards pre-fire suppression conditions. Arkle and Pilliod (2010) suggest that aseasonal prescribed burning in riparian forest did not mimic the ecological effects of natural fire, potentially eliminating an important natural disturbance from these habitats. Roche *et al.* (1998) found that season of stimulation of the soil seed bank had a profound effect on seedling emergence and survival, with spring stimulation (equivalent to winter and spring prescribed burning) resulting in a collapse in seedling survival during the first summer, in comparison with a previous summer or autumn ignition.

Importantly, Fernandes (2018) identifies several deficiencies and knowledge gaps in current prescribed burning practices in southern Europe that appear common throughout mediterranean regions. These include the role of prescribed burning in facilitating invasive plant species (and how such species alter ecosystem flammability), a general lack of research into the effects of prescribed burning (particularly aseasonal burns) on the diversity and behaviour of fauna, and poor understanding of the cumulative ecological effects of prescribed burning at different spatial and temporal scales (Haslem *et al.* 2011).

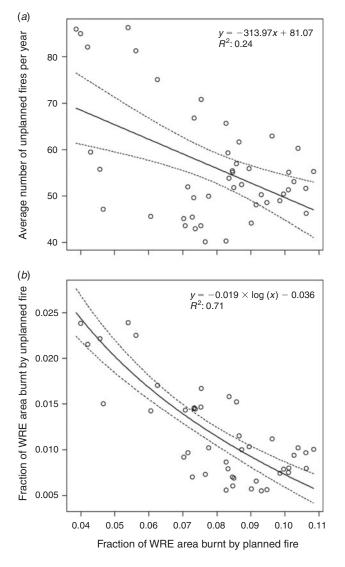
Critically, given hazard reduction as a stated primary aim, studies indicate that prescribed burning has no or only a modest effect on subsequent unplanned fire in mediterranean regions, or may increase flammability, as found in other biomes including south-eastern Australian woodlands and forest (Zylstra 2018). Boer et al. (2009) present evidence that the percentage of the area treated by prescribed burning over a preceding period of up to 6 years had a significant negative effect on the percentage of the area burned by unplanned fire in south-west Australian forests. Fernandes et al. (2013) suggest that prescribed fire application in Europe is unlikely to reduce wildfire hazard and Van Wilgen et al. (2010) conclude that prescribed burning is broadly ineffective at reducing the incidence of wildfires in fynbos. This is unsurprising if the best results of prescribed fire application are likely to be attained in heterogeneous landscapes and in climates where the likelihood of extreme weather conditions is low, as suggested in a global review by Fernandes and Botelho (2003). Most, if not all mediterranean regions are characterised to some degree by broad- rather than fine-scale turnover of vegetation communities, and frequent extreme weather conditions. Current fire management practices are unlikely to appreciably reduce the threat to infrastructure assets, but may significantly negatively impact biodiversity (Driscoll et al. 2010a), and it is unlikely that prescribed burns can replace unplanned 'wild' fire (Price 2012). Prescribed burning is generally not necessary to provide sufficient fire for regeneration in fynbos (Van Wilgen et al. 2010), and is thought to have little utility for managing biodiversity in southern Europe (Fernandes et al. 2013; Fernandes 2018). It is also of limited efficacy in biodiversity conservation in arid grasslands in Australia owing to taxon-dependent and unpredictable species responses (Pastro et al. 2011). Despite the evidence from these studies, there is a political dimension to prescribed burning, with government agencies often unwilling to prioritise the environment over the perception of safety issues (Morrison et al. 1996; Driscoll et al. 2010a; Buizer and Kurz 2016).

In south-western Australia, in particular, there are alternatives to reduce flammability while enhancing biodiversity. A significant factor in the build-up of litter is the role played by animals that regularly burrow, tunnel or construct mounds, plough through soil, ingest soil or dig pits while foraging; these animals are referred to as bioturbators (Valentine 2014). In places where the bioturbators continue to be active, the litter layer is thin. However, in many forests, predation by feral cats and foxes has decimated the population density of bioturbators (Short and Smith 1994; Abbott 2002; Short 2004), and the litter layer has increased. Better control of feral animals should be an element of a holistic approach to manage litter and fire risks (Fleming *et al.* 2014). Invasive weeds may also exacerbate fire hazards in bushland and threaten native biodiversity (Milberg and Lamont 1995), which may be mitigated by mechanical or herbicidal removal of flammable invasive weeds, such as the veld grass *Ehrharta calycina* in Western Australia (Dixon *et al.* 1995*b*, 1995*c*).

Recent research suggests that it is possible to conduct prescribed burning in a manner that would have neutral biodiversity impacts (Monimeau et al. 2002; Ubeda et al. 2005; Van Wilgen et al. 2010; Fernandes et al. 2013; Moreno and Rouco 2013; Céspedes et al. 2014; Casals et al. 2016; Sagra et al. 2017). However, the current global emphasis on burning, on often increasing scales for human safety rather than for ecological considerations, is of concern. If the argument for burning as a safety tool is set aside, evidence suggests that prescribed burning throughout mediterranean regions is being undertaken almost ubiquitously at too high a frequency, during ecologically inappropriate seasons, with inadequate scientific justification, and with poor spatial management - factors likely to result in significant impacts on ecosystem function in some of the most notable global biodiversity hotspots (Acácio et al. 2009). An example of the negative impact that prescribed burning can have on a rare and endangered species is the Proteaceae shrub Mimetes stokoei in the fynbos. This plant is quite short-lived, survives inter-fire periods as seeds that are buried by ants (Bond and Slingsby 1983), and requires high-temperature fires for their germination. Several 'slow, cool prescribed burns' in 1971 and 1984 failed to trigger germination of any seedlings, and the species was declared 'extinct'. In 1999, the area was burnt in an extremely hot uncontrolled wildfire, and 24 seedlings emerged (Slingsby and Johns 2009), changing its status from 'extinct' to 'critically endangered'. This example illustrates the failure of 'safe' prescribed burns to ensure the conservation objective, and it is likely that ecosystem managers would not have permitted higher-intensity fires for safety reasons (Van Wilgen 2013). Although large catastrophic wildfires, and how they might be avoided, are the focus of much of the attention at present, there is appreciation that conservation outcomes may not always be disastrous following such events (Bradstock 2008; Keane et al. 2008; Yates et al. 2008).

## How effective is prescribed burning at preventing wildfires in mediterranean-climate ecosystems?

Prescribed burning, unless on a massive scale, is unlikely to reduce wildfire hazard in Europe (Fernandes *et al.* 2013; Fernandes 2018), the fynbos (Van Wilgen *et al.* 2010), or in temperate regions such as the biodiverse region of Tasmania (Furlaud *et al.* 2018). A major long-term study of prescribed burning over a 52-year period in the south-west Australian biodiversity hotspot provides some of the best evidence available to assess its ability to reduce the impact and frequency of wildfires (McCaw *et al.* 2005; Boer *et al.* 2009). Prescribed fire had a statistically significant effect in reducing the incidence of wildfire up to 6 years following the prescribed fire. There was no analysis, however, of the potential effects of prescribed burning on the behaviour of unplanned fire, or of any protective effects



**Fig. 1.** Six-year running means of the annual number (*a*), and extent (*b*) of unplanned fires against 6-year running means of the annual extent of planned fire (1958–2003). Fire extent shown as fractions of the current surface area of the Warren Region Estate. Black continuous lines are for fitted regression models. Dashed lines show 95% confidence intervals (from Boer *et al* 2009 with permission).

that might result from the fuel reduction. When burnt areas over the whole 6-year period were averaged, 71% of the variation in the mean annual extent of unplanned fires was explained by the area prescribed-burned over the same 6-year period, but the slope of the regression was only -0.26 (Fig. 1). This figure is a direct measure of the 'leverage' prescribed burning has on mitigating unplanned fire, defined as the unit reduction in unplanned fire area resulting from one unit of previous fire. The figure of Boer *et al.* (2009) of -0.26 means that approximately four times the area needs to be burned in order to protect any given area from wildfire. Higher and more effective leverage values have been reported in Portugal and some areas in the United States (Loehle 2004; Price *et al.* 2015*a*). The question of leverage is an important one and a recent review on the effectiveness of fuel reduction burning (FRB) in south-west and south-east Australia notes:

'There is as yet no clear scientific agreement concerning the protection or ecological benefits of treating larger area by FRB, and recent studies into leverage suggest that FRB programs provide a poor return on investment in terms of area of wildfire reduced relative to area treated by FRB' (Enright and Fontaine 2014).

A recent paper by Price et al. (2015b) investigated geographic variation in leverage value from prescribed burns in Australia and found they were, with two exceptions, all lower than the figure of 0.26 cited in the study of Boer et al. (2009), with many zero or even negative (i.e. no protective effect of prescribed burning at all, or an increased risk of fire due to the PB). In the Australian Alps, for example, leverage was only 0.086, meaning that almost 12 times the area to be protected needs to be prescribed-burned (Zylstra 2018). The latter study makes it very clear that the West Australian model for wildland fire protection is not exportable to other ecosystems and is further supported by a study of global patterns in fire leverage (Price et al. 2015a). A recent study simulating the effectiveness of prescribed burning at altering wildfire behaviour in Tasmania concluded that ' prescribed burning can theoretically mitigate wildfire, but that an unrealistically large area would need to be treated to affect fire behaviour across the island' (Furlaud et al. 2018). They go on to recommend investigating alternative methods of reducing fuel loads instead of prescribed burning, including strategic mechanical thinning, but one would need to ensure that bioturbators are protected.

