

Fire as a key driver of Earth's biodiversity

Tianhua He^{1,2*} , Byron B. Lamont¹ and Juli G. Pausas³

¹*School of Molecular and Life Sciences, Curtin University, Perth, Australia*

²*College of Science, Health, Engineering and Education, Murdoch University, Murdoch, Australia*

³*CIDE-CSIC, Valencia, Spain*

ABSTRACT

Many terrestrial ecosystems are fire prone, such that their composition and structure are largely due to their fire regime. Regions subject to regular fire have exceptionally high levels of species richness and endemism, and fire has been proposed as a major driver of their diversity, within the context of climate, resource availability and environmental heterogeneity. However, current fire-management practices rarely take into account the ecological and evolutionary roles of fire in maintaining biodiversity. Here, we focus on the mechanisms that enable fire to act as a major ecological and evolutionary force that promotes and maintains biodiversity over numerous spatiotemporal scales. From an ecological perspective, the vegetation, topography and local weather conditions during a fire generate a landscape with spatial and temporal variation in fire-related patches (pyrodiversity), and these produce the biotic and environmental heterogeneity that drives biodiversity across local and regional scales. There have been few empirical tests of the proposition that 'pyrodiversity begets biodiversity' but we show that biodiversity should peak at moderately high levels of pyrodiversity. Overall species richness is greatest immediately after fire and declines monotonically over time, with postfire successional pathways dictated by animal habitat preferences and varying lifespans among resident plants. Theory and data support the 'intermediate disturbance hypothesis' when mean patch species diversity is correlated with mean fire intervals. Postfire persistence, recruitment and immigration allow species with different life histories to coexist. From an evolutionary perspective, fire drives population turnover and diversification by promoting a wide range of adaptive responses to particular fire regimes. Among 39 comparisons, the number of species in 26 fire-prone lineages is much higher than that in their non-fire-prone sister lineages. Fire and its byproducts may have direct mutagenic effects, producing novel genotypes that can lead to trait innovation and even speciation. A paradigm shift aimed at restoring biodiversity-maintaining fire regimes across broad landscapes is required among the fire research and management communities. This will require ecologists and other professionals to spread the burgeoning fire-science knowledge beyond scientific publications to the broader public, politicians and media.

Key words: fire regime, pyrodiversity, biodiversity, environmental heterogeneity, intermediate disturbance hypothesis, patch mosaic burning.

CONTENTS

I. Introduction	1984
II. Fire regime and pyrodiversity explained	1984
III. Fire as a driver of biodiversity	1988
(1) Individual fire components as drivers of biodiversity	1988
(2) Diversity through time: fire resets community dynamics	1990
(3) The intermediate disturbance hypothesis	1992
(4) The pyrodiversity–biodiversity hypothesis	1994
(5) Mixed fire regime and intermediate disturbance hypothesis	1997
(6) Fire and biodiversity at broad scales	1997
IV. Fire as an evolutionary driver of biodiversity	1998
(1) Fire-driven evolution and adaptation	1998
(2) Fire and diversification of plant lineages	1999

* Author for correspondence (Tel.: +61 8 9457 7164; E-mail: tianhua.he@curtin.edu.au)

(3) Mutagenic effects of heat and chemicals released by combustion	2001
V. Implications for biodiversity conservation and fire management	2002
VI. Future research directions and outcomes	2003
VII. Conclusions	2004
VIII. Acknowledgements	2004
IX. References	2004
X. Supporting Information	2010

I. INTRODUCTION

Many terrestrial ecosystems are fire prone, and fire controls their composition and structure (Bond, Woodward & Midgley, 2005; Krawchuk *et al.*, 2009; Pausas & Keeley, 2009; Pausas & Ribeiro, 2013; Archibald *et al.*, 2018; He & Lamont, 2018a). Where these ecosystems have a long history of recurrent fire (over geological time scales), they harbour exceptionally high levels of species richness and endemism (Bond & Parr, 2010; Rundel *et al.*, 2016; Fernandes *et al.*, 2018) and are considered biodiversity hotspots (Myers *et al.*, 2000). Environmental heterogeneity and resource availability (climate, soils) have long been regarded as the most important factors that determine species richness at the regional scale (O'Brien, 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003; Krefl & Jetz, 2007). For example, the exceptionally high species richness of the Cape flora in South Africa has been hypothesised to be the result of geographic and parapatric radiation in the region *via* a mosaic of distinctive habitats due to localised soils, microclimates and altitudinal variations (Linder, 2005; Schnitzler *et al.*, 2011). The relatively stable post-Miocene history and establishment of semi-arid and highly seasonal (Mediterranean-type) climates in southwestern Africa have also been assumed to be major contributors to diversity (Goldblatt & Manning, 2000). Although a role for the presence of wildfire as a stimulus for species diversification was proposed long ago (Mutch, 1970), it has only received attention more recently (He, Lamont & Manning, 2016; Rundel *et al.*, 2016, 2018) and has been shown to have a dominant, even pre-emptive, role compared with other likely environmental constraints (Hu *et al.*, 2018; Lamont, He & Yan, 2019b). In attempts to understand the distribution and diversity of species, disturbance by fire as a key agent of selection has long been overlooked, and continues to be so (Pausas & Lamont, 2018; Magadzire *et al.*, 2019; Pausas & Bond, 2019). However, there is increasing evidence to suggest that prevailing fire regimes make a major contribution to explaining plant diversity at both the community (Bourke, Myers & Belote, 2015; Hu *et al.*, 2018) and global (Pausas & Ribeiro, 2017) scales compared with other possible constraints.

Within the wide range of agents of selection available (e.g. climate, soil, pollinators, microsymbionts, herbivores), a role for fire in the diversification of floras has long been postulated (Wells, 1969; Cowling, 1987). It is now known that fire has been a leading determinant of species diversity in fire-prone ecosystems over the last 100 million years (Simon *et al.*, 2009; Bytebier *et al.*, 2011; Crisp *et al.*, 2011; He,

Lamont & Downes, 2011; He *et al.*, 2012; He *et al.*, 2016), and has led to the development of an extraordinary diversity of plants (Rundel *et al.*, 2016). Studies on fire-stimulated responses under a wide range of fire regimes, and on the role of fire in the ecology and evolution of non-plant groups (fungi, insects, birds and mammals), are emerging (McMullan-Fisher *et al.*, 2011; Hutto *et al.*, 2016; Stawski *et al.*, 2017; Pausas & Parr, 2018; Carbone *et al.*, 2019). The long co-existence between these organisms and fire suggests that they have adaptive traits allowing them to persist in fire-prone environments. Given that fire may kill organisms while at the same time opening up new niches, our central question is: to what extent do different fire regimes shape species diversity among and within biomes globally? Species diversity is shaped by multiple drivers under the umbrella of environmental factors, disturbance, and species interactions (e.g. Schnitzler *et al.*, 2011; Stein, Gerstner & Krefl, 2014; Van der Niet, Peakall & Johnson, 2014; Cramer & Verboom, 2017; Pausas & Lamont, 2018); their relative roles may depend both on their intensity and history. Here we focus on fire as an agent of disturbance and the mechanisms that enable recurrent fire to act as a significant ecological and evolutionary force that promotes and maintains biodiversity over different spatiotemporal scales. To do so, we address a range of factors, including time-since-fire, mixed fire regimes, intermediate disturbance, and pyrodiversity, as they impact biodiversity at the landscape scale, through to fire's direct role as a mutagenic agent.

II. FIRE REGIME AND PYRODIVERSITY EXPLAINED

Each particular fire, which we refer to as a *fire event*, has a unique set of properties characterised by its spatial and temporal dimensions (Bradstock, 2008). The fire event is controlled by the type of vegetation and its moisture state, the topographic features of the fire-prone area, and the local weather conditions during the fire event. A given fire event can be defined by: fire intensity (heat per unit time generated by the fire), size (total burnt area), its horizontal (patchiness) and vertical (strata burnt) spread pattern, the time since (the previous) fire, and the season in which it occurred (Fig. 1). These conditions define the type of fire (*fire type*), in terms of which of the two extremes of each of the six components is exhibited by the fire, and it is independent of the ignition source (Fig. 1). Note that not all combinations

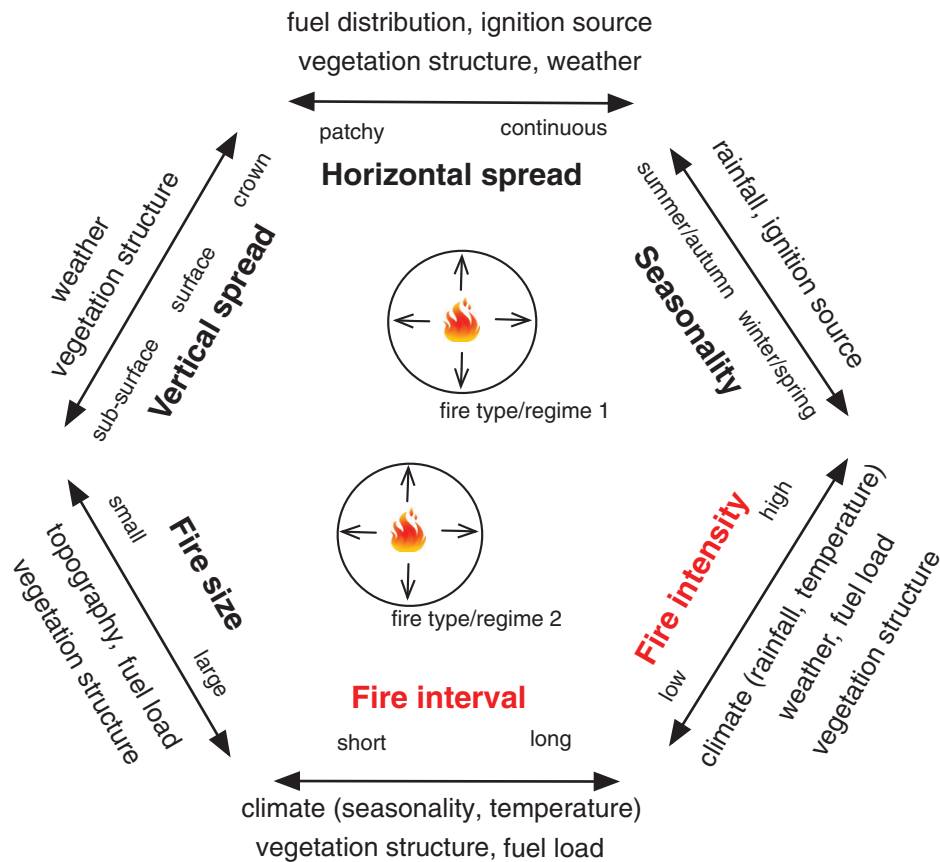


Fig. 1. The six components (the two ‘core’ components in red) of individual fires (fire events) and environmental factors that control the properties of each component to define the fire type. Ignition source (lightning, anthropogenic) may affect the properties of each component but is not itself a component of fire. ‘Fire interval’ refers to the time since last fire for individual fires and mean fire interval for the fire regime. The fire regime arises from repeated patterns (means plus variance) over time of the properties of the components for each fire. For a certain vegetation structure under a given climate, fire regime is relatively predictable (as indicated by the circles) and selects for an adapted group of plants, microflora and associated fauna.

of descriptors are possible and that there are correlations among descriptors. A given fire creates a landscape patch, and this patch has a fire history. Parameters that define the temporal component are: (i) time since last fire (fire age), (ii) mean fire interval (mean time between successive fires), and (iii) variability about this mean (Fig. 2). Since it can only be recognised from the imprint of the last fire on the vegetation, a *patch* is usually defined by the area covered by that fire and the time since the previous fire occurred. A patch may also be recognised as an unburnt area within the larger confines of the total area burnt by more recent fires. The distribution of different fire-related patches forms a mosaic over the reference area. The reference area usually refers to a stated community type, but can be extended to the landscape or regional scales. This mosaic varies through time and space as more fires occur in different locations and time since fire increases until a new fire occurs. When records are available over many years, the mean fire interval can be inverted to give fire frequency, the number of fire events per time interval that can include time since last fire (Fig. 2). However, neither parameter gives any indication of

variation about the mean (stochasticity) that can have major long-term effects on plant responses (Enright *et al.*, 1998). Although rarely formalised, this can be represented by the coefficient of variation among fire intervals.

