

*Commentary***The third dimension: How fire-related research can advance ecology and evolutionary biology****Byron B. Lamont and Tianhua He***Byron B. Lamont (*B.Lamont@curtin.edu.au*), School of Molecular and Life Sciences, Curtin University, PO Box U1987, Perth, WA 6845, Australia**Tianhua He, College of Science, Health, Engineering and Education, Murdoch University, Murdoch, WA 6150, Australia***Abstract**

Most of the Earth's vegetated surface is fireprone but the relevance of fire in understanding how nature works is not always recognized. We aim to show that, by adding the fire dimension to observations on biological phenomena, interpretations can be improved; how fire-related research can be used to answer 'fundamental' questions in ecology; and how theories/models developed for fireprone ecosystems can be applied to advancing disturbance ecology, biogeography and evolutionary biology more generally. We compiled lists from the world-wide web of the most highly cited papers in fire ecology, and examined papers that had been approached from multiple viewpoints, including fire. We show that great advances over the last 20 years have been made in our understanding of the pivotal role of fire as a driver of many ecological processes and a powerful selective agent/evolutionary trigger among biota. We document 21 sets of observations originally interpreted in the context of the two traditional dimensions, prevailing environment and biotic interactions, but can also be shown to have a strong, if not dominant, historical link to fire. We note that fire-related research is able to address 55 of the 100 questions considered 'fundamental' in ecology and that many have already received some attention in fireprone ecosystems. We show how theories/models that had their origins in fireprone systems can be applied to other disturbance-prone systems and thus have wide application in ecology and evolutionary biology. Fire and other disturbances should be included as variables in research about possible critical environmental and biotic constraints controlling ecosystem function in general. Adding this third dimension to research endeavours greatly enriches our understanding of how nature works at the global scale in an era where ecosystems are

changing rapidly and novel species-environmental interactions are emerging.

Keywords: evolutionary processes, fire-driven evolution, fire ecology, fundamental ecological questions, natural disturbances

"Fire is a natural process that is as fundamental to ecosystems as rain and the sun and (thus) we need a theory that rises out of this fact." (Pyne 2016)

Introduction

Traditionally, the distribution and associated traits of plants over the Earth's terrestrial surface have been interpreted in terms of abiotic environmental constraints (essentially climate, soils, topography) and biotic interactions (pollination, herbivory, diseases, competition). The third dimension/component, disturbance (especially fire), has often received less attention or even been ignored (Pausas and Bond 2019). For example, among the 100 papers published in journals of the British Ecological Society (BES) and considered most influential by the editors (Grubb and Whittaker 2014), only one (Lavorel and Garnier 2002) cites fire or heat. In accompanying commentaries on these papers, the generic term, disturbance, is raised five times but there is no mention of fire, whereas other environmental constraints (such as soil, nutrients, water, climate, temperature and plant-animal interactions) are mentioned many times. But it would be premature to conclude from this report that fire is not an active field of research, nor that it is only a minor environmental force with limited relevance to

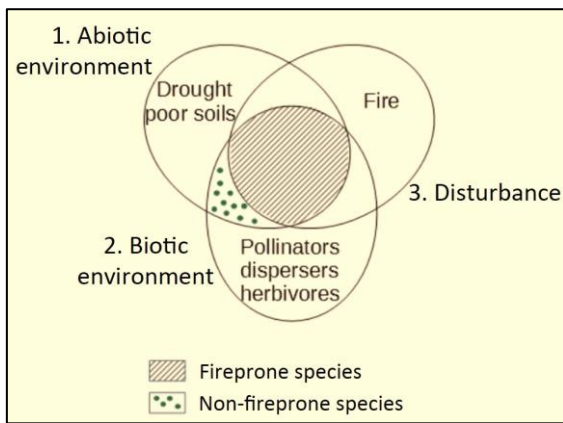


Figure 1. Venn diagram showing how the three dimensions of environmental constraints interact to control the ecology and evolution of the Earth’s terrestrial biota, with non-fireprone species limited in abundance by comparison. Examples of possible constraints have been added to the zone of influence of each dimension. Adapted from Pausas and Lamont (2018).

explaining ecological processes. On feeding in the key words “fire” (for the paper title) and “ecology” (to identify the journal) into Google Scholar, of the first 1,000 BES papers that appeared, we noted that a substantial 206 papers dealing with fire were published in BES journals, but apparently they must lack ‘influence’. We propose that disturbance/perturbations, especially fire, should be raised to equal status with abiotic and biotic constraints as controlling the ecology and evolution of plants and animals across the Earth’s terrestrial surface (Figure 1).

Fires have burned on Earth ever since the evolution of terrestrial plants 420 million years ago (Glasspool et al. 2004), and subsequently have had profound impacts on the Earth system (Bowman et al. 2009, Archibald et al. 2018). Currently, most of the Earth’s vegetated surface is fireprone, and on average 5% of the Earth’s vegetated surface is burnt every year, and 60% over any given 15-year period (Archibald et al. 2013). Great advances over the last 20 years have been made in our understanding of the pivotal role of fire as a driver of many ecological and Earth processes and as a powerful selective agent/evolutionary trigger among biota (Bond et al. 2005, Bowman et al. 2009, He and Lamont 2018a, He et al. 2019). Fires affect Earth system processes through altering the structure and composition of ecosystems (Pausas and Keeley 2009), controlling the distribution and diversity of biomes (Bond et al. 2005, Pausas and Ribeiro 2017), and shaping the evolution of functional traits (Keeley et al. 2011, Lamont et al. 2019a). Emissions from fire affect the cycling of carbon, phosphorus, and nitrogen (Wang et al. 2015, Wittkuhn et al. 2017). Fires alter the Earth’s surface energy budgets and regional to

global climate through increasing the land surface albedo, and emissions of greenhouse gases, aerosols and particulates (Randerson et al. 2006). Recently, Pausas and Lamont (2018) demonstrated how the inclusion of fire as a variable (the third dimension) greatly improved understanding of the distribution of the iconic plant family, Proteaceae, across Australia by taking the presence of fireproneness of the vegetation, as well as the other two dimensions, into account.

Here, we show that a) not only has fire-related research produced a suite of theories/models that can be applied throughout the fireprone regions of the world but also b) these theories have generality for relatively fire-free regions as well, especially those prone to disturbances other than fire. These objectives are achieved through four approaches. The first is to collate highly cited papers with ecological/biological effects of fires as a major part of their subject matter that illustrate the many issues that fire research can encompass. The second is to review phenomena that were initially interpreted in a non-fire context, mainly climate and herbivory (the first two dimensions), and then, with further observations, shown to benefit from the inclusion of fire-related explanations. The third is to demonstrate that many key questions in ecology, biogeography and evolutionary biology originally raised in a non-fire context can be, and have been, addressed by fire ecologists. Finally, we note that fire is a particular type of disturbance/perturbation and consider how the theories/models resulting from fire-related research can be applied more broadly in scientific endeavours.

Highly influential papers that included fire as a key part of their subject matter

We compiled a list of 25 highly cited papers with fire effects as (one of) their foci (Appendix Table A1). We excluded papers that dealt just with the properties of fire, i.e., as an end in itself. With a total of 31,542 (Web of Science) and 52,134 (Google Scholar) citations, as of 10 July 2019, these show that papers based on fire ecology have been well received by the scientific community. The topic of fire in these papers covers a wide range of disciplines, from organic chemistry, species invasion ecology, ecosystem dynamics, soil science, biodiversity evolution, forestry and climate change science. This shows that fire-related research has wide applicability in ecology. The role of fire as an ecological and evolutionary driver of ecological processes has received much less attention and detailed research on fire as an evolutionary trigger and mutagenic agent has only begun to emerge during the last decade (Simon et al. 2009, Crisp et al. 2011, Lamont and He 2017, He and Lamont 2018b). It is papers such as these that enabled us to prepare a list of theories/models developed for fireprone systems that could be tested for their generality in other disturbance-prone systems (see below). We also note that the periodic lists of Current Titles in

Table 1. Ranking of 21 paired sets of observations on botanical phenomena (Table A2) according to whether observed fire-related or non-fire-related constraints gave scientifically sounder explanations (five ranks) and the evolutionary sequence (three ranks) in which the fire-related and non-fire-related constraints occurred together with their interaction.

Time of origin of fire-related constraint	Importance of fire-related constraint relative to non-fire-related constraint					Subtotal
	Unclear (1)	Less (2)	Equal (3)	More (4)	Replaces (5)	
Before non-fire-related (1)	0	0	0	8	6	14
Same time or unclear (2)	1	2	1	1	0	5
After non-fire-related (3)	0	0	1	1	0	2
Subtotal	1	2	2	10	6	21

Wildland Fire (<https://fireecologyjournal.org/current-titles-in-wildland-fire>, curated by Jason Greenlee) reached 118,000 publications by the end of 2019 with a mean listing per month of about 400 new publications, and 70 books published over the last five years. There can be no question that studies centred on fire are currently an area of exceptional activity, perhaps rivalled only by that on climate change.

Fire as an alternative explanation for understanding certain biological phenomena

We searched the literature for observations on plant traits and geography that have been interpreted in both a non-fire context, and, usually later, in a fire-related context. If this leads to possible bias, as suggested by a reviewer, then it is either because few research projects have considered all three dimensions as potentially relevant explanatory variables or because our literature search was inadequate. This yielded 21 paired sets of observations/interpretations supported by 65 studies (Appendix Table A2), i.e., no single study examined all three dimensions, with each research group approaching the topic from the perspective with which they felt ‘comfortable’ (Pausas and Lamont 2018). These dealt with five aspects of soil-stored seeds; two with plant-stored seeds; three with growth form; three with biogeographic traits, originally related to climate and/or soils; four with protective plant traits (biotic or abiotic); and three with aridity-related traits. We then examined both sets of evidence and ranked the importance (weight of evidence in support) of the fire-related interpretation versus the non-fire-related interpretation as unclear, less, equal, more, or the latter could replace the former entirely.