Several studies also considered the level of protection of property afforded by prescribed burning of surrounding bushland. In a study carried out following the Black Saturday fires in Victoria in 2009, all fuel treatments were more effective if undertaken closer to built infrastructure. For example, 15% fewer houses were destroyed if prescribed burning occurred at the observed minimum distance from houses (0.5 km) for controlling fire spotting, rather than the observed mean distance from houses (8.5 km) (Gibbons *et al.* 2012). These results imply that a shift in emphasis away from broad-scale fuel reduction to intensive fuel treatments close to property will more effectively mitigate impacts from wildfires on infrastructure.

# What is the impact of frequent prescribed burning on biodiversity? The south-west Australian biodiversity hotspot as an exemplar

Essential to any debate on the impact of fire on biodiversity in the South-west Australian hotspot is knowledge of the fire regime(s) under which that biodiversity evolved. There is a strongly held belief too, known as the 'historical-fire-regime concept', that replicating the pattern of fires ignited by lightning or pre-industrial humans best promotes native species in fire-prone regions (Freeman *et al.* 2017). Aborigines arrived in Australia c.50 000 years ago (Turney *et al.* 2001; Clarkson *et al.* 2017), but the biodiversity long predated this and evolved in concert with a pre-Aboriginal fire regime. Recent archaeological excavations on Barrow Island, some 1400 km north of the Western Australian capital Perth, have shown that its rich biodiversity has persisted unchanged, despite the absence of Aboriginal burning on the island for c.7000 years (Veth *et al.* 2014, 2017). This suggests that other factors, such as the introduction of exotic predators and competitors, are likely responsible for the recent loss of small mammals in desert regions in the absence of traditional burning practices (Morton 1990; Short and Turner 1994; Bowman 1998).

What little information there is on pre-European fire regimes in south-western Australia comes from several sources: archaeological charcoal deposits, burn scars in old growth trees and early European records. Although early explorers and settlers reported on much smoke and fire generated by Aborigines, they had no way of estimating the area of land being burnt (Abbott 2003), though Aboriginal oral evidence points to selectivity rather than ubiquity as being the norm in the south-west (Prober et al. 2016). We have evidence of the frequency of natural fires in Australia and Western Australia during the previous 2-3 million years (Mooney and al. 2011). This is based on carbon fragments and pollen grains of fire-following species of the Gyrostemonaceae found in cores drilled into the base of ancient lakes, and at the Yallalie impact crater east of Jurien Bay (Hassell and Dodson 2003; Dodson et al. 2005). Fire frequencies in the fire-prone sandplain habitat at Yallalie averaged 12-14 years 3 million years ago, compared with 81 years in the jarrah forest before European settlement (Burrows et al. 1995), and from 80 to 100 years 3000-4000 years ago on the south-eastern coast of Western Australia, now the Fitzgerald River National Park (Hassell and Dodson 2003). The best evidence of pre-Aboriginal fire regimes indicates that they were extremely variable, potentially of limited landscape-scale impact and depended on location, with fire frequencies ranging from 12-14 years in semiarid parts of Western Australia to 80-100 years in the jarrah forest on the Darling Scarp and along the south coast (Enright and Thomas 2008). Significantly, a recent study of the impact of fire interval on trees in a banksia woodland in Eneabba, near the Yallalie impact crater, found that the lowest rates of mortality of the trees were associated with a fire interval of 10-14 years (Enright et al. 2011), which approximates the pre-human fire frequency for the region.

The burn frequencies currently employed in south-west Western Australia are linked with desired fuel levels of 8 tonnes  $ha^{-1}$  for jarrah forests and 19 tonnes  $ha^{-1}$  for karri forests. Current prescribed burn frequencies are 5-7 years in jarrah forest and 8-11 years in karri forest (Burrows et al. 2008). This contrasts with a pre-European burn frequency in the jarrah forests of 81 years (Burrows et al. 1995) and much longer in karri forests (Rayner 1992). For the purposes of fire control, the landscape has been divided into three Land Management Zones (LMZs) 1, 2 and 3. LMZ 1 refers to areas close to (5 km) and surrounding town sites and other such infrastructure, which must be protected, but LMZs 2 and 3 cover much of the southwest biodiversity hotspot, and together have a target of 180 000 ha to be burned per annum out of the total 200 000 ha (Fig. 2). Given the leverage, this amount of burning would only protect an area of ~45 000 ha from wildfire. However, the main

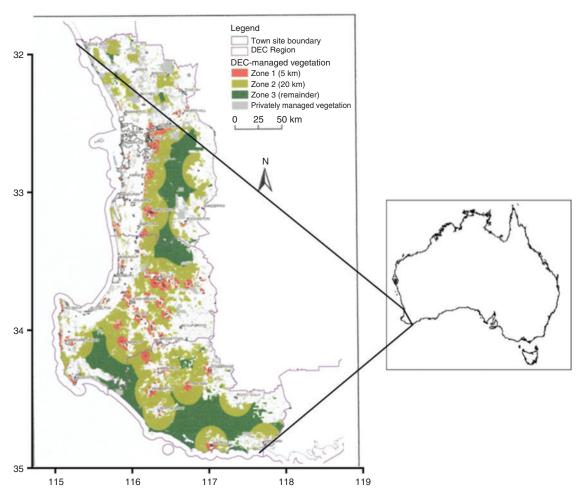
driver of when to impose fire is related to time since last prescribed burn (which for the south-west hotspot is 6 years – see below) independently of fuel loads with low fuel-carrying ecosystems, such as kwongkan hyperdiverse shrublands now subject to the practice.

After a large fire in Western Australia's south-west in January 2016 that partially destroyed the small town of Yarloop, the Ferguson Review established after the fire recommended that:

'The annual objective is to treat a total of 60 000 hectares of priority hazard reduction per annum, ... the strategic objective will be that a fuel age of less than six (6) years will be maintained across 45% of the landscape on State Forest, National Parks and other Parks and Wildlife managed lands in the South West and Perth Hills' (Ferguson 2017)

Inherent in this recommendation is the belief that many Australian plant species require fire to complete their life cycle and are 'fire-adapted' and will not be harmed by recurrent burning, i.e. regeneration cycles of plants are 6 years or less. This assumption has been questioned (Main 1996; Hopper 2003; Bradshaw et al. 2011) and is a critical one, as it is one of the main justifications for the use of so-called 'biodiversity conservation burns'. The idea that many Australian plant species depend on fire to successfully complete their reproduction is a concept embedded in the national psyche (Horton 2000). Trees such as banksias and hakeas that store seeds for many years in the canopy, a trait known as serotiny or bradyspory, are exemplars of this stratagem and it is widely believed that the seeds are only released by fire (Gill 1981; Burrows and Abbott 2003; Keeley et al. 2012). There is no doubt that many species do release their seeds immediately following fire, but less well known is the fact that many species of banksia and other serotinous species release seed over time if a fire does not occur. The common candle banksia, for example, Banksia attenuata, relies on a proportion of seed release in the inter-fire period, with total release of remaining seeds in the canopy in concert with fire (Enright et al. 1998).

There is anecdotal evidence that some trees and shrubs senesce and die after many years in the absence of fire (Gent and Morgan 2007; Close et al. 2009) and in the Eneabba study of Enright et al. (2011), mortality of Banksia attenuata and Melaleuca leuropoma (but not Hibbertia hypericoides) was significantly greater in areas that had not been burnt for 39-42 years. It is well established that disturbance of some kind is needed to maintain species that are associated with particular seral stages in a climax succession (Connell 1978; Fox 1979). Thus, if a given plant or animal is not associated with the climax state of the succession, but with one of the seral states leading to the climax, it will require a major disturbance of some kind (fire, tornado, etc.) for gap creation with a return of the ecosystem to an earlier seral state. An example of a disturbance producing an effect usually associated with fire is provided by Bald Island marlocks (Eucalyptus conferruminata) growing in an area on the south coast that was stripped of vegetation by a severe tornado in 2007, which responded with epicormic sprouting, similarly to their response after fire (Bradshaw et al. 2011).



**Fig. 2.** Department of Biodiversity, Conservation and Attractions (DBCA) Land Management Zones (LMZs). LMZ 1 (20 000 ha) refers to a 'Community Protection Zone' within a 5-km radius of town sites and other such infrastructure, where prescribed burning would be at a frequency of <4 years; LMZ 2 (70 000 ha) is a 'Bushfire Modification Zone' where prescribed burning would be maintained at a frequency of 5–7 years over a further 20-km radius; LMZ3 (110 000 ha) refers to a 'Biodiversity Management Zone' where one-third of the area would be prescribed burned at a frequency of <4 years, a further third at 4–7 years, and one-third at >7 years (adapted from DPaW (2017) and Burrows and McCaw 2013). DEC, Department of Environment and Conservation.

Many Australian plants germinate only after fire, and some of the so-called 'fire ephemerals' are also thought to be 'obligate' fire followers, i.e. they depend on fire without which they cannot germinate. Flowering after fire, so-called 'pyrogenic' flowering, was identified in 9 species from a total of 429 in south-west Australian shrublands, 7 of which were thought to be obligate fire-stimulated flowering species (Pate *et al.* 1984). Post-fire flowering is known to be stimulated by ethylene gas produced by the fire, which is also produced by senescing and rotting vegetation (George 1993).

The discovery in 1995 that smoke alone stimulates germination in a range of Western Australian plants with dormant seeds (Dixon *et al.* 1995*a*) initially reinforced the paradigm that fire is essential for the reproduction of many species, including in mediterranean regions (De Lange *et al.* 2018). Subsequent research, however, isolating and identifying the chemical compound in smoke responsible for the effect (Dixon et al. 2009) has led to a more nuanced understanding of the process. The major stimulant, a butenolide known as karrikinolide, is produced by the oxidation of plant tissue, and thus, most likely, occurs in low concentrations in rotting vegetation as well. Fire involves a massive increase in rates of oxidation of plant tissue and smoke that is rich in karrikinolide. The fact that smoke-induced germination has now been described in a wide range of plants, including lettuce, celery, corn and red rice (Chiwocha et al. 2009), none of which is associated with fire-prone environments, makes it clear that the role of fire in the process is incidental. Whether there are in fact any plant species that fail to reproduce in the absence of fire is not known with any certainty. Pyrorchis nigricans, a 'pyrogenic' orchid, for example, flowers only after fire in the south-west of Western Australia, but flowers without fire in the south-eastern part of its range, near Ravensthorpe.



