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PERSPECTIVE

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Ecology and biogeography in 3D: The case of the Australian Proteaceae

Abstract

The key biophysical pressures shaping the ecology and evolution of species can be broadly aggregated into three dimensions: environmental conditions, disturbance regimes and biotic interactions. The relative importance of each dimension varies over time and space, and in most cases multiple dimensions need to be addressed to adequately understand the habitat and functional traits of species at broad spatial and phylogenetic scales. However, it is currently common to consider only one or two selective pressures even when studying large clades. We illustrate the importance of the all-inclusive multidimensional approach with reference to the large and iconic plant family, Proteaceae: we review life-history traits related to these three dimensions for the 46 genera occurring in Australia and show that this family can be considered the product of a long history of harsh environments, recurrent fires and strong faunal interactions. Because most Proteaceae species occur in fire-prone ecosystems and possess fire-adaptive traits that are both ancient and essential for their survival, disturbance by fire is likely to explain much of this family's ecology, evolution and distribution. Approaches that only examine prevailing environmental variables may fail to identify the mechanisms that drive a taxon's biogeography; they need to consider the likely mechanisms of adaptation and accept or reject plausible alternative hypotheses as the evidence allows. As multidisciplinary teams that consider all aspects of a taxon's ecology are assembled, and databases and numerical tools become increasingly available, studies on the ecology, biogeography and diversity of organisms at broader spatial and phylogenetic scales will arrive at more realistic conclusions.

1 | EVOLUTIONARY DIMENSIONS

The phenotype and genotype of organisms, and the distribution of taxa across the world, are the product of a long evolutionary history. Over millions of years, plants and animals have been constantly reshaped in response to many evolutionary pressures, and the importance and intensity of each agent of selection has changed over time and across space. From the snapshot we see today, an important objective of biogeography is to identify the key factors explaining *how* and *why* biodiversity has arisen on our planet.

Here, we argue that the main evolutionary pressures that shape biodiversity can be aggregated along three axes: environmental conditions (including climate and resources such as soil nutrients and water availability), disturbance regimes and biotic interactions (Figure 1a). The relative importance of each type of pressure has varied over time and across space (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). For instance, in regions where the climate (e.g. arid or cold ecosystems) or substrate (e.g. wetlands) is relatively extreme, environmental factors (temperature, water availability, salinity) are likely to play a major role in shaping species traits and distributions. Under intermediate and seasonal climatic conditions (e.g. tropical savannas, mediterranean ecosystems), disturbance is likely to play a major role (Bond, Woodward, & Midgley, 2005; Keeley, Bond, Bradstock, Pausas, & Rundel, 2012). In contrast, under benign and largely aseasonal conditions (e.g. rain forests), species interactions are predicted to predominate (Galetti et al., 2013). The importance of these different evolutionary pressures changes through time as climate, atmospheric composition, disturbance regime and interacting species have changed throughout the history of the Earth (Barnosky, Koch, Feranec, Wing, & Shabel, 2004; He & Lamont, 2017; Keeley et al., 2012; Pausas & Keeley, 2009).

Of course, these three dimensions are not always independent; for instance, disturbance regimes may be linked to climate, and thus some plant traits may be correlated. This is the case with fire-prone ecosystems, because they undergo a dry season, many plants in theses ecosystems show important adaptations to drought in addition to adaptations to fire (Lamont & He, 2017a; Pausas et al., 2016; Vilagrosa, Hernández, Luis, Cochard, & Pausas, 2014). Furthermore, these evolutionary dimensions may interact. For instance, poor soils may increase plant flammability and frequent fires in turn will further reduce soil fertility (Ojeda, Pausas, & Verdú, 2010); or frequent fire may modify biotic interactions and affect the fitness of flammable species (García, Castellanos, & Pausas, 2016). Despite these correlations and interactions, many plant traits are readily assignable to particular dimensions (Table 1), and for a mechanistic understanding of plant phenotypes and their distribution, it is important to consider the relevance of each of the three dimensions.