We determined that the inclusion of fire as a variable provided a more likely explanation of the critical constraints for almost half of the phenomena we examined (Table 1). For these, non-fire related limiting factors have an ancillary role (Appendix Table A2). Climate (seasonal drought or heat waves) were secondary constraints in seven cases compared with fire, with an eighth, on the switch from C3 to

C4 grasses, partly relating to decreasing rainfall and temperatures, and lower carbon dioxide levels (Osborne 2008). Plant-consuming animals appear to have had a minor role in three cases, and landscape variability provides little insight into the ratio of fire-stimulated resprouters to nonsprouters in one case. Of most interest are the five cases where a fire-related explanation is sufficient to replace the earlier interpretation. Four included reference to climate, with two of these including plant-animal interactions, and a fifth involving scarification of hard seeds by soil processes (that proved to be ineffective, unlike fire heat). One is of particular interest, for this was a well-executed test of the proposal that a warming climate was responsible for the apparent upward shift of chaparral species in the Santa Rosa Mountains, California (Kelly and Goulden 2008). Schwilk and Keeley (2012) showed that it was an artefact of the differences in fire history of the sites (at least for the key fire-killed species that they were able to examine in detail).

Thus, it seems, for phenomena occurring in fireprone environments, that fire often has the more important role in explaining plant traits and distribution patterns when compared with those originally proposed. Nevertheless, a few phenomena are not essentially fire adaptive, with non-fire-related functions equally important in two cases, two less important, and one (highly flammable terpenoids that are also known to deter some herbivores) uncertain as to their principal function. Clearly, there is a need for simultaneous tests of the hypothesised relevant variables so that their relative contribution to explaining the phenomenon can be assessed. Distinguishing a high summer-temperature from a fire-heat effect on breaking seed dormancy (Moreira and Pausas 2012) provides one of the few examples of what is required.

Our analysis of the evolutionary sequence of the different possible constraints was less formal here as this topic has been comprehensively reviewed elsewhere (Lamont et al. 2019a,b and references therein). We used this background to show that 14 of the 16 cases where the phenomenon could essentially be explained by its relationship with fire (columns 4 and 5 in Table 1) that fireproneness also

preceded the advent of the less critical constraints such as climate seasonality (as it affects plant phenology) or granivores (as they affect the need for seed protection). It was not possible to distinguish the timing of the presence of fire from other possible constraints in five cases. Thus, the presence of fire was associated with the origin of the highly fire-tolerant leptospermoid Myrtaceae, especially *Eucalyptus*, as an advanced trait over its immediate ancestors but it is unknown if the universally present terpenoids arose then as well or earlier (Crisp et al. 2011). The same is true for the timing of the critical selective agents for ant-attracting arils on seeds that ensure their burial (was the key selective agent increasing granivory or intensifying fire?), succulence, geophyty, finely divided foliage and plants with C4-type photosynthesis. It is clear that additional ancestral trait assignments (the techniques themselves need refining) are required on multiple hypothesised constraints to distinguish the timing at which they were imposed on clades (Lamont et al. 2019b).

Scope for fire-related research to address key questions in ecology and evolution

Looking to highlight priorities for future research in ecology, Sutherland et al. (2013) identified 100 ‘fundamental’ questions. Such an objective is laudable provided it does justice to the three dimensions of environmental constraints in ecology and evolutionary biology. Regarding the third dimension, the closest is question 26 that asks, “What demographic traits determine the resilience of natural populations to disturbance and perturbation?” Since the word fire is not mentioned in the document we decided to check the literature to see to what extent fire-related research has been undertaken on any of the ‘fundamental’ questions asked by Sutherland. The authors might respond that the questions are generic (as did a colleague) so you would not expect such a specific process as fire to be mentioned. That response is hard to defend as processes such as dispersal (mentioned four times), disease, parasitism, mutualism, allelopathy, weather and human behaviour are all the subject of questions (why not fire effects?). Abiotic components of ecosystems are raised, such as soil, nutrients (including nitrogen and phosphorus), microbes (five times) and groundwater, and such ecosystems as marine, terrestrial, and freshwater are highlighted (why not fireprone?), and such traits or growth forms as body size, leaf area, grasses, woody plants, megafauna are noted (why not seed storage, resprouters, bark thickness...?).

We found that 55 of these questions have indeed been examined in the context of fire (Appendix Table A3). This showed that fire-related research is particularly suited to addressing questions that deal with the control of population and community dynamics, biodiversity, ecosystem functioning and evolutionary ecology, including adaptive responses to environmental change (Figure 2). We suggest that

a more thorough literature research would show almost all of these questions have been given some attention in the past but all await thorough investigation even in fireprone systems. Thus, we need to add a further question (101): “What is (i.e., ecology), and has been (i.e., evolutionary biology), the significance of fire among the world’s biota compared with other environmental constraints?” Addressing this question would include testing if the biota is non-fire-tolerant in non-fireprone systems as the null model. Demonstrating that particular dynamics can be attributed to disturbances other than fire is equally relevant. Even where fire tolerance is demonstrated by biota in non-fireprone systems it immediately returns to issues of possible exposure to fire during their phylogenetic history (Lamont and He 2017).

Testing fire-related theories for their wider applicability in nature

Fire ecology fits more generally into the discipline of *disturbance ecology*. This field encompasses resistance, avoidance and adaptive responses to damage, dieback or mortality due to the presence of any kind of natural or anthropogenic disturbance. This includes diseases and pests, drought, flooding, frost, ice or heat waves; lightning strikes; wind, hail or snow storm damage; abrasion from flying objects in hurricanes or rubbing by large animals; landslides, rock and falling trees; treefall gaps; mammal trampling and vertebrate digging; volcanic activity (barren rock substrates); prolonged cloudiness from volcanic activity, meteorite impact; earthquake damage; invasion by exotic species; scouring by fast moving water; creation of new substrates by retreating water bodies, lava flows, island emergence; and human-caused disturbances – harvesting, herding; dryland salinity, landclearing; buildings, roads and rubble; and polluted air, water and soil.

We searched the fire ecology/evolution literature for apparent paradigms in this field of research and then examined the possible applicability of these more generally in ecology and evolutionary biology, at least in the context of disturbance ecology and disturbance-induced evolution. There are four options available for relating fire-centred research to more general ideas in ecology and evolution:

1. A given theory developed without considering fire effects could be tested for its generality in the context of fire
2. A given theory developed for fireprone systems could be tested for its generality in other disturbance-prone systems
3. A given theory developed for fireprone systems uniquely applies to them as the idea is based on the unique properties of fire, such as causing ignition or producing heat exceeding that possible from sunlight alone
4. A given theory developed for non-fireprone systems cannot apply to fireprone systems,

such as pertaining to the unique properties of aquatic systems or succulent desert vegetation.

Our purpose here is to consider the first two options as they allow for the issue of generality to be explored (Figure 3). These all involve the interplay between inductive and deductive logic. For our purposes, early case studies are used to develop general theories/models either in fire-free (Figure 3A) or fireprone (Figure 3B) systems (induction, it consistently applies in the particular, so probably applies more generally). The questions raised in Sutherland et al. (2013) are at this stage in a research program. The case studies in fireprone systems that we cite (Table 2, Table A2) are an attempt to formulate a theory that applies to both disturbed and non-disturbed systems. The fire-free theory is tested in a fireprone system (deduction, if it applies generally, then it must apply in the particular) to confirm its generality. If it is shown not to apply (induction), then the theory is abandoned or modified (it is general, except for/provided...). Alternatively, theories/models are developed in fireprone systems and the challenge is now to see if they also apply more generally. These ideas are less

likely to apply universally but are more likely to be relevant to disturbed systems. Thus, fire-related theories should have some generality.

We identified 20 theories/models developed in, and for, fireprone systems that have potential application in disturbance-prone systems more generally (Table 2). These theories/models have some parallels with the 55 ‘fundamental’ ecological questions that we consider fire-related research can help address but our list gives much more prominence to evolutionary processes (Figure 2). Most are well-established paradigms in fire ecology, especially those related to the fitness function of fire-related traits (theories 2, 4–6, 9, 13, 18). Some have probably not been articulated before, mainly because they are too new to have matured into a widely accepted hypothesis through extensive (deductive) testing (7, 14–17, 19, 20). Some have yet to be couched solely in terms of fire. For example, Vanneste et al. (2014) attributed high levels of genome duplication close to the Cretaceous–Paleogene boundary to “severe disturbance events” but gave no details. However, we know that this was the close of one of the most flammable periods in the Earth’s history—the fiery Cretaceous (Brown et al.

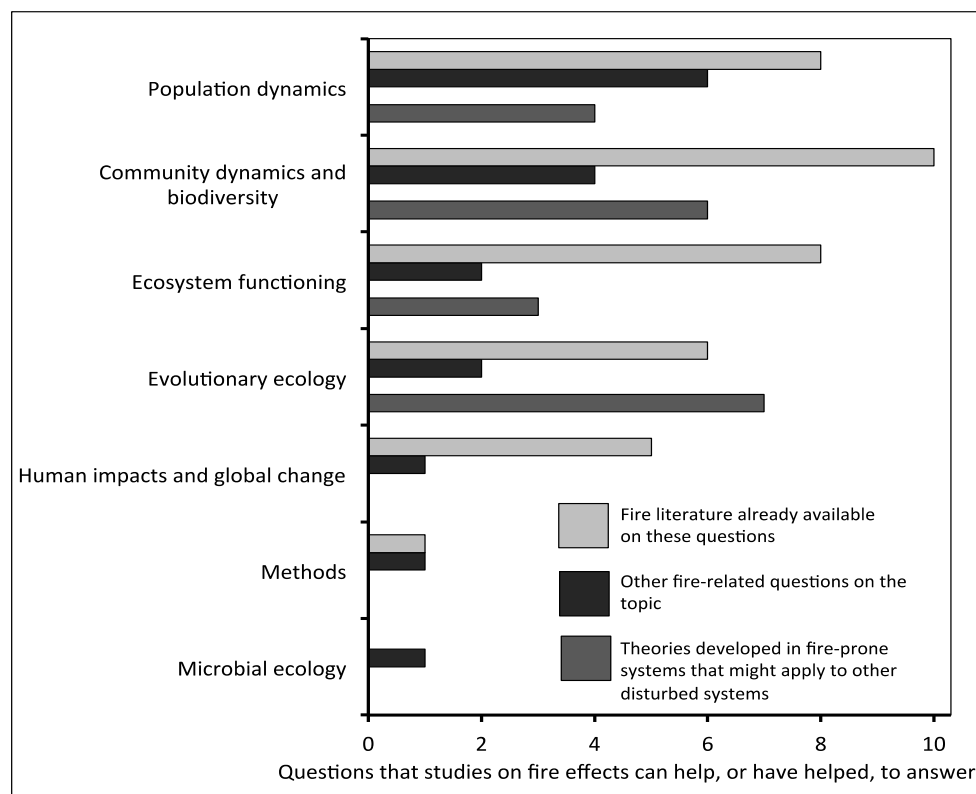


Figure 2. Collation of 55 ‘fundamental’ ecological questions of the 100 compiled by Sutherland et al. (2013) that we show can be addressed in the context of fire effects (Table A3). Our survey shows that a number of these (two-thirds) have already received some attention in the fire literature (light grey bars) and that a more thorough literature survey might show that some research has been undertaken on the remainder (black bars). No question has been examined exhaustively and fireprone systems are ideal settings for addressing many of them. In addition, we identified 20 theories/models derived from fire-related research (Table 2) and collated them here with the same headings as used for the ecological questions for comparative purposes (dark grey bars).