Fig. 3. The unintended consequences of prescribed burning on biodiversity result in species losses. (a) Prescribed burning in the south-western Australian biodiversity hotspot peat swamps results in the loss of peat beds accumulated over a period of  $\sim$ 5000 years. (b) The exposed lignotuber and roots of a dead *Homalospermum firmum* (Myrtaceae), owing to 60 cm of peat burnt away through high-intensity fire, contrasted with a surviving Albany pitcher plant (*Cephalotus follicularis*, Cephalotaceae) (insert, photo June 2018, S. D. Hopper). (c) Prescribed burning of banksia woodland in south-western Australia. (d) Prescribed burning of a nature reserve south of Perth resulted in the death of this translocated critically endangered western ringtail possum (*Pseudocheirus occidentalis*) (photo A. Dixon).

Managers have sought to base burn frequencies in south-west Western Australia on fundamental regeneration indices of the ecosystem. A 'rule-of-thumb' adopted by most fire managers is that the shortest interval between burns should be double the time to flowering of the slowest obligate seeder in the community (Burrows and Wardell-Johnson 2003). A survey of 639 plant species in forests and associated ecosystems in south-west Western Australia recorded that 97% of understorey species reached flowering age within 3 years of fire and all species within 5 years (Burrows et al. 2008). It is important to note, however, that the 'juvenile period' was defined by the authors as 'the time taken for at least 50% of individuals in a population to reach flowering age after fire'. In determining a minimum time, the authors made no attempt to establish the extra time needed for seed production sufficient to support replacement of plants lost through fire, even though many species such as banksias produce low levels of viable seed in the first years after flowering (Enright et al. 1996; Wooller et al. 2002). Within a drying climatic environment in temperate Australia, it is probable that the time intervals to parent plant replacement post fire will be substantially extended as plant growth and productivity decrease in response to declining rainfall, with ecosystems at the drier margins likely to require substantially longer fire-free periods (Enright *et al.* 2015).

A separate study detailed times to flowering of a variety of forest species and recorded 24 species from a total of 198 in the jarrah forest that take 6 years or more to flower from germination (Muir 1987). This should mandate a minimum burn frequency of at least 12 years in jarrah forest, keeping in mind that this does not take into account the extra time taken between flowering to seed set and release (Muir 1985). In hyperdiverse kwongkan heathland, Meney *et al.* (1994) recommended fire-free intervals of 15 years or longer for the major plant families Ericaceae and Restionaceae.

At the community level, a most vulnerable habitat to fire are peat swamps, harbouring Gondwanan relicts such as the Albany pitcher plant *Cephalotus follicularis* (Fig. 3) and endangered species such as the monotypic giant sedge *Reedia spathacea* and the sunset frog *Spicospina flammocaerulea*. When burned intensely by prescribed burning or wildfire, the entire peat layer ignites and a 5000+-year-old community is destroyed (Horwitz *et al.* 1999). Granite outcrops rich in vulnerable endemics and old growth forests deserve similar focus and protection from fire.

Studies of the impact of wildfire and prescribed burning on fauna have been much less focused than those on plants (Fox et al. 1985; Friend and Wayne 2003), and scepticism is expressed in the literature on the benefits of the practice (Shugg 1979; Main 1998; Dellasala et al. 2004; Parr and Anderson 2006; Clarke 2008; Kelly et al. 2011; Pastro et al. 2011; Penman et al. 2011; Taylor et al. 2012; Taylor et al. 2013). There are two significant studies suggesting fire-dependence for long-term persistence of populations. The best known is a study of the impact of fire on the Australian tammar wallaby (Notamacropus (formerly Macropus) eugenii) (Christensen 1980). The study showed that tammars were agile at avoiding fire, returned to the burnt area soon after, and concluded that 'It lives in thickets of scrub species which provide periodic intense fires under dry conditions to regenerate as suitable habitat. A fire frequency of 25 to 30 years is necessary to maintain populations of this species'. The quokka, Setonix brachyurus, was also identified as a species requiring dense thickets unburnt for 10-20 years for its survival (Christensen and Kimber 1975). The use of prescribed burning as a conservation tool to create localised patches forming a 'mosaic' of burnt and unburnt habitat has recently been promoted as a means to enhance long-term survival of fragmented quokka populations in jarrah forest in south-west Western Australia (Burrows and Abbott 2003; Burrows et al. 2003; Bradstock et al. 2005; Bain et al. 2016). In both cases, rather than being described as 'fire-dependent', tammars and quokkas could perhaps better be described as 'infrequent-firedependent'.

#### A synopsis of published studies on the impact of frequent fire on targeted species in the south-west biodiversity hotspot

Considerable research has been devoted to documenting the impact of frequent fire on plant and animal species in the southwest of Western Australia and the following summarises some of the major findings.

#### Vertebrate animals

The tiny 10-g marsupial honey possum, *Tarsipes rostratus*, is the only non-volant vertebrate that completely depends on nectar and pollen for its survival (Bradshaw and Bradshaw 2012) and is thus extremely vulnerable to fire. Field studies using isotopic turnovers in free-ranging individuals have shown that a 9-g adult consumes 7 mL of nectar and 1 g of pollen per day, and will die within a matter of days without access to fresh blossoms (Bradshaw and Bradshaw 1999). A recent long-term population study in Scott National Park in the south-west of Western Australia estimates that the population will take 25.6 years to recover to pre-burn densities from two fires lit 6 years apart (Bradshaw and Bradshaw 2017). An extensive trapping survey in banksia woodland, 30 km north of Perth, also found

*Tarsipes rostratus* to be the most common of the nine native species recorded, and densities were greatest in areas that had not been burned for 20–26 years (Wilson *et al.* 2014). In the Fitzgerald River National Park on the south coast of Western Australia, capture rates of honey possums increased to a peak 30 years after fire, with a slight decline in vegetation unburnt for 50–60 years (Everaardt 2003; Wooller and Wooller 2014).

Another small marsupial, the litter-dependent mardo, Antechinus flavipes, is also most abundant in habitats that have not been burned for 40 years and very rare in forests that have been burned 5 years previously (Hindmarsh and Majer 1977). Christensen and Kimber (1975) note 'population levels are generally very low in the regularly burnt habitat', and the 'study in dry sclerophyll forest demonstrated the preference of the mardo for an area from which fire had been excluded for a long period'. The critically endangered western ringtail possum, Pseudocheirus occidentalis, is particularly vulnerable to fire as it is a slow-moving canopy-living folivore with a preference for highly flammable oil-rich peppermint trees (Wayne et al. 2006). Burning of banksia woodland at frequencies less than 16 years has also been shown to disadvantage a mixed reptile fauna with many species absent or diminished in number at current fire frequencies (6-12 years) (Valentine et al. 2012).

Long-term field studies of the splendid fairy wren, Malurus splendens, show that optimum densities require fire intervals of at least 12 years between fires, which must not occur during the winter and spring breeding season (Rowley and Brooker 1987). Optimal fire intervals of 20-40 years for mallee heath and >55 years for mallee vegetation have been identified for the longterm maintenance of mallee fowl (Leipoa ocellata) populations in south-west Western Australia (Parsons and Gosper 2011; Gosper et al. 2012). Old marri trees with hollows used for breeding by endangered forest red-tailed black cockatoos (Calyptorhynchus banksii naso) in the northern jarrah forest in Western Australia average 220 years in age and need to be protected against fire (Johnstone et al. 2013). Carnaby's whitetailed black cockatoo (Calyptorhynchus latitrostris) is another closely related endangered species that relies on hollows in old wandoo and salmon-gum eucalypt woodlands for breeding; this species is threatened by recurrent fire and climate change (Saunders et al. 2011). The noisy scrub-bird, Atrichornis clamosus, is one of Australia's rarest birds. It was presumed extinct until a population was discovered at Two Peoples Bay, east of Albany in Western Australia, in the 1960s. They require dense ground cover wetlands with very dense leaf litter to feed on the leaf-degrading invertebrates that form their diet. The scrub-bird has only been recorded in areas that have not been burnt in the previous 50 years and fire is the greatest threat to their long-term survival (Smith 1985).

#### Plants and soil invertebrates

The vulnerability of banksias, the primary food source of honey possums, is highlighted by a study of flowering and fruiting of *Banksia baueri*, *B. nutans* and *B. baxteri* in kwonkgan heathland on the south-west coast of Western Australia in which all three were extinguished from an area burnt twice in an interval of 9 years (Wooller *et al.* 2002). Burning at 3–4-year intervals resulted in significant reduction in the abundance of key obligate

seeder species in the south-west, such as *Acacia browniana* and *Crowea angustifolia* (Burrows and Wardell-Johnson 2003). *Banksia sessilis* flowers freely 3–4 years after fire, but does not set seed until 8 years after fire and reaches maximum honey production only after 12–15 years (Muir 1985). Burning on a 4-year cycle in Kings Park in central Perth led to the demise of *Banksia* trees (Dixon *et al.* 1995*b*) and the abandonment of the practice (Dixon *et al.* 1995*c*; Wells *et al.* 2004). Young karri trees (*Eucalyptus diversicolor*) are fire-sensitive for up to 25 years (DPaW 2016) and in jarrah (*Eucalyptus marginata*) and other forests, research suggests prescribed burning on a 5–7-year rotation is likely to permanently simplify the litter flora and invertebrate fauna, with far-reaching effects on forest hygiene (Springett 1976; York 1999*b*, 1999*a*, but see Abbott *et al.* 2002).