Fire ‘intensity’ should not be confused with fire ‘severity’. *Severity* refers to the impact of the fire event on the associated biota and is often gauged as the fraction of biomass that is consumed by the fire or a surrogate for that, e.g. the mortality rate of the affected species (Keeley, 2009; Taille *et al.*, 2018). Consequently, severity may depend on the species survival traits (e.g., bark thickness, bud bank) and vegetation characteristics (e.g. density, continuity, flammability), while intensity is a physical component of the fire itself. Severity is often closely associated with fire intensity but also with extremes in other fire properties, e.g. unusually frequent fires might also be regarded as having severe effects on the viability of particular biota. Alternatively, occasional extremes in fire resilience and intensity justify distinguishing the two concepts, such as historically fire-protected (non fire-prone) vegetation failing to recover from even low-intensity fires (Cochrane & Barber, 2009; Balch *et al.*, 2015). Of some

Fire history of a given location in a reference area

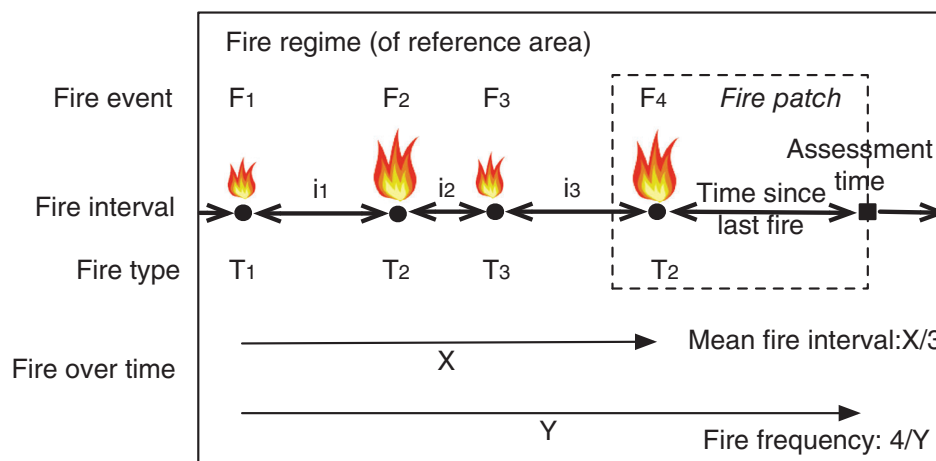


Fig. 2. Illustrations of time-related fire concepts. Recurrent fires occur at each location in a reference area (fire events, F) and usually vary in their properties – see Fig. 1 for the six components that together describe the fire type, T. Times between successive fires vary (fire interval, i) that can be summed and their mean taken. The area occupied by a particular fire event and time since the last fire define a patch. When the occurrence of fires is monitored over an extended period they can be used to estimate fire frequency. The fire regime is the mean and range of fire types experienced throughout the reference area over a sufficiently long period to be able to calculate fire frequency.

value in the forest literature is the concept of *mixed-severity fires* or just mixed-fire regimes. To be ‘mixed’, the reference area is considered to include a moderate abundance of ‘stand-replacing patches’ (Agee, 1993; Collins & Stephens, 2010; Hessburg *et al.*, 2016) although this assumes that all dominant species do not survive intense fire so it is mainly applicable to certain conifer forests. More generally, ‘mixed’ simply implies wide variation about the mean of one or more fire properties or its effects. Here, adaptive traits can be expected to show intermediate properties (e.g. weak serotiny; Enright *et al.*, 1998) or high levels of phenotypic plasticity (He *et al.*, 2019). Alternatively, the species pool contains species/ecotypes with a wide range of traits on which each patch type can draw. ‘Mixed-severity’ has some elements in common with ‘high pyrodiversity’ (Taille *et al.*, 2018) but the latter is a broader concept, with stand replacement just one of many options for defining patchiness (Section III.4).

The proposition that fire promotes and maintains biodiversity does not mean that any vegetation type, and the species within it, are adapted to fire *per se* (Keeley *et al.*, 2011). Rather, species possess a set of functional traits that enable them to respond favourably to a certain fire regime. The concept of fire regime is therefore central to understanding the role of fire as a critical ecological and evolutionary factor. *Fire regime* refers to the typical properties of all fire events in a given reference area (community to region) gauged over an extended time period. It is defined by the repeated patterns of each fire component (Fig. 1). For example, it may be characterised as experiencing intense crown fires in summer–autumn at moderate frequency, widespread and with little patchiness. The two core components, fire frequency and intensity, have upper and lower limits to which a species is adapted in an ecological/evolutionary

sense (Keeley *et al.*, 2011). These have major effects on other components, especially the spread pattern (strata that burn, patchiness) and total area burnt. Often distinguished are crown and surface fire regimes: the former is a response to intense fires at low/moderate frequency that reach the upper stratum, and the latter to less-intense fires, usually at high frequency or managed fires under mild weather conditions, that burn only the ground stratum in shrublands or the understorey in woodlands/forests. Mixed-severity fire regimes require patches of both crown and surface fires.

Fire frequency and intensity are controlled by the vegetation age and composition as they determine the available fuel *via* net primary production (Fig. 3), and by the weather at the time of each fire event. Both are confounded by climate that controls the type of vegetation and sets the bounds within which weather occurs, but also has independent effects such as the incidence and seasonality of lightning and litter dryness (Fig. 1). For example, in (sub)tropical biomes with mid-to-high net primary productivity, and with much fuel potentially available to be burnt (Fig. 3), the amount of moisture in fuel is the strongest determinant of fire frequency and intensity (drought-driven fire regimes; Pausas & Ribeiro, 2013). At the other end of the spectrum, in areas where the available fuel is generally meagre, such as deserts, alpine regions and tundras, the availability of fuels produced during a pulse of elevated resources (e.g. higher-than-average rainfall) in the growing season has more influence on the fire pattern (fuel-driven fire regimes; Pausas & Ribeiro, 2013; Archibald *et al.*, 2018). In regions with medium productivity, such as grasslands/savannas and evergreen shrublands, fire activity is much more frequent and predictable (the intermediate fire-productivity model; Pausas & Ribeiro, 2013).

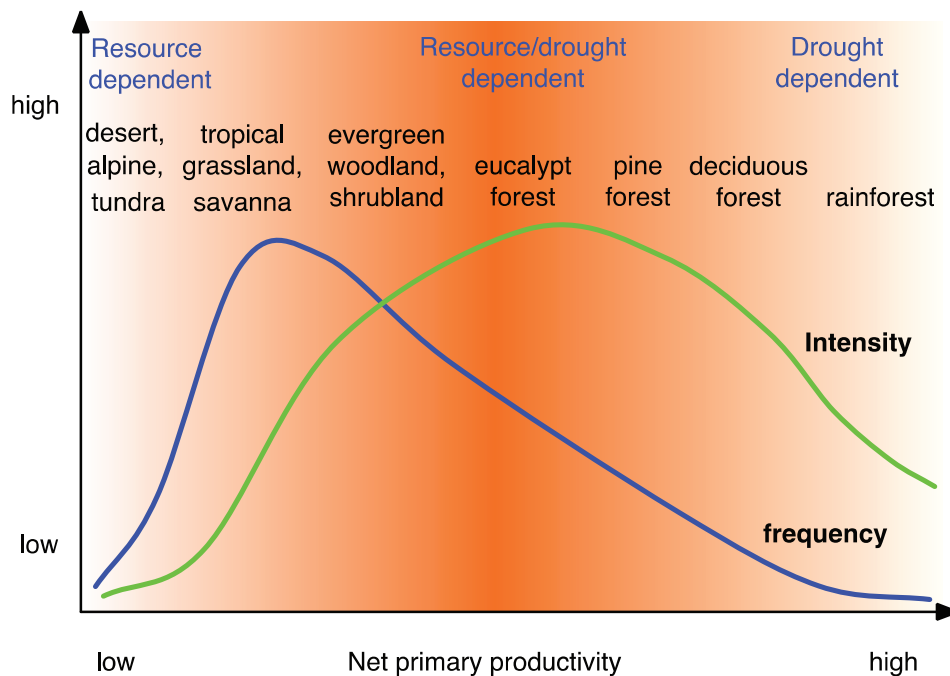


Fig. 3. Fire intensity and frequency in ecosystems with different levels of net primary production. The intensity of orange (background color) indicates the level of fire proneness of each vegetation type. The extent to which fire occurrence in each vegetation type is dependent on critical levels of resources or drought is also shown.

Fire regime has four additional components: the total size of the burnt area under consideration (fire size), the mean seasonality of the fire, and the spread patterns: horizontal (overall grain of patchiness) and vertical (usual strata burnt) (Fig. 1). With fire regime, the time component is given by fire frequency or mean fire interval. These components are influenced by both biotic and abiotic factors, including vegetation structure, topographic heterogeneity, local weather during each fire event, and the ignition source (Collins *et al.*, 2007; Kane *et al.*, 2015). The fire regime, therefore, filters biotas, selecting for adaptations that persist in particular fire-prone environments at the scales of both population (Hernández-Serrano *et al.*, 2013; Lamont, He & Downes, 2013; Vandvik *et al.*, 2014) and community (Cavender-Bares *et al.*, 2004; Verdú & Pausas, 2007). Through the feedback cycle, fire shapes the vegetation structure that reinforces the tendency for a specific fire regime (with predictable fire frequency and intensity) to prevail (Archibald *et al.*, 2018). Where fire heterogeneity patterns tend to stabilise over time, i.e. the range of variation in the components becomes predictable, a fire regime for the reference area may be defined.

Local variations in the distribution of fuel, topography, moisture levels, weather conditions and ignition sources cause properties of the spatial/seasonal components (Fig. 1) to vary continuously over the landscape. Together with temporal components (time since previous fire, previous history of fire intervals for individual patches), they produce a mosaic of fire-related landscape patches (see Fig. 1 in Agee, 2005 for an excellent demonstration of fire-related mosaics), with

distinct composition, structure and fire history, that control the level of pyrodiversity (Martin & Sapsis, 1992). Thus, *pyrodiversity* is the level of fire-caused heterogeneity (diversity of patches) in a given area at a stated time (Krawchuk & Moritz, 2011). The patch components are not independent, such that the time interval between the most recent fire and the previous one may be a surrogate for the amount and distribution of fuel and hence fire intensity, patch size and which strata burn. The temporal pattern of fire histories, such as varying historical intensity and fire intervals across the landscape, has sometimes been termed the ‘invisible (fire) mosaic’ as usually only the most recent postfire patches can be recognised (Bradstock *et al.*, 2005; Parr & Andersen, 2006; Bradstock, Tozer & Keith, 2008), and represents the temporal dimension of pyrodiversity.

Mathematically, pyrodiversity may be treated as a numerical summation of the scaled range of spatial variation in the fire components within a stated area. Different ranges of the various components can sum to a similar level of pyrodiversity, just as different species compositions and abundance spread may produce similar species diversities, and even biodiversity: both can be low, moderate or high. Thus, it is possible to quantify pyrodiversity using standard indices of diversity such as Shannon’s index, classically used for species diversity, and thus compare them. For further interpretation, the relative levels of the components need to be examined to explain how each diversity estimate was reached (Davies *et al.*, 2018). The term pyrodiversity has been used increasingly in the literature, as it is seen to be aligned with the ecological hypothesis that ‘diversity begets

diversity' (Parr & Andersen, 2006; Bowman *et al.*, 2016; Kelly & Brotons, 2017). In practice only one or a few components are assessed on the understanding that they are a surrogate for others or that other components do not vary significantly (Martin & Sapsis, 1992; Sitters *et al.*, 2014; Ponisio *et al.*, 2016; Davies *et al.*, 2018).

In contrast to pyrodiversity, the concept of fire regime describes the specific properties of each of the fire-related components as gauged over many years. The properties of the six components of each fire at a given location in the reference area determine what species will be present in each patch. Fire regime may include reference to variation about the mean where it is pronounced, e.g. mixed-severity fire regime (Collins & Stephens, 2010), although quantifying/ranking that variation is more the province of pyrodiversity. While the various fire-related patches have a local effect on population viability, it is the level of pyrodiversity, and its causes, that dictate overall species presence and abundance at that time, and the long-term impact of the fire regime that determines what species will remain. Their impacts on biodiversity are examined in the following sections.

With regard to the concept of biodiversity, we usually equate this with species diversity. We recognise that species diversity has at least two components, number of species (richness, *S*) and evenness (the extent to which total abundance is spread among the species, *E*). *S* is highlighted as this is easily assessed and conceptualized and is usually correlated with *E* (dominance is more likely with fewer species). Other possible species-diversity components, such as phylogenetic or genetic disparity, are not considered here. We also accept that biodiversity has two other components highly relevant to fire-prone systems: structure and function (Noss, 1990; Lamont, 1995). These are referred to when discussing the effect of fire on vegetation type, successional processes and fire-related traits that control ecosystem function.

III. FIRE AS A DRIVER OF BIODIVERSITY

Fire has been present since terrestrial plants invaded land 420 million years ago (Scott, 2018). It has long been recognised that fire is a natural ecological factor in many forest, woodland, shrubland, and grassland systems around the world (Rundel, 1981; Bond & Keeley, 2005; Bond, 2008; Pausas & Keeley, 2009), and that it has a major role in maintaining biodiversity and ecological processes in fire-prone ecosystems (Bond & Parr, 2010; Rundel *et al.*, 2016, 2018; Pausas & Keeley, 2019). Fire plays many important ecological roles in ecosystems that cannot be duplicated by any other natural events. Fire affects key processes in the ecosystem, dictates what species are present in that ecosystem and determines how they are arranged in space and time. Environmental heterogeneity and resource availability are among the most important factors that determine species-richness gradients (Stein *et al.*, 2014), and, in many ecosystems, these are controlled by the incidence

of fire. Here, we review the ecological role of fire in creating environmental heterogeneity, and generating and maintaining biodiversity. We focus initially on the effect of variation in fire components on biodiversity at a given location (temporal scale, Sections III.1–3) then turn to their variation over the landscape (spatial scale, Sections III.4–6).