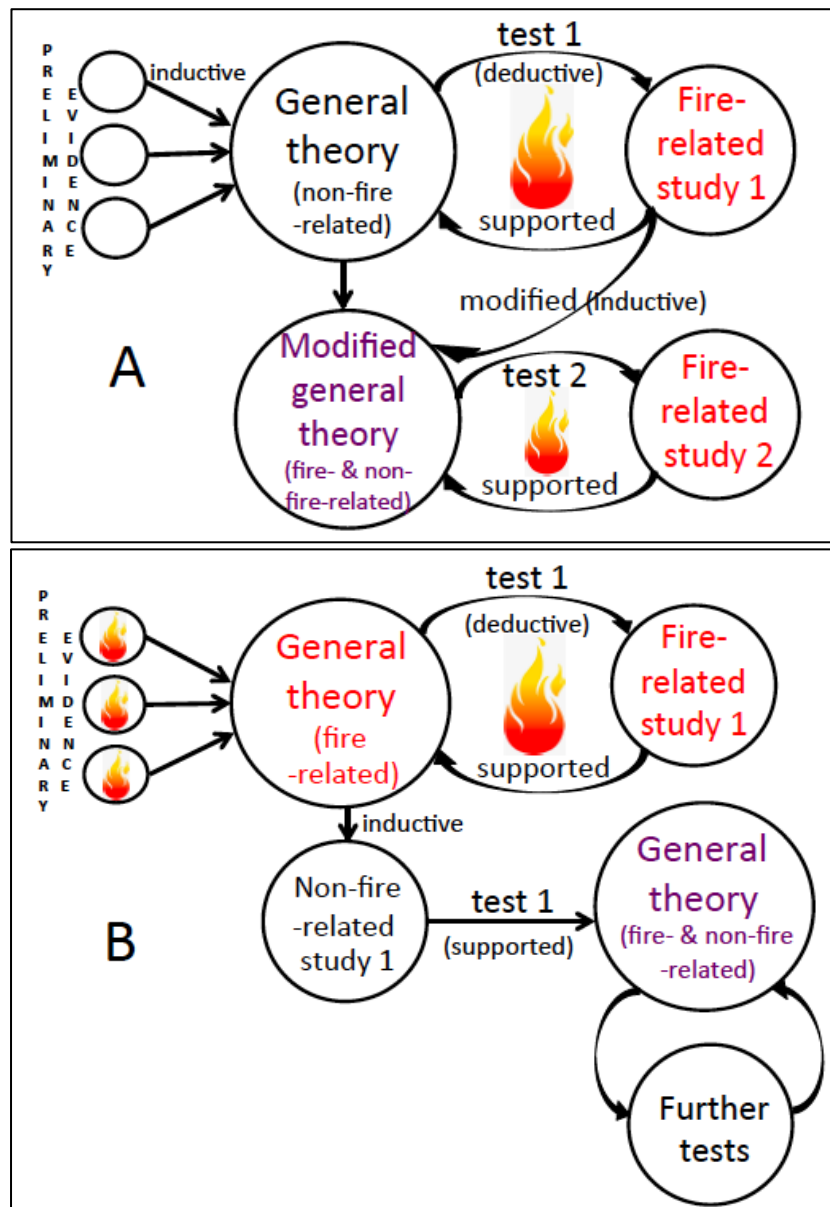


Figure 3. Procedures for testing the generality of theories and models developed initially for A) non-fireprone systems (to determine if they also apply to fireprone systems) and B) fireprone systems (to determine if they also apply to non-fireprone systems). It is most likely that systems that experience recurrent disturbance will conform with scenario B

2012, He et al. 2012). Moreover, there is much evidence of the ability of heat, ash, smoke particulates and fire-released volatiles to induce DNA mutations and polyploidisation in plants, bacteria and animals (Pettersen 1961, Pécrix et al. 2011, He and Lamont 2018b).

Our main purpose here has been to show that current fire-related theories/models may well be applied to other ecosystems, especially if they are disturbed on a recurrent basis. Much depends on the extent to which other disturbances can imitate fire properties (e.g. fire-mimicking, Lamont and He 2017) or fire effects. For example, disturbances that result in bare ground can be combined with a substantial soil-stored seed bank. This would only mimic the colonizing (patch-creating) property of fire, but not the cue for prolific germination. Greater exposure to sunlight, and thus a greater diurnal range of temperatures (Brits 1987), will promote dormancy breaking (Santana et al. 2013) but, as already noted, this would not be of the same order as under postfire conditions. Nevertheless, this scenario may promote synchronized germination and enable the testing of theories 1 and 9 (Table 2) under a variety of densities, species mixes and microsite sizes (Lamont et al. 1993).

Since there has been little theory development in other disturbance-prone systems, we essentially draw attention to the scope for comparing the effects of the wide array of disturbances that exist against our 20 fire-based theories/models in the search for generality (Table 2). In particular, we note what

Table 2. Twenty theories and models that were developed for fireprone systems that could be applied to non-fireprone systems (or fireprone that also undergo disturbances from causes other than fire) to gauge their applicability and generality. Unless cited elsewhere in the text, references cited in this table are listed at the end of Appendix Table A3.

Theory developed in a fireprone context	Supporting phenomena/literature from fireprone systems	What and how to test in non-fireprone systems
<i>Population dynamics</i>		
1. Competition among seedlings is maximised when their establishment is synchronised (i.e., postfire), especially when serotiny/pyriscence dominates the recovery pattern	Postfire microsite studies, Enright and Lamont (1989), seedling thinning – Lamont et al. (1993)	Identify disturbance conditions that promote synchronized seedling establishment (e.g., treefall gaps), set up a trial that varies planting density possibly including enclosures in addition to controls to compare against herbivore effects
2. Heat tolerant/avoidance traits are adaptive responses to recurrent high temperatures (exceeding that possible via heat from sunlight)	Seeds in fireprone systems are held in woody, heat-resistant cones or fruits, or seeds are buried by ants insulated by soil, buds are stored beneath thick bark or belowground, Enright et al. (2007), Pausas et al. (2018)	This hypothesis is uniquely applicable to fireprone systems. It would need to be completely modified to apply to particular disturbance types of interest. Thus the relevant tolerant/avoidance traits would refer to such constraints of interest as frost, severe winds, bare ground, trampling, flooding and it would be necessary to demonstrate a history of association with them over evolutionary time
3. Pyrophilic insects can detect fire and smoke from great distances away (up to >100 km)	Pyrophilic Jewel beetles (<i>Melanophila</i>) have infrared smoke detectors (Schütz et al. 1999)	Observe other animals (insects, birds, mammals) for movement and migration dynamics as a response to other disturbances that produce signals (visual, olfactory, auditory) to which they respond positively
4. Seed storage in fireprone systems is a syndrome of traits that includes a) insulation from fire heat or heat tolerance, b) increased longevity mechanisms, c) responses to fire-related cues that break dormancy, and d) protection from, or tolerance of, granivores, diseases, detritivores and ingestion by dispersal agents	Serotiny/pyriscence, hard-seededness/heat-stimulated germination, decay-resistant seeds with smoke-stimulated germination – reviewed in Lamont et al. (2019a)	Impose agents of disturbance on seeds produced by species native to disturbance-prone ecosystems (plus controls) and gauge their ability to survive. Test their ability to remain viable after decade-long periods of storage in soil, presence of pathogens and decomposers, ingestion by local granivores and omnivores. Impose dormancy-breaking cues likely to be encountered as a result of the disturbance (abrasion, waterlogging, lower or higher temperatures, pollutants...) and note effects on viability and post-treatment germination
<i>Community dynamics and biodiversity</i>		
5. Fire (disturbance) induces ultimate responses that increase fitness via specialized survival and/or reproductive traits	Serotiny/pyriscence; fire-stimulated resprouting, flowering and germination (Lamont and Downes 2011, Causley et al. 2016, Pausas et al. 2018)	Assess adaptive species traits that resist, avoid or respond to damage/dieback/mortality due to presence of all types of disturbances (see main text for details)

