Historical links between climate and fire on species dispersion and trait evolution

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Abstract The interaction effects between climate and fire regime in controlling the type of vegetation and species composition is well established among the Earth’s biomes. Climate and the associated fire regime are never stable for long, and annual temperatures, atmospheric carbon dioxide and oxygen levels, and burn probability have varied radically over the last 350 million years. At the scale of thousands of years, floras have oscillated between spreading and retracting as climate and the dependent fire regime have fluctuated. At the scale of millions of years, distinct traits have evolved along three lines: fire resistance, fire-stimulated dormancy release, and rapid postfire growth, all limited by the type of fire (as controlled by climate) and postfire weather. Eight pairings of fire- and postfire-related traits resulting from the interplay between fire and climate are noted here. Smoke-released seed dormancy is beneficial on two counts: it increases the chance of recruitment under the present fireprone climate and increases the chances of survival should the wet season shift to another time of year where temperatures are higher or lower. Four pathways can be recognized with respect to the fire regimes induced by climate changes: (1) from non-fireprone to fireprone habitats (gains fire-adapted trait, 13 studies covering the last 115 million years (My) described here); (2) from a surface fire to a crown fire-type habitat (gains a different fire-adapted trait, 13 studies); (3) from a crown fire-type to surface fire-type habitat (loss of fire-adapted trait, 12 studies); and (4) from moderately burnt (crown fire) to non-fireprone habitat, such as desert, rain-forest, or alpine habitats (loss of fire-adapted trait, 6 studies). Four case studies, at decreasing taxonomic rank, are used to illustrate the intimate relationship between climate change with its associated vegetation and fire regime change as they promote adaptive trait evolution: gain then loss of heat-released seed dormancy in Dipterocarpaceae–Cistaceae–Bixaceae over 90 My, gain then loss of serotiny in Callitroid Cupressaceae over the last 65 My, gain then loss of smoke-released seed dormancy in Proteoid Proteaceae over the last 120 My, gain then loss of resprouting and serotiny among Hakea species (Grevilleoid Proteaceae) over the last 20 My. Examples of within-species rates of migration and trait change, including a model describing increasing degree of serotiny with intensifying drought, are given. The relevance of this historical approach to current (anthropogenic) climate change and associated fire regime alteration is discussed. Despite major threats expected to species...
conservation status at both the macro-(biome) and micro-(population) scales, I conclude that insufficient time or opportunities remain for effective migration to less-stressed areas or suitable adaptive responses to climate-fire regime change to evolve.

Keywords Climate change · Climate–fire interactions · Dipterocarpaceae · Fire-adapted traits · Mediterranean climate · Soil seed storage

Introduction

The close link between vegetation, its associated flora, and the prevailing fire regime, is well established (He et al. 2019). For example, Bond and Keeley (2005) have shown how structure of the Earth’s vegetation would be quite different in the absence of fire. Consider Fig. 1. In this overview, current major vegetation types are initially defined by climate, as revealed through a gradient of precipitation and/or temperature as these affect plant growth. Rainfall and temperature effects are usually positively correlated with growth rates, except with increase in altitude (wet but cold) and closeness to mid-latitudes (warm but dry) where they become negatively correlated. The second dimension is fire frequency that is equally important and essentially follows two parallel pathways: (a) less-frequent fires that are more intense and burn the tree and shrub canopies as well as the ground-hugging flora (crown fires) and (b) more-frequent fires that are less intense and tend to burn only the herbaceous flora which is usually dominated by grasses (surface fires). The ‘boomerang’ shape of the relationship is created by seasonality that is a property of both the climate and fire regime: seasonality is greatest at intermediate rainfall levels and fires are most intense and frequent under moderate conditions as well. A crucial difference in the seasonality of ecosystems with crown and surface fires is that the former tend to be summer-dry and fire-prone from late spring to late autumn. Those with surface fires tend to be summer-wet and burn only in late winter to early summer. The intimate relationship between climate and fire is again demonstrated by lightning strikes, by far the most important source of ignitions historically, whose frequency increases as annual rainfall and temperature rise. Historical changes in atmospheric oxygen and carbon dioxide levels alter both climate and fire-proneness and affect the boundaries of the ‘boomerang.’ It is the aim of this review to examine such climate–fire interactions over various time scales and show how these have affected the dispersion of species over shorter time frames and evolution of plant traits over longer time frames.

Changes in climate and fire regime over evolutionary time scales

Weather is never constant at all time scales, varying over a few hours to millions of years. But over decades it does form patterns that define the climate. Given sufficient time, climates also change as the weather patterns change. Similarly, fire events accumulate over time to form patterns that also define the fire regime (He et al. 2019). Since climate controls the fire regime, this implies that fire regimes change as the climate changes. Both have varied radically over scales of tens of millions of years. Consider Fig. 2. At a broad scale that ignores latitudinal effects, marked peaks in mean annual temperature...
occurred ~250, 150, 100 (mid-Cretaceous), and 40 million years ago (Ma) reaching the highest level of ~20 °C at 100 Ma (some models put this much higher, at 24 °C then, Scotese et al. 2021). Currently it is ~15.8 °C. Marked troughs occurred at ~300, 225, 175, and 60 Ma, reaching the lowest level of ~14 °C at 300 Ma. Currently, the Earth is in a trough that has been ongoing for ~40 My from the late Eocene. Refinements in these trends since the end of the Cretaceous (65.5 Ma) will be discussed later.

Changes in world temperatures closely mirror that of atmospheric carbon dioxide levels [CO$_2$] (Fig. 2). The major difference is that [CO$_2$] has varied by an order of magnitude over the last 350 million years (My), whereas temperature has varied by only a few degrees. There is also a tendency for the [CO$_2$] pattern to be out of phase with (precede) the temperature pattern by a few million years at this course scale. This can be attributed to the classic ‘greenhouse’ effect where the [CO$_2$] level controls temperature. Thus, [CO$_2$] reached 1300 mL/10$^3$L at 350 Ma and 1200 mL/10$^3$L in the mid-Cretaceous with a local rise to ~800 mL/10$^3$L in the mid-Eocene (45 Ma), falling to 300 mL/10$^3$L prior to the Industrial Revolution. It is currently at 400 mL/10$^3$L in highly populated parts of the Earth (Keeling et al. 2017, https://gml.noaa.gov/ccgg/trends).