# Discussion: should burning at a 6-year interval in mediterranean-climate biodiversity hotspots be recognised as a 'key threatening process'?

A significant issue in the long history of prescribed burning in Western Australia is that the regulatory body has set a target of 200 000 ha to be burned annually, 180 000 ha of which is in the south-west biodiversity hotspot, regardless of environmental conditions. In practice, this means that National Parks, although fairly free of human habitation, are burnt more frequently than State forests in an effort to meet the quota (McNamara 2010). These 'strategic burns' are primarily conducted to protect fire-sensitive immature post-logging regrowth in adjacent State forest but are flagged as 'conservation burns' to protect and enhance the biodiversity in the National Parks. Conservationists and foresters alike agree that large uncontrolled fires are catastrophic for biodiversity (Bradstock et al. 2005; Bradstock 2008); hence, the current focus is on 'mosaic' burning that is meant to maintain a range of habitats with varying fire histories (Burrows et al. 2003; Bowman et al. 2008; Burrows 2008; Burrows and McCaw 2013; Bain et al. 2016). This practice, however, is not without its critics and sufficient research has yet to be carried out to justify its claims and show how it can be effectively implemented (Short and Turner 1994; Dellasala et al. 2004; Lloyd and Krasnostein 2005; Parr and Anderson 2006; Clarke 2008; Pastro et al. 2011; Kelly et al. 2017).

It seems intuitively obvious that burning at a 6-year interval of south-west Australian forests, which in the past had been burnt at intervals of 80-100 years, and longer in the case of karri (Rayner 1992), would engender substantial changes in the ecosystem. Plants that have a juvenile period of more than 6 years, such as Banksia baueri, B. nutans and B. baxteri (all keystone nectar-producing species) would gradually be eliminated, and species associated with late seral stages or climax states of the ecosystem, such as tammar wallabies, quokkas and honey possums, would disappear. The time of the year at which burning takes place will also have a substantial impact. The preferred burning times of winter and spring, when fires are less intense and easier to control, coincide with the time when most birds in Australia are breeding or fledging their young, and when kangaroo and wallaby young are just emerging from the pouch to feed on new vegetation. Burning in autumn, when the vegetation is much drier and more flammable, coincides with the time that many reptiles, such as bobtail lizards (*Tiliqua rugosa*), king skinks (*Egernia kingii*) and tiger snakes (*Notechus scutatus*), are giving birth to their live young. Fires in either season are thus likely to have negative, but divergent, impacts on wildlife that will be compounded if occurring at short 6-year intervals.

A study comparing the mediterranean ecosystems of southwest of Western Australia and south-eastern France with divergent fire regimes (dominated by unplanned wildfires in France, compared with planned fires in south-west Australia) found that the Australian landscape was characterised by areas with either high or low pyrodiversity, contrasting with French fire mosaics that were characterised by greater variation in time-since-fire values (Faivre *et al.* 2011). Principal component analysis of the two fire mosaics revealed similar spatial distributions of the data, but differed in their location along the fire-frequency axis. Thus, despite the disparate fire regimes, the two environments fell in a pyrodiversity continuum, suggesting that the intensively managed fire mosaics in south-west Western Australia may approximate those resulting from unplanned fire in the Provence region of France.

The problem that must be resolved is how to balance the overarching need to protect human life and assets without endangering the rich biodiversity that characterises mediterranean-climate ecosystems. There have been some recent attempts to address this problem by applying decision theory to high-risk situations. Driscoll et al. (2010a) highlight the need for trade-offs between biodiversity conservation and asset protection to be addressed explicitly and transparently. They consider the two most limiting factors in the current debate over prescribed burning to be knowledge of (i) the effectiveness of the full range of management actions in protecting assets, and (ii) the influence of these management actions on biodiversity. Community perceptions are also crucial in the currently polarised debate over the benefits and dangers of prescribed burning (Morrison et al. 1996; Pausas et al. 2008; Syphard et al. 2009; Gomez-Gonzalez et al. 2010). Buizer and Kurz (2016) argue that the question of vulnerability, both of human life and the environment, drives the essentially incompatible viewpoints that dominate the current debate. An analysis of submissions to the Parliamentary Inquiry following the large fires in southern Australia in 2009 found that, surprisingly, those both for and against prescribed burning shared common views on the value of nature, human life and assets, but differed in their interpretation of the ethics of risk imposition in the use of prescribed burning (Altangerel and Kull 2013). Antagonists of prescribed burning discounted the value of assets built in fire-prone areas, seeing them as voluntary risk exposure, and highlighted the damage done to wildlife. Adherents of the practice, however, saw themselves and their assets as being involuntarily at risk from wildfires, worsened by a lack of prescribed burning, and discounted the harm done to wildlife (Altangerel and Kull 2013). Attempts to reach general agreement on the pros and cons of prescribed burning are in their infancy, with recent publications including (i) a critique of the 'historical-fireregime concept' (Freeman et al. 2017); (ii) a recommendation to use a 'worldview lens' (Ruane 2018); and (iii) the use of multi-objective decision-making based on Pareto optimality theory (Kennedy et al. 2008).

The current situation in the South-west Australian hotspot is best summarised by a quote from Wells *et al.* (2004):

'Understandably, no studies address the role of fire in maintaining and protecting all biodiversity. The literature is selective as to species and communities investigated, with a focus on some vascular plants and some vertebrates. ... A few descriptive studies where effects of more than a single fire have been documented show changes in the relative abundance of some plants and animals. Rigorous experimental science has been applied to hypotheses relating to life history attributes with obvious fire effects, such as the role of smoke and heat on germination of many vascular plants. ...However, trends in meta-population dynamics under different fire regimes are known for few organisms, and even less has been documented about interactions between fire effects and those caused by other processes such as disease attack, predation, herbivory, salinity, etc.'

There is a major need for targeted research on key issues inherent in the use of prescribed burning. Foremost amongst these, as recommended by Driscoll et al. (2010b), is a mechanistic understanding of the responses of a range of plants and animals to fire regimes, followed by knowledge of how species are influenced by the timing and spatial arrangement of fires. Little, if any, research has also been devoted to comparing the difference between 'natural' and intensively managed fire regimes, and their long-term ecological impact. One study in the south-western Australian biodiversity hotspot compared the 'resilience' of sites burnt at different frequencies in recovering from a large wildfire, claiming that there was little difference (Wittkuhn et al. 2011). One problem with the study was that it used an 'unbalanced design', measuring biodiversity 4-5 years after the large fire, but had no control showing the initial state before the fire. What was measured in this study was the slow invasion of a suite of animals from unburnt areas in the early stages of regeneration of the vegetation after the fire. This is unlikely to be influenced, however, by whether the site had been burnt frequently or not for long periods, unless the frequently burnt sites lacked some fire-sensitive species.

The impact of global warming is a major future research priority and the probability of wildfires is likely to vary geographically, increasing with changes in vegetation productivity (Krawchuk *et al.* 2009). Mediterranean-climate ecosystems are particularly vulnerable, owing to their long hot, dry summers and highly flammable vegetation (Pausas and Fernandez-Munoz 2012). Future changes in water balance and water potential in Australia have been modelled under various climate change scenarios and predict that shifts from fuel-dryness-type fires to fuel-productivity fires will occur in the south-west biodiversity hotspot by 2080 (Boer *et al.* 2016).

Given that projected changes in the climate due to global warming are likely associated with more frequent and intense fires (Enright *et al.* 2015) in the south-west of Western Australia, adhering to a fixed and vast area that must be prescribed-burned each year, two-thirds of it at an interval of 4–7 years (Burrows and McCaw 2013), can only compound the problem of protecting the unique biodiversity of this hotspot. Rather than adhering to a fixed and unsubstantiated target of 200 000 ha each year for

prescribed burning in the south-west Australian hotspot, we advocate initiating an adaptive management approach (e.g. Dixon *et al.* 1995*b*, 1995*c*). This would focus on protecting targeted assets of both infrastructure and vulnerable biodiversity, combined with flammable weed removal and promoting bioturbators that reduce the litter layer, and less on burning large tracts of bushland remote to key assets such as towns.

## Conclusion: prescribed burning in Mediterranean-climate ecosystems

A long-term study of the efficacy of prescribed burning in mitigating wildfires in the south-west of Australia found that the area treated for up to 6 years had a negative effect on the percentage of the area burned by unplanned fire. This effect, however, did not extend beyond 6 years, which has given rise to the recommendation that prescribed burning needs to be this frequent to be effective. Numerous studies show that the impact of burning on a 6-year cycle would be catastrophic for many species of plants and animals that are unique to the south-west biodiversity hotspot and will have a deleterious cascade effect on the entire ecosystem, increasing the 'extinction debt' (Kuussaari et al. 2009). Leverage values are low, indicating that an area approximately four times larger than that to be protected needs to be prescribed-burned. Other studies indicate that burning closer to habitation and infrastructure is more effective in protecting these assets than broad-scale burning of bushland areas kilometres distant. Similar arguments can be advanced for the other four mediterranean-climate ecosystems, although planned fire is used less extensively there than in south-west Australia. Together, these areas - the fynbos, the Chilean matorral, the Californian chaparral, the Mediterranean basin and south-west Western Australia - account for almost 9% of plant species worldwide, and some of the rarest. Methods other than prescribed burning are needed if we are to protect and preserve the unique biological assemblages that are now further threatened by climate change.

#### **Conflicts of Interest**

The authors declare no conflicts of interest.