6. There is a dichotomy in responses to fire (disturbance) – either survival (resprouting) or mortality followed by recruitment of offspring	Wells (1969), Lamont and Wiens (2003), Pausas and Keeley (2014). [The model of Bellingham and Sparrow (2000) is in a wider context than fire]	Assess ways that the component species respond to a particular disturbance type to determine to what extent the dichotomy holds, including varying the properties of the disturbance, such as intensity and frequency
7. Pyrodiversity promotes biodiversity	Different fire events create patches varying greatly in size, structure, intensity and time since fire (He et al. 2019), the fire-maintained prairies of N America (Martin and Spasis 1992), diversity of marsupials in N. Australia (Davies et al. 2018)	Any system with varying levels of patchiness (mosaics) from a range of causes (e.g., mosaics of soil, invasive species, micro-topography) within matched areas of equal total size can be used to test this hypothesis
8. “Initial floristic composition” model of community succession, also called “autosuccession”– the same biota are present immediately postfire (post-disturbance) as were present prefire (pre-disturbance) though the slopes and peaks of their abundance curves may not coincide	Noble and Slatyer (1980), Enright et al. (2007), He et al. 2019, also persistence niche theory (Bond and Midgley 2001)	Assess species composition before and after applying a particular disturbance type and examine the reasons for the match or mismatch
9. Species are cued to release or germinate their seeds in response to disturbance (i.e., postfire) as conditions for recruitment are optimal then. <i>Corollary:</i> lack of fire-stimulated germination occurs when the disturbance is so frequent that seed storage is redundant or maladaptive	Postfire seed release, fire-stimulated germination of soil-stored seeds, water/light/nutrients high, disease low, Cowling and Lamont (1987), Causley et al. (2016), lack of seed storage in savanna grasslands (Lamont et al. 2017)	Determine the optimal conditions for stimulating germination and seedling recruitment – this requires simultaneous comparison of a number of disturbance or stress constraints, possibly varying in intensity, against a common control, ideally undertaken in the field
10. Alternative vegetation states are mediated by fire, such that the types of vegetation and species now clothing the Earth would be quite different in the absence of fire	Shrubland vs forest (Odion et al. 2010), shrubland vs hummock grassland (Wright 2018), savanna vs forest (Bond and Parr 2010), vegetation models in the absence of fire (Bond et al. 2005)	Impose widespread disturbance and gauge vegetation and species presence/diversity change and to what extent they are self-perpetuating (Odion et al. 2010)

Ecosystem functioning

11. The rate of disturbance (fire frequency) controls the rate of carbon and nutrient cycling	Goldammer et al. (2009), Wittkuhn et al. (2017), Archibald et al. (2018)	Field trials are required where the disturbance type of interest varies in intensity and the effect on carbon or nutrient cycling is monitored. Where the ability to manipulate the system is limited, modelling will help to predict the outcomes
12. Volatilization of carbon and mineral nutrients (due to fire) is a key contributor to their ecosystem cycling	Goldammer et al. (2009), Wang et al. (2016), Wittkuhn et al. (2017), Archibald et al. (2018), Butler et al. (2018)	Volatilization is difficult to study directly. One approach is to determine base levels of carbon or nutrients and what remains after the disturbance and the difference is what has been lost in volatilization

13. Specificity of plant-animal relations and animal-animal relations is relaxed in disturbed systems (due to frequent change in species presence and abundance)	Many animals that have major impacts on ecosystem functioning are omnivores or generalists, emus (seed dispersers), honeyeaters (pollinators), cockatoos (granivores), ants (seed buriers), insects generally (Koltz et al. 2018)	Present animals with a wide range of potential diet items, whose presence and abundance vary with the intensity of disturbance, and monitor what they select via direct observations or examination of droppings or stomach contents
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Evolutionary processes

14. Fire-heat is a key agent for inducing genome duplication and polyploidization among flowering plants	Pettersson (1961), Pécirix et al. (2011), much polyploidization occurred either side of the fiery K-T event (Vanneste et al. 2014, He and Lamont 2018b)	Genome duplication and polyploidization are proposed as significant mechanisms in the diversification of plants but their cause over the long evolutionary time of life on Earth is unclear. Vanneste et al. (2014) attribute high levels around the K-T boundary to “severe disturbance” events but give no details. The discovery of fire-heat induced genome duplication and polyploidization may be the key to diversification of flowering plants but other sources of disturbance need to be tested as well
15. Fire-(disturbance)-related traits are fire-(disturbance)-adapted as they evolved after (or rarely coincidentally with) the onset of fire-(disturbance)-proneness within their ancestral habitats	Confirmed for the Pinaceae, Proteaceae, Orchidaceae, Haemodoraceae, Xanthorrhoeaceae, Restionaceae, Fabaceae using trait-assignment techniques (Lamont and He 2017, Lamont et al. 2019b)	Comprehensive dated phylogenies are required for clades whose adaptive traits to specific disturbances among its extant species are well established. Independent evidence for the presence of the relevant agent of disturbance at the time of the estimated time of origin of the trait is desirable. Validity of the results is enhanced when there is strong support from dated fossils for dating the phylogeny, estimating the evolutionary environment and providing direct evidence of the existence of the trait through time
16. Fire (disturbance) promotes speciation via population turnover and dispersal effects but, more fundamentally, because fire itself is a source of mutagens	Plants (Wells 1969, He and Lamont (2018b), insects (Koltz et al. 2018)	Set up a field trial to test if the disturbance type of interest promotes population turnover and record pre- and post-disturbance genotypes. There is evidence that cold treatments can induce mutagenesis and other disturbance types could be assessed for their mutagenicity
17. Abundance and impact of somatic mutations depends on the intensity and length of exposure of meristems to mutagenic agents, and opportunities for their expression via bud burst (i.e., postfire)	Lamont and Wiens (2003), Fowler et al. (2018), He and Lamont (2018b)	The accumulation of mutagens is difficult to study. However, determining to what extent the disturbance type of interest promotes bud burst by resprouters is the expression part of mutagenesis that is easily studied and compared against controls

18. Evolution of flammability and fire-adapted traits is the result of niche construction processes at all scales	Mutch (1970), Bond and Midgley (1995), Zedler (1995), Schwilk and Ackerly (2001), Schwilk (2003), He et al. (2011), He et al. (2012), Pausas et al. (2017), Staver and Schertzer (2018)	Assess if the increase of fire activities in otherwise relatively fire-free ecosystems leads to increased flammability and fire-adapted traits, thereby increasing fire activities through niche construction process and promoting an evolutionary feedback loop. As fire-adapted traits and flammability could be predicted from the fire regime the vegetation experiences, it may be feasible to use niche construction theory to make a general, formal predictions about organism traits and responses
19. Wildfire (widespread disturbance) causes rapid genetic/phenotypic adaptation among the impacted biota	Genetically based melanism among grasshoppers (<i>Tetrix subulata</i>) is negatively correlated with time since fire (Forsman et al. 2011), insects (Koltz et al. 2018)	Sudden and widespread disturbances are severe selective agents but are short-lived. To the extent that rapid adaptation is required (especially if the biota remains resident), genotype/phenotype fluctuations can be assessed by comparing them against disturbance events for their levels of synchronization.
20. Fluctuating levels of atmospheric oxygen and carbon dioxide over geological time scales have had a key role in controlling fireproneness (habitat flammability), evolution of fire-related traits and plant speciation rates, and pre-empted control by rainfall seasonality	Oxygen levels control flammability (Belcher et al. 2010), major plant orders arose during the fiery Cretaceous (He and Lamont 2018a), evolution of fire-related traits and speciation rates correlate with oxygen levels (He and Lamont 2018b, Lamont et al. 2019a), seasonal effects took over from oxygen levels in the late Cenozoic (Lamont and He 2017). The importance for plants of the changes in atmospheric O ₂ through geological time (Bond and Scott 2010)	This hypothesis gives causal explanations for fluctuating fire regimes over geological timespans and thence its effects on the associated biota. Unexplored is how these same atmospheric fluctuations may have affected the incidence of other disturbances and the consequent effects on evolutionary processes. There are geological records for the incidence of disturbances noted under (5) above and correlations can be undertaken. Models are available for the effect of the 'greenhouse effect' (high carbon dioxide) on the incidence of flooding, hurricanes and the like, and meteorites on cloudiness, temperatures and the like. It is doubtful that varying oxygen levels affect other disturbance types.

disturbance types most likely apply to particular fire-related theories and suggest suitable methodological approaches for testing them. As the opposite of fire heat, bouts of extreme cold can be expected to have a profound effect on population and community dynamics and evolutionary processes (Rabosky et al. 2018). Frost prunes back plants in a way equivalent to fire and it has been suggested is responsible for evolution of the subshrub geoxyllic growth form in African grasslands (Finckh et al. 2016). Although it has since been shown to be historically implausible in this case (fire effects on such a growth form preceded frost-proneness, Lamont et al. 2017), frost-resistance may evolve among young plants in frost-prone populations (Prunier et al. 2012) while cold-tolerant genes can be ‘switched on’ by low temperatures (Rensink et al. 2005).

As a further example, the reviewer, Marcelo Simon, points out that seasonal flooding of vegetation in river floodplains has parallels with fire disturbance: the incumbent plants are either flood tolerant or recolonize the plain after the water retreats (Parolin et al. 2003, Arias et al. 2018). This is equivalent to resprouters and nonsprouters (re-establish from seeds) in fireprone ecosystems, and their dynamics can be compared with theories 1, 4 to 10 in Table 2 developed for fireprone floras.

Finally, we outline the steps that we have previously taken in seeking to understand the role of fire in plant evolution (Box 1). We offer this as a template that could be used for research programs on other disturbance types that may have an evolutionary impact. This approach requires comprehensive dated phylogenies for clades whose adaptive traits to specific disturbances among its extant species are well known. Independent evidence for the presence of the relevant agent of disturbance at the time of the estimated time of origin of the trait is desirable. Validity of the results is enhanced when there is strong support from dated fossils for giving a time dimension to the phylogeny, estimating the evolutionary environment and providing direct evidence of the existence of the trait through time (Lamont et al. 2019a).

Conclusions

Progress in ecology, biogeography and evolutionary biology is made through synthesising accumulated results into general patterns, identifying underlying mechanisms and testing consistency of predictions derived from hypotheses (Knapp et al. 2004). Most advances will be made when these procedures are undertaken on the three dimensions (major groups of constraints) that control the structure and dynamics of ecosystems (environmental factors, biotic interactions, and disturbances). Although it is the most prominent disturbance in nature, any explanatory role for fire is sometimes overlooked, misunderstood or dismissed (Pausas and Lamont 2018, Pausas and Bond 2019)

or branded as an unnatural destructive force to be suppressed (Pyne 2016). Yet much is known about the key role of fire in ecosystem functioning and as a selective agent in trait evolution and speciation. Although none of the 100 ‘fundamental’ questions (Sutherland et al. 2013) specifically mentions fire and its role in ecosystem and evolutionary processes, we show that fire-related research can address, or already has shed light on, 55 of them. Further, we identify 20 theories/models developed in fireprone systems that we believe need to be taken seriously by the rest of the ecological/evolutionary community in order to avoid “reinventing the wheel”. We outline ways that these ideas and approaches can be tested in other systems for their applicability, especially in

Box 1. The steps involved in documenting the evolution of fire-adapted traits and fire-stimulated speciation that can be used as a template for pursuing evolutionary processes in other disturbance-prone systems.