It is instructive to relate the probability of fire to climate properties at evolutionary time scales. The lower 25% percentile for burn probability (see Belcher et al. 2010 for how it is estimated) shows greatest fluctuations over the last 350 My (Fig. 2). The pattern mimics those for temperature and atmospheric CO$_2$ except that it is much lower at 350 Ma and the peak is much sharper at 100 Ma (hence the ‘fiery’ Cretaceous, He et al. 2012). Of most interest is the gradual decline from this maximum with a local peak at 50 Ma (Mid-Eocene Climatic Maximum) again. The extent to which fuel creates heat is a function of fuel load that depends on vegetation productivity—that is a function of temperature and rainfall in terms of climate. Here [CO$_2$] is a surrogate for productivity since this gas is the primary resource for photosynthesis and temperature is a surrogate for the rate at which metabolism occurs. These expected correlations between burn probability, temperature, and CO$_2$ are demonstrated in Fig. 2. The extent to which atmospheric CO$_2$ is available for photosynthesis will determine to some extent on how much oxygen [O$_2$]), as a waste product of photosynthesis, is present as well. This is supported in Fig. 2, apart from the low levels at 350 Ma, indicating low productivity among terrestrial floras at this early stage in the evolution of green plants. Also, the gradients in [O$_2$] variation over time are much gentler.

Of course, combustibility is also a function of [O$_2$] levels (Belcher et al. 2010) and this correlation comes through as well. Up to the last 40 My, it is considered that burn probability was most strongly impacted by the prevailing [O$_2$] levels in the presence of sufficient lightning strikes [again indicated by temperature and [CO$_2$] as a surrogate for fuel]. Even sodden fuel ignited during the high [O$_2$] levels of the Cretaceous (Belcher and Hudspith 2017). Once the Eocene Climatic Maximum passed and [O$_2$] levels began to decline, it is likely that increasing seasonality became the dominant influence on the fire regime (Fig. 1). As seasonality intensifies, biomass loss and fire frequency will depend on the increasing interaction between (a) the level of fuel dryness during the fire
season and (b) fuel availability as controlled by moisture and temperature levels during the wet season. In this regard, litter is crucial as prime fuel to be ignited by lightning historically (Westcott et al. 2014) and its build-up will depend on (a) plant properties [growth rates, seasonal leaf fall, resistance to decay (presence of nitrogen, tannins, lignin), leaf architecture], (b) seasonality (moisture content and temperature during the wet season as they affect activity of saprophytic organisms), and (c) time since fire.

**Climate and fire effects on plant dispersion and traits**

Climate affects the properties of fire events that in turn affect species dispersion in the medium term and trait evolution in the long term. Species that lack adaptations to a changed climate or fire regime become locally extinct in the short term and their distribution is reduced or they retreat to matched climates and fire regimes elsewhere. Other environmental factors such as nutrient availability and herbivore pressure will also exert influences but are downplayed here as they are outside our task that is to highlight the historical interactions between climate and fire. Species that can adapt to the changed climate and fire regime survive and expand their distribution as these new conditions spread elsewhere. Here, fire-adapted traits refer to any genetically based trait that increases the plant’s fitness and hence that of the species, to a particular fire regime. Thus, fire-released seed dormancy is adaptive in forests on the expectation of occasional intense fires that create large bare patches suitable for seedling recruitment, while heat resistance without dormancy is more adaptive in tropical grasslands on the expectation of almost annually occurring fires of low intensity (Pausas and Lamont 2022a). The sequence can be grouped into prefire and postfire processes, summarized as follows (arrows refer to the passage of time):

1. **Climate prefire promotes fire** → recurrent fires → distribution of species with non-fire-adapted trait 1 contracts (dispersion) → fire-adapted traits change (evolution) → distribution of species with fire-adapted trait 2 expands (dispersion).

2. **Climate postfire promotes growth** → recurrent fires → distribution of species with weak postfire growth trait 3 contracts (dispersion) → postfire climate-adapted traits change (evolution) → distribution of species with strong postfire growth trait 4 expands (dispersion).

**Dispersion**

The impact of recurrent fires in the medium term is to affect the dispersion of species and hence of their associated vegetation. With speciation cycles dependent on the severity of environmental change, rates of mutation, life cycle duration (fire frequency or mean fire intervals), number of genes and alleles involved in trait change, and the level of change required to be adaptive in the new environment (Lamont et al. 2020), evolution of adaptive traits is only a long-term solution to climate and fire-regime change. The quicker response is variation (retreat or expansion) in species dispersion. Consider Fig. 3. This documents the relative abundance of fireprone sclerophyll

![Fig. 3 Modeled relationship between abundance of fireprone (pyrophytic) eucalypt fires and essentially non-fireprone rainforest in NE Queensland during the late Pleistocene and projected annual rainfall based on current relationships of vegetation types with rainfall in the region. Red dot shows that at ~2.5 × 10^4 years ago (ya), the vegetation was dominated by eucalypts that would have been favored by the drier, more fire-prone conditions. Green dot shows in the Holocene, ~0.5 × 10^4 ya, the reverse contractions and expansions occurred as rainfall increased to 3000 mm. Simplified and redrawn from Hopkins et al. (1993)](image_url)
forests, dominated by eucalypts and non-fireprone mesophyll rainforests, dominated by a wide mixture of non-eucalypts, in NE Queensland over the last 30,000 years (late Pleistocene). The model uses extrapolated annual rainfall based on current relationships of vegetation types with rainfall in the region (Hopkins et al. 1993). At ~25,000 years ago (ya), annual rainfall was relatively low (~1500 mm), and the vegetation was dominated by eucalypts that would have been favored by the drier, more fireprone conditions. Thus, as rainforest was continually burnt at its margins, its flora would gradually be replaced by sclerophyllous species (Tang et al. 2003). In the Holocene, ~5000 ya, the reverse contractions and expansions occurred as rainfall increased to 3000 mm that favored replacement of eucalypt vegetation by rainforests. The scope for species migration under current climate change is raised under the Discussion.

Evolution

Evolution of traits adapted to the new climate and associated fire regime is the only long-term solution for survival of the clade. A selective advantage is provided among plants that have both fire-adapted and postfire climate-adapted traits in the new environment. Three possible short-term (proximate) responses to the presence of fire in the ecosystem can be recognized. Plant traits of adaptive significance associated directly with the fire involve enabling meristematic tissues of the plant or its dormant offspring to (a) survive the fire, then using properties of that fire (heat, smoke) to (b) overcome dormancy of the surviving meristematic tissues. Other fire-related traits enable the plant or its offspring to take advantage of postfire conditions to then (c) promote division of the meristematic tissues whose effectiveness is constrained by (i) the type of fire and (ii) subsequent weather as a feature of particular climates. The presence of these fire-related traits are the result of ultimate (adaptive) responses to the changed conditions. In the presence of recurrent fire, extinction, selection, and genetic innovations gradually evolve and diversify (i) in response to the fire and (ii) in response to the postfire growing conditions. Table 1 lists eight fire-related categories that can express both such fire-adapted traits (a: fire tolerance and b: dormancy release) and postfire climate-adapted traits (c: rate of recovery by resprouters and extent of recruitment by seedlings).