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#### References

- Abbott I (2002) Origin and spread of the cat, *Felis catus*, on mainland Australia, with a discussion of the magnitude of its early impact on native fauna. *Wildlife Research* 29, 51–74. doi:10.1071/WR01011
- Abbott I (2003) Aboriginal fire regimes in south-west Western Australia: evidence from historical documents. In 'Fire in ecosystems of southwest Western Australia: impacts and management'. (Eds I Abbot and N Burrows) pp. 119–146. (Backhuys: Leiden, the Netherlands)
- Abbott I, Burbidge T, Strehlow K, Mellican A, Wills A (2002) Logging and burning impacts on cockroaches, crickets and grasshoppers, and spiders in jarrah forest, Western Australia. *Forest Ecology and Management* 5915, 1–17.

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- Acácio V, Holmgren M, Rego F, Moreira F, Mohren GMJ (2009) Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? *Agroforestry Systems* 76, 389–400. doi:10.1007/ S10457-008-9165-Y
- Altangerel K, Kull CA (2013) The prescribed burning debate in Australia: conflicts and compatibilities. *Journal of Environmental Planning and Management* 56, 103–120. doi:10.1080/09640568.2011.652831
- Arkle RS, Pilliod DS (2010) Prescribed fires as ecological surrogates for wildfires: a stream and riparian perspective. *Forest Ecology and Management* 259, 893–903. doi:10.1016/J.FORECO.2009.11.029
- Bagne K, Purcell K (2011) Short-term responses of birds to prescribed fire in fire-suppressed forests of California. *The Journal of Wildlife Management* 75, 1051–1060. doi:10.1002/JWMG.128
- Bain K, Wayne A, Bencini R (2016) Prescribed burning as a conservation tool for management of habitat for threatened species: the quokka, *Setonix brachyurus*, in the southern forests of Western Australia. *International Journal of Wildland Fire* 25, 608–617. doi:10.1071/ WF15138
- Boer MM, Sadler RJ, Wittkuhn R, McCaw WL, Grierson PF (2009) Longterm impacts of prescribed burning on regional extent and incidence of wildfires – evidence from 50 years of active fire management in SW Australian forests. *Forest Ecology and Management* 259, 132–142. doi:10.1016/J.FORECO.2009.10.005
- Boer MM, Bowman DMJS, Murphy BP, Cary GJ, Cochrane MA, Fensham RJ, Krawchuk MA, Price OF, De Dios VR, Williams RJ, Bradstock RA (2016) Future changes in climatic water balance determine potential for transformational shifts in Australian fire regimes. *Environmental Research Letters* 11, 065002. doi:10.1088/1748-9326/11/6/065002
- Bond WJ, Slingsby P (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science* **79**, 213–233.
- Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. *New Phytologist* **165**, 525–538. doi:10.1111/J.1469-8137.2004.01252.X
- Bowman DMJS (1998) Tansley Review No.11. The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* 140, 385– 410. doi:10.1046/J.1469-8137.1998.00289.X
- Bowman DMJS, Boggs GS, Prior LD (2008) Fire maintains an Acacia aneura–Triodia mosaic in central Australia. Journal of Arid Environments 72, 34–47. doi:10.1016/J.JARIDENV.2007.04.001
- Bradshaw SD, Bradshaw FJ (1999) Field energetics and the estimation of pollen and nectar intake in the marsupial honey possum, *Tarsipes rostratus*, in heathland habitats of south-western Australia. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* 169, 569–580. doi:10.1007/S003600050257
- Bradshaw SD, Bradshaw FJ (2012) The physiology of the honey possum, *Tarsipes rostratus*, a small marsupial with a suite of highly specialised characters: a review. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* **182**, 469–489. doi:10. 1007/S00360-011-0632-9
- Bradshaw SD, Bradshaw FJ (2017) Long-term recovery from fire by a population of honey possums (*Tarsipes rostratus*) in the extreme southwest of Western Australia. *Australian Journal of Zoology* 65, 1–11. doi:10.1071/ZO16068
- Bradshaw SD, Dixon KW, Hopper DS, Lambers H, Turner SR (2011) Little evidence for fire-adapted traits in mediterranean climate regions. *Trends* in *Plant Science* 16, 69–76. doi:10.1016/J.TPLANTS.2010.10.007
- Bradstock RA (2008) Effects of large fires on biodiversity in south-eastern Australia: disaster or template for diversity? *International Journal of Wildland Fire* 17, 809–822. doi:10.1071/WF07153
- Bradstock RA, Bedward M, Gill AM, Cohn JS (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* 32, 409–423. doi:10. 1071/WR02114

- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonesca GB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16, 909–923. doi:10.1046/J.1523-1739. 2002.00530.X
- Brown PJ, Manders PT, Bands DP, Kruger FJ, Andrag RH (1991) Prescribed burning as a conservation management practice: a case history from the Cederberg Mountains, Cape Province, South Africa. *Biological Conservation* 56, 133–150. doi:10.1016/0006-3207(91) 90014-Z
- Buizer M, Kurz T (2016) Too hot to handle: depoliticisation and the discourse of ecological modernisation in fire management debates. *Geoforum* 68, 48–56. doi:10.1016/J.GEOFORUM.2015.11.011
- Burge DO, Thorne JH, Harrison SP, O'brien BC, Rebman JP, Shevock JR, Alverson ER, Hardison LK, Rodríguez JD, Junak SA, Oberbauer TA, Riemann H, Vanderplank SE, Barry T (2016) Plant diversity and endemism in the California Floristic Province. *Madrono* 63, 3–206. doi:10.3120/MADR-63-02-3-206.1
- Burrows N (2008) Linking fire ecology and fire management in south-west Australian forest landscapes. *Forest Ecology and Management* 255, 2394–2406. doi:10.1016/J.FORECO.2008.01.009
- Burrows N, Abbott I (2003) Fire in south-west Western Australia; synthesis of current knowledge, management implications and new research directions. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot and N Burrows) pp. 437–452. (Backhuys: Leiden, the Netherlands)
- Burrows N, McCaw WL (2013) Prescribed burning in south-western Australian forests. *Frontiers in Ecology and the Environment* **11**, e25– e34. doi:10.1890/120356
- Burrows N, Wardell-Johnson G (2003) Fire and plant interactions in forested ecosystems of south-west Western Australia. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot and N Burrows) pp. 225–268. (Backhuys: Leiden, the Netherlands)
- Burrows ND, Ward B, Robinson AD (1995) Jarrah forest fire history from stem analysis and anthropological evidence. *Australian Forestry* 58, 7–16. doi:10.1080/00049158.1995.10674636
- Burrows N, Liddelow G, Green D, Bain K, Middleton T, Freebury G, Shedley E (2004) Fire-induced habitat mosaics in south-west landscapes: The Fire Mosaic Project. Department of Conservation and Land Management, unpublished report, pp. 1–19. (Perth, WA, Australia)
- Burrows N, Wardell-Johnson G, Ward B (2008) Post-fire juvenile period of plants in south-west Australia forests and implications for fire management. *Journal of the Royal Society of Western Australia* 91, 163–174.
- Casals P, Valor T, Besalú A, Molina-Terrén D (2016) Understory fuel load and structure eight to nine years after prescribed burning in Mediterranean pine forests. *Forest Ecology and Management* 362, 156–168. doi:10.1016/J.FORECO.2015.11.050
- Céspedes B, Torres I, Pérez B, Luna B, Moreno JM (2014) Burning season does not affect post-fire regeneration but fire alters the balance of the dominant species in a seeder-dominated Mediterranean shrubland. *Applied Vegetation Science* 17, 711–725. doi:10.1111/AVSC.12102
- Chiwocha SDS, Dixon KW, Flematti GR, Ghisalberti EL, Merritt DJ, Nelson DC, Riseborough JM, Smith SM, Stevens JS (2009) Karrikins: a new family of plant growth regulators in smoke. *Plant Science* 177, 252–256. doi:10.1016/J.PLANTSCI.2009.06.007
- Christensen PES (1980) The biology of *Bettongia penicillata* Gray, 1837, and Macropus eugenii (Desmarest, 1804) in relation to fire. Forests Department of Western Australia Bulletin no. 91 (Perth, WA, Australia.
- Christensen PES, Kimber PC (1975) Effect of prescribed burning on the flora and fauna of south-west Australian forests. *Proceedings of the Ecological Society of Australia* **9**, 85–106.
- Clarke MF (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research* **35**, 385–394. doi:10. 1071/WR07137