1. The ecosystem becomes fireprone for the first time or the fire regime changes (Lamont and He 2017)
2. Fire causes population turnover and promotes emergence of novel genotypes and may itself be a source of mutagens that may cause changes in the genome of individuals in the affected population (He and Lamont 2018b)
3. Directional selection takes place, depending on genetic variation in the population and the type of mutations caused by fire, some individuals (phenotypes) respond negatively (local extinction or reduced fecundity) and others respond positively (local survival or increased fecundity)
4. The genetic structure of the population changes, and thus new trait types arise that increase fitness under the new fire regime (Simon et al. 2009, Maurin et al. 2014)
5. The new genotypes proliferate (stabilizing selection) and further speciation may now occur under the influence of other (secondary) agents of selection present in the new habitats now occupied (Lamont et al. 2019a)
6. The extent of speciation will depend on a) the range of fire regimes available to the ancestral species, as each regime type will induce a separate evolutionary pathway, b) the range of other selective agents present within a given fire regime, c) the genetic heterogeneity of the component clades, and hence trait options available to respond positively to the new fire regime, d) the mutagenic properties of the fires that occur, e) (meta)population dynamics of the affected species, and f) the passage of geological time available (Dolan et al. 2008)

response to sources of disturbance and severe stresses other than fire.

The Anthropocene is an era with unprecedented biotic mixing, where ecosystems are altered and novel plant-trait combinations are emerging. Flammability is not only prominent in fireprone ecosystems, but is also becoming relevant in previously relatively fire-free regions with climatic change and plant invasion; and the impact of wildfire in many regions is escalating (Moritz et al. 2014). Note the wide occurrences of severe fires in Eastern Australia and California in 2019–20 that show how this dimension can have a profound effect on ecosystems not previously thought to be highly fireprone (Clarke et al. 2020). We exhort field biologists and theoreticians alike to include fire and other disturbances in their thinking about possible critical environmental constraints operating on the biota and ecosystems that they study. Adding the third dimension to research endeavours may require a change in the objectives of some projects but it will greatly enrich our understanding of how nature works at the global scale.

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- necessary clues as to their optimal conservation management. It is a major, and now perhaps urgent, task for researchers to find out what these properties are. This knowledge needs to be passed onto land managers whose objectives must include biodiversity conservation as well as protection of life and property.
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Response to Referee

It is encouraging to have support for our commentary from such an authority on the place of fire on Earth as Stephen Pyne (e.g., Pyne 2019). Others might just see our exhortations as sour grapes over perceived lack of interest in our research endeavours. On the contrary, Pyne (2020) considers that we do not go far enough. We argue for fire, and disturbance ecology in general, as worthy of equal status with the traditional controlling influences, climate, topography and soils (abiotic factors) and to a lesser extent, biotic interactions (herbivory, pollination and the like) in research. Pyne sees fire as even more fundamental in understanding nature than these. This is because fire is inextricably part of nature. In support of this view, we have argued elsewhere (Lamont, He and Yan 2019) that fire pre-empts these other influences historically in many instances; that is, they only have a secondary, ‘fine-tuning’ role that comes into operation after fire has shaped the basic adaptations of plants in particular.

Pyne's comments are so insightful that for us to sprinkle them through the manuscript would have been an act of plagiarism. He alone must take credit for them. It is surely a classic comment from him that fire studies got relegated to forestry who did not want it and then this land management authority did all it could to suppress fire so that they did not have to deal with it—recent events in California and Australia show that fire has certainly come back to bite the hand that fed it (so well)! The dilemma is that, while (wild)fire is fundamental to maintaining nature's processes (He et al. 2019), it is incompatible with the presence of humans in the landscape. Yet humans now control the incidence of fire and we accept the criticism that we have not addressed the implications of this adequately in arguing for a greater recognition of fire-related biology in our research endeavours.

Creative management must find ways to let fire-prone ecosystems operate in such a way as to maintain biodiversity (*ad hoc* fire suppression is not effective land management) while keeping human-occupied areas fire-free. We believe that the fire-related traits possessed by biota provide the

Appendices

Table A1. 25 highly influential papers that include fire ecology as part of their subject matter. The last two columns are the number of citations recorded by two web services (as at 10 July 2019) with the listing order determined by the first. The 11 papers whose main theme is fire effects are indicated by *.

Title	Authors	Year	Journal	Vol	Pages	Web of Science	Google Scholar
Biotic invasions, causes, epidemiology, global consequences, and control	Mack, R.N., Simberloff, D. Lonsdale, W.M., et al.	2000	Ecological Applications	10	689–710	3508	6283
Warming and earlier spring increase western US forest wildfire activity*	Westerling, A.L., Hidalgo, H.G., Cayan, D.R., et al.	2006	Science	313	940–943	2430	4009
Northern peatlands - role in the carbon-cycle and probable responses to climatic warming	Gorham, E.	1991	Ecological Applications	1	182–195	2161	3503
Emission of trace gases and aerosols from biomass burning*	Andreae, M.O., Merlet, P.	2001	Global Biogeochemical Cycles	15	955–966	2071	3308
Nitrogen limitation on land and in the sea - how can it occur?	Vitousek, P.M., Howarth, R.W.	1991	Biogeochemistry	13	87–115	2040	3196
Biological invasions by exotic grasses, the grass fire cycle, and global change	Dantonio, C.M., Vitousek, P.M.	1992	Annual Review of Ecology and Systematics	23	63–87	1855	3339
Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model	Sitch, S., Smith, B., Prentice, I.C., et al.	2003	Global Change Biology	9	161–185	1708	2642
Tree-grass interactions in savannas	Scholes, R.J., Archer, S.R.	1997	Annual Review of Ecology and Systematics	28	517–544	1427	2285
Disturbance, diversity, and invasion - implications for conservation	Hobbs, R.J., Huenneke, L.F.	1992	Conservation Biology	6	324–337	1295	2590
Predicting changes in community composition and ecosystem functioning from plant traits, revisiting the Holy Grail	Lavorel, S., Garnier, E.	2002	Functional Ecology	16	545–556	1430	2223

Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009)*	van der Werf, G.R., Randerson, J.T., Giglio, L., et al.	2010	Atmospheric Chemistry and Physics	10	11707–11735	1407	1931
Fire in the Earth System*	Bowman, D.M.J.S., Balch, J.K., Artaxo, P., et al.	2009	Science	324	481–484	1113	1704
Effects of fire on properties of forest soils, a review	Certini, G.	2005	Oecologia	143	1–10	1102	1913
Climate change and forest disturbances	Dale, V.H., Joyce, L.A., McNulty, S., et al.	2001	BioScience	51	723–734	1062	1897
The global distribution of ecosystems in a world without fire*	Bond, W.J., Woodward, F.I., Midgley, G.F.	2005	New Phytologist	165	525–537	937	1447
Fire as a global 'herbivore', the ecology and evolution of flammable ecosystems*	Bond, W.J., Keeley, J.E.	2005	Trends In Ecology & Evolution	20	387–394	926	1546
Fire effects on belowground sustainability, a review and synthesis	Neary, D.G., Klopatek, C.C., DeBano, L.F., et al.	1999	Forest Ecology and Management	122	51–71	812	1484
Ecology of sprouting in woody plants, the persistence niche	Bond, W.J., Midgley, J.J.	2001	Trends In Ecology & Evolution	16	45–51	783	1179
Effects of invasive alien plants on fire regimes*	Brooks, M.L., D'antonio, C.M., Richardson, D.M., et al.	2004	BioScience	54	677–688	733	1329
Fire, resprouting and variability, a recipe for grass-tree coexistence in savanna*	Higgins S.I., Bond W.J., Trollope, W.S.W.	2000	Ecology	88	203–229	577	924
Plant diversity in Mediterranean-climate regions	Cowling, R.M., Rundel, P.W., Lamont, B.B., et al.	1996	Trends In Ecology & Evolution	11	362–366	562	855
What limits trees in C-4 grasslands and savannas?*	Bond, W.J.	2008	Annual Review of Ecology Evolution and Systematics	39	641–659	444	727

Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by <i>in situ</i> evolution of adaptations to fire*	Simon, M.F.; Grether, R., de Queiroz, L.P., et al.	2009	Proceedings of The National Academy of Sciences of The United States of America	106	20359–20364	403	566
Effects of fire and herbivory on the stability of savanna ecosystems*	van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., et al.	2003	Ecology	84	337–350	384	643
A burning story, the role of fire in the history of life*	Pausas, J.G., Keeley, J.E.	2009	BioScience	59	593–601	372	611

Table A2. Twenty-one (21) cases of observations on species traits and distribution interpreted in a non-fire context and additional observations and interpretations in a fire-related context that provide alternative explanations to the non-fire related observations. X, Y at the end of the the pair of numbers, X, Y, in the fire-related interpretation column refer to ranks given in Table 1 for relative importance of fire-related interpretation (X) and relative time of origin of fire-related constraint (Y)

Observations	Interpretation not taking fireproneness into account	References	Fire-related observations	Fire-related interpretation	References
<i>Soil-stored seeds</i>					
1. Seeds dispersed onto soil in South American savanna lack or have weak dormancy	Adaptation to a reliable wet season suitable for recruitment in any year	Dayrell et al. 2016	Vegetation burnt every 1–3 years at start of wet season, seeds survive fire but germination is fire-independent	Seeds heat tolerant but dormancy redundant as conditions may be suitable for germination within the year so that a fire cue is not required and storage could come at a ‘cost’. 4, 1	Lamont et al. 2017
2. Aril-(elaiosome)-bearing seeds are carried by ants some distance from their source and into their nests from which they may germinate; this includes crypsis from granivores	Elaiosomes are an adaptation for increasing dispersal to ‘safe sites’ among seeds that are otherwise passively dispersed	Ness et al. 2004, Christian and Stanton 2004	Elaiosome-bearing species are confined to fireprone ecosystems; seeds are carried by ants to depths that insulate them from the full heat of fire but still enable them to receive a heat pulse that breaks dormancy and promotes germination; the distances seeds are carried by ants is on average only a few metres; unless the aril is removed, seeds are still vulnerable to granivory by rodents	The distance aril-bearing seeds are carried by ants is too short and crypsis too unreliable to be of adaptive significance; elaiosomes ensure that ants bury the seeds to variable depths which can receive moderate heat pulses that break dormancy as a ‘bet-hedging’ strategy. 3, 2	Gómez and Espadaler 1998, Christian and Stanton 2004, Kwit et al. 2012, Beaumont et al. 2018
3. Hard (impermeable) seeds worldwide lack aroma, occur in seasonally dry climates and/or survive digestion by granivores	Hard seeds not detectable by smell-sensitive granivores (cryptic); can better survive strongly seasonal climates; increase fitness by surviving digestion	Paulsen et al. 2013, Wyse and Dickie 2018	Hard seeds survive in the long absence of fire but fire is required to break dormancy and most seedlings recruit immediately postfire; regions with strongly seasonal climates are also the most fireprone; seasonality in itself does not break dormancy or else seeds would germinate every year; seeds may survive digestion but they are still not primed to germinate—fire heat is required	Hard seeds increase longevity that exceeds intervals commensurate with fire frequency; fire both signals the onset of optimal conditions for recruitment and is the mechanism for breaking dormancy. 4, 1	Calviño-Cancela et al. 2008, Lamont et al. 2019a