(1) Individual fire components as drivers of biodiversity

The fire-biodiversity relationship has been tested for a wide range of taxa worldwide in fire-prone regions (Table 1). These studies have examined species diversity at various temporal and spatial scales. The parameterisation of fire type is usually based on variation in one component, such as fire frequency, fire size, strata burnt, fire intensity, or seasonality, at different locations or sometimes a combination of two or three components (Table 1). The results either demonstrate a significant positive relationship (13 studies), negative (9), a positive relationship dependent on the component considered (7), or no relationship (1) between changes in the fire component and (component of) biodiversity. Species diversity tends to be positively correlated with increasing fire severity within limits (Sitters *et al.*, 2014; Tingley *et al.*, 2016) but a plateau or decrease at high severity is also common (Taille *et al.*, 2018). Time-since-fire may be critical in the abundance of biota and a humped relationship is the norm (Lazarina *et al.*, 2017; Taille *et al.*, 2018). Decreases/increases in mean fire interval may have a positive/negative (8 studies), negative/positive (6) or variable/nil (7) effect on species diversity. Temporal aspects are considered further in Section III.2 as the outcome depends very much on the range of intervals used and the ecosystem under study.

The diversity of ants, spiders and termites usually responds positively to greater fire activity. Birds, reptiles, small animals, and intensity of plant–animal interactions generally benefit from diverse fire types with varying intensity, while varying fire size and frequency do not affect their diversity (Table 1). Among plants, shortened fire intervals often lead to decreased species richness and diversity of plant functional traits in the community, especially among woody species (Bradstock *et al.*, 1997; Bradstock *et al.*, 1998; Schaffhauser *et al.*, 2011; Bowman, O'Brien & Goldammer, 2012; Enright *et al.*, 2014). Bowman *et al.* (2016) noted that these mixed results could be the outcome of failing to include spatiotemporal heterogeneity among fire types (pyrodiversity; see Section III.4), and assessing study areas over too short a time scale. Thus, the level of species diversity is overwhelmingly associated with the fire regime to which the area is subjected.

Are changes in fire-biodiversity relationships always driven by changes in fire properties as the independent variable? Directional variation in the fire regime resulting from climate change has been shown to lead to changes in species richness and associated functional traits (Lamont *et al.*, 2013), i.e. fire drives biodiversity. Conversely, areas that are similar climatically but have different fire regimes produce different vegetation types that confirm the tight relationship between the fire regime and biodiversity. Thus,

Table 1. Examples of studies that examined individual fire components as a driver of biodiversity. Time span refers to the period within which fire events were monitored. BACI: before-after-control-impact design

Taxon group	Ecosystem	Fire components assessed	Biodiversity components assessed	Time span of study (years)	Relationship demonstrated	Reference
Ants	Brazilian Cerrado	Fire interval	Species composition	16–37	Positive	Maravalhas & Vasconcelos (2014)
Ants	Northern Australia	Fire history (interval)	Species richness	10	Positive	Anderson <i>et al.</i> (2014)
Termites	African savanna	Fire interval and intensity	Species diversity	65	Positive	Davies <i>et al.</i> (2012)
Termites	Semi-arid Australia	Fire age (time since fire) patchiness	Species diversity	35	No relationship	Davis <i>et al.</i> (2018)
Insects	SE Australia	Fire history	Species richness	75	Positive	Brown & York (2017)
Spiders	Western Australia	Fire history heterogeneity	Species richness, abundance	20	Positive	Langlands, Brennan & Ward (2012)
birds	Montane California, USA	Fire severity	Species diversity	10	Positive	Tingley <i>et al.</i> (2016)
Birds	SE Australia	Fire size, intensity	Species diversity	BACI	Positive	Sitters <i>et al.</i> (2014)
Birds	SE Australia	Fire history (interval)	Species richness	35	No relationship to positive	Taylor <i>et al.</i> (2012)
Reptiles	Central Australia (arid)	Fire size	Species diversity	<1	No relationship to positive	Pastro, Dickman & Letnic (2014)
Reptiles	SE Australia	Fire history (interval)	Species richness	35	Negative	Nimmo <i>et al.</i> (2013)
Reptiles	Western Desert, Australia	Fire size (burnt area)	Abundance	20	Positive	Bird <i>et al.</i> (2013)
Reptiles	Semi-arid Australia	Time since fire	α , β , γ diversity	13	No relationship to positive	Farnsworth <i>et al.</i> (2014)
Small mammals	Australian tropical savanna	Fire interval	Persistence	6	Positive	Griffith, Garnett & Brook (2015)
Small mammals	SE Australia	Fire history (interval)	Species richness	35	No relationship to positive	Kelly <i>et al.</i> (2012)
Small mammals	Northern Australia	Fire size, interval	Species diversity	8	Negative	Lawes <i>et al.</i> (2015)
Medium-sized mammals	Northern Kimberley, Australia	Fire history (interval)	Species richness, abundance	4	Negative	Radford <i>et al.</i> (2015)
Mammals	Central Australia (arid)	Fire size (burnt area)	Species diversity	<1	No relationship to positive	Pastro <i>et al.</i> (2014)
Mammals	N Australian savanna	Fire frequency patchiness	Species diversity	9	Positive	Davies <i>et al.</i> (2018)
Plant–pollinator communities	National parks, California, USA	Fire interval, age, extent, severity	Bee-plant interactions	10	Positive	Ponisio <i>et al.</i> (2016)
Plants	SW Australia	Fire interval	Species richness	32	No relationship to positive	Witkuhn <i>et al.</i> (2011)
Plants	Mediterranean, Corsica Island	Fire interval	Species richness	13000	No relationship to positive	Leys, Finsinger & Carcaillet (2014)

Table 1. Continued

Taxon group	Ecosystem	Fire components assessed	Biodiversity components assessed	Time span of study (years)	Relationship demonstrated	Reference
Plants	SW Australia	Fire interval	Woody species richness, fire trait abundance	20	Negative	Enright <i>et al.</i> (2014)
Plants	SE Australia	Fire interval	Species richness, functional traits	200 (simulation)	Negative	Bradstock <i>et al.</i> (1998)
Plants	SE Australia	Fire interval	Species richness, functional traits	3	Negative	Watson, Bradstock & Morris (2009)
Plants	SE Australia	Fire interval	Species richness, functional traits	3	Negative	Bradstock, Tozer & Keith (1997)
Plants	Mediterranean, SE France	Fire interval	Species richness, functional traits	50	Negative	Schaffhauser, Curt & Taton (2011)
Plants	Tasmania	Fire interval	Species richness	20	Negative	Bowman <i>et al.</i> (2016)
Vegetation	SE Australia	Fire severity, time since fire patchiness	Heterogeneity in vegetation structure	3–20	Positive	Bassett <i>et al.</i> (2017)
Vegetation	SE Australia	Fire interval patchiness	Heterogeneity in vegetation structure	55	Positive	Foster <i>et al.</i> (2017)

areas burnt frequently to maintain grasslands (savannas) have different species composition and diversity than surrounding areas that burn rarely (forests) (Bond & Parr, 2010; Dantas, Batalha & Pausas, 2013). These different floras have different flammability traits that maintain different fire regimes and contrasting vegetation although under a similar climate (stabilising feedbacks). Some areas under different environmental constraints and fire regimes may nevertheless have similar vegetation structurally, although differing greatly in terms of species, such as sub-alpine and savanna grasslands. Thus, certain components of biodiversity may sometimes be independent of the fire regime, while species composition may invert the usual relationship by driving the fire regime instead.

(2) Diversity through time: fire resets community dynamics

By consuming biomass, fire creates vegetation gaps and initiates population and community recovery. In fire-prone ecosystems, most plant species present before the fire either recover vegetatively and/or germinate from stored seeds (Keeley *et al.*, 2012). Seeds released by serotinous fruits/cones in response to fire spread through and across adjacent burnt communities and immediately add to the species available for recruitment (Merwin *et al.*, 2012). Short-lived or geophytic species that had long completed their aboveground life cycle become visible as their seeds or belowground bud banks break dormancy and their foliage appears above the soil (Pausas *et al.*, 2018b). In fire-prone ecosystems, almost all plant species in the postfire community recorded prefire are evident within 12 months of a fire (Herath *et al.*, 2009) – this phenomenon conforms with the ‘autosuccession’ (Hanes, 1971) or ‘initial floristic composition’ (Noble & Slatyer, 1980; Enright *et al.*, 2007) models of community succession. The subsequent rapid decline in population size is accompanied by a gradual increase in vegetative growth of survivors, a period of escalating fecundity, then declining foliage and seed production, and eventual death or return to belowground dormancy. However, the key to understanding community dynamics is that individual species undertake their bell-shaped response curve at different rates (Fig. 4A). Some annuals are only evident the year following fire (pyroendemics; Keeley & Pausas, 2018), although most linger in the increasingly scarce bare patches. Other herbaceous species complete their (aboveground) life cycle within a few years (Hinman & Brewer, 2007; Lamont & Downes, 2011), weakly woody shrubs may survive for about a decade, strongly woody shrubs lacking persistent budbanks may survive for several decades, strongly woody plants with persistent budbanks may survive for hundreds of years, and clonal species with belowground budbanks may survive for thousands of years (Lamont & Wiens, 2003; Merwin *et al.*, 2012; Pausas *et al.*, 2018b).

As particular plant species and growth forms take turns to dominate the community, and the structure and availability of habitat types changes progressively, the apparent successional stages are due to alternating maximum

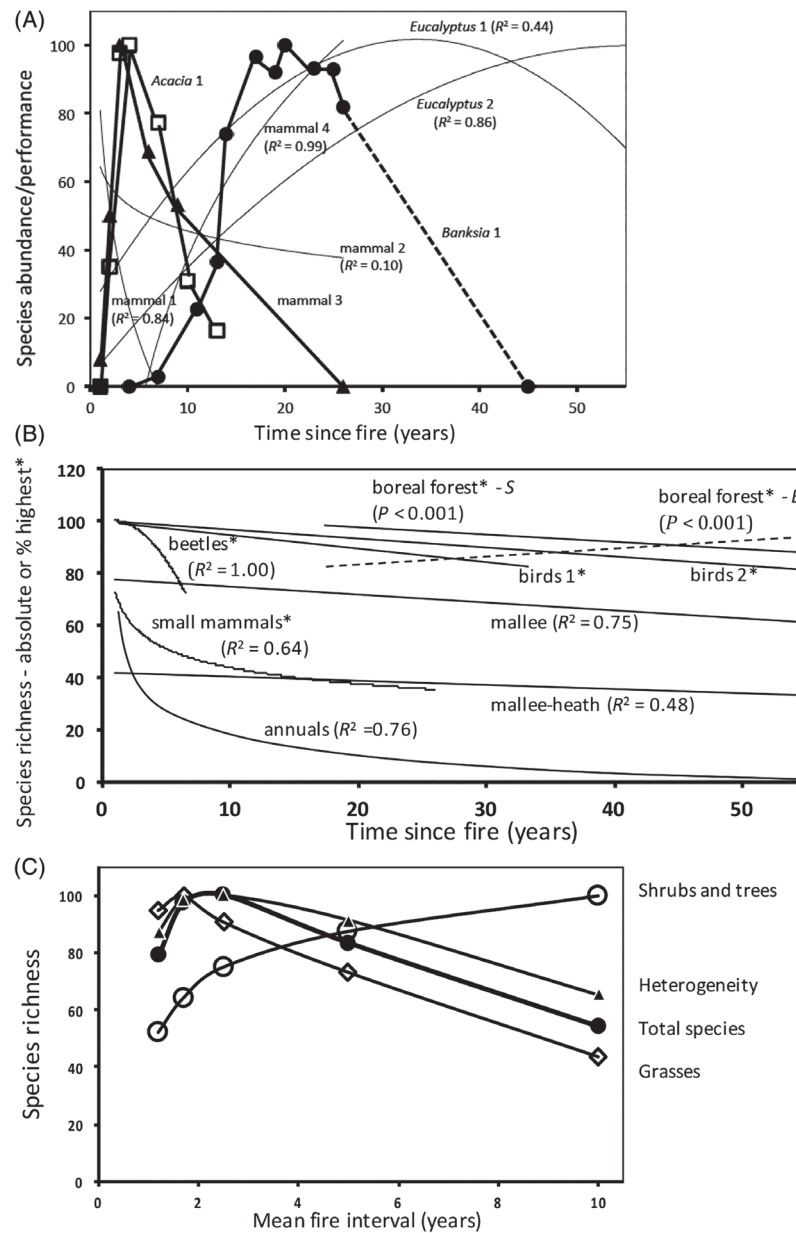


Fig. 4. (A) Postfire abundance/performance of individual species relative to the highest value in each data set. Curve fits are based on the best-fit lines using at most two variables (shown with R^2), or are lines joining the raw data points. Time-since-fire effects are given for four species in SW Australia: *Acacia* 1 (fire-killed) is for annual seed production; population size decreased by 20-fold over the period shown (Monk, Pate & Loneragan, 1981). *Banksia* 1 (fire-killed) is for on-plant seed storage (serotiny) with up to 200 released seeds per plant after fire reducing one individual by 15 years, and with mean longevity estimated at 45 years (Lamont & Enright, 2000). *Eucalyptus* 1 and 2 represent the stature of a mixture of resprouting eucalypts over time (Gosper *et al.*, 2012). Time-since-fire effects are also given for the abundance of four mammals in savanna grasslands of Brazil (Briani *et al.*, 2004). Note that all plant species are present from year 1, but some animals enter the system later. (B) Trend lines for species richness (S , * indicates values are plotted relative to highest values) in a given community based on the processes shown in A. Beetles in N Australian savanna (Orgeos & Anderson, 2001, birds 1 (functional richness in heathland) and birds 2 (wet forest) in SE Australia (Sitters *et al.*, 2016), small mammals in Brazil (Briani *et al.*, 2004), boreal forest trees in Canada [both S and evenness (E)], for data over 50 years since fire (Yeboah, Chen & Kingston, 2016), mallee and mallee-heath in SW Australia (Gosper *et al.*, 2012), and annuals in pine forest, Greece (Kazanis & Arianoutsou, 2004). (C) Relative S for different growth forms and total species, and relative species heterogeneity ($1 - \text{mean similarity index between quadrats}$) in relation to mean fire interval (inverse of fire frequency) for a forest–grassland ecotone in central Northern USA (Peterson & Reich, 2008) (quadratic fit for all lines, $P < 0.01$).