However, historically, few studies have dealt with multiple evolutionary dimensions at the same time, in part because they are linked to different approaches and expertise of the various research groups (e.g. ecophysiology, disturbance ecology, reproductive biology). In addition, the lack of suitable data and numerical tools for such multidimensional (multidisciplinary) analyses may have limited the use of this approach. As databases and phylogenetic and numerical tools become increasingly available (Benson, Karsch-Mizrachi, Lipman, Ostell, & Wheeler, 2005; Kattge et al., 2011; Paradis, 2012; GBIF.org), studies on the ecology, biogeography and diversity of organisms at broader spatial and phylogenetic scales become feasible.

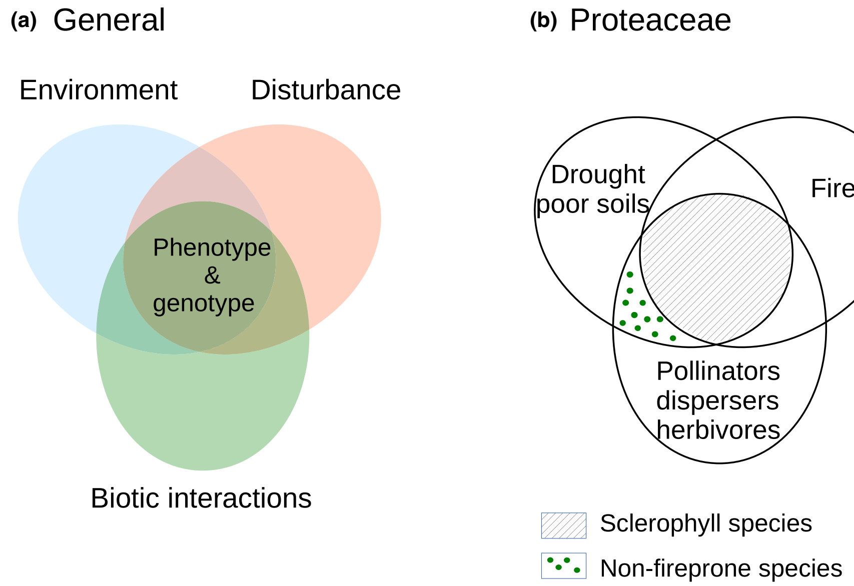

FIGURE 1 The evolutionary pressures that shape the phenotype and genotype of an organism can be aggregated into three dimensions (a): environmental factors (e.g. climate, soils, topography), disturbances, and biotic interactions; each of these dimensions is related to a particular set of traits (Table 1). In the case of the Australian Proteaceae (b), the factors determining these three dimensions define the characteristics of most species (sclerophyllous species; Figure 3 right); excluding one dimension (fire) define the few Proteaceae species that occur in non-fireprone ecosystems (Figure 3 left) [Colour figure can be viewed at wileyonlinelibrary.com]

Thus, technology now matches desirability when considering multiple evolutionary dimensions (Araújo & Luoto, 2007; Staniczenko, Sivasubramaniam, Suttle, & Pearson, 2017).

The interplay between the different evolutionary dimensions can be illustrated by the iconic plant family Proteaceae (Figures 1b and 2). With more than 115 million years of history, the Proteaceae has radiated into over 80 genera and 1,700 species essentially distributed in the Southern Hemisphere; its species are especially abundant in Australia and southern Africa, with southwestern Australia as the main diversity hotspot (Cowling & Lamont, 1998; Figure 3, Table S1). In the following section, we summarize how the three evolutionary dimensions noted above have contributed to the ecology, distribution and diversity of the Proteaceae.