4. High summer temperatures in vegetation gaps produce significant dormancy breakage and germination of soil-stored seeds	Germination of soil-stored seeds is cued by high summer temperatures (exposure to strong light) that signal the presence of vegetation gaps	Santana et al. 2013, Ooi et al. 2014	Fire induces much higher levels of germination than summer-type temperatures, larger vegetation gaps, optimal conditions for recruitment and much higher levels of fecundity than interfire recruits. Interfire recruits will be younger when experiencing the next fire so producing fewer, if any, seeds	Fitness at the individual and species levels is best promoted by fires that occur at fitful intervals as germination, survival and fecundity are maximized postfire compared with interfire recruits. 4, 3	Moreira and Pausas 2012, Enright et al. 1998, Jaganathan et al. 2017, Causley et al. 2016, Lamont et al. 2019a
5. Soil-stored seeds become permeable with time or when passing through digestive tract of animals	Decay processes, soil abrasion, digestion provide the mechanisms for breaking dormancy of hard seeds	Soriano et al. 2014, Zalamea et al. 2015	Most seeds do not become permeable simply with the passage of time when soil-stored though their threshold temperature requirement may decrease; decay and soil abrasive agents and digestion ineffective at breaking dormancy; only heat (usually from fire) effective in breaking dormancy	Soil and digestion processes are ineffective at priming hard seeds for germination and heat is still required to break dormancy. 5, 1	Calviño-Cancela et al. 2008, Zalamea et al. 2015, Liyanage and Ooi 2017

Plant-stored seeds

6. On-plant seed storage (serotiny) common among pine trees in the Mediterranean-type climate of California	Serotiny (closed cones) is associated with summer-dry, winter-wet climates (no mention of fire in the entire review)	Raven and Axelrod 1978	Serotiny associated with woody cones/fruits is restricted to fireprone floras; seed release is initiated by fire heat; most recruitment occurs after fire	Seeds held in fire-tolerant structures that release their seeds in response to fire heat that signals the onset of optimal conditions for seedling recruitment. 5, 1	Lamont and Enright 2000
7. Woody fruits/cones are rarely penetrated by granivores	Woody fruits/cones serve to deter granivores from reaching the nutritious seeds	Groom and Lamont 1997, Lamont et al. 2016	Woody fruits/cones protect seeds from the elements until conditions are suitable for seedling recruitment as after fire; woody fruits insulate seeds from full heat of fire; high temperatures cause the rupture of woody fruits and release of their seeds onto an optimal seedbed	Woody fruits/cones are fire-related adaptations that protect the seeds from decay, granivores and fire heat during storage, and that respond to fire heat by dehiscing (pyriscence) and releasing their seeds under optimal conditions for seedling recruitment. 4, 1	Bradstock et al. 1994, Lamont and Enright 2000

Growth form

8. South African subshrub geoxyles (short woody resprouters) occur in frost-prone uplands	Low stature is a response to pruning by frost and the woody underground structures enable them to resprout and recover	Finckh et al. 2016	The subshrub geoxyle habit is associated with fireprone habitats whether frost-prone or not and fire adaptations (e.g. lignotuber) can be traced to fireprone, preMiocene times via ancestral trait assignment	The geoxyle habit evolved under fireprone conditions that long preceded the onset of recurrent frost in the Miocene. 5, 1	Maurin et al. 2014, Lamont et al. 2017
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9. Savanna grasses possess the highly efficient C4 photosynthetic pathway when CO ₂ is limiting growth	Grasses with the C4 pathway has given them an adaptive advantage over C3 grasses	Taylor et al. 2010	C4 grasses dominate highly fireprone grasslands; C4 grasses survive fire much better than C3 grasses because they are fire-tolerant through possessing soil-buried buds (rhizomes)	C4 grasses have a competitive edge over C3 grasses because of their ability to survive fire. 4, 2	Scheiter et al. 2012; Pausas and Paula 2019
10. Resprouters among Restionaceae relatively more abundant in Australia than South Africa	The mountainous landscape (greater altitudinal variation) of South Africa promotes diversification of nonsprouters	Litsios et al. 2014	Resprouters are associated with a greater range of fire frequencies than nonsprouters that require specific fire regimes; most Restionaceae require smoke to break seed dormancy (ancestral condition); rhizomatous habit gives fire protection and is ancestral; SW Australia has a longer and more intense fire history than S. Africa	Restionaceae probably arose in highly fireprone Australia where the rhizomatous habit gives fire protection and smoke promotes germination; nonsprouting is a later development associated with more reliable, intermediately frequent fires more likely in S. Africa. 4, 1	López-Villalta 2014, He et al. 2016, Lamont et al. 2019b
<i>Biogeographic traits, originally related to climate and/or soils</i>					
11. Most Australian Proteaceae have small scleromorphic leaves, occur under highly seasonal climates in 'open' vegetation, and fossils can be traced to > 70 million years ago; they also occur in nutrient-impooverished soils	Small leaves are an adaptation to drought and Proteaceae can be traced to open, Mediterranean-type vegetation using ancestral trait assignment, poor soils promoted diversification of Proteaceae	Onstein et al. 2016, Prentice et al. 2017	Oldest Australian clades were fireprone at the time and long preceded a mediterranean climate; all species show fire adaptations essential for their survival and reproduction; Proteaceae abundant in both open (shrubland) and closed (forest) vegetation that share high flammability rather than high light or strong summer droughts	Fire adaptations were critical in the origin and diversification of the Australian sclerophyllous Proteaceae (by ancestral trait assignment) long before strong seasonality in the Neogene and openness of vegetation in itself is not the critical constraint. 4, 1	Lamont and He 2012, Pausas and Lamont 2018
12. Distribution, diversification and plant and leaf size traits in the S African genus Protea shows strong correlation with climatic gradients in the Cape Floristic Province	Climate gradients have played a key role in species diversification and distribution of Cape proteas, summer-rainfall species have smaller size, larger leaves	Mitchell et al. 2018	Coincident with climate change was a change in the fire regime, initiation of summer rainfall to the east and north-east in the Miocene produced grasslands that burn at 1-3 year intervals; all grassland proteas are nonserotinous and resprout after fire, frequently burnt plants will be smaller as frequently pruned by fire	Invasion of the grasslands was not possible until proteas evolved nonserotiny and the ability to resprout in response to frequent fire from ancestors that were serotinous and fire-killed (ancestral trait assignment). 4, 1	Lamont et al. 2013, Lamont et al. 2017

13. Distribution of chaparral species increased in Santa Rosa Mountains, S California by 65 m from 1977 to 2007	The upward shift in species distribution can be attributed to a warming climate (less snow, more rainfall variability) not air pollution or increased fire frequency	Kelly and Goulden 2008	Stem ring analysis of the fire-killed <i>Ceanothus greggii</i> showed that the study sites had an elevational bias in fire history that led to lower levels of mortality in that period at the higher altitudes so that there has been no altitudinal increase in distribution	The greater survival of <i>C. greggii</i> at the higher elevations was due to differences in fire history (time since the last fire) not due to climate warming. 5, 1	Schwilk and Keeley 2012
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Protective plant traits (biotic or abiotic)

14. Terpenoids are abundant in palatable parts of some plant species and these deter consumption by herbivores	Terpenoids function to deter herbivory	Lawler et al. 2000, Jones et al. 2003	Terpenoids are highly flammable; are abundant in some fireprone species and are concentrated in highly exposed foliage; the associated species possess many fire-adapted traits, such as serotiny (leptospermoid Myrtaceae), thick bark (<i>Eucalyptus</i>), soil-stored seeds (Rutaceae); ineffective against many herbivores, e.g. koalas	Terpenoids are a flammability trait that is associated with strong fire adaptations of the host species that serves to increase fitness by reducing competition from less fire-tolerant species and ensures fire-adapted traits are expressed. 1, 2	Owens et al. 1998, Pausas et al. 2016
15. Thick bark is protective against herbivore attack or water loss	Thick bark has evolved to deter herbivory and minimize water loss	Paine et al. 2010, Pausas 2015	Bark thickness is a function of fireproneness of the ecosystem; insulating properties of bark are (largely) a function of bark thickness; thick bark does not prevent infestation by bark beetles; exten of bark stripping not a function of bark thickness; species with thin bark may occur in deserts	Thick bark is an adaptation for minimizing temperature rise at the position of the cambium during the heat pulse from a fire; it may have other functions in non-fireprone systems. 4, 1	Vines 1968, Gill 1992, Bertheau et al. 2009, Brando et al. 2012, Pausas 2015
16. Grasses with a blanket of dead leaves in savanna grasslands lack herbivory and survive frost	Dead leaf retention is an adaptation for reducing the likelihood of herbivory and/or frost damage	Finckh et al. 2016, Mingo and Oesterheld 2009	Dead leaves increase combustibility of the plant; savanna grasses are fire tolerant via soil-buried (heat-insulated) buds; fireproneness long preceded the advent of recurrent frost that is only present among upland grasslands; frost reduction will also benefit competing neighbours; fire recycles nutrients and opens up grasses to light	Dead leaves increase flammability of savanna grasses that reduces competition from less heat-tolerant neighbours and favours improvement in growing conditions; soil-buried buds enabled fire survival long before the advent of recurrent frost (exaptation). 5, 1	Wakeling et al. 2012, Moore et al. 2019, Pausas and Paula 2019