performance by persistent species rather than continual colonisation and exodus as expected in non-fire-prone systems and among some animal groups (Pausas & Parr, 2018). Most animals are recorded surprisingly early in postfire communities, with some surviving in cryptic refuges (Kiss & Magnin, 2006), or attracted by enhanced food sources (Lamont, Ralph & Christensen, 1985; Curtis, 1998; Pausas & Parr, 2018) or by predator reduction (Pausas *et al.*, 2018a), then decline as the habitat continues to change (Raphael, Morrison & Yoder-Williams, 1987). Others must wait for the return of more mature stands to meet their niche requirements (Bradstock *et al.*, 2005; Smucker, Hutto & Steele, 2005; Moretti, Duelli & Obrist, 2006; Jacquet & Prodon, 2009; Santos, Badiane & Matos, 2016; Fig. 4A). Some fire-killed epiphytes, such as mistletoes, enter the community from unburnt stands also after some delay, depending on the availability of suitable aerial substrates. However, among both plants and animals, there is a general decline in species richness (S) with time since fire (TSF, Fig. 4B), confirming that succession is essentially a function of the species present initially. As a rule of thumb (including certain functional groups following their sharp initial decline in S), the data collated here indicate a typical slope for both plants and animals of ~ 0.2 , i.e. a decline of about 10% in S every 50-year interval since the last fire. But TSF is not the only temporal variable that affects S : fire frequency (range of fire intervals) must also be taken into account.

In addition, both plants and animals can recolonise burned habitats when they suffer local extinction. Species co-existence is achieved because species are differentially adapted to different successional stages (i.e. different habitat openness) and these stages (TSF) vary across the landscape, while their long-term persistence is achieved through metapopulation dynamics, as species migrate to suitable habitats (He *et al.*, 2004, 2009). Frequent fires retard the over-dominance of the most competitive species, and allow less-competitive species to persist (Grubb, 1977). Similarly, vegetation patches that were burnt in severe fires may lead directly to increased gamma biodiversity, as intense fires create habitats for pioneer species (Tingley *et al.*, 2016). Boucher *et al.* (2012) showed that successional changes in species composition were more pronounced in burned sites than in those with a girdling treatment, which indicates that the contribution of fire-generated habitats to regional diversity includes promoting successional processes. Consequently, these mechanisms allow species climaxing at different successional stages to coexist in space and time, facilitating the maintenance of diverse communities over landscape and regional scales.

(3) The intermediate disturbance hypothesis

Consider the outcome of a range of successive fire intervals. Imagine a stand is intensively burnt again after a few years: many juveniles of fire-killed woody species have not yet reached maturity (immaturity risk; Zedler, 1995). Fire-intolerant species that regenerate *via* seeds (especially if stored on the plant), can potentially be eliminated, as

the seed bank is depleted and becomes insufficient to maintain population viability (Enright *et al.*, 2014). Declines in abundance, and even local extinction or exclusion, with increased fire frequencies have been documented among many plants and animals (Evans, 1988; Watson & Wardell-Johnson, 2004; Kiss & Magnin, 2006; Moretti *et al.*, 2006; Griffith *et al.*, 2015). With the decline in supply of propagules, multiple extinctions are possible (Enright *et al.*, 2015). Bowman *et al.* (2012) observed conversion of serotinous *Eucalyptus regnans* forests in SE Australia to grassy shrublands after sites burnt in 2003 and 2007 were reburnt in 2009 and 2013 while trees were still immature (lacking seeds), explaining complete regeneration failure. Resprouters are likely to be more resilient to frequent fires, especially among grasses, but there is evidence of a reduction in woody resprouters with anthropogenic increases in fire frequency through invasion by annual species (Pausas & Keeley, 2014a). This may be due to insufficient time for starch reserves to build up or because of the exhaustion of resprouting buds.

At the other extreme, consider a stand unburnt for much longer periods, e.g. several decades. By then many geophytes, evergreen herbs and short-lived shrubs ('fireweeds') have retreated to dormant belowground bud banks or completed their life cycle (Fig. 4C). Dead serotinous plants will no longer represent a source of seeds should a fire occur (as any fruits/cones on dead plants are incinerated; Lamont, 1995), while the longevity of some soil-stored seeds may only span a few years. Palmquist, Peet & Weakley (2014) recorded a 30–40% decline in S in Florida pine savannas when fire was withheld for 30 years, especially among herbs, that for many species was permanent when fire was re-introduced (the propagules had presumably perished). Dee & Menges (2014) noted the importance of postfire bare patches (gaps) for recruitment of herbs and shrubs lacking persistent bud banks and that these became unavailable within 26 years in Florida shrublands due to the accumulation of impenetrable litter, with a consequent decline in species diversity. Animals dependent on these species for their survival decline in parallel. This reduction is simply the long tail of the negative S versus TSF slopes described in Fig. 4B and applies to both plants and animals. By contrast, rare species are finally eliminated or excluded and species evenness (E) increases (Fig. 4B).

If the potential presence of species in the community is curtailed by both frequent short-interval and rare long-interval fires, it follows that there must be an optimum moderate-interval fire regime for promoting species diversity (Fig. 5). Somewhere between a mean fire interval of a few years and some decades is a range of intervals where most species are present – they are producing or storing sufficient seeds for self-replacement should a fire occur (Enright *et al.*, 1998). This principle is known as the *intermediate disturbance hypothesis* (IDH) (Connell, 1978; Huston, 2014). This model has been applied to total S , but also to the Shannon diversity index ($H = S \times \text{evenness}$), mean S of n patches, and species heterogeneity (mean pairwise dissimilarity of n patches based on S or H) (Peterson & Reich, 2008). For the latter index,

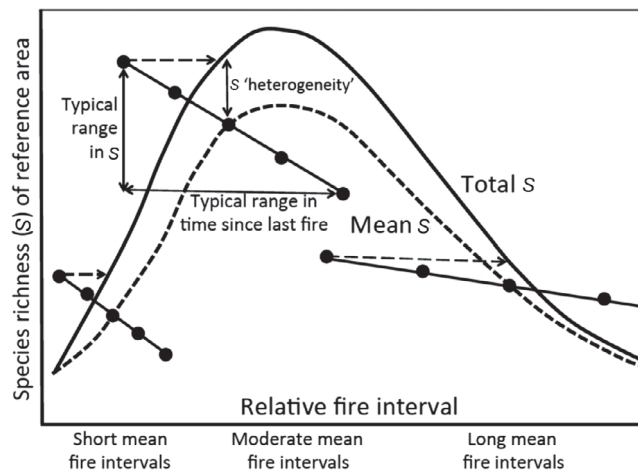


Fig. 5. Conceptualised relationship between species richness (S) of a reference area (community, landscape, region) and mean fire interval (fire regime). For a given fire regime, there is a mosaic of patches defined by different times since the last fire (represented by black circles) about the mean time interval. For convenience, these two measures of time are plotted against a common time axis but in reality time-since-fire forms a third dimension, with, for example, the furthest left dot at each of the three intervals possibly representing the same time-since-fire. Each patch is associated with a different S whose mean S at the different mean intervals describe a bell-shaped curve (broken line). One (or a combination) of the patches (here taken as the one at shortest time-since-fire on the grounds that this usually has the highest S) accounts for the highest S under that regime (total S) and collectively they describe a bell-shaped curve (solid line). The difference between total and mean S is an approximate index of species heterogeneity (biodiversity) in the study area. Note that the curves are asymmetric with there being a sharp decline in S as intervals become shorter and a much more gradual reduction in S at long intervals. This model is consistent with the intermediate disturbance hypothesis (see Fig. 4C).

heterogeneity will be a function of (i) the scale of patchiness of species distributions, and (ii) the range of TSF patches (and their fire history) present in the community – the mosaic effect. As S declines with each repeated short- or long-interval fire, variation about the mean due to TSF patchiness, gauged as (total S – mean S) or mean dissimilarity, will also reduce (Fig. 4C). This means that total S , mean S and heterogeneity will peak under moderate mean fire intervals but highest S can be attributed to just one (recently burnt) patch, whereas mean S and heterogeneity are a function of the net values for all patches. If the initial composition successional pathway holds for plants, then total S may provide an adequate diversity measure for botanists; if the replacement successional pathway holds for animals, then mean S and heterogeneity, with their emphasis on mosaics, will be of more relevance to zoologists (Sitters *et al.*, 2016).

The IDH has been well supported for fire-prone vegetation (Dee & Menges, 2014; Gordijn, Everson & O'Connor, 2018; Fig. 4C) but there has been little relevant work done on animals (Lazarina *et al.*, 2019). If the species trajectories we have outlined above hold generally, it follows that the model must apply to fire-prone systems generally. In that case, failure to support the model (Schwilk, Keeley & Bond, 1997) could be due to limitations of the test rather than inapplicability of the model. Beckage & Stout (2000) showed a $P = 0.08$ quadratic fit to their Florida pine forest diversity data, but if we compare the two most diverse sites at moderate fire frequency with the four sites having lesser and greater fire frequency, a one-tailed t -test with equal variances yields $P = 0.006$. This indicates a problem of inadequate sample size.

Another problem is uncertainty that the full range of mean fire intervals has been covered – there is the risk that only one side of the ‘bell’ has been included because of logistic limitations. While species composition/structure at the frequent and infrequent ends of the fire-interval spectrum may be quite different, whether these values increase at moderate frequencies as expected (Gordijn *et al.*, 2018) may not be evident at the community scale but will apply at the landscape scale (Keith & Tozer, 2012). Other claims of lack of support for the hypothesis have been due to failure to appreciate that the theory only applies to closed systems, i.e. with a fixed species pool – gamma diversity might continue to rise with increasing disturbance in landscapes subject to invasion by exotic species (Kuneš, Abraham & Herben, 2019) although diversity might decrease at the local (alpha) scale if the alien species start to outcompete the indigenous flora (Milberg & Lamont, 1995; Fisher *et al.*, 2009). This is elaborated further in Section III.5.

One potentially confounding issue is the difficulty of subjecting vegetation at different fire intervals to the same fire intensity. Thus, Maikano, Cohn & Di Stefano (2018) obtained higher species diversity at greater fire intensities due to enhanced germination in SE Australian woodland and forest. Among birds, burn intensity may greatly affect the shape of the response curve to time-since-fire (Taille *et al.*, 2018). Individual species of birds in North American forests are favoured by either absence of fire, or low, moderate or intense fires (Smucker *et al.*, 2005; Taille *et al.*, 2018). These variations could distort their relative positions on the graph. In conclusion, fire resets community dynamics and increases species richness and diversity from the outset. Repeated fires

modify the responses and set up new patterns but the basic bell-shaped response curve to increasing mean fire intervals may still be expected.

(4) The pyrodiversity–biodiversity hypothesis

Environmental heterogeneity is considered one of the most important factors that determine species-richness gradients (Stein *et al.*, 2014) and fire is one of the major natural sources of such heterogeneity. Every fire has unique outcomes, as the burning of each stand of vegetation is the combined effect of local weather conditions, available fuel, and topography of the reference area. Thus, the spatiotemporal variation in fire types, and time since each fire occurred, may create a diverse fire-caused mosaic over the landscape that is quantified as pyrodiversity. Because different plants and animals may depend on different resources and habitat conditions that are created by fire, it has been argued that high pyrodiversity produces a wider range of habitats that can support more species in the total area. Fire-generated environmental heterogeneity is regarded as a useful framework for understanding species co-existence at local and regional scales (Dantas *et al.*, 2013; Bowman *et al.*, 2016), population divergences (He, 2013; Castellanos, González-Martínez & Pausas, 2015; He *et al.*, 2019), and the presence of specific fire-related traits in fire-prone ecosystems (Simon *et al.*, 2009; Lamont & He, 2012; Talluto & Benkman, 2013; Pausas, 2015). Diverse plant communities create different niches for fauna (Stevens & Tello, 2011) and more opportunities for synergistic species interactions (Janz, Nylin & Wahlberg, 2006; Ponisio *et al.*, 2016; García, Castellanos & Pausas, 2018; Carbone *et al.*, 2019).