An excellent example of the interactions between climate and fire is provided by the Triassic (215 Ma) conifer, Agathaxylon arizonicum (Fig. 4). This ancient tree also illustrates the three trait categories: fire tolerance, postfire stimulated meristematic activity, and rapid regrowth. A reduction in tracheid width indicated the onset of severe continuous drought over ~24 months as a drought-tolerant response (Byers et al. 2020). A severe fire then occurred, no doubt facilitated by the accumulation of dry fuel during that time. The heat resulted in incineration of part of the bark to form an 85-cm-long scar on the studied tree stump of 30 cm diameter. Despite the injury, the tree survived; thus it provides an example of heat tolerance. Whether there is a threshold in tree size for survival in relation to fire intensity remains unknown. Cambial activity was then stimulated with the severed bark edge gradually regrowing toward the scar, as a healing response. Third, general rejuvenation of the tree followed, indicated by increasing tracheid diameter, over the next 24 months (described by Byers as “growth release”), then settling back to a lower growth rate. This growth spurt can also be viewed as a fire-related trait, although it would need to be compared with the survival and fecundity of other species that do not show such a high growth rate at that time to confirm it as a special adaptive trait.

Other pairings of fire- and postfire-related traits are given in Table 1. For example, finely divided foliage is highly flammable but is also easily replaced rapidly after fire, and some of its properties are best explained as adaptations to drought and/or nutrient-impoveryed soil (Lamont et al. 2015). Some of the best-documented examples of such pairings are soil-stored diaspores—these do not germinate, even if ideal recruitment conditions prevail, until their inherent (primary) dormancy is broken by fire heat (high summer temperatures are rarely, or not as, effective, Moreira et al. 2010; Lamont et al. 2022). First, they must survive fire heat, dependent on the temperature and duration to which the buried seeds are subjected. If heat stimulated, then a heat threshold must be exceeded that results in fracturing of the seedcoat or opening of the so-called water gap (Nandi 1998). Then they remain under enforced (secondary) dormancy until the soil temperature drops below a threshold and soil moisture levels exceed a threshold.

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Table 1  Climate initially controls species composition and vegetation structure and thence the type of fire. Particular traits of plants are adapted to properties of the fire for survival and as a stimulus for subsequent growth. Different traits can also be adapted to take advantage of postfire conditions, especially the subsequent weather as controlled by climate. Eight such pairings are described here.

| Fire-related trait                      | Fire-adapted traits                                      | Postfire climate-adapted traits                                      |
|----------------------------------------|----------------------------------------------------------|---------------------------------------------------------------------|
| 1. Tree trunk with thick bark          | Trunk resistant to fire-type heat, scarring minimal and heals readily, epicormic buds insulated from heat | Fast rate of restoration of bark thickness, density, and healing |
| 2. Finely divided foliage              | Finely divided leaves and twigs, presence of essential oils, increase flammability, and promote expression of other fire-adapted traits | Fast rate of restoration of foliage (among resprouters) and type of postfire foliage (level of sclerophylly, leaf size) are also a function of climate |
| 3. Soil-stored seeds                   | Survive heat, inherent dormancy broken by fire-type heat, increased diurnal fluctuations and/or smoke | Induced dormancy until minimum temperature range and sufficient soil moisture available for germination and growth, greater range of weather/climates tolerated, fast rate of germination once soil moist |
| 4. Plant-stored (serotinous) seeds     | Seeds with induced dormancy survive and released by fire-type heat | Induced dormancy maintained until minimum temperature range and sufficient soil moisture available for germination and growth |
| 5. Stored seeds on plant or in soil    | Fire-type heat-tolerant but dormancy not broken           | Dormancy broken by cold or warm stratification that follow, decay processes escalate over wet periods |
| 6. Postfire resprouting shrub or creeper| Plant incinerated but survives via underground bud-storing organs | Prolific postfire regrowth |
| 7. Plant killed by fire                | Produces abundant soil- or plant-stored seeds            | Prolific postfire germination and recruitment |
| 8. Fire-simulated (pyrogenic) flowering | Bud-storing organs survive with prolific flowering in response to fire, obligate/facultative peak | Prolific flowering/seed set take advantage of ideal postfire growing conditions, with high pollinator activity also controlled by severity and patchiness of fire and postfire weather |
Species in biomes that receive erratic bouts of rain, as in the Mediterranean Basin, are adapted to germinate quickly under postfire conditions, compared with those with much more reliable extended winter rains, as in the Cape, South Africa, and SW Australia (Pérez-Fernández et al. 2000; Cowling et al. 2005).

Seeds with heat-stimulated dormancy release have two distinct phases: heat-released dormancy, dependent on the extent that fire heat reaches the buried seeds, followed by climate-released dormancy, dependent on the postfire weather. By contrast, seeds with smoke-released dormancy may have limited environmentally controlled dormancy, as the smoke chemicals (karrikins, hydrocyanins) are adsorbed by soil particles in the dry season and may only enter the permeable seeds once dissolved in soil water produced from seasonal rains—inherent dormancy is broken and followed immediately by activation of metabolism that initiates germination. Nevertheless, there are records of dry seeds absorbing smoke chemicals but remaining dormant until wetted (Montalvo et al. 2002). And of course, if germination conditions remain suboptimal, then temperature may still limit the extent to which secondary dormancy is broken once the seed is wetted (Mackenzie et al. 2016).

The smoke response highlights the strong interactions possible between fire and climate. Consider Fig. 5. First, smoke promotes maximum germination in the immediate post-autumn fire environment coinciding with the standard growing season, say winter (Collette and Ooi 2021). But, provided sufficient moisture is available, the smoke response also enables the seeds to germinate under non-standard growing seasons and thus the trait is multifunctional, related to both fire and climate. This phenotypic plasticity is an example of an exapted trait (if such extremes were encountered in its historical past) or

Fig. 4 Example of double fire-related traits described in Table 1. Mean diameter of tracheids in a petrified trunk of a Triassic (215 Ma) conifer, Agathaxylon arizonicum, six or so years before and after a fire that caused severe scarring (location of transect indicated by double arrow on the image showing recovery after scarring with position of scar ring indicated by red line and dot). Note how severe drought preceded (narrow tracheids) and apparently created conditions conducive to the intense fire, followed by gradual rejuvenation of growth (increasing tracheid diameter). Simplified and redrawn from Byers et al. (2020)