- Clarkson C, Jacobs Z, Marwick B, Fullagar R, Wallis L, Smith M, Roberts RG, Hayes E, Lowe K, Carah Florin SA, McNeil J, Cox D, Arnold LJ, Hua Q, Huntley J, Brand HEA, Manne T, Fairbairn A, Shulmeister J, Lyle L, Salinas M, Page M, Connell K, Park G, Norman K, Murphy T, Pardoe C (2017) Human occupation of northern Australia by 65,000 years ago. *Nature* 547, 301–310. doi:10.1038/NATURE22968
- Close DC, Davidson NJ, Johnson DW, Abrams MD, Hart SC, Lunt LD, Archibald RD, Horton B, Adams MA (2009) Premature decline of *Eucalyptus* and altered ecosystems processes in the absence of fire in some Australian forests. *Botanical Review* 75, 191–202. doi:10.1007/ S12229-009-9027-Y
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310. doi:10.1126/SCIENCE.199.4335.1302
- De Lange JH, Brown NAC, Van Staden J (2018) Perspectives on the contributions by South African researchers in igniting global research on smoke-stimulated seed germination. *South African Journal of Botany* 115, 219–222. doi:10.1016/J.SAJB.2017.12.015
- Dellasala DA, Williams JE, Williams CD, Franklin JF (2004) Beyond smoke and mirrors: a synthesis of fire policy and science. *Conservation Biology* 18, 976–986. doi:10.1111/J.1523-1739.2004.00529.X
- Di Castri F, Goodall DW, Specht RL (Eds) (1981) 'Mediterranean-type shrublands.' (Elsevier Scientific Publishing Company: Amsterdam, the Netherlands)
- Dixon KW, Roche S, Pate JS (1995a) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101, 185–192. doi:10.1007/BF00317282
- Dixon R, Keys K, Hopper DS, Wycherley P (1995b) A fifty-year record of fire management in Kings Park bushland. In 'Fire and urban bushland'. (Ed. J Harris) pp. 15–18. (Urban Bushland Council: Perth, WA, Australia)
- Dixon R, Keys K, Paynter R, Keighery B, Dixon KW, Hopper SD (1995*c*) 'Kings Park Bushland Management Plan 1995–2005.' (Kings Park and Botanic Garden: Perth, WA, Australia)
- Dixon KW, Merritt DJ, Flematti GR, Ghisalberti EL (2009) Karrikinolide a phytoreactive compound derived from smoke with applications in horticulture, ecological restoration and agriculture. *Acta Horticulturae* (813), 155–170. doi:10.17660/ACTAHORTIC.2009.813.20
- Dodson JR, Robinson M, Tardy C (2005) Two fine-resolution Pliocene charcoal records and their bearing on pre-human fire frequency in southwestern Australia. *Austral Ecology* **30**, 592–599. doi:10.1111/J.1442-9993.2005.01490.X
- DPaW (2016) Karri silvicultural burning manual. FEM072 Forest Management Series. Department of Parks and Wildlife. (Perth, WA, Australia)
- DPaW (2017). Department of Parks and Wildlife 2016–17, Annual Report, pp. 140. (Perth, Western Australia)
- Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gill M (2010*a*) Resolving conflicts in fire management using decision theory: assetprotection versus biodiversity conservation. *Conservation Letters* 3, 215–223. doi:10.1111/J.1755-263X.2010.00115.X
- Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF, Dexter N, Fensham R, Friend G, Gil M, James S, Kay G, Keith DA, MacGregor C, Russell-Smith J, Salt D, Watson JEM, Williams RJ, York A (2010b) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation* 143, 1928–1939. doi:10.1016/J.BIOCON.2010.05.026
- Enright NJ, Fontaine JB (2014) Climate change and the management of fireprone vegetation in south-west and south-east Australia. *Geographical Research* 52, 34–44. doi:10.1111/1745-5871.12026
- Enright NJ, Thomas I (2008) Pre-European fire regimes in Australian ecosystems. *Geography Compass* 2, 979–1011. doi:10.1111/J.1749-8198.2008.00126.X
- Enright NJ, Lamont B, Marsuala R (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub *Banksia hookeriana. Journal of Ecology* 84, 9–17. doi:10.2307/2261695

- Enright NJ, Marsula R, Lamont BB, Wissel C (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *Journal of Ecology* 86, 946–959. doi:10.1046/ J.1365-2745.1998.00312.X
- Enright NJ, Fontaine JB, Westcott VC, Lade JC, Miller BP (2011) Fire interval effects on persistence of resprouter species in Mediterraneantype shrublands. *Plant Ecology* **212**, 2071–2083. doi:10.1007/S11258-011-9970-7
- Enright NJ, Fontaine JB, Bowman DMJS, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* 13, 265–272. doi:10.1890/ 140231
- Everaardt A (2003) The impact of fire on the honey possum, *Tarsipes rostratus*, in the Fitzgerald River National Park, Western Australia. PhD thesis, Murdoch University, Perth, WA.
- Faivre N, Roche P, Boer MM, McCaw L, Grierson PF (2011) Characterization of landscape pyrodiversity in Mediterranean environments: contrasts and similarities between south-western Australia and south-eastern France. *Landscape Ecology* 26, 557–571. doi:10.1007/S10980-011-9582-6
- Ferguson E (2017) Reframing rural fire management. Report of the Special Inquiry into the January 2016 Waroona fire, Part 1. Waroona Fire Special Inquiry published by Government of Western Australia, p. 19. (Perth, Western Australia)
- Fernandes PM (2018) Scientific support to prescribed underburning in southern Europe: what do we know? *The Science of the Total Environment* 630, 340–348. doi:10.1016/J.SCITOTENV.2018.02.214
- Fernandes PM, Botelho HS (2003) A review of prescribed burning effectiveness in fire hazard reduction. *International Journal of Wildland Fire* 12, 117–128. doi:10.1071/WF02042
- Fernandes PM, Davies GM, Ascoli D, Fernández C, Moreira F, Rigolot E, Stoof CR, Vega JA, Molina D (2013) Prescribed burning in southern Europe: developing fire management in a dynamic landscape. *Frontiers* in Ecology and the Environment 11, e4–e14. doi:10.1890/120298
- Fettig CJ, Mckelvey SR, Cluck DR, Smith SL, Otrosina WJ (2010) Effect of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. *Forest Ecology and Management* 260, 207–218. doi:10.1016/J. FORECO.2010.04.019
- Fleming PA, Anderson H, Prendergast AS, Bretz MR, Valentine LE, Hardy GE (2014) Loss of Australian digging mammals and ecosystem function. *Mammal Review* 44, 94–108. doi:10.1111/MAM.12014
- Fox JF (1979) Indeterminate disturbance hypothesis. Science 204, 1344– 1345. doi:10.1126/SCIENCE.204.4399.1344
- Fox BJ, Quinn RD, Breytenbach GJ (1985) A comparison of small-mammal succession following fire in shrublands of Australia, California and South Africa. *Proceedings of the Ecological Society of Australia* 14, 179–197.
- Freeman J, Kobziar L, Rose EW, Cropper W (2017) A critique of the historical-fire-regime concept in conservation. *Conservation Biology* 31, 976–985. doi:10.1111/COBI.12942
- Friend G, Wayne A (2003) Relationships between mammals and fire in south-west Western Australian ecosystems: what we know and what we need to know. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot & N Burrows ) pp. 363–380. (Backhuys: Leiden, the Netherlands)
- Furlaud JM, Williamson GJ, Bowman DMJS (2018) Simulating the effectiveness of prescribed burning at altering wildfire behaviour in Tasmania, Australia. *International Journal of Wildland Fire* 27, 15–28. doi:10.1071/WF17061
- Gent ML, Morgan JW (2007) Changes in the stand structure (1975–2000) of coastal *Banksia* forest in the long absence of fire. *Austral Ecology* 32, 239–244. doi:10.1111/J.1442-9993.2007.01667.X

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- George EF (1993) 'Plant propagation by tissue culture. Part 1: The technology.' (Exegetics Ltd: Edington, UK)
- Gibbons P, Van Bommel L, Gill AM, Cary G, Driscoll DA, Bradstock R, Knight E, Moritz MA, Stephens SL, Lindenmayer D (2012) Land management practices associated with house loss in wildfires. *PLoS One* 7, e29212. doi:10.1371/JOURNAL.PONE.0029212
- Gill AM (1981) Adaptive responses of Australian vascular plant species to fire. In 'Fire and the Australian biota'. (Eds AM Gill, RH Groves & IR Noble) pp. 243–272. (Australian Academy of Science: Canberra, ACT, Australia)
- Gillon D, Rapp M (1989) Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. *Plant and Soil* **120**, 69–77. doi:10.1007/BF02370292
- Gioia P, Hopper SD (2017) A new phytogeographic map for the South-west Australian Floristic Region after an exceptional decade of collection and discovery. *Botanical Journal of the Linnean Society* 184, 1–15. doi:10. 1093/BOTLINNEAN/BOX010
- Goldblatt P, Manning JC (2002) Plant diversity of the Cape Region of South Africa. Annals of the Missouri Botanical Garden 89, 281–302. doi:10. 2307/3298566
- Gomez-Gonzalez S, Torres-Diaz C, Valencia G, Torres-Morales P, Cavieres LA, Pausas JG (2010) Anthropogenic fires increase alien and native annual species in the Chilean coastal matorral. *Diversity & Distributions* 2010, 1–10.
- Gosper CR, Yates CJ, Prober SM, Parsons BC (2012) Contrasting changes in vegetation structure and diversity with time since fire in two Australian mediterranean-climate plant communities. *Austral Ecology* 37, 164–174. doi:10.1111/J.1442-9993.2011.02259.X
- Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister KE, Spence-Bailey LM, Clarke MF, Bennett AF (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology* 48, 247–256. doi:10.1111/J.1365-2664.2010.01906.X
- Hassell CW, Dodson JR (2003) The fire history of south-west Western Australia prior to European settlement in 1826–1829. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot & N Burrows) pp. 71–85. (Backhuys: Leiden, the Netherlands)
- Hindmarsh R, Majer JD (1977) Food requirements of mardo (Antechinus flavipes [Waterouse]) and the effect of fire on mardo abundance. Forests Department of WA, Research Paper No 31. (Perth, WA, Australia)
- Hopper SD (2003) An evolutionary perspective on south-west Western Australian landscapes, biodiversity and fire: a review and management implications. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot & N Burrows) pp. 9–35. (Backhuys: Leiden, the Netherlands)
- Hopper SD (2014). Sandplain and Kwongkan: historical spellings, meanings, synonyms, geography and definition. In 'Plant life on the sandplains in Southwest Australia: a global biodiversity hotspot'. (Ed H Lambers) pp. 23–33. (University of Western Australia Publishing: Perth, WA)
- Horton DR (2000) 'The pure state of nature: sacred cows, destructive myths and the environment.' (Allen & Unwin: Sydney, NSW, Australia)
- Horwitz P, Pemberton M, Ryder D (1999) Catastrophic loss of organic carbon from a management fire in a peatland in south-western Australia.
  In 'Wetlands for the Future. Proceedings of INTECOL V', 22–28 Deptember 1996, Peth, Western Australia. (Eds AJ McComb and JA Davis) (Gleneagles Press: Adelaide, SA, Australia)
- Johnstone RE, Kirkby T, Sarti K (2013) The breeding biology of the forest red-tailed black cockatoo *Calyptorhynchus banksii naso* Gould in southwestern Australia. I. Characteristics of nest trees and nest hollows. *Pacific Conservation Biology* 19, 121–142.
- Keane RE, Agee JK, Fulé P, Keeley JE, Key C, Kitchen SG, Miller RD, Schulte LA (2008) Ecological effects of large fires on US landscapes:

benefit or catastrophe? *International Journal of Wildland Fire* **17**, 696–712. doi:10.1071/WF07148