Martin & Sapsis (1992) were the first to explore the consequences on biodiversity of variation in the burning pattern in fire-defined habitat mosaics. The pyrodiversity–biodiversity hypothesis recognises that fires create landscape heterogeneity (patch mosaics with different vegetation structure and openness) that cause resource partitioning over the landscape, thus promoting and maintaining multiple plant functional types and their associated fauna. There is a range of possible ecological mechanisms under which pyrodiversity may promote biodiversity (Table 2). Species have finely partitioned niches that match these spatially heterogeneous habitats. For example, fire generates spatially or temporally localised release of mineral nutrients for plant growth (Stock & Allsopp, 1992) and pockets of food for fauna. Diverse habitat types are associated with more niches that are favoured by different species (Parr & Brockett, 1999; Bond & Keeley, 2005; Bird *et al.*, 2008; Kelly *et al.*, 2012; Cohn *et al.*, 2015). Different species are favoured at various times after the fire disturbance (see Section III.2). Variations in fire intensity create niches varying greatly in resource availability (light, moisture, nutrients, space) that have different effects on survival of individual biota, seed germination and plant growth rates (Pausas *et al.*, 2003), and finally, selection, divergence and speciation. For example, Howard & Hill (2007) reported fire-stimulated reproduction in the Prairie

mole cricket (*Gryllotalpa major*) in Oklahoma, and hypothesised that burnt grassland sites may be more efficient for acoustic communication than more complex unburnt sites with dense surface vegetation, with responding females spending less effort discovering mates, therefore improving reproductive efficiency. Thus, the presence of burnt patches fosters the presence of this mole cricket in grasslands.

Fire-generated landscape mosaics also enhance environmental heterogeneity at the regional scale, creating differentiated species selection and promoting regional biodiversity (Talluto & Benkman, 2013; Castellanos *et al.*, 2015). For example, in tropical ecosystems, Dantas *et al.* (2013); Dantas *et al.* (2016) showed that different types of fire have driven the alternative states of forest and savanna under a given climate, with both containing a different set of species with markedly different traits (Table 2). Therefore, such fire-driven savanna–forest mosaics contribute to enhancing regional plant diversity, which in turn, contributes to the generation of heterogeneous habitats that provide diverse niches and resources for animals (Bond & Parr, 2010; Bowman *et al.*, 2016; Ponisio *et al.*, 2016). Landscape mosaics as a result of diverse fire patterns may also drive phenotypic and genetic divergence within species (Gómez-González *et al.*, 2011; Pausas *et al.*, 2012; Hernández-Serrano *et al.*, 2013; Vandvik *et al.*, 2014; Pausas, 2015; He *et al.*, 2019). In addition, increased patchiness of fires increases habitat edge, and attracts birds and other animals since both shelter and new food sources become available (Longhurst, 1978; Parkins, York & Di Stefano, 2018).

Mathematical constraints also contribute to explaining the level of pyrodiversity because, as the reference area is divided up into more (fire-related) patches, the number of patches increases exponentially and the size of patches declines linearly (Fig. 6). Given that each patch has a different fire history, species composition will differ among patches, and the species richness in each patch will depend on its species–area relationship, which in turn depends on the growth and life form of the species present, growing conditions and historical factors (Keeley & Fotheringham, 2003; Magadzire *et al.*, 2019). This relationship is asymptotic and suggests that as the area (x -axis in Fig. 6A) is reduced, the reduction in the number of species (y -axis) is small at first until a point is reached where a small reduction in area generates a large decrease in species richness (rare species are lost). Thus, with increasing pyrodiversity (i.e. an increasing number of patches of decreasing size), the number of species is likely to increase until a point is reached where it drops because the patches are so small that the number of species in each patch decreases at a faster rate than the area. Thus, the pyrodiversity–diversity relationship is likely to be humped, with the peak towards the upper end of the pyrodiversity gradient (left-skewed; Fig. 6). In addition, with increasing subdivision, the vegetation and fire history become less different among patches (spatial autocorrelation), so that it takes more patches to give an equal increase in pyrodiversity. Overall, there is a theoretical limit to support for the ‘pyrodiversity begets diversity’ hypothesis.

Table 2. Possible mechanisms underpinning the hypothesised pyrodiversity-biodiversity relationship, with examples

Mechanism	Interpretation with examples	Scale of diversity	References
Resource partitioning promoted at fine scales	Fire patchiness promotes coexistence of multiple plant functional types	Local	Martin & Sapsis (1992)
Cross-trophic interactions promoted	Intermediate disturbance maintains species co-existence as species with different resource requirements are not excluded	Local	Bond & Keeley (2005); Bird <i>et al.</i> (2008); Kelly <i>et al.</i> (2012); Cohn <i>et al.</i> (2015); Beale <i>et al.</i> (2018)
	Fire stimulates flowering, leading to more species interactions, and species-rich pollinator communities	Local	Campbell, Alfaro & Hawkes (2007); Grundel <i>et al.</i> (2010); Van Nuland <i>et al.</i> (2013); García <i>et al.</i> (2018)
	Regular fires may promote species with canopy seed banks, and cues simultaneous seed release – providing abundant food resources for granivorous animals	Local	Benkman & Siepielski (2004)
	Black-backed woodpeckers are attracted to post-wildfire conditions because of the abundance of wood-boring beetle species attracted to the fire-killed trees	Regional	Hutto (1995); Dixon & Saab (2000); Hoyt & Hannon (2002); Rota <i>et al.</i> (2014)
Environmental heterogeneity enhanced at the landscape scale	Savannas and forests harbour different species, and different fire regimes generate savanna–forest mosaics with high regional diversity	Regional	Dantas <i>et al.</i> (2013); Dantas <i>et al.</i> (2016); Pausas (2015); Bond & Parr (2010)
	Landscape mosaics are a suitable setting for population divergences and selective processes in fire-prone ecosystems	Regional	Talluto & Benkman (2013); Castellanos <i>et al.</i> (2015); Pausas <i>et al.</i> (2012); Hernández-Serrano <i>et al.</i> (2013); Vandvik <i>et al.</i> (2014); Pausas (2015); Davies <i>et al.</i> (2018); He <i>et al.</i> (2019); Gordijn <i>et al.</i> (2018)
New niches for fire-dependent species created through elevated food supply	Animal diversity is enhanced by landscape mosaics through their association with particular plant communities	Regional	Law & Dickman (1998); Bond & Parr (2010); Bowman <i>et al.</i> (2016); Ponisio <i>et al.</i> (2016)
	Some moss and lichen species are relatively restricted to severely burnt forest conditions	Regional	Ahlgren & Ahlgren (1960)
	The mushroom <i>Morchella elata</i> , and the shrub <i>Geranium bicknellii</i> , are promoted by immediate postfire conditions	Regional	Heinselman (1981); Pilz <i>et al.</i> (2004)
	Fungi differ in their adaptations to recently burnt and long-unburnt conditions	Regional	McMullan-Fisher <i>et al.</i> (2011)
	Several beetle species are relatively restricted to recently burnt forests	Regional	Saint-Germain, Drapeau & Hebert (2004); Boucher <i>et al.</i> (2012); Pausas <i>et al.</i> (2018a)
	White-headed woodpeckers (<i>Leuconotopicus albolavatus</i>) are more abundant in burnt (wildfire) than unburnt forest	Regional	Hollenbeck, Saab & Frenzel (2011); Lorenz <i>et al.</i> (2015)
	In aquatic systems, severe fire events can rejuvenate stream habitats by causing large amounts of gravel, cobble, woody debris, and nutrients to be imported, resulting in increased productivity and aquatic-insect emergence rates	Regional	Benda <i>et al.</i> (2003); Burton (2005); Malison & Baxter (2010); Jackson & Sullivan (2015)
	Succession processes allow species with different postfire stage preferences to replace each other, thus promoting species-rich communities, with their associated fauna and soil biota, when different stages co-exist among a mosaic of fire intervals	Local	See Section III.4
Fires buffer stress, and maintain local diversity	Fire mitigates drought by reducing transpiration of a site; the resprouting plants and newly emerged seedlings postfire should benefit from higher resource availability	Local and regional	Alfaro-Sánchez <i>et al.</i> (2016); Pausas <i>et al.</i> (2003)

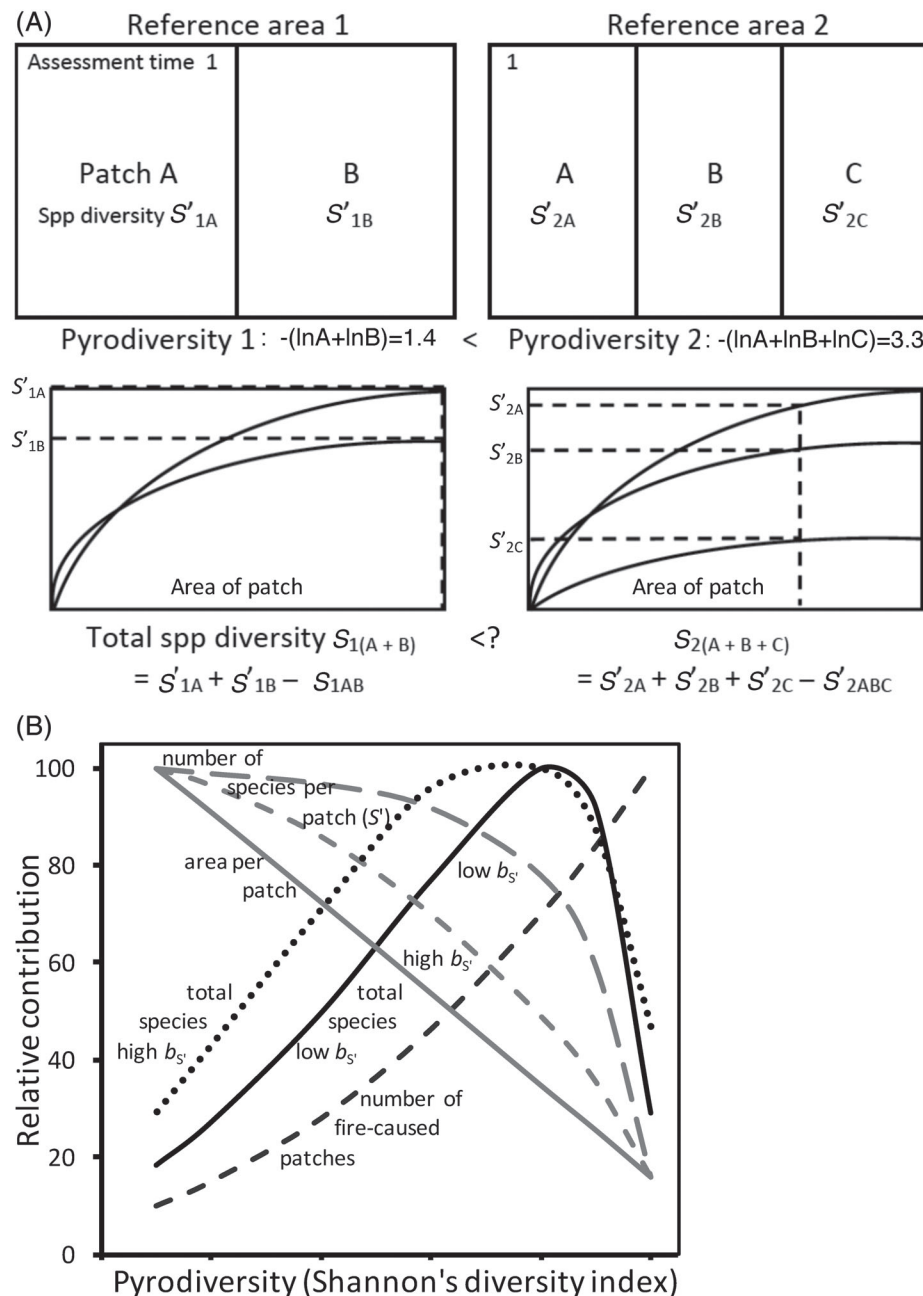


Fig. 6. (A) The upper two diagrams show the conceptual relationship between different fire-caused patches (A, B, C) within two reference areas (1, 2) of the same size and species diversity (S' for the patch, S for the reference area) assessed at the same time (Assessment time 1). The mosaic of patches in each area can be combined to give an estimate of the range of variation in fire events, pyrodiversity (P), of that area. Here, we use Shannon's diversity index to show that the area with three fire-related patches has more than twice the P of that with two, with each patch in the reference area making an equal but different contribution to P . Using the same index for species diversity (lower two graphs) shows that the relationship between S' and patch size depends on the slope and asymptote of the species-area curve and where the patch area fits along the area axis. S'_{AB} and S'_{ABC} represent the number of species in common between the various patches that has to be subtracted from the number of species in each patch, reducing the certainty that $S_2 > S_1$. (B) Model outcomes showing possible relationships between P and biodiversity (here given by S). The number of patches (N) rises exponentially as the mean area per patch declines linearly. The mean number of species per patch (S') is based on Fig. 6A, with a mean slope (b) modelled here that is relatively high (approaches linear, e.g. $b = 0.9$, for the power function) or low (strongly curvilinear, e.g. $b = 0.6$). Multiplying N by S' at a given P gives the total number of species (S) present. The two extreme scenarios given here show a marked peak in S at moderately high and high P values. All parameters were scaled between 0 and 100 to facilitate comparison.