Fig. 5 Example of a multifunctional trait related to both fire and climate tolerances. Responses to smoke at incubation temperatures equivalent to those prevailing in winter, spring/autumn, and summer among eight Rutaceae shrubs native to eucalypt forest in SE Australia with a moderate rainfall having a minor summer maximum. While there is great variation between species, as indicated by the large 95% confidence intervals, all differences are significant at <5% with a one-tailed, paired t test (Vasserstats© 2021). Note how the smoke is not only an adaptive trait to fire but also increases the range of climates in which the species might be competitive. Collected, statistically analyzed, and graphed by BL from data in Collette and Ooi (2021)
a pre-adapted trait (if such extremes have not been experienced before, Lamont and He 2017a, b) in the face of climate change. Thus, if the climate warms and the rainy season shifts toward summer, fires now occur in spring and smoke sensitivity enables enhanced germination in the wet summer as well. Merritt et al. (2006) obtained a similar pattern of seasonal responses among three daisies in SW Australia. Smoke also improved germination of three of six grasses, endemic to mesic grassland in South Africa, when seeds were incubated at 25 and 30 as well as 35 °C (Ghebrehiwot et al. 2009).

**Evolution of fire-related reproductive traits in relation to climate change**

Table 2 summarizes how climate change over the last 115 My has resulted in the development of different vegetation types that led to altered fire regimes and the evolution of new fire-related reproductive traits among 44 studies and an additional six studies that involved substrate changes within the same climate type. This table is collated from Table S1 in the Supplementary Material that gives additional information on the clades, geographic location, and pre-climate change habitats, fire regimes, and ancestral traits, as well as the relevant references. The climates were divided into five major types and compared pairwise, giving 20 possible pairs, allowing for climate change in either direction between pairs. Thirteen of the 20 possible changes have entries here, all with multiple examples. Most (22) climate changes involved an increase in rainfall seasonality, seven a reduction in annual rainfall, and six a return to an exceptionally warm and wet, uniform climate. The most ancient changes were recorded in the 12 studies where the warm, ever-wet climates became more seasonal, starting from 109–65–23 (oldest–mean–youngest) Ma in the dated phylogeny, i.e., at the basal node of the stem leading to the crown node where the actual record has been made (see Lamont et al. (2019b) for the rationale to this method of ancestral trait assignment). The oldest of these were those leading to summer-wet, monsoon climates, on average occurring 68 Ma. The youngest of these changes were those leading to Mediterranean-type climates, on average occurring 20 Ma, that might provide a clue as to when this climate type arose generally in the Cenozoic (Lamont and He 2017b). However, the data imply that Mediterranean-type climates may even have existed in the late Upper Cretaceous and that is in need of confirmation.

Throughout the last 115 My, there are cases of the restoration of rainforest climates from summer-wet monsoon forests, 95–36–4 Ma. More recently on average, some moderate-rainfall climates with minor summer seasonal rain converted to strongly summer-wet climates, 41–25–0.3 Ma. Strongly seasonal climates are the most recent pathway to climate change, 47–18–6.4 Ma, leading either to low-rainfall deserts or moderate-rainfall alpine climates. Most recent of all have been substrate changes (rock outcrops, edges of saline water bodies) within a given climate type, 9–3–0.5 Ma. This has only been recorded in Mediterranean-type climates so far, but, like all the data presented here, this is likely to be biased by where the studies were undertaken. Table 2 shows that climate change leads to the development of the full range of possible vegetation types and fire regimes. Four migration or in situ pathways can be recognized with respect to the fire regimes induced by these climate changes: (A1) from non-fireprone to fireprone habitat (gains fire-related trait); (A2) from one fireprone habitat type to a crown fire-type (gains a different fire-related trait); (B1) from crown fire-type habitat to surface fire-type habitat (loss of fire-related trait); and (B2) from moderately burnt (crown fire) habitat to non-fireprone habitat (loss of fire-related trait). Thirteen of the 50 studies collated here were of type A1, with non-serotiny (seeds released at maturity) replaced by serotiny, non-stored diaspores replaced by soil-stored, with either fire-type heat or smoke-released dormancy, and the seeds often becoming arillate and ant-dispersed (Pausas and Lamont 2022a). The impetus here was the conversion of non-fireprone rainforests to shrublands, woodlands, or dense forests with highly seasonal climates where the accumulation of much dry fuel over the dry season made them highly vulnerable to recurrent fire. Lamont et al. (2019b) described this evolutionary pathway as primary directional selection.
Table 2 Climate change effects on 50 clades and their traits through evolutionary time, including the associated dates of change, new vegetation, and fire regime. Attribute change: ↑ from left row climate heading to upper column climate heading; ← from upper column climate heading to left row climate heading. Migration pathways:

| Climate Change | Summer drought (moderate rainfall) | Summer wet (moderate rainfall) | Annually dry (desert) or cold (alpine) | Moderate rainfall, minor seasonality | Uniformly very wet |
|----------------|-----------------------------------|---------------------------------|--------------------------------------|-------------------------------------|-------------------|
| Number of studies |                                  |                                 |                                      |                                     |                   |
| Summer drought | 6                                 | ↑4                              | ↑1                                   | ←6                                  | ←5                |
| Summer wet     |                                   |                                  |                                      |                                     |                   |
| Annually dry or cold |                |                                  |                                      |                                     |                   |
| Moderate rainfall, minor seasonality | ↑9                      | ↑7                              | ←5                                   |                                      |                   |
| Uniformly very wet |                             | ↑5                              | ↑1                                   |                                      |                   |

Date of change (base of stem, Ma)

| Climate Change | Summer drought (moderate rainfall) | Summer wet (moderate rainfall) | Annually dry (desert) or cold (alpine) | Moderate rainfall, minor seasonality | Uniformly very wet |
|----------------|-----------------------------------|---------------------------------|--------------------------------------|-------------------------------------|-------------------|
|                | 9.1, 9, 19, 0.5                  | 13, 12.4                        | 4.7, 41, 7, 12                       |                                     |                   |
|                | 27, 23                           | 22, 6.4                         | 41, 37.3, 22, 0.8                    | 95, 40, 32, 5, 7, 4                |                   |
|                | 1                               |                                 |                                      |                                     |                   |
|                | 33, 28, 18, 17, 5                | 114, 80, 71, 45, 32             |                                     |                                     | 23                |
|                | 70, 70, 56, 3, 50, 44            | 109, 95, 77                     | 73.5, 73.5, 61, 64, 44, 23           |                                     |                   |