17. Dead leaf and flower retention in <i>Banksia</i> shrubs gives extra shade to stems and cones and renders them less exposed to borers and granivores	Dead leaf and flower retention are an adaptation to reduce summer drought desiccation and reduce detection by predators	He et al. 2011	Dead leaves and flowers are highly combustible and increase the likelihood of heat-induced follicle opening of serotinous cones and release of nutrients for recruitment of seedlings among fire-killed species; strong evolutionary association between dead leaf retention and nonsprouting, and flower retention and serotiny	Dead leaf and flower retention are an adaptation to enhance heat-induced follicle opening and seed release and nutrient availability when conditions for recruitment are optimal. 5, 1	Low and Lamont 1990, He et al., 2011
18. Geophyty (shoots die back annually to underground storage structures with buds e.g. corms, bulbs, tubers) is associated with strongly seasonal climates, eg cold winters	Geophyty is an adaptation to environments with seasonal temperature extremes with reliable growing season rainfall that enable the dormant plant to recover once the stress is over	Procheş et al. 2005	Geophyty is often associated with fireprone ecosystems that are also highly seasonal; the dead aboveground parts are highly flammable while the storage structures are insulated from fire heat; some geophytes evolved under fireprone conditions preMiocene while frost-prone, seasonally dry conditions increased from the Miocene; many geophytes respond to fire by early flowering (protanthy) that takes advantage of postfire conditions for reproduction; some geophytes remain underground for many years until stimulated to shoot/flower by fire	Many geophytes are adapted to both highly seasonal and fireprone conditions (savannas, mediterranean) and both warmer or wetter conditions and fire may break bud dormancy and promote shoot growth and flowering. 3, 3	Lamont and Downes 2011, He et al. 2016, Pausas et al. 2018

Traits associated with aridity

19. The Australian grasstree, <i>Xanthorrhoea</i> , has long thin leaves whose xeromorphic structure includes a thick cuticle, sunken stomates and bands of fibres	The structure and orientation of <i>Xanthorrhoea</i> leaves is designed to minimize transpirational water loss	Fahn 1954	<i>Xanthorrhoea</i> retains its pendulous leaves after death to form a dense 'skirt' around the caudex; both living and dead leaves are highly flammable and burn at > 1000°C; <i>Xanthorrhoea</i> survives the most intense of fires because of mantle of non-ignitable leafbases; ignition releases ethylene that promotes fire-stimulated flowering; ignition melts the leafbase resin that then fills the airspaces	The unique arrangement, structure and retention of leaves in <i>Xanthorrhoea</i> is an adaptation for maximizing its flammability that reduces competition from less fire-tolerant neighbours, ensures flowering when recruitment conditions are favoured, and seals the caudex against stem damage by borers. 4, 1	Lamont et al. 2004, Wittkuhn et al. 2017
20. Finely divided, sclerophyllous foliage (many small leaves and branchlets per unit mass) is associated with drought-prone ecosystems	Dense, sclerophyllous foliage is an adaptation to climates with a hot dry summer that reduces water loss per unit mass	Lamont et al. 2003, Westoby and Wright 2003	Species with finely divided, sclerophyllous foliage are abundant in fireprone vegetation; finely divided foliage is highly flammable; species with finely divided foliage possess other fire-adaptive traits such as resprouting, serotiny, soil-stored seeds; fire promotes the evolution of flammability traits.	Dense, sclerophyllous foliage is highly combustible and serves to a) reduce competition from less fire-tolerant neighbours, and b) ensure advantage is taken of its other fire-adapted traits, such as fire-stimulated resprouting, seed release and germination. 2, 2	Burger and Bond 2015, Calitz et al. 2015, Pausas et al. 2012

21. Leaf and stem succulence are associated with arid climates and have extremely low transpiration rates

Succulence is an adaptation for conserving water under drought stress

Lamont and Lamont 2000

Many succulents occur in fireprone vegetation; succulents survive fire as they are non-flammable and have a large thermal mass when exposed to heat

Succulence is a fire-avoiding mechanism that allows species in fireprone vegetation to survive. Calitz et al. 2015 2, 2

Table A3. Fifty-five of the 100 ‘fundamental’ questions for ecology selected by Sutherland et al. (2013) that we show fire considerations help to address. The original numbers of the questions have been retained. We have made no attempt to review the relevant literature but simply use the cited papers to illustrate how many of the questions have already been tackled.

Fundamental ecological question	Examples of how the question has been, or can be, addressed in fireprone systems
<i>Evolutionary processes</i>	
1 What are the evolutionary consequences of species becoming less connected through fragmentation or more connected through globalization?	Increasing patchiness (fragmentation) of fires will deter long-distance dispersal of seeds (He et al. 2009) while many invasive species are fire-adapted, both suited for studying their evolutionary consequences.
3 How local is adaptation?	Fire properties can be manipulated across the landscape to determine the limits of adaptation to fire of particular species
4 What are the ecological causes and consequences of epigenetic variation?	There are scores of fire byproducts in smoke and fire-heated air (eg methyl groups) that could be checked for their epigenetic properties and effects on plant fitness
5 What are the relative contributions of different levels of selection (gene, individual, group) to life-history evolution and the resulting population dynamics?	The evolution of plant flammability is contentious, especially at what scale it operates. Elements of flammability are determined by genes (e.g., those controlling leaf area and mass, branching pattern, water content, volatile oils, dead biomass retention/accumulation), it is manifested at the individual plant level (e.g., where dead biomass is located on the plant), and expressed at the community level (fuel structure in horizontal and vertical dimensions). The question can even be examined from the perspective of life-history evolution, population dynamics and community structure and function (Pausas and Keeley 2014)
6 What selective forces cause sex differences in life history and what are their consequences for population dynamics?	Fire-stimulated flowering/coning can increase the incidence of female gametes (e.g., <i>Stirlingia</i> , cycads, Lamont and Downes 2011)
8 How do the strength and form of density dependence influence feedbacks between population dynamics and life-history evolution?	Since germination is synchronized by fire, fireprone populations are ideal for studying seedling density effects that vary between microsite types and among resprouters/nonsprouters (Lamont et al. 1993)
9 How does phenotypic plasticity influence evolutionary trajectories?	Fire is a deterministic process, but it also has considerable stochastic properties, creating ample opportunity for the development of phenotypic plasticity. The divergence of the fire regime over geographic scales as a result of environmental and climatic variation; such phenotypic plasticity will take the evolution of relevant traits on different trajectories (He et al. 2019)
10 What are the physiological bases of life-history tradeoffs?	Resprouters (few seeds) and nonsprouters (many seeds) are ideal for studying the physiological basis of tradeoffs in seed set and seedling recruitment (Lamont and Wiens 2003, Pate et al. 1990, Bowen and Pate 2017)

Population dynamics

- 11 What are the evolutionary and ecological mechanisms that govern species' range margins? Fire regime interzones are well recognized as they are indicated by change in vegetation type. They are quite stable but can be manipulated by fire regime change so are ideal for studying control mechanisms
- 13 How do species and population traits and landscape configuration interact to determine realized dispersal distances? The patchy distribution of populations in fireprone landscapes, where fire may also prompt long-distance dispersal (LDD), makes this scenario ideal for such studies (e.g., LDD in *Banksia*, e.g., He et al. 2009)
- 14 What is the heritability/genetic basis of dispersal and movement behaviour? The LDD traits of plant species in fireprone landscapes (e.g., wing load) are ideal for studies of their heritability (e.g., Merwin et al. 2012)
- 16 How do organisms make movement decisions in relation to dispersal, migration, foraging or mate search? Plants cannot make decisions, but, from an evolutionary viewpoint, the varying patchiness of fires coupled with genotype parent assignment is ideal for studying dispersal and migration patterns and potential
- 17 Do different demographic rates vary predictably over different spatial scales, and how do they then combine to influence spatio-temporal population dynamics? Resprouters (few seeds) and nonsprouters (many seeds) are ideal contrasting life forms to study their demographic rates over varying spatial scales and how they influence spatiotemporal population dynamics in response to fire
- 18 How does demographic and spatial structure modify the effects of environmental stochasticity on population dynamics? Fire events are stochastic while the demography and spatial structure of fireprone species vary greatly so are ideal for studying their effects on population dynamics
- 19 How does environmental stochasticity and environmental change interact with density dependence to generate population dynamics and species distributions? Fires synchronize species establishment so there are strong density effects that interact with fires that are stochastic and climates that are changing (stronger drought effects) to challenge population dynamics and species viability (Enright et al. 2014)
- 20 To what degree do trans-generational effects on life histories, such as maternal effects, impact on population dynamics? Fire-stimulated resprouters traverse many fire cycles that kill nonsprouters—this enables them to persist through times of poor recruitment conditions—the storage effect of Miller and Chesson (2009), population stability of resprouters vs. nonsprouters (Groeneveld et al. 2002)
- 21 What are the magnitudes and durations of carry-over effects of previous environmental experiences on an individual's subsequent life history and consequent population dynamics? Fire controls population dynamics as interfire recruitment is usually negligible—thus the carry-over effect of the type of fire and fire interval on individuals is profound (Enright et al. 1989, Lamont et al. 1993)

22 What causes massive variability in recruitment in some marine systems?	There is also massive variability in fireprone systems due to the great range in fire properties and frequency
23 How does covariance among life-history traits affect their contributions to population dynamics?	It is commonly observed that a specific fire regime selects for a suite of fire-related traits that allows plants to persist. e.g., serotiny and dead branch retention are coupled in pines (Schwilk and Ackerly 2001, He et al. 2012).
24 What is the relative importance of direct (consumption, competition) vs. indirect (induced behavioural change) interactions in determining the effect of one species on others?	Fireprone systems are suitable for such studies and many interactions are triggered by fire such that interactions are affected by time since the last fire. Thus, the changing impact of plant species on other biota can be followed with time since fire
25 How important is individual variation to population, community, and ecosystem dynamics?	Many fireprone species vary phenotypically in different climates/vegetation types (He et al. 2018) so that their varying effects on dynamics at different scales can be assessed. Within population variation of individuals can also vary greatly (e.g., fecundity, phenology) with effects on the rate of hybridization receiving some study (Lamont et al. 2003)
26 What demographic traits determine the resilience of natural populations to disturbance and perturbation?	Fireprone systems are ideal for the study of resistance and resilience, with contrasts available in the way seeds are stored and whole-plant responses to fire (Enright et al. 2014)