Despite increasing adoption of the mosaic-burning approach in fire management (Kelly & Brotons, 2017), there have been few tests of the validity of the pyrodiversity-biodiversity hypothesis. Davies *et al.* (2018) modelled the effect of different-sized patches varying in fire frequency on its known relationship with the presence and abundance of seven mammal taxa in northern Australian savanna. Pyrodiversity (P) was based on Shannon's index and, since the type of patches was fixed, P increased as the size of the patches (E) became more equal. Mammal diversity peaked at intermediate P . Had the deleterious effect of small patch size on population viability been taken into account (the area was dimensionless), this may have pushed the optimum further to the right, i.e. generating a more left-tailed distribution not unlike our model (Fig. 6), even though our data are based only on S rather than $S \times E$. Gordijn *et al.* (2018) also noted that species diversity should be greatest with a mixture of patches at different fire frequencies as the extremes were quite different in species composition (although any effect of patch size on S was not considered). Others have observed no effect (Davis *et al.*, 2018) or a negative effect (Bassett *et al.*, 2017; Foster *et al.*, 2017). The extent to which this fails to support intermediate P as maximizing biodiversity due to (i) testing an inadequate range of P , thus observing only part of the 'hump', (ii) not using a fixed reference area, thus not appreciating that increasing patch type is at the expense of patch area and thus species—area limitations come into play, or (iii) using different indices of P and diversity, requires further investigation. In practice, the specific pyrodiversity—biodiversity relationship will depend on the ecosystem under study, the taxonomic group examined (as these will have different species—area relationships), the range of patchiness that can be applied, and the indices of P and diversity used. However, theory and empirical studies that are area-constrained indicate that the relationship will be essentially humped and left-skewed.

(5) Mixed fire regime and intermediate disturbance hypothesis

Since a mixed-severity fire regime (MSR) promotes maximum biodiversity, a parallel can be drawn with the IDH. Arno, Parsons & Keane (2000) and Perry *et al.* (2011) seem to have been among the few to recognise that MSRs conform with the IDH at the landscape scale, i.e. both represent the peak of the hump along a fire component gradient (Fig. 4). Our contribution is to demonstrate that species diversity is also humped when plotted against P (Fig. 6). This integrates the three concepts (IDH, P and MSR) to show that biodiversity is maximal at moderate levels of patch diversity, disturbance and fire severity over the landscape. But the optimal fire-regime conditions represented by each term are not identical. Biodiversity is greatest when there is a wide range of fire types corresponding to moderately high P and fire severity. In terms of the IDH, biodiversity is greatest when the fire types range around the midpoint between the extremes (Fig. 5): this would be equivalent to a

moderately low P . The greatest range of patch heterogeneity corresponds to the highest P but biodiversity falls as the mean size of patches is now so small that each patch contains few rare species and population viability of those present is threatened (the Allee effect; Lamont, Klinkhamer & Witkowski, 1993). With the IDH, species most favoured by low or high fire frequency are usually still present but rare, as well as the majority of species that optimise at moderate levels of disturbance. Patch-size constraints are not relevant to the IDH provided that the optimal patch types are present and are large enough to support rare species. MSRs also incorporate the mean and frequency range of the three possible fire types but patch size variation is limited (moderate) otherwise the required mean would not be reached (Agee, 1998).

(6) Fire and biodiversity at broad scales

Fire is almost ubiquitous in global terrestrial ecosystems (Archibald *et al.*, 2018). Simulation studies show that biome distributions in the absence of fire would be very different from their current patterns (Bond *et al.*, 2005). However, different environments, and different geographical regions within the same environment, may have quite different fire histories and pyrodiversity levels (Rogers, Soja & Randerson, 2015; Archibald *et al.*, 2018). The IDH is often proposed as the most likely pattern for maximising species diversity (Huston, 2014; Section III.3). However, this is not the case when studying fire-diversity patterns at broader scales; instead, these show a monotonic positive relationship with increasing fire activity for plants (Pausas & Ribeiro, 2017) and vertebrates (Beale *et al.*, 2018). Fire frequency gradients at the biogeographical scale cannot be equated with different fire frequencies at given sites. This is because an increase in a disturbance at the local scale takes place within a given species pool, and thus is likely to include fire regimes beyond the historical range (which could decrease diversity). By contrast, biogeographical studies include gradients of disturbance across different species pools, and in each species pool, the fire regime may be within the historical range (e.g. from fire-sensitive ecosystems with low fire activity to fire-prone ecosystems with high fire activity). In addition, fires in many ecosystems are frequent and predictable enough to have selected species with adaptive traits for persisting under the historical fire regime (Keeley *et al.*, 2012; Charles-Dominique *et al.*, 2015; Pausas, 2015). Consequently, frequent fires do not always imply species loss, and thus the decrease in diversity at the high end of the disturbance gradient (as in the IDH) is unlikely for broad areas that cover numerous fire-prone ecosystems. The overall trend is therefore that at broad scales diversity increases along the fire activity gradient (Pausas & Ribeiro, 2017).

Broad-scale species diversity is also strongly controlled by environmental factors (Kreft & Jetz, 2007) and variations in productivity (Gillman & Wright, 2006) that modulate the fire regime to some extent. So, the question that arises is to what extent can the increasing species diversity be attributed to fire, or to the environmental factors that mediate it? The

current evidence indicates that both environmental factors and fire are important and complementary dimensions in explaining biogeographical patterns of biodiversity. For instance, once productivity, environmental variables and their heterogeneity are included in the model, fire activity explains a major fraction of the variability in the diversity of plants at the global scale (Pausas & Ribeiro, 2017) and mammals and birds at the continental scale (Africa; Beale *et al.*, 2018). In fact, for global plant diversity, fire activity is the best single variable that accounts for the level of plant diversity.

IV. FIRE AS AN EVOLUTIONARY DRIVER OF BIODIVERSITY

Evidence is mounting that fire has been a significant force in the selection and evolution of terrestrial biotas through geological time and has shaped the structure and function of global biomes throughout the 420-million-year history of terrestrial life on Earth (Pausas & Keeley, 2009; Belcher, Collinson & Scott, 2013; He & Lamont, 2018a). The species richness of current fire-prone ecosystems can be explained by high diversification rates associated with fire (Cowling & Pressey, 2001; Barraclough, 2006; Pausas & Lamont, 2018). Thus, fire has been a strong driver of diversification through promoting mutation, selection, divergence, and speciation (Lamont *et al.*, 2013; He & Lamont, 2018b). In this section, we focus on how fire has driven the evolution and adaptations of terrestrial floras but also refer to some recent advances in other taxon groups. We further compare the net speciation rate of plant groups with sister lineages in fire-prone and non-fire-prone habitats. Finally, we propose that fire itself is a source of mutagens that can generate genetic novelties in plants.

(1) Fire-driven evolution and adaptation

The diversity of life histories and morphologies uniquely related to proliferation and persistence in fire-prone environments (Table 3; Table S1) challenges the long-held belief that diversity patterns can be explained solely by climate, topography and soil (Pausas & Bond, 2019). Abundant evidence shows that much of the world's vegetation has been strongly fire prone since the Mid-Cretaceous, taking precedence over Cenozoic drought as the critical agent of selection in the evolution of adaptive traits (Brown *et al.*, 2012; He *et al.*, 2012; He *et al.*, 2016; Lamont, He & Yan, 2019b). There has been debate over whether adaptations to fire or drought (exaptations to fire) came first among plants in fire-prone ecosystems (Keeley *et al.*, 2011; Bowman *et al.*, 2016). Recent research indicates that the presence of fire-related traits among plants has been a direct response to the unique characteristics of the local fire regime as fire was already present before or synchronously with the advent of these traits (Lamont & He, 2017). Almost no fire-related traits emerged through

'fire-mimicking' disturbances, such as severe drought and hot summers, but were selected for by the constraints imposed by the prevailing fire regime. Excellent reviews already exist that conclude that fire has been a significant agent of natural selection in driving the evolution of terrestrial biota for 420 million years (Bond & Scott, 2010; Keeley *et al.*, 2011; Rundel *et al.*, 2016; Archibald *et al.*, 2018; He & Lamont, 2018a; Pausas *et al.*, 2018b).

The roles of fire in the evolution and adaptation of animals have received little attention (reviewed by Pausas & Parr, 2018). The long co-existence over evolutionary time between organisms and fire suggests that these organisms must have evolved to adapt to, even rely on, recurring wildfires to persist in fire-prone environments (i.e. 'pyrophilous' species; Table S2). Organisms that depend on fire-disturbance for their long-term survival may be regarded as adapted to fire-prone habitats (Hutto *et al.*, 2016; Pausas & Parr, 2018), although the evidence for unique fire adaptations in animals has rarely been explored (Nimmo *et al.*, 2019). Recent studies (Stawski *et al.*, 2015, 2017; Matthews *et al.*, 2017; Nowack *et al.*, 2018) indicate that torpor (a state of decreased physiological activity) is used extensively among terrestrial mammals in Australia to deal with fires, or the scorched postfire environment, suggesting that fire may act as a signal, and leads to adaptive changes in animal behaviour and physiology. There are also many pyrophilous fungi species (Robinson, Mellican & Smith, 2008), i.e. fungi that are dependent on fire to stimulate spore germination and mycelial growth, analogous to fire-stimulated flowering in plants.

Fires generate a wider range of habitat types than possible in their absence, that in turn leads to increased selection pressure to occupy such environments. From the perspective of evolutionary processes that promote fitness in fire-prone habitats, two main response types exist in plants: species with fire-stimulated resprouting, and those killed by fire (non-resprouters) but coupled with fire-stimulated germination of fire-surviving seeds (obligate seeders). These two major persistence syndromes both have special genetic mechanisms that promote rapid diversification (Pausas & Keeley, 2014b). Obligate seeders have short generation times that track the mean fire intervals of the region. For example, the longevity of many fire-killed banksias in SW Australian heathlands is about 45 years in the absence of fires (Burgman & Lamont, 1992; Enright, Lamont & Marsula, 1996) but they are likely to be burned at 10–30-year intervals (Miller *et al.*, 2007; Enright & Thomas, 2008). Species with shorter generation times evolve faster as the result of the accumulation of more DNA replication errors per unit time, as observed in both animals (Bromham *et al.*, 2015) and plants (Soria-Hernanz *et al.*, 2008; Yue *et al.*, 2010; Buschiazzi *et al.*, 2012), and the effect is stronger when there is no overlap between generations as occurs among obligate seeders. Thus, frequent fires further shorten the generation time of obligate-seeder species, creating the potential for more rapid molecular evolution and therefore contributing to rapid diversification in a landscape with diverse fire-driven opportunities for the selection of novel genotypes.

Table 3. Plant morphological traits whose evolution and diversification are promoted in fire-prone ecosystems, and their contribution to fitness

Trait type	General category	Specific example	Contribution to fitness
Protection (heat-insulated regenerative structure)	Aerial bud bank	Epicormic bud	Survival
	Belowground bud bank – woody	Apical bud	Survival
		Lignotuberous bud	Survival
		Rhizomatous bud	
	Belowground bud bank – non-woody	Root sucker	Survival/recruitment (ramets)
		Bulbous, tuberous, cormous buds	Survival/recruitment (ramets)
	Heat-insulated seed store	Canopy storage	Survival/recruitment
		Soil storage	Survival/recruitment
	Heat-insulated meristems	Thick bark	Survival
	Fire-stimulated flowering	Some geophytes, grasses, shrubs	Recruitment
Reproduction (fire initiates reproduc- tive/recruitment cycle)	Fire-stimulated seed release	Woody follicles, cones	Recruitment
		Smoke stimulated	Recruitment
	Fire-stimulated germination	Heat stimulated	Recruitment
	Finely divided foliage	Small leaves, highly branched twigs	Indirect
	Retention of dead biomass	Flowers, leaves, branches	Indirect
	Flammable secondary compounds	Essential oils, resins	Indirect
	Flammable tissues	High cellulose, lignin; low moisture content	Indirect
	Fire deterrent	Crown and litter discontinuity	Indirect
Fire suppression (trait reduces flammability)	Low combustibility	High moisture content	Indirect
	Poor flame transmitter	Branch shedding	Indirect

Fire-stimulated budburst during postfire resprouting can promote the expression of somatic mutations through mechanisms described in Section IV.3. Somatic mutations accumulate during plant growth. Gametes produced late in a plant's life cycle are likely to possess such somatic mutations and these can be transmitted to the next generation (Bobiwash, Schultz & Schoen, 2013; Watson *et al.*, 2016). In regions with short fire intervals (e.g. 10–30 years in heathlands of SW Australia and the Cape, 1–5 years in sub-tropical savannas), resprouting species usually live for hundreds to thousands of years, e.g. 300–1200 years for some *Banksia* species (Enright *et al.*, 1996; Merwin *et al.*, 2012), or 3800 years for *Jacaranda decurrens* (Alves *et al.*, 2013), passing through tens to hundreds of fire cycles in that time and creating abundant opportunities for the expression of somatic mutations as a source of novel traits among resprouting plants.