Vegetation (after climate change)

| Climate Change | Summer drought (moderate rainfall) | Summer wet (moderate rainfall) | Annually dry (desert) or cold (alpine) | Moderate rainfall, minor seasonality | Uniformly very wet |
|----------------|-----------------------------------|---------------------------------|--------------------------------------|-------------------------------------|-------------------|
|                | Rock outcrops, salt lake margins  | Grassy savannas                 | Subalpine forest/woodland, desert shrublands |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |

Fire regime (after climate change)

| Climate Change | Summer drought (moderate rainfall) | Summer wet (moderate rainfall) | Annually dry (desert) or cold (alpine) | Moderate rainfall, minor seasonality | Uniformly very wet |
|----------------|-----------------------------------|---------------------------------|--------------------------------------|-------------------------------------|-------------------|
|                | Non-fireprone                     | Frequent surface fires in spring | Non-fireprone                        |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |
|                |                                  |                                  |                                      |                                     |                   |

Plant traits (after climate change)

| Climate Change | Summer drought (moderate rainfall) | Summer wet (moderate rainfall) | Annually dry (desert) or cold (alpine) | Moderate rainfall, minor seasonality | Uniformly very wet |
|----------------|-----------------------------------|---------------------------------|--------------------------------------|-------------------------------------|-------------------|
|                | Non-serotinous, non-dormant, not smoke/heat-sensitive | Resprouting, loss of serotiny | No longer smoke-sensitive, non-arillate, gain dormancy (Pinus) | Loss of smoke or heat sensitivity, not arillate | No longer dominant, non-arillate |
|                |                                  |                                 |                                      |                                     |                   |
|                |                                  |                                 |                                      |                                     |                   |
|                |                                  |                                 |                                      |                                     |                   |
|                |                                  |                                 |                                      |                                     |                   |
|                |                                  |                                 |                                      |                                     |                   |

Migration pathways:

- from non-fireprone to fireprone habitat (gains fire-related trait);
- from one fireprone habitat type to a crown-fire-type (gains a different fire-related trait);
- from crown-fire-type habitat to surface-fire-type habitat (loss of fire-related trait);
- from moderately burnt (crown-fire) habitat to non-fireprone habitat (loss of fire-related trait).
Another 13 studies were of type A2. Here, the climate was mildly seasonal and some fire-related traits were already present before becoming strongly seasonal. This pathway can be described as secondary directional selection. Thus, among some pines, fire-resistant trees lacking serotiny became fire killed, retaining the old-side branches with their intact cones that released their seeds in response to fire that could now reach their crowns (He et al. 2012). The climate aspect of these trait innovations in pines is not completely clear. Three-quarters of current serotinous species occur under Mediterranean climates (Lamont et al. 2020). Trees in *Pinus*, subgenus *Pinus*, were non-serotinous up to ~114 Ma. They experienced surface fires that imply a summer-rainfall savanna climate with a grassy ground cover, equivalent to present-day savannas (Lamont et al. 2013). It appears that annual rainfall increased but the summer maximum rainfall was maintained. Thus, it is also likely that fire frequency decreased. Scattered trees would now form forests, with extra fuel that would enable fire to reach their crowns and travel from one tree to another. Serotiny would be promoted along with dead-branch retention that creates a ‘ladder’ effect for carrying flames to the crown.

The main reason for lack of serotiny in summer-rainfall savannas is that it has no adaptive advantage in habitats where fire can be expected in most years and selection might now shift to, say, taking advantage of exceptionally wet summers (Lamont et al. 2020). Thus, serotiny should be favored not just in Mediterranean climates but also under moderately high rainfall climates that support dense tree or woody shrub vegetation with mild summer seasonality that favors occasional fires. Here serotiny would be beneficial (along with soil-stored seeds). Such a scenario currently exists in extant SE Australia, with abundant rain and a minor summer maximum, where serotiny (and geospory) are well represented in the sclerophyll woodlands and forests (Lamont et al. 2020; Collette and Ooi 2021).

Interestingly, Table 1 indicates that, with the predicted increase in aridity in this biome with time, such traits will become increasingly adaptive.

Six studies involved changes from crown fire-type habitats to surface fire-type habitats as rainfall consolidated to summer and fire frequency increased (type B1). With frequent low-intensity ground fires, seed storage became redundant: pines in particular now shed their old branches, reducing the ability of flames to ‘climb’ to the crown (He et al. 2012) and serotinous cones were discarded, heat- and smoke-released dormancy lost their advantage once fires could occur in successive years, and resprouting replaced non-sprouting as there was now insufficient time to produce enough seeds for self-replacement after fire. This too is an example of secondary directional selection. At the opposite pole of fire-promoting climates are three extreme climates that suppress fires: (a) low rainfall, hot or cold, deserts, (b) cold tundras and mountainous uplands, and c) ever-wet rainforests. Twelve such cases of type B2 are recorded here. The six cases of clades returning to the rainforest are worth highlighting as the usual perception is that closed, ever-wet forests are strictly ancestral environments that is shown here to be a biased view (see further evidence under Dispersion).

The apparent paradox is that habitats which become either frequently burnt or fire free both lose their fire-adapted traits but for different reasons and often in different ways. Thus, fire-killed species with prolific production of dormant seeds are no longer adaptive in savannas as there is insufficient time to produce enough seeds for self-replacement, whereas fire-released dormant seeds are redundant in deserts and rainforests where fire is not available as a dormancy breaker. At both vegetation extremes, legume seeds in particular are no longer arillate—further evidence that ant dispersal is essentially an adaptive response to intense fires, as ultimately controlled by climate (Pausas and Lamont 2022a). However, other traits may be gained, such as cold stratification to break seed dormancy in the uplands (Montalvo et al. 2002). These
Fig. 6 Dated phylogeny of the Cistaceae together with its ancestors, Dipterocarpaceae and Bixaceae, showing how four phases (separated by broken lines) in the evolution of this superclade can be recognized (described in the text). Clade 1: Dipterocarpoid Dipterocarpaceae in tropical Asia, 2: Sarcolaenaceae in tropical Madagascar, 3: Monotoid Dipterocarpaceae in tropical Africa (savanna), 4: Bixaceae (mostly Cochlospermum) in savannas in the Southern Hemisphere, 5: Pakaraimaea in tropical Africa (savanna), [6–13 Cistaceae], responses might now be better described as examples of primary directional selection, for new traits arise under selection from limiting environmental factors unrelated to fire (e.g., aridity, low temperatures, continuous rain). It is a moot point whether these new traits (non-serotiny, non-dormancy) could still be regarded as fire-related traits, as they are responses to fire regimes at the extremes of the range (Lamont et al. 2020), exceptionally frequent fires on the one hand and essentially non-fireprone on the other.