- Keeley JE, Bond WJ, Brackstock RA, Pausas JG, Rundel PW (2012) 'Fire in Mediterranean ecosystems.' (Cambridge University Press: New York, NY, USA)
- Kelly LT, Nimmo DG, Spence-Bailey LM, Haslem A, Watson SJ, Clarke MF, Bennett AFB (2011) Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity & Distributions* 17, 462–473. doi:10.1111/J.1472-4642.2011.00754. X
- Kelly LT, Brotons L, Mccarthy MA (2017) Putting pyrodiversity to work for animal conservation. *Conservation Biology* 31, 1–4.
- Kennedy MC, Ford ED, Finney M, Agee JK (2008) Informed multiobjective decision-making in environmental management using Pareto optimality. *Journal of Applied Ecology* **45**, 181–192. doi:10.1111/J. 1365-2664.2007.01367.X
- Krawchuk MA, Moritz MA, Parisien M-A, Dorn JF, Hayhoe K (2009) Global pyrogeography: the current and future distribution of wildfire. *PLoS One* 4, e5102. doi:10.1371/JOURNAL.PONE.0005102
- Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Partel M, Pino J, Roda F, Stefanescu C, Teder T, Zobel M, Steffan-Dewenter I (2009) Extinction debt: a challenge for biodiverity conservation. *Trends in Ecology & Evolution* 24, 564–571. doi:10. 1016/J.TREE.2009.04.011
- Lloyd N, Krasnostein A (2005) Historical perspectives on mosaic burning in Western Australia's south-west forests. In '6th National Conference of the Australian Forest Historical Society Inc., 2005', 12–17 September 2004, Perth, WA. (Ed. MC Calver) pp. 439–450. (Millpress: Rotterdam, the Netherlands)
- Loehle C (2004) Applying landscape principles to fire hazard reduction. Forest Ecology and Management 198, 261–267. doi:10.1016/J. FORECO.2004.04.010
- Main AR (1996) Ghosts of the past: where does environmental history begin? Environmental History 2, 97–114. doi:10.3197/096734096779522428
- Main BY (1998) 'Prescribed burning and relictual species: Gondwanic refugia.' (Environment Protection Authority: Perth, WA, Australia)
- McCaw WL (2013) Managing forest fuels using prescribed fire a perspective from southern Australia. *Forest Ecology and Management* 294, 217–224. doi:10.1016/J.FORECO.2012.09.012
- McCaw WL, Hanstrum B (2003) Fire environment of mediterranean southwest Western Australia. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbot & N Burrows) pp. 1–8. (Backhuys: Leiden, the Netherlands)
- McCaw WL, Hamilton T, Rumley C (2005) Application of fire history records to contemporary management issues in south-west Australian forests. In '6th National Conference of the Australian Forest Historical Society Inc., 2005', 12–17 September 2004, Perth, WA. (Ed. MC Calver) pp. 555–563. (Millpress: Rotterdam, the Netherlands)
- McNamara K (2010) 'Senate Select Committee on agricultural and related industries.' (Hansard (Commonwealth of Australia)): Canberra, ACT, Australia)
- Meney KA, Nielssen GM, Dixon KW (1994) Seed bank patterns in Restionaceae and Epacridaceae after wildfire in heath (kwongan) in south-western Australia. *Journal of Vegetation Science* 5, 5–12. doi:10. 2307/3235632
- Milberg P, Lamont BB (1995) Fire enhances weed invasion of roadside vegetation in south-western Australia. *Biological Conservation* 73, 45– 49. doi:10.1016/0006-3207(95)90061-6
- Mittermeier RA, Robles-Gil P, Hoffmann M, Pilgrim JD, Brooks TM, Mittermeier CG, Lamoreux JL, Fonseca G (Eds) (2004) 'Hotspots revisited: Earth's biologically richest and most endangered ecoregions.' (Cemex: Mexico City, Mexico)
- Monimeau L, Mouillot D, Fons R, Prodon R, Marchand B (2002) Impact of prescribed burning on the survival rates of the wood mouse (*Apodemus*

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*sylvaticus*). *Acta Oecologica* **23**, 51–58. doi:10.1016/S1146-609X(02) 01133-5

- Mooney SD, Harrison SP, Bartlein PJ, Daniau AL, Stevenson J, Brownlie KC, Buckman S, Cupper M, Luly J, Black M, Colhoun E, D'Costa D, Dodson J, Haberle S, Hope GS, Kershaw P, Kenyon C, McKenzie M, Williams N (2011) Late Quaternary fire regimes in Australia. *Quaternary Science Reviews* **30**, 28–46. doi:10.1016/J.QUASCIREV.2010.10.010
- Moreira-Muñoz A (2011) 'Plant geography of Chile.' (Springer Science & Business Media)
- Moreno S, Rouco C (2013) Responses of a small-mammal community to habitat management through controlled burning in a protected Mediterranean area. Acta Oecologica 49, 1–4. doi:10.1016/J.ACTAO.2013.02. 001
- Morrison DA, Buckney RT, Bewick BJ, Cary GJ (1996) Conservation conflicts over burning bush in south-eastern Australia. *Biological Conservation* 76, 167–175. doi:10.1016/0006-3207(95)00098-4
- Morton SR (1990) The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**, 201–213.
- Muir BG (1985) Fire exclusion: a baseline for change? In 'Fire ecology and management in Western Australian ecosystems'. (Ed. J Ford) pp. 119– 128. (Western Australian Institute of Technology: Perth, WA, Australia)
- Muir B (1987) Time between germination and first flowering of some perennial plants. *Kingia* 1, 75–83.
- Myers N, Mittermeier R A, Mittermeier C G, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858. doi:10.1038/35002501
- Parr CL, Anderson AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* 20, 1610–1619. doi:10.1111/J.1523-1739.2006.00492.X
- Parsons BC, Gosper CR (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. doi:10.1071/WF09099
- Pastro LA, Dickman CR, Letnic M (2011) Burning for biodiversity or burning biodiversity? Prescribed burn vs wildfire impacts on plants, lizards, and mammals. *Ecological Applications* 21, 3238–3253. doi:10. 1890/10-2351.1
- Pate JS, Dixon KW, Orshan G (1984) Fire in the kwongan. In 'Kwongan: plant life of the sandplain'. (Eds JS Pate and JS Beard) pp. 177–204. (University of WA Press: Perth, WA, Australia)
- Pausas JG, Fernandez-Munoz S (2012) Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. *Climatic Change* 110, 215–226. doi:10.1007/S10584-011-0060-6
- Pausas JG, Llovet J, Rodrigo A, Vallejo R (2008) Are wildfire a disaster in the Mediterranean basin? A review. *International Journal of Wildland Fire* 17, 713–723. doi:10.1071/WF07151
- Pellegrini A F A, Ahlstrom A, Hobbie SE, Reich PB, Nieradzik LP, Staver AC, Scharenbroch BC, Jumpponen A, Anderegg WRL, Randerson JT, Jackson RB (2017) Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553, 194–198. doi:10. 1038/NATURE24668
- Penman TD, Christie FJ, Anderson AN, Bradstock RA, Cary G, Henderson MK, Price O, Tran C, Wardle GM, Williams RJ, York A (2011) Prescribed burning: how can it work to conserve the things we value? *International Journal of Wildland Fire* 20, 721–733. doi:10.1071/ WF09131
- Pignatti E, Pignatti S, Ladd PG (2002) Comparisons of ecosystems in the Mediterranean Basin and Western Australia. *Plant Ecology* 163, 177– 186. doi:10.1023/A:1020968010349
- Price OF (2012) The drivers of effectiveness of prescribed fire treatment. *Forest Science* **58**, 606–617. doi:10.5849/FORSCI.11-002
- Price OF, Pausas JG, Govender N, Flannigan M, Fernandes PM, Brooks ML, Bkiege Bird R (2015*a*) Global patterns in fire leverage: the

response of annual area burnt to previous fire. *International Journal of Wildland Fire* **24**, 297–306. doi:10.1071/WF14034