(2) Fire and diversification of plant lineages

If fire is a major driver of ecological and evolutionary processes, and other agents of selection are minor or

apply equally across all habitats, then lineages that occur in fire-prone habitats should be better represented here than in non-fire-prone habitats. To test this hypothesis, we searched the literature for studies that contained dated phylogenies of seed plants with sister lineages in fire-prone and non-fire-prone habitats. We estimated net speciation rate of each lineage as $(\log_{10}N)/t$, where N is the number of extant species in the lineage, and t is the stem age of the lineage (Magallón & Sanderson, 2001). We performed 39 comparisons (in 20 plant families) containing sister clades with >90% of their species in either fire-prone or non-fire-prone habitats (Fig. 7; Table S1). For 26 comparisons the number of species in fire-prone lineages was higher than that in the non-fire-prone lineages, so contributing significantly to biodiversity in their respective ecosystems (Fig. 7; Table S1). Overall, speciation rates are significantly higher in fire-prone habitats, and the number of pairs in each direction (26 and 13) is also significant with more lineages containing higher species numbers in fire-prone habitats than in non-fire-prone habitats (Fig. 7). The number of families (12) containing lineage pairs with higher speciation rates in fire-prone lineages was not significantly greater than the number of

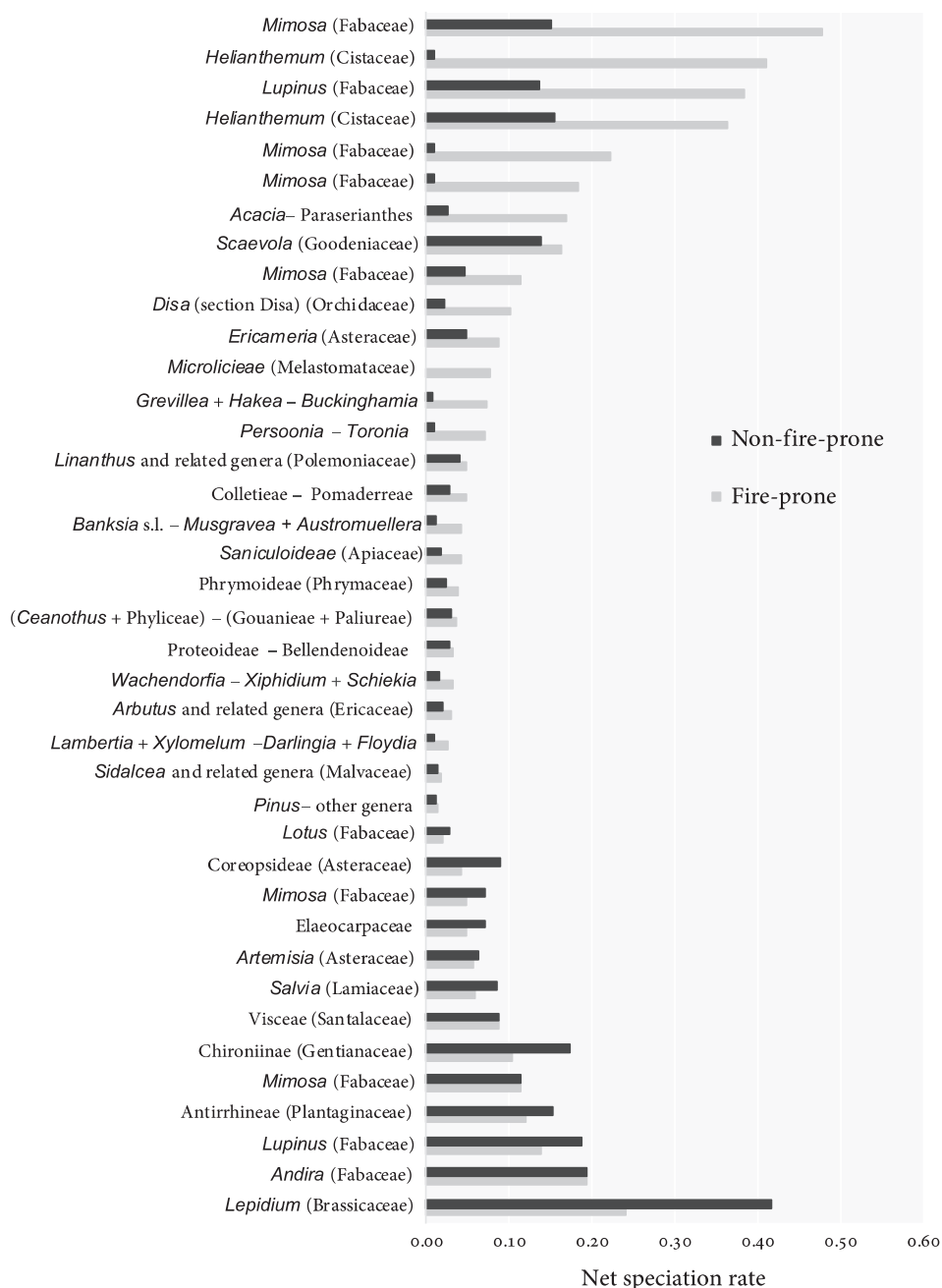


Fig. 7. Logarithm of net speciation rate for sister lineages in fire-prone (fp) and non-fire-prone (nfp) habitats. Data derived from Table S1. — separates fp lineages on the left from nfp on the right. Lineages are listed from highest to lowest speciation rate for the fp lineage when it exceeds the nfp lineage then lowest to highest speciation rate for the nfp lineage when it exceeds the fp lineage. Speciation rates are significantly higher in fp than in nfp habitats ($P = 0.008$; paired, one-tailed t -test); and there are significantly more lineages containing higher species numbers in fp habitats than in nfp habitats (26 and 13, respectively; $P < 0.05$, chi-squared test with Yate's correction).

families (11) containing pairs with higher speciation rates in non-fire-prone lineages ($P > 0.05$); thus, the differences in diversification rates are likely operating at below the family level. While these results are decisive, we note that the sample size is limited, that some clades are related and the taxon groups available may not be representative of seed plant taxa in general.

Some extremely species-rich groups, such as *Acacia* (Fabaceae) with 1065 species and hard, arillate seeds, and *Grevillea* (ant-dispersed) + *Hakea* (serotinous) with over 510 species, are found overwhelmingly in fire-prone habitats, compared with only a few species in their non-fire-prone sister lineages (Fig. 7, Table S1). Other speciose fire-prone taxon groups that were not included here (due to a lack of

clear, non-fire-prone sister lineages) are *Eucalyptus* and *Erica*. *Eucalyptus* (Myrtaceae, > 850 species, including *Angophora* and *Corymbia*) has fire-stimulated resprouting with the majority present in fire-prone Australia (Crisp *et al.*, 2011), and only nine species occurring in non-fire-prone Indonesia and New Guinea. In *Erica* (Ericaceae, fire-stimulated germination, some species with lignotubers) 690 species (out of 860) occur in the fire-prone Cape of South Africa and Mediterranean Basin, with the remainder in relatively non-fire-prone parts of Africa/Madagascar and Europe. These two cases suggest that our comparison in Fig. 7 is conservative. Among the 26 cases with higher speciation rates in fire-prone habitats, the lineages migrated from non-fire-prone ancestral habitats (e.g. rainforest) into fire-prone environments in 24 cases. The two exceptions are *Scaevola* (Goodeniaceae) where limited dispersal occurred more recently from fire-prone Australia to the non-fire-prone Pacific rim (Jabaily *et al.*, 2014), and a few species of *Disa* (Orchidaceae) dispersing from fire-prone fynbos to rarely burnt riverbanks (Bytebier *et al.*, 2011). On acquiring fire-adapted traits, vast new habitats become available that create new speciation opportunities in terms of the altered physical environment (climate, soil, topography) and different plant–animal interactions (pollinators, herbivores, granivores) become possible (Lamont *et al.*, 2013; Pausas & Lamont, 2018).

For 13 comparisons, the number of species in non-fire-prone habitats was higher than in fire-prone habitats, with eight of these cases in California (Lancaster & Kay, 2013). Higher species numbers were also recorded in another seven fire-prone lineages of California. The non-fire-prone *Elaeocarpus* alliance has produced six times more species than the fire-prone Tremandraceae (Fig. 7) since the two groups diverged in the Paleogene. The high speciation rate in *Elaeocarpus* followed migration events from Australian rainforest to continental Asia, Madagascar, New Zealand and the Pacific (Phoon, 2015). It therefore seems that, while fire may often increase speciation of lineages in fire-prone habitats, it is not the only, nor always the ‘best’, environment to promote diversity. Fire-free areas (e.g. rainforest) may also present novel agents of selection in association with extensive new habitats and foster speciation. Nevertheless, migration to fire-free habitats among essentially fire-prone lineages is relatively recent and the comparatively low levels of speciation observed might simply be attributed to their restricted numbers (Bytebier *et al.*, 2011; Jabaily *et al.*, 2014; Lamont *et al.*, 2019b). Overall these results suggest that fire is as good, or an even more powerful, driver of diversification than the traditionally considered agents of selection (climate, soils, biogeography and species interactions; Pausas & Lamont, 2018).

(3) Mutagenic effects of heat and chemicals released by combustion

Mutations are the ultimate genetic basis for adaptation and diversification. There is increasing evidence pointing to the potential for fire to act as a mutagen, generating novel genetic

material for trait innovation and speciation (He & Lamont, 2018b). There are two main components of a natural fire: heat (from sub-lethal to >1000°C; Wittkuhn, Lamont & He, 2017) and products of combustion (~4000 chemicals in smoke; Flematti *et al.*, 2004). Abundant evidence exists that both components can induce mutations.

Fire heat causes ignition and death of unprotected combustible tissues (Pausas *et al.*, 2018b). A ground-breaking discovery of the effect of heat on plant mutations was made by Pettersson (1961), who used a magnifying lens to concentrate sunlight onto the flower buds of plant species and subsequently germinated the seeds set from the heated flowers. Many plants possessed extra leaves per node, bud proliferation, and odd leaf shapes and sizes. Surprisingly, many of these mutants resembled traits of (untreated) congeneric species. Pécix *et al.* (2011) showed that mild heat may cause meiotic dysfunctioning and lead to the formation of diploid pollen. The formation of diploid gametes may have a significant role in speciation and diversification, as fertilisation by the diploid pollen and eggs produce novel polyploids. It is also a mechanism that overcomes the reproductive failure of triploids when a diploid species crosses with a polyploid species (Ramanna & Jacobsen, 2003). Polyploidy, sometimes as result of whole-genome duplication, is considered an important mechanism for the rapid diversification of flowering plants across the Cretaceous–Cenozoic boundary (Vanneste *et al.*, 2014). In support of this, the Myrtaceae and Proteaceae, two prominent plant families in the fire-prone floras of Australia and South Africa, ancient whole-genome duplication was estimated to have occurred in the Mid-Cretaceous–Paleocene (Johnson & Briggs, 1975; Myburg *et al.*, 2014) when fire activity is estimated to have been at the highest level during the last 350 million years (Belcher *et al.*, 2010).

It is also well known that smoke from numerous sources carries mutagens and carcinogens (Simoneit *et al.*, 2000; Nolte *et al.*, 2001; Vu *et al.*, 2012). Polycyclic aromatic hydrocarbons (PAHs) are well-known components of the gas and particulate components of smoke from burning biomass (Schmidl *et al.*, 2008). Research indicates that PAHs can be absorbed by plants and cause mutations (Nisbet & LaGoy, 1992). PAH extracts from burning the Australian tree, *Eucalyptus globulus*, were more mutagenic than those from trees and shrubs native to Spain (Sharma & Tripathi, 2009; Sojinu, Sonibare & Zeng, 2011). Studies that have used plant species from fire-prone vegetation as a source of fire-related mutagens showed that these cause among the highest levels of mutagenesis (White *et al.*, 1983; de Oliveira Alves *et al.*, 2011; Vu *et al.*, 2012; Orecchio *et al.*, 2016).