Case studies on the evolution of plant traits under changing climates and fire regimes

Dipterocarpaceae–Cistaceae–Bixaceae (fireprone Mediterranean Basin in particular)

The families Dipterocarpaceae, Cistaceae, and Bixaceae form a natural superclade within the order Malvales. Dipterocarpaceae currently is the major tree clade in non-fireprone tropical Asia, the Cistaceae is largely a prominent shrub clade in the highly fireprone Mediterranean Basin flora, and Cochlospermum (Bixaceae) is one of the Earth’s most widespread savanna genera, spanning South America to Australia. Four phases in the evolution of this suborder can be recognized with respect to
climate and fire (Fig. 6): (1) the most basal clades occur in ever-wet rainforest that is non-fireprone and its seeds are non-dormant, often recalcitrant (Appanah and Turnbull 1998); (2) new clades migrate or adapt to summer-wet, monsoonal savannas that are fireprone, most of whose seeds are physically dormant and are stimulated to germinate by fire-type heat; (3) migration or adaptation to winter-wet Mediterranean climates that are strongly fireprone that fosters marked speciation, most of whose seeds are physically dormant and are stimulated to germinate by fire-type heat; and (4) most species in the two most advanced clades of *Helianthemum* (Cistaceae) migrate to fire-free habitats usually within the Mediterranean Basin (rock outcrops, saline wetlands, desert margins) that retain hard seeds but lose their fire heat responsiveness with some becoming annuals at the driest margins.

**Callitroid Cupressaceae (fireprone Australia in particular)**

Figure 7 depicts the evolution of lineages among the Callitroidae (family Cupressaceae), widespread in the Southern Hemisphere, in relation to putative mean world temperatures and atmospheric oxygen levels over the last 65 My. There has been a general increase in number of serotinous and non-serotinous lineages during the entire Cenozoic. This is despite the general decline in average world temperatures during that time and atmospheric oxygen as a surrogate for burn probability (Fig. 2). But it is the anomalies that are of

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**Fig. 7** Evolution of serotinous and non-serotinous lineages among Callitroidae (family Cupressaceae) over geological time scales in relation to putative mean world temperatures (redrawn from Zachos et al. (2008)) and atmospheric oxygen levels (redrawn from Bergman et al. 2004). Callitroid data from Crisp et al. (2019, Supplementary Materials). Reanalyzed and redrawn from Lamont et al. (2019b)
most interest for they show that climate and fireprone-
ness continue to have major influences on the subfam-
ily’s rate of speciation and level of serotiny. Thus, the
decline in speciation during the 40–30-Ma interval
that may be attributed to the 4 °C drop in temperature
coinciding with the final separation of Australia from
Antarctica and onset of the Southern Ocean circula-
tion pattern (with an expected decline in fire activity).
This was followed by enhanced speciation with a rela-
tive increase in serotinous lineages during the warmer
early Miocene with increase in [O₂] levels (with an
expected increase in fire activity). Unlike patterns
among some other clades, the mid-Miocene Climatic
Maximum was not accompanied by a marked increase
in fire-related traits (Lamont et al. 2019b), but there
was a dip in [O₂] levels that may have been relevant.
Finally, there was a marked increase in speciation,
with a relative decline in serotinous clades, over the
last 10 My with speciation promoted as the subfamily
moved into summer-rainfall savannas and non-fire-
prone uplands, deserts, and rainforests where serotiny
is non-adaptive.

![Dated phylogeny of part of the proteoid Proteaceae
clade highlighting diversification in section Proteae in rela-
tion to climate, vegetation, fire regime, and seed dormancy
types. The rainforest-type climates (green pathways) with
lack of fire and seed dormancy are ancestral and can be traced
to > 120 Ma. The summer-wet grasslands (orange pathways)
with surface fires and heat-tolerant seeds arose from 13 Ma.
The shrubland floras with highly seasonal climates (maroon
pathways) are of Mediterranean type with strongly fire-adapted
seeds and appeared as early as 95 Ma. Collated from Lamont
and He (2012), Lamont et al. (2013), He et al. (2016a, b),
Lamont et al. (2017a, b), and Pausas and Lamont (2018), with
some dates revised by Tianhua He (personal communication)]
Proteoid Proteaceae (fireprone South Africa in particular)

Figure 8 provides a dated phylogeny of part of the proteoid Proteaceae clade highlighting diversification in section Proteae in relation to climate, vegetation, fire regime, and the two-seed dormancy types, smoke- and heat-released. The association of ancestral rainforest-type climates with the absence of fire and seed dormancy is clear. Present from 13 Ma are summer-wet grasslands with surface fires and heat-tolerant seeds lacking fire-stimulated germination. The extant shrubland flora mostly under Mediterranean-type climates can be traced to 95 Ma and is characterized by strongly fire-adapted seeds that are either serotinous and released in response to branch incineration or soil stored with dormancy broken by smoke and/or heat (see Newton et al. 2021 for a comprehensive study of Leucadendron). The trait pairing changed from (a) non-sprouting with seed storage to (b) resprouting with non-storage following the migration to summer-wet grasslands is notable (Lamont et al. 2017b). We could use these traits to impute Mediterranean-type climates up to the mid-Cretaceous by ancestral trait assignment techniques as undertaken here but there is no paleontological evidence to support seasonality as summer-dry then that limits the value of this approach. Provided fires incinerated the vegetation (canopy-type) and were only of moderate frequency it is possible that ancestral fires along these pathways were associated with moderate rainfall with a minor summer maximum, as occurs in SE Australia currently (also see the earlier discussion about type A2 traits under Evolution of fire-related reproductive traits in relation to climate change).

Hakea (fireprone SW Australia in particular)

The twin ancestral fire-related traits in Hakea were postfire resprouting and serotiny and demonstrate that the genus arose in a fireprone environment. From this we can also surmise that the fires were initially of overall moderate frequency (>5–45 years intervals). If fires were at the high frequencies associated with summer-wet savannas (<5-year intervals) the plants would have stayed non-serotinous, like their ancestors (Lamont et al. 2013). If fire intervals exceeded plant longevity, say 45 years, then, upon death in the absence of fire, serotinous seeds would be released onto a hostile seedbed that rarely yields recruits (Causley et al. 2016). Highly variable annual rainfall favors resprouting over non-sprouting. However, within 4 My, a non-sprouting clade, with its need for fires at moderate intervals followed by reliable rains, had arisen (Lamont et al. 2017a, El-ahmir et al. 2015). The outcome was strong transitioning to both resprouting and non-sprouting in the Miocene and all epochs were dominated by an almost universal proliferation of serotinous descendants (Table 3). Of note are both the continuing transitions to non-sprouting in the Pliocene and its steady increase throughout Hakea’s history (from 38.6 to 58.3% of all fire-response proliferations). It is likely that the trend for increasing aridity and seasonality and declining atmospheric oxygen and carbon dioxide (Figs. 2, 7) led to less frequent, but more reliable, fires, and promotion of non-sprouting (Lamont et al. 2011, 2013). Today, resprouters are better represented in the more fireprone, strongly seasonal northern sandplains of SW Australia and non-sprouters in the less-fireprone southern parts, especially on deeper soils where recruitment and adult survival are more likely (Lamont and Markey 1995; Groom and Lamont 1996).