Disease and Micro-organisms

32 What is the relative importance of biotic vs. abiotic feedbacks between plants and soil for influencing plant growth?	Depleted soil nutrients over the long term create vegetation types that are adapted to infertile soils, and promote plants with highly flammable traits (e.g., small leaves, finely divided foliage, dead mass retention), and forming feedback cycles.
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Community dynamics and diversity

39 How well can community properties and responses to environmental change be predicted from the distribution of simple synoptic traits, e.g. body size, leaf area?	Fire tolerance of species in fireprone systems (changing in intensity) can be predicted from their fire-related traits depending on the extent to which it has been shown that they increase fitness (Lamont and He 2017)
42 How widespread and important are indirect interactions (e.g. apparent competition, apparent mutualism) in ecological communities?	Many food webs and other interactions exist in fireprone systems and some of these are mediated by fire itself (Lamont 1994). Those that involve symbiotic microbes may be keystone (Lamont 1992)

- 43 How do spatial and temporal environmental heterogeneity influence diversity at different scales? Spatially and temporally varying fire events create spatial and temporal heterogeneity at different scales that affect alpha diversity and promote beta and gamma diversity (pyrodiversity begets biodiversity)
- 44 How does species loss affect the extinction risk of the remaining species? Fire can be the cause of species extinction (interval too long, too short) and the effect will depend on the level of species interactions and any keystone role they may have had (Lamont 1992)
- 45 What is the relative importance of stochastic vs. deterministic processes in controlling diversity and composition of communities, and how does this vary across ecosystem types? Fire has strong stochastic properties but it can be treated as deterministic (fire at fixed intervals) in models and any differences in outcome can be explored (Enright et al. 1998). Stochasticity varies greatly under different fire regimes in different ecosystems
- 46 How do we predict mechanistically how many species can coexist in a given area? Fire-response traits of co-occurring species are well-known for particular ecosystems with some work on competitive sorting but these seem to have little impact on species spatial relations (Perry et al. 2017)
- 47 To what extent are local species composition and diversity controlled by dispersal limitation and the regional species pool? Fireprone systems are ideal to test this. Fire patchiness and the need for dispersal and recruitment to coincide with fire events help to quantify dispersal limitations (He et al. 2009).
- 48 What are the contributions of biogeographical factors and evolutionary history in determining present day ecological processes? Fire has been a potent evolutionary force since the ‘fiery’ Cretaceous when the major orders of flowering plants were evolving (He and Lamont 2018a) and will have had a profound effect on current ecological processes
- 49 To what extent is primary producer diversity a driver of wider community diversity? Fire tolerance of primary producers will control their diversity and impact on other community biota
- 51 What is the relative importance of trophic and nontrophic interactions in determining the composition of communities? Trophic interactions can be controlled by the fire regime while simultaneous postfire recruitment heightens nontrophic interactions (Lamont et al. 1993)
- 52 How important are dynamic extinction-recolonization equilibria to the persistence of species assemblages in fragmented landscapes? Fire events can be manipulated to promote both extinction and recolonization (He et al., 2009); fires create temporal-spatially varying environmental heterogeneity – dynamic fragmented landscapes that provide a unique testing ground for persistence (Enright et al. 2014)
- 53 Which mechanisms allow the long-term coexistence of grasses and woody plants over a wide range of ecosystems? This question cannot be answered satisfactorily without considering fire. Fire, resprouting and variability of life history-disturbance interactions are key to explaining long-term grass-tree coexistence in savannas (Higgins et al. 2000)

- 54 How do resource pulses affect resource use and interactions between organisms? There is no better cause of a resource pulse than fire. Fire regulates resource availability in ecosystems across trophic levels, facilitating the maintenance of diverse communities in space and time. Fire releases nutrients that are locked up in biomass, creating resource pulses in the short term, promoting the dynamics of populations and species co-existence patterns across trophic levels (Bowman et al. 2016, Ponisio et al. 2016)
- 56 What is the feedback between diversity and diversification? Fire is both a cause of extinction and force for trait innovation and proliferation and fireprone clades and regions are among the world's most speciose

Ecosystem functioning

- 58 Which ecosystems are susceptible to showing 'tipping' points and why? Fireprone ecosystems should be one of the types of ecosystems susceptible to 'tipping' points. A certain vegetation type is maintained by a relatively fixed fire regime. A change in fire regime, especially as it interacts with increasing drought, could change ecosystem properties (Enright et al. 2014). However, some fire-response types, e.g., resprouters, are more persistent than others
- 59 How can we tell when an ecosystem is near a 'tipping' point? Since fire properties (e.g. fire interval) are easily manipulated it should be possible to identify the community's 'tipping' point. Fire intervals are relatively stable over the long-term in a certain vegetation type. Ecosystems show clear symptoms in response to unprecedented fire events and intervals, providing a unique system to observe the approach of a 'tipping' point (Enright et al. 2014)
- 60 Which factors and mechanisms determine the resilience of ecosystems to external perturbations and how do we measure resilience? Fire might be considered an external perturbation in ecosystems normally considered fire-free (tundra, rainforest, desert); mechanisms of fire tolerance include postfire survival and recruitment as measures of resilience (Enright et al. 2014)
- 61 Which ecosystems and what properties are most sensitive to changes in community composition? Fireprone ecosystems are sensitive to invasion by more fire-tolerant/flammable species. Invasive pines have altered natural fire regimes in South Africa through changes to the flammable biomass. Pines are larger than native plants and increase the fuel load and support more intense fires (Kraaij et al. 2018). In Australia, exotic grasses invade and outcompete the native ground flora (Milberg and Lamont 1995)
- 62 How is ecosystem function altered under realistic scenarios of biodiversity change? Invasion of a fireprone ecosystem by species with different fire-related traits provides the opportunity to examine any change in its function (Milberg and Lamont 1995). Research also shows that transition from relatively fire-free forests to fire-frequent savanna grasslands, as consequence of spreading C4 plants, completely changes ecosystem properties and function (van Langevelde et al. 2003)
- 66 How does spatial structure influence ecosystem function and how do we integrate within and between spatial scales to assess function? Fire events vary horizontally (mosaics) and vertically (surface, canopy) that create spatial structure in environmental properties, and these spatial structures are dynamic as fire events also vary at temporal scales – dynamic environmental heterogeneity (He et al. 2019); thus, their effects on biodiversity and ecosystem function are readily assessed. Fire patchiness and time since fire affects the presence and movement of animals (Davies et al. 2018)

68 To what extent is biotic invasion and native species loss creating ecosystems with altered properties?	Fireprone ecosystems in South Africa and Australia are readily invaded by ‘fireweeds’ at the expense of native species (Milberg and Lamont 1995, Brooks et al. 2004) and this enables their functional effect to be measured. Invasions can affect native ecosystems by changing fuel properties that in turn affect fire behaviour and, ultimately, alter fire regime characteristics, such as frequency, intensity, extent, type, and seasonality of fire. If the regime change subsequently promotes dominance by the invaders, then an invasive plant–fire regime cycle is established.
70 Which, if any, species are functionally redundant in the context of stochastic or directional environmental changes?	Fire can be stochastic or directional (frequency change) so is an ideal tool to test functional redundancy
71 Is hysteresis the exception or the norm in ecological systems?	Hysteresis (fire history determines species diversity, structure and function) dictates ecology of fireprone ecosystems at any point in time
72 Can we predict the responses of ecosystems to environmental change based on the traits of species?	Fire-related traits can be used to model the effects of fire regime change on population viability (Enright et al. 1998)

Human impacts and global change

74 What is the role of evolution in recovery from exploitation and responses to other forms of relaxed selection?	Climate change is inducing fire regime change – how species are responding ultimately rather than proximately is subject to selection and diversification – there is some evidence of changes in genotype distribution within populations in response to drought, and the effect of increased fire (directional selection) and no fire (relaxed selection) is a suitable goal to explore as well (Lamont et al. 2019a)
76 What are the major feedbacks and interactions between the Earth’s ecosystems and the atmosphere under a changing climate?	A changing climate implies a change in the fire regime and thus in heat and gas transfers to the atmosphere and must be included in cycling models
77 What are the key determinants of the future magnitude of marine and terrestrial carbon sinks?	Fires release enormous amounts of carbon into the atmosphere. Fire activity is predicted to increase with climate change. The increase in carbon dioxide as a result promotes plant growth and increases its role as a carbon sink but the rate is reduced by the incidence of fires (Goldammer et al. 2009).
78 How will atmospheric change affect primary production of terrestrial ecosystems?	Fire activity is predicted to increase with climate change. The increase in carbon dioxide as a result promotes plant growth and increases its role as a carbon sink but the rate is reduced by the incidence of fires throughout the Earth (Goldammer et al. 2009).
81 How do natural communities respond to increased frequencies of extreme weather events predicted under global climate change?	Extreme weather creates extreme fires. Much is known about the relationship between fire intensity and plant responses such as resprouting, seed release and germination but whole community responses has received little attention to extreme fire events, though the effect of increased fire frequencies has received some attention (Enright et al. 2014)

82 In the face of rapid environmental change, what determines whether species adapt, shift their ranges or go extinct? The innate tolerance/avoidance of species to various fire properties is well known, also their postfire seed dispersability—evidence for *Banksias* indicates that range shifts would be inadequate under predicted climate change while resprouters have a greater range and tolerance of climate change than nonsprouters (Witkowski and Lamont 2006, Merwin et al. 2012)

Methods

94 How is our understanding of ecology influenced by publication bias?	Papers on the 65% of the vegetated surface of Earth that is highly flammable are historically interpreted in terms of non-disturbance constraints, giving a biased view of nature (Pausas and Lamont 2018)
100 How can the feedbacks between human behaviour and ecological dynamics be accounted for in ecological models?	Much is known about human causes of, and responses to, fire events and the effects of different fire types on ecosystem dynamics, making fire ideal for feedback studies

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