Flower buds rarely survive fire but insulated vegetative buds (either *via* thick bark or soil) usually do (Pausas *et al.*, 2018b). Sublethal heating of stored seeds and protected meristems during fire might act as a mutagenic agent, and these buds could be a potent source of somatic mutations for promoting speciation (Lamont & Wiens, 2003). Fowler *et al.* (2018) reported somatic mutations in resprouting *Banksia*

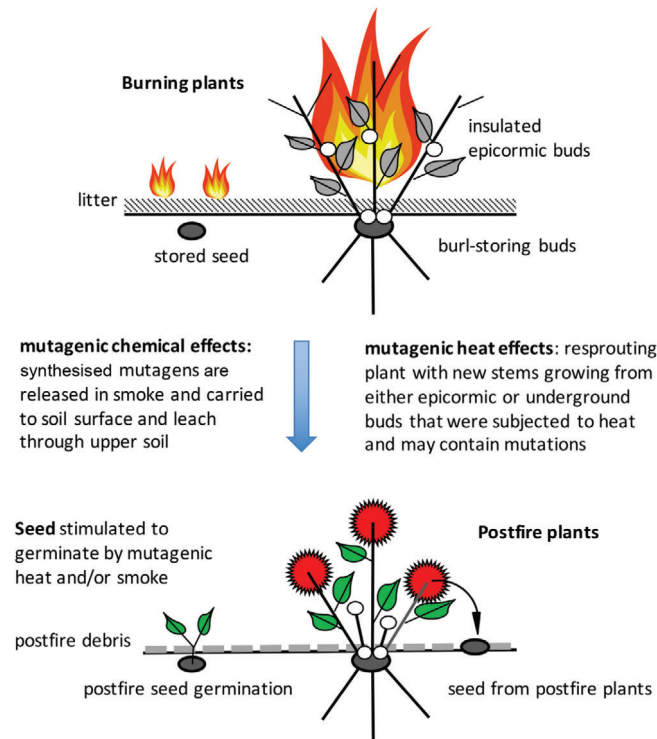


Fig. 8. Possible fire-based mutagenic pathways in fire-prone ecosystems (small white ovals are buds). Modified from He & Lamont (2018b).

attenuata in SW Australia. Litter and foliage consumption by fire opens the vegetation and exposes stored seeds and buds to heat and fire-related chemicals. Burning plants and litter release aerosols and gases containing mutagens including PAHs and terpenoids that spread through the plant community *via* the atmosphere, and most of these mutagens reach the soil surface or are deposited on unburnt leaves, buds or other surviving plant parts (Fig. 8). Mutagens then enter seeds or seedlings through the growing medium. The critical step is mutagen uptake by the root system (Zach & Sheppard, 1991).

Although no work has been done specifically in the context of wildfire as a mutagenic agent that might lead to trait innovation and speciation, current research collectively supports the view that fire (and its byproducts) can induce mutations in meristems and seeds (He & Lamont, 2018b). In turn, this provides a mechanism that can explain how fire may have a direct role in stimulating plant speciation in fire-prone environments. To what extent smoke may be a source of mutations among animals remains unknown, but insects with immature stages (eggs, larvae, or pupae) in the soil are likely to receive mutagenic agents from wildfires.

V. IMPLICATIONS FOR BIODIVERSITY CONSERVATION AND FIRE MANAGEMENT

The bigger picture that emerges from this review is that fire is a major ecological and evolutionary force that promotes

and maintains biodiversity at local, regional and global scales which is manifested through relatively stable and predictable fire regimes that set upper and lower limits to trait selection. Not only is fire a mechanism that consumes biomass (fuel) and creates environmental heterogeneity that drives biodiversity, it also promotes and maintains biodiversity by serving as an agent of natural selection in evolution and speciation, and by regulating nutrient cycles and biotic interactions.

Global fire-dependent ecosystems are not an artefact of recent anthropogenic burning as commonly believed. Instead, they have existed for so long that they have enabled the evolution of distinctive fire-adapted species and communities (Bond *et al.*, 2005; Pausas & Keeley, 2009; Bond, 2015; Archibald *et al.*, 2018; Karp, Behrensmeier & Freeman, 2018; He & Lamont, 2018a). Doerr & Santín (2016) reported an overall decline in fire activity over the past century, and argued that much of the world suffers from the harmful consequences of fire-management strategies centred on ‘fire suppression’. As fire is a natural and integral part of many terrestrial ecosystems, fire-management strategies that attempt to remove fire from these areas to protect human life and property may have negative consequences on biodiversity conservation (Kitchen, 2012). Active fire suppression has resulted in less-frequent but higher intensity fires, causing fundamental changes in stand structure and composition, and greater risk to life and property (Schoennagel *et al.*, 2017). Management strategies such as intensive logging and clearfelling might be able to reduce fire risks to some extent but they will be detrimental to

maintaining ecosystem biodiversity, structure and function. Fire itself is the most important and naturally available tool used in landscape/vegetation management and provides a range of services to humankind (Pausas & Keeley, 2019), but current sociocultural, political and economic factors, together with historical biases (Pausas & Bond, 2019), greatly influence acceptable fire-management practices (Buizer & Kurz, 2016).

Prescribed burning (vegetation burnt under mild weather conditions) has long been recognised as an effective strategy for reducing fire risk. This revolutionary technique with its underlying philosophy of using fire to ‘fight’ fire was developed in Western Australia in the early 1960s (Shea, 1994) although we note that ‘wildfires’, to which most species will be adapted, are not part of this protocol. It was later adopted by fire-management authorities throughout Australia and the USA. The hypothesis that pyrodiversity begets biodiversity has become increasingly influential in guiding land management and biodiversity conservation over recent years (Kelly & Brotons, 2017). The practice of patch (mosaic) burning, creating spatial variation in components of the fire regime, has recently been promoted as the preferred fire-management protocol to maintain biodiversity based on the pyrodiversity-biodiversity hypothesis (Bowman *et al.*, 2016; Kelly & Brotons, 2017). Evidence in support of this proposal is currently mixed, while our modelling indicates that there is a ceiling to its benefits.

Similarly, the IDH, that there is an optimum fire activity for maximizing biodiversity, is supported by ecological principles when variations in fire frequency are considered but the theory does not recognise that species composition at the extremes of the fire gradient may be quite different from those at moderate levels (Davies *et al.*, 2018; Gordijn *et al.*, 2018). When and where the fire occurs in a landscape are determined by the vegetation, season, local climate/weather, habitat topography and ignition source. The interaction between fire and biodiversity depends on context, and its properties vary among species, ecosystems and across spatial scales. High pyrodiversity may have theoretical support but variation in its components must be within the bounds of the natural fire regime that has assembled the vegetation in the region over millions of years to maintain the current species composition and diversity. Further, fires may open up the vegetation and promote invasion by exotic species, that, once established, may outcompete indigenous species. Thus, an unintended consequence of patches of more frequent fires (higher pyrodiversity) may in fact be a decrease in biodiversity (Fisher *et al.*, 2009). This can never be an objective of conservation management.

In the absence of a complete understanding of how fire regimes are maintained, it is likely that random production of fire-caused patches will not always generate optimal fire mosaics for maintaining biodiversity. Fire-management practices that recognise historical fire regimes have positive nature conservation outcomes in many systems. Evidence exists that inappropriate fire regimes, as result of ill-planned prescribed burning, could also

lead to species decline and forest degradation (Driscoll *et al.*, 2010). An understanding of how lightning-caused wildfires structure landscapes is essential when considering prescribed burning (anthropogenic ignition) to manage and restore fire-dependent ecosystems (Ghazoul & Chazdon, 2017; Gordijn *et al.*, 2018). Although the ecological and evolutionary roles of fires are increasingly understood by fire ecologists and fire-management authorities, their implementation remains controversial among the public and decision-makers as they continue to view fire as essentially destructive (Ingalsbee, 2017). This could lead to undesirable fire-management outcomes for plant communities and the environment. Science-based fire management of fire-dependent ecosystems requires an understanding of the feedbacks between ecosystem structure, biodiversity values, and societal perceptions (Moritz *et al.*, 2014; Pausas & Keeley, 2019). A paradigm shift to restore natural fire regimes across broad landscapes is required among fire research and management communities, and requires fire ecologists and other professionals to spread fire-ecology knowledge beyond scientific publications to reach the broader public, politicians and the media. Failure to appreciate that floras in fire-prone regions are fire-adapted can only undermine our ability to use fire effectively, and undermine public confidence in fire-management practices.

VI. FUTURE RESEARCH DIRECTIONS AND OUTCOMES

To advance our understanding of ecological processes and biodiversity patterns, we must move away from the traditional view that biodiversity is controlled solely by climate and soils, and accept fire as a major ecological factor and evolutionary force that shapes the distribution and abundance of biota (Keeley *et al.*, 2011, 2012; Bond, 2015; Pausas & Lamont, 2018; He & Lamont, 2018a; Pausas & Bond, 2019). The relationships between fire properties and biodiversity are likely to vary among species and ecosystems. It is essential that policy-makers recognise that natural ecosystems contain different species with different fire-regime requirements. Fire management should be guided by demonstrated knowledge on the fire ecology of plants and animals in the landscape that they inhabit. Research focused on the population dynamics of target species (Groeneveld *et al.*, 2013) is essential for understanding how different species respond to different fire regimes.

The fundamental question at the centre of the relationships between fire and biota is how does fire stimulate the evolution of new species? To answer this question, we must move from a descriptive and process-based narrative on the role of fire in speciation to a mechanism-based approach. For example, research examining direct evidence that fire (and its byproducts) act as a source of mutagens that induce mutations upon which selection can act, leading to divergence and adaptation, will advance our knowledge on the fundamental role of fire in the evolution of terrestrial biota (He & Lamont,

2018b). Current genomic advances are contributing to an understanding of the genetic architecture of plant adaptive traits, including those related to fire (Castellanos *et al.*, 2015; He *et al.*, 2019). Ultimately, we need research into the underlying genetic basis of ecological adaptations of fire-prone floras.

The notion that ‘pyrodiversity begets biodiversity’ is increasingly advocated in fire management, where fires are manipulated to create a mosaic of patches with different fire histories across space and time (Kelly & Brotons, 2017). Our preliminary modelling indicates that there are limits to the benefits of pyrodiversity, but more sophisticated approaches are required, such as calculating the effect of varying patch size. To what extent are the various components of pyrodiversity correlated and how does it increase as the size of patches decreases? The logistic constraints in research and implementation in management should also be evaluated.

Finally, fire has not featured strongly in the development of current ecological and evolutionary theories in general because of the prevailing cultural bias against viewing fire as a significant ecological factor and fundamental agent of natural selection (Pausas & Bond, 2019; Lamont *et al.*, 2019a). Fire ecologists should communicate current understanding of fire–biodiversity relationships to fellow biologists, the general public, the media, and policy-makers, so that the key role of fire on ecological and evolutionary processes in much of the Earth’s terrestrial biota is incorporated into nature conservation and management.

VII. CONCLUSIONS

(1) Many biodiverse ecosystems are fire prone and, by examining mechanisms and fire-related gradients operating at ecological and evolutionary scales, we show that the relationship is usually causal.

(2) Ecological responses are controlled by six fire components whose properties vary greatly through space and time and define the type of fire during a fire event, and the fire regime over extended periods.

(3) Fire intensity (vertical spread) and frequency are the major components controlling species composition, vegetation structure, and plant functional traits. In turn, species composition may feed back to control the fire regime.

(4) Species diversity is greatest immediately postfire and declines gradually, although the abundance of individual plant and animal species peaks at different times; postfire immigration/emigration are rare among plants (autosuccession) but common among animals.

(5) The intermediate disturbance hypothesis (IDH) regarding conditions that favour maximum species diversity can be applied to fire-prone landscapes and is supported, provided there is a fixed species pool.

(6) Pyrodiversity (P) emphasises patchiness of the landscape caused by varying fire types and time since fire across the landscape. Species—area constraints mean that there is a limit to P as a promoter of biodiversity within a defined area:

the biodiversity relationship with P is hump-shaped, with the peak at relatively high P (left-skewed).

(7) Mixed-severity (fire) regimes (MSRs) are a particular type of high P involving stand replacement. The relationships of biodiversity with increasing fire frequency/severity are hump-shaped for both the IDH and MSR.

(8) Species associated with recurrent fire have evolved many traits that increase their fitness in the presence of fire. For 39 comparisons, the number of species in 26 fire-prone lineages is much higher than that in their non-fire-prone sister lineages.

(9) Fire itself may be a mutagenic agent and can produce novel traits, although its significance in driving biodiversity has yet to be explored.

(10) A paradigm shift aimed at restoring biodiversity-maintaining fire regimes across broad landscapes is required from both research and management perspectives.

VIII. ACKNOWLEDGEMENTS

The research of T.H. and B.B.L. on fire-driven evolution was supported by the Australian Research Council (DP120103389). J.G.P. acknowledges support from the Spanish and Valencia Regional Governments (projects CGL2015-64086-P, PGC2018-096569-B-I00, PROMETEO/2016/021).

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Species richness of sister lineages in fire-prone and non-fire-prone habitats. – separates fire-prone lineages

on the left from non-fire-prone lineages on the right. Number of species was estimated as the species that occur exclusively in the specified habitat. Whenever possible, all species in the lineage were evaluated, and the number of species is given; otherwise, the number of species in the published phylogeny is given, assuming that a representative sample was in the original study. When there are multiple migrations between fire-prone and non-fire prone habitats within the taxon group, the number of species and divergent time for each migration are given. My, million years.

Table S2. List of the currently known non-plant pyrophilous species (fungi, insects, amphibians and birds). *, documented attraction to ongoing fire (open fire, hot ash or smoke);? indicates the absence of confirmative literature. Region: NA: North America; SA: South America; EA: Eurasia; AU: Australia; AF: Africa. Data compiled from Wikars (1997), Hjältén *et al.* (2007), Hutto *et al.* (2008); Hutto, Bond & DellaSala (2015), McMullan-Fisher *et al.* (2011) and Klocke *et al.* (2011).

(Received 3 April 2019; revised 19 June 2019; accepted 21 June 2019; published online 12 July 2019)