Transitions to non/weak serotiny were rare but five of the six independent origins were in the late Miocene and their proliferation was restricted to the recent Pliocene (Table 3). Reasons include migrations to frequently burnt, summer-wet savannas (H. divaricata lineage), or rarely burnt arid lands (H. recurva). The novel fire-free granite outcrops exposed from ongoing lowering of the landscape were colonized by drought-adapted species lacking serotiny (H. clavata), and the presence of eucalypt forests with reliable winter rains enabled the appearance of weakly serotinous species that could recruit interfir (H. trifurcata lineage) (Lamont et al. 2020). This pattern has limited parallels with Protea in South Africa where a single transition to non-serotiny in savanna grasslands was followed by increasingly extensive stabilization there (Fig. 8, Table 3) that failed to occur in Australian savanna grasslands. However, in both biomes, stabilization of serotiny in the presence of the increasingly prevailing mediterranean climate (Lamont and He 2017b) was by far the dominant process and reversals were negligible. By contrast, the well-known lability in whole-plant fire responses (He et al. 2011) was expressed in both Protea and Hakea, although 80% of reversals...
were to resprouting in *Hakea* in the Miocene, perhaps reflecting periods of increased or more stochastic fire frequencies associated with less reliable rainfall as the clade moved to drier parts of Australia (Lamont et al. 2016). These historic variations in fire frequency coupled with the severity of seasonal droughts serve well to help interpret the present relative abundances and distributions of resprouters and non-sprouters among hakeas, ericas, and proteas (Ojeda 1998; Lamont et al. 2013). The dominant role of climate lies behind the conclusion of Litsios et al. (2014) that a more heterogeneous (altitude-dependent) but overall mesic climate explains why Restionaceae non-sprouters are so well represented in South Africa compared with Australia, but this can be more parsimoniously explained by their evolution in a less-fireprone landscape than SW Australia during the Cenozoic (Lamont et al. 1985, 2011, 2019b; Bond et al. 2003).

### Table 3

| Trait that evolved | Genetic process | Within trait (%) | Across trait (%) | Fire response | Serotiny | No. of reversals |
|--------------------|-----------------|------------------|-----------------|--------------|---------|----------------|
| Resprouter (ancestral) | Stabilization | 86.1 | 100.0 | 0.0 | 0.0 | 92.2 | 9 |
| Resprouter (ancestral) | Transition | 13.9 | 100.0 | 0.0 | 0.0 | 7.8 | 33 |
| Nonsprouter (ancestral) | Stabilization | 79.4 | 88.2 | 100.0 | 11.8 | 86.2 | 9 |
| Nonsprouter (ancestral) | Transition | 20.6 | 100.0 | 0.0 | 0.0 | 13.8 |
| Speciation promotion rate | 1.95 | 1.95 | 2.40 | 2.02 |

All node-to-node steps in the phylogeny were treated as diversification events. Where the ancestor was ambiguous this event was omitted from the counts as the process was unclear. Reversals refer to transitions back to the previous trait. Speciation promotion rate (SPR) is given by SPR = 100/Y where Y is the percentage of events that retain the ancestral trait; speciation is promoted when > 1 due to a trait change (1 = no effect). Speciation rates are based on non-logged formula.
Evolution at the population scale

Biotic responses to environmental change begin at the micro-scale, i.e., via population dynamics. There are many studies that demonstrate within-species trait changes/differences in the context of fire (Pausas et al. 2012; Leonard et al. 2018) and fire–climate interactions (Groom and Lamont 2011; He et al. 2018). Sometimes it is unclear if these are genotypic (ultimate) or just phenotypic plasticity (proximate) responses to variations in fire proneness, climate, or local growing conditions, such as nutrient and water availability. Nevertheless, it is clear that both types of responses can be considered adaptive (Groom and Lamont 2011). However, there are no empirical data on the rates of genetic change comparable with that at the clade level as described here and certainly nothing on the mechanisms of change at the gene level.

There has been a recent attempt to model changes in the degree of serotiny at the population scale where serotiny is adaptive (Lamont et al. 2020). I extend that simple deterministic model here in the context of intensifying summer drought such that a) crown fires are more severe and less patchy, b) seedling recruitment is restricted to the postfire environment only, and c) genetically non-serotinous seeds are released interfire before serotinous seeds. Thus, the issue of declining rainfall reliability with increasing drought (Cowling et al. 2005) is avoided, as postfire germination and recruitment conditions will always be better than interfire that is considered zero. The model assumes that the degree of serotiny of an average plant is 22.2, that is, already relatively high (Lamont 2020), i.e., 5% of seeds are released each year, and that wastage of seeds through viability and granivory losses increase at 5% per year. Following each fire, the population is made up of individuals varying genetically in their degree of serotiny such that some will release most of their seeds interfire and others will only release them in response to fire (tree death through burning). Further, assume that the tree or shrub takes 10 years to commence production of mature seeds, fires occur regularly at 20-year intervals, and the plant produces 55 seeds in its first year and five more with each successive year. Finally, assume that seed production and postfire seedling recruitment decline at 6.5% per year compared with the initial level in response to the gradually declining rainfall. The outcome for three fire cycles is given in Fig. 9.

The model shows a gradual increase in the fraction of seeds stored on the plant that is serotinous with each successive fire cycle, despite declining seed production (Fig. 9). From a position of half the seeds genetically serotinous, attrition of non-serotinous seeds results in an increase to a fraction of 0.605 serotinous by 10 years from the onset of seed production. This rises to 0.686 by the end of the second generation.
fire cycle and 0.778 by the end of the third fire cycle. This yields a rapid adaptive response to climate–fire regime change: the recovered populations would be almost completely serotinous within 120 years.