- Price OF, Penman TD, Bradstock RA, Boer MM, Clarke H (2015b) Biogeographical variation in the potential effectiveness of prescribed fire in south-eastern Australia. *Journal of Biogeography* 42, 2234–2245. doi:10.1111/JBI.12579
- Prober SM, Yuen E, O'connor MH, Schultz L (2016) Ngadju kala: Australian Aboriginal fire knowledge in the Great Western Woodlands. *Austral Ecology* 41, 716–732. doi:10.1111/AEC.12377
- Rayner ME (1992) Application of dendrochronology, stem analysis and inventory data in the estimation of tree and stand ages in Karri forest. Department of Conservation and Land Management, Technical Report No. 27. (Perth, WA, Australia).
- Rix MG, Edwards DL, Byrne M, Harvey MS, Joseph L, Roberts JD (2015) Biogeography and speciation of terrestrial fauna in the south-western Australian biodiversity hotspot. *Biological Reviews of the Cambridge Philosophical Society* **90**, 762–793. doi:10.1111/BRV.12132
- Roche S, Dixon KW, Pate JS (1998) For everything a season: smokeinduced seed germination and seedling recruitment in a Western Australian banksia woodland. *Australian Journal of Ecology* 23, 111– 120. doi:10.1111/J.1442-9993.1998.TB00709.X
- Rowley I, Brooker MG (1987) The response of a small insectivorous bird to fire in heathlands. In 'Nature conservation: the role of remnants of native vegetation'. (DA Saunders, GW Arnold, AA Burbidge and AJM Hopkins) pp. 211–218. (Surrey Beatty: Chipping Norton)
- Ruane S (2018) Using a worldview lens to examine complex policy issues: a historical review of bushfire management in the south-west of Australia. *Local Environment* 23, 777–795. doi:10.1080/13549839.2018.1467390
- Sagra J, Moya D, Plaza-Álvarez PA, Lucas-Borja ME, Alfaro-Sánchez R, De Las Heras J, Ferrandis P (2017) Predation on early recruitment in Mediterranean forests after prescribed fires. *Forests* 8, 1–3. doi:10.3390/ F8070243
- Saunders DA, Mawson PR, Dawson R (2011) The impact of two extreme weather events and other causes of death on Carnaby's black cockatoos: a promise of things to come for a threatened species? *Pacific Conservation Biology* 17, 141–148. doi:10.1071/PC110141
- Short J (2004) Mammal decline in south-western Western Australia perspectives from Shortridge's collections of mammals in 1904–07. *Australian Zoologist* 32, 605–628. doi:10.7882/AZ.2004.006
- Short J, Smith A (1994) Mammal decline and recovery in Australia. Journal of Mammalogy 75, 288–297. doi:10.2307/1382547
- Short J, Turner B (1994) A test of the vegetation mosaic hypothesis: a hypothesis to explain the decline and extinction of Australian mammals. *Conservation Biology* 8, 439–449. doi:10.1046/J.1523-1739.1994. 08020439.X
- Shugg HB (1979) Fire control and nature reserves. SWANS 9, 9-11.
- Slingsby P, Johns A (2009) 'T. P. Stokoe: the man, the myths, the flowers.' (Baardskeerder: Cape Town, South Africa)
- Smith GT (1985) Fire effects on populations of the noisy scrub-bird (Atrichornis clamosus), western bristle-bird (Dasyornis longrostris) and western whip-bird (Psophodes nigrogularis). In 'Fire ecology and management of Western Australian ecosystems'. (Ed. J Ford) pp. 95– 102. (Western Australian Institute of Technology: Perth, WA, Australia)
- Springett JA (1976) The effect of prescribed burning on the soil fauna and on litter decomposition in Western Australian forests. *Australian Journal of Ecology* 1, 77–82. doi:10.1111/J.1442-9993.1976.TB01094.X
- Syphard AD, Volker CR, Hawbaker TJ, Stewart SI (2009) Conservation threats due to human-caused increases in fire frequency in mediterranean-climate ecosystems. *Conservation Biology* 23, 758–769. doi:10. 1111/J.1523-1739.2009.01223.X
- Taylor RS, Watson SJ, Nimmo DG, Kelly LT, Bennett A, Clarke MF (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity & Distributions* 18, 519– 529. doi:10.1111/J.1472-4642.2011.00842.X

- Taylor RS, Watson SJ, Bennett A, Clarke MF (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. doi:10.1016/J.BIOCON.2012.12.005
- Turney CSM, Bird MIL, Fifield LK, Roberts RG, Smith M, Dortch CE, Grün R, Lawson E, Ayliffe LK, Miller GH, Dortch J, Cresswell RG (2001) Early human occupation at Devil's Lair, south-western Australia 50,000 years ago. *Quaternary Research* 55, 3–13. doi:10.1006/QRES. 2000.2195
- Úbeda X, Lorca M, Outeiro LR, Bernia S, Castellnou M (2005) Effects of prescribed fire on soil quality in Mediterranean grassland (Prades Mountains, north-east Spain). *International Journal of Wildland Fire* 14, 379–384. doi:10.1071/WF05040
- Underwood EC, Viers JH, Klausmeyer KR, Cox RL, Shaw MR (2009) Threats and biodiversity in the Mediterranean biome. *Diversity & Distributions* 15, 188–197. doi:10.1111/J.1472-4642.2008.00518.X
- Valentine LE (2014) Ecosystem services of digging mammals. In 'Plant life on the sandplains in south-west Australia, a global biodiversity hotspot'. (Ed. H Lambers) pp. 255–262. (UWA Publishing: Perth, WA, Australia)
- Valentine LE, Reaveley A, Johnson B, Fisher RA, Wilson BA (2012) Burning in banksia woodlands: how does the fire-free period influence reptile communities. *PLoS One* 7, e34448. doi:10.1371/JOURNAL. PONE.0034448
- Van Wilgen BW (1981) Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. *South African Forestry Journal* **118**, 42–55. doi:10.1080/00382167. 1981.9630524
- Van Wilgen BW (1982) Some effects of post-fire age on the above-ground biomass of fynbos (macchia) vegetation in South Africa. *Journal of Ecology* 70, 217–225. doi:10.2307/2259874
- Van Wilgen BW (2009) The evolution of fire and invasive alien plant management practices in fynbos. *South African Journal of Science* 105, 335–342.
- Van Wilgen BW (2013) Fire management in species-rich Cape fynbos shrublands. Frontiers in Ecology and the Environment 11, e35–e44. doi:10.1890/120137
- Van Wilgen BW, Bond WJ, Richardson DM (1992) Ecosystem management. In 'The ecology of fynbos: nutrients, fire and diversity'. (Ed. RM Cowling) pp. 345–371. (Oxford University Press: Cape Town, South Africa)
- Van Wilgen BW, Forsyth GG, De Klerk H, Das SK, Khuluse S, Schmitz P (2010) Fire management in mediterranean-climate shrublands: a case study from the cape fynbos, South Africa. *Journal of Applied Ecology* 47, 631–638. doi:10.1111/J.1365-2664.2010.01800.X
- Veth P, Ditchfield K, Hook F (2014) Maritime deserts of the Australian north-west. Australian Archaeology 79, 156–166. doi:10.1080/ 03122417.2014.11682032
- Veth P, Ward I, Manne T, Ulm S, Ditchfield K, Dortch J, Hook F, Petchey F, Hogg A, Questiaux D, Demuro M, Arnold L, Spooner N, Levchenko

V, Skippington J, Byrne C, Basgall M, Zeanah D, Belton D, Helmholz P, Bajkan S, Bailey R, Placzek C, Kendrick P (2017) Early human occupation of a maritime desert, Barrow Island, north-west Australia. *Quaternary Science Reviews* **168**, 19–29. doi:10.1016/J.QUASCIREV. 2017.05.002

- Wayne AF, Cowling A, Lindenmayer D, Ward CG, Vellios CV, Donnelly CF, Calver M (2006) The abundance of a threatened arboreal marsupial in relation to anthropogenic disturbances at local and landscape scales in Mediterranean-type forests in south-western Australia. *Biological Conservation* 127, 463–476.
- Wells G, Hopper SD, Dixon KW (2004) Fire regimes and biodiversity conservation: a brief review of scientific literature with particular emphasis on south-west Australian studies. Environmental Protection Authority. (Perth, WA, Australia).
- Williams RJ, Bradstock RA (2008) Large fires and their ecological consequences: introduction to the special issue. *International Journal of Wildland Fire* 17, 685–687. doi:10.1071/WF07155
- Williams KJ, Ford A, Rosauer DF, De Silva N, Mittermeier R, Bruce C, Larsen FW, Margules C (2011) Forests of east Australia: the 35th biodiversity hotspot. In 'Biodiversity hotspots'. (Eds FE Zachos and JC Habel) pp. 295–310. (Springer-Verlag: Berlin and Heidelberg)
- Wilson BA, Kuehs J, Valentine LE, Sonneman T, Wolfe KM (2014) Guidelines for ecological burning regimes in Mediterranean ecosystems: a case study on *Banksia* woodlands in Western Australia. *Pacific Conservation Biology* 20, 57–74.
- Wittkuhn R, McCaw WL, Wills A, Robinson R, Anderson AN, Van Heurck P, Liddelow G, Cranfield R (2011) Variation in fire interval sequences has minimal effects on species richness and composition in fire-prone landscapes of south-west Western Australia. *Forest Ecology* and Management 261, 965–978. doi:10.1016/J.FORECO.2010.10.037
- Wooller RD, Wooller SJ (2014) 'Sugar and sand: the world of the honey possum.' (Swanbrae Press: Perth, WA, Australia)
- Wooller SJ, Wooller RD, Brown KI (2002) Regeneration by three species of *Banksia* on the south coast of Western Australia in relation to fire interval. *Australian Journal of Botany* 50, 311–317. doi:10.1071/ BT01078
- Yates C, Edwards AC, Russell-Smith J (2008) Big fires and their ecological impact in Australian savannas: size and frequency matters. *International Journal of Wildland Fire* 17, 768–781. doi:10.1071/WF07150
- York A (1999a) Long-term effects of frequent low-intensity burning on the abundance of litter-dwelling invertebrates in coastal blackbutt forests of south-eastern Australia. *Journal of Insect Conservation* 3, 191–199. doi:10.1023/A:1009643627781
- York A (1999b) Long-term effects of repeated prescribed burning on forest invertebrates. In 'Australia's biodiversity: responses to fire'. (Eds AM Gill, CZ Woinarski and A York) pp. 181–266. (Department of Environment and Heritage: Canberra, ACT, Australia)
- Zylstra P (2018) Flammability dynamics in the Australian Alps. *Austral Ecology* **43**, 578–591. doi:10.1111/AEC.12594