However, simplistic also means idealistic. Species in some situations can now rarely respond to fire in such a way that leads to certain self-replacement. Populations in some remnants never burn so that there is no generation turnover (essential in this model) and seeds are wasted; others are in such small populations that Allee effects (inbreeding) take over and seed production per plant may even fall to zero (Lamont et al. 1993). With climate change, extreme weather events increase, fires are more intense coupled with higher fuel loads, and greater incineration of seeds and buds follows. Some fire management/control authorities try to emulate perceived aboriginal practices by burning at shorter intervals that threaten adequate seed production by non-sprouters for self-replacement (Enright et al. 2014). Urbanization leads to more-frequent fires for many reasons outside the control of management (Syphard et al. 2017). Other authorities specifically aim to suppress fires as soon as they start, leading to long unburnt stands. Some land managers implement ‘cool’ out-of-season fires that fail to reach tree crowns so that adults no longer die nor do they release their stored seeds as flames fail to reach the crowns as they did during pre-human evolution when fires were more stochastic. Exotic, highly combustible weeds invade vegetation remnants and pastoral lands, depending on their distance from transport routes and become permanent components of the vegetation at the expense of native plants (Milberg and Lamont 1995). Fireproneess of the hybrid vegetation increases.

Discussion

In this review, I have highlighted how climate controls the type of vegetation and how both dictate the fire regime that develops in response. Atmospheric carbon dioxide is not considered a component of climate but its levels both control the climate (temperature, rainfall, humidity, seasonality) generally and movement of climate belts latitudinally and altitudinally. It also has direct effects on plants as a resource for photosynthesis that in turn affects atmospheric oxygen levels and thence flammability of fuel. As [O$_2$] levels declined over the last 50 My, seasonality, as it affected dry fuel accumulation, took over as a key determinant of fire events. Until the recent evolution of humans, lightning, as a property of the climate and expressed through weather events, dictated the incidence of fires. No interaction between two phenomena could be closer historically than that of climate and fire. All this changed with the Industrial Revolution and now they are decoupled (Syphard et al. 2017). However, the Industrial Revolution also brought with it an increase in atmospheric CO$_2$ and other potent ‘greenhouse’ gases, such as methane. To what extent can we expect history to repeat itself with adaptive changes in plant dispersion and the evolution of new climates and fire-sensitive traits as I have shown here have occurred over the last 120 My?

This is the first time in 50 My that atmospheric CO$_2$ has clearly trended upward (Fig. 2). We can therefore expect a reverse trend of increasing mean temperatures, burn probability, and atmospheric O$_2$ [provided this is accompanied by greater productivity (Gamage et al. 2018) that depends on rainfall]. Rainfall is increasing in the tropics but decreasing in the mid-latitudes as the rain-bearing westerly systems are pushed Poleward. Plant productivity is at present being maintained as the higher photosynthesing [CO$_2$] balances out increasing drought due to higher temperatures and lower rainfall. Fuel production is maintained but it is now drier so that fires are more intense and frequent (Syphard et al. 2017). Fires now occur in uplands, boreal forests, and rainforests traditionally considered non-fireprone. Mid-latitude forests begin to experience the type of scenario revealed 215 Ma for the conifer Agathaxylon arizonicum, with drought at multi-annual, not seasonal, scales, with marked postfire recovery if the species are already fire tolerant and local extinction if they are not.

When vegetation spread freely over the Earth, species became locally extinct when the tolerance range of their fire-adapted traits was exceeded by the new climate-fire combination. But they could migrate to areas where the previous conditions were retained. Thus, vegetation types shrank or expanded accordingly (Fig. 3). Currently, two major obstacles have arisen: a given vegetation type is fractured or decimated and often now exists only as isolated remnants, rendering migration of its component species unlikely. Population size is so small that Allee effects come into play (Lamont et al. 1993) and the nucleus
of fertile plants is insufficient to produce and spread propagules, even by long-distance dispersal (LDD) mechanisms, in the random directions where suitable habitats may exist. Serotinous species depend on fire for the release of their seeds and the remnants may now rarely burn or are burnt so frequently that plant immaturity risk is a problem (inadequate seed production for self-replacement).

Despite demonstrating the presence of LDD agents, Merwin et al. (2012) concluded that the clonal shrub, Banksia candolleana, occurring widely on scattered dunes in a large conservation reserve, would only traverse < 800 m over 200 years, rendering propagule dispersal as an ineffective mechanism for coping with rapid climate change. For a similar clonal shrub, B. goodii, with far fewer opportunities for LDD as it occurs in dense forest, the estimated distance was ~200 m in 200 years (Witkowski and Lamont 2006). However, as slow-growing shrubs whose longevity may exceed 1000 years, resilience is the main survival mechanism available to these species. For other co-occurring banksias, such as B. hookeriana, with 100% mortality in the presence of fire, other mechanisms are needed, such as high recruitment efficiency (seedling recruits to parent ratio, Merwin et al 2012).

The alternative is the evolution of novel traits adapted to the new climate–fire combination. Evolutionary change in this review is treated at the macro-scale. But trait change expressed at the species level is extremely slow. For example, consider Table 3. For both Hakea in Australia and Protea in South Africa, the average net diversification rate over the last 20 My was ~4 species per one million years. The rates were greatest in the Miocene when there were marked long-term variations in climate and the fire regime (Fig. 7). Speciation rates were an order of magnitude lower in the Pliocene and Quaternary, when there was a marked decline in mean temperatures, especially during the so-called Ice Ages of the Pleistocene that occurred at about 100,000 years intervals and presumably fires were rare then as well. For these genera, fire clearly promoted (at least doubling) the incorporation of the novel traits of resprouting or non-sprouting into the daughter species over this period (Table 3). Fire was less effective at promoting serotiny or non-serotiny into the new species (8% or 25% increase respectively), essentially because serotiny was already advantageous and simply remained with the daughter species. While novelty of traits is invariably emphasized in studies of this type, retention of traits that are already adaptive (stabilization), e.g., serotiny in the face of intensified fire with climate change, deserves greater recognition. See He and Lamont (2018) and He et al. (2019) for details on the mechanisms by which fires promote speciation, which can include direct effects on the genome.

In conclusion, I consider that future opportunities for adaptation to climate–fire regime change via migration or trait evolution as described here are close to non-existent. The most disturbing change is declining rainfall with intensifying drought and more frequent and severe fires, mostly of anthropogenic origin. Here, increasing serotiny, soil seed storage, heat resistance, resprouting, and fecundity/recruitment efficiency would have adaptive advantages. But the likelihood of these evolving naturally is remote. Selection/breeding programs can aim to incorporate these traits into cultivated plants and species used in rehabilitation programs and thus short-circuit adaptive processes. However, the evidence presented here shows that both insufficient time and suppressive circumstances render future adaptive change in the conservation estate untenable. Nature can no longer run its course as time is now the limiting factor. Here, the only practical solutions in the face of the current onslaught of anthropogenic climate change appear to be restricted to (a) reliance on phenotypic plasticity (e.g., Fig. 5) and (b) species resilience (Witkowski and Lamont 2006; Clarke et al. 2015).

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