2 | PROTEACEAE IN 3D

2.1 | Environment

The Proteaceae is well-known for its production of "proteoid" roots, specialized root clusters for enhancing nutrient uptake that occur in most species of the family (Figure 4). These roots exude organic acids that increase phosphorus-uptake efficiency as an alternative pathway to mycorrhizal symbioses for survival in nutrient-impoverished soils. Many Proteaceae also have highly scleromorphic leaves, and include species regarded among the world's most sclerophyllous (Lamont, Hanley, Groom, & He, 2016; Lamont, He, & Lim, 2016); these traits are considered a response to both infertile soils (high leaf density) and drought (high leaf thickness) (Lamont, Groom, Williams, & He, 2015). These features contrast with the basal, bifacial meso-macrophylls associated with the rain forest taxa (Flora of Australia 1995).

2.2 | Disturbance

Another well-known feature of the Proteaceae is the prevalence of serotiny (on-plant seed storage), a clear adaptation to recurrent crown fire (Keeley et al., 2011; Lamont & Enright, 2000). Where resources for seed production are limited, accumulation of seeds in the crown enables the critical number for self-replacement to be reached following disturbance. Fire is both the cue for seed release and the cause of ideal recruitment conditions. No other family has so many serotinous species and the diversity of serotinous structures is without peer; it is especially common among the most species-rich genera (Figure 4). Recent studies show that serotiny is an ancestral trait that arose during the fiery Cretaceous (Lamont & He, 2012). Less well-known, but also common among Proteaceae, is the presence of a soil seed bank with fire-stimulated (heat and smoke-cued) germination (Figure 4). Again germination is cued to the period when recruitment is most likely to be successful (interfire establishment makes a negligible contribution to population dynamics).

The Proteaceae also includes other fire adaptations such as species with enhanced flammability around the serotinous cones and retention of dead foliage that ensure seed release (He, Lamont, & Downes, 2011; Table S1), some with thick bark and epicormic resprouting that enable trees to survive fire (Groom & Lamont, 2015), and many with large belowground bud banks located in lignotubers, root crowns or woody rhizomes that enable shrubs to recover from fire (Cowling & Lamont, 1998; Myerscough, Whelan, &

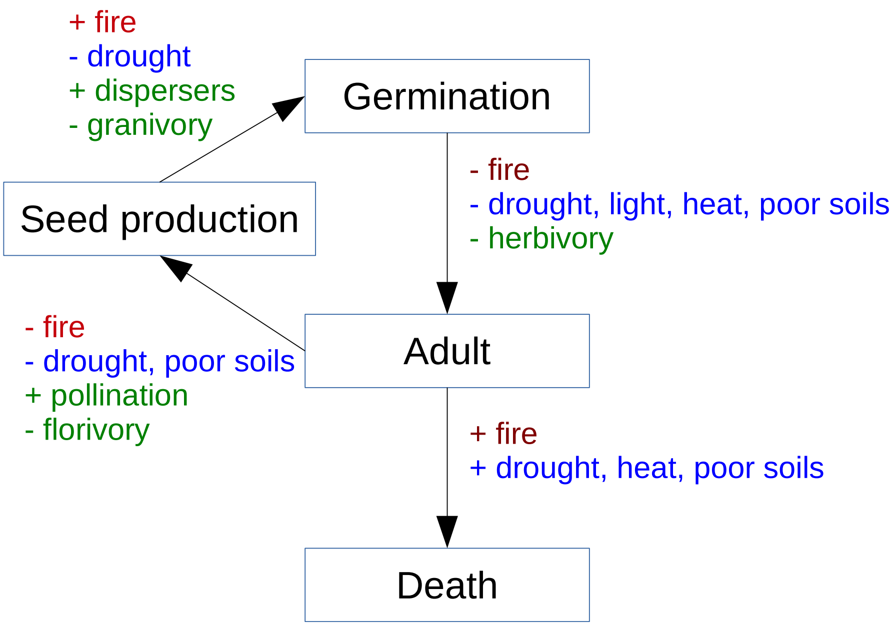

FIGURE 2 The way different ecological drivers promote (+) or retard (–) the life cycle of most Proteaceae species. Note that fire is a vital factor in their successful reproduction (fire stimulates seed release and dispersal or germination; Figure 4) [Colour figure can be viewed at wileyonlinelibrary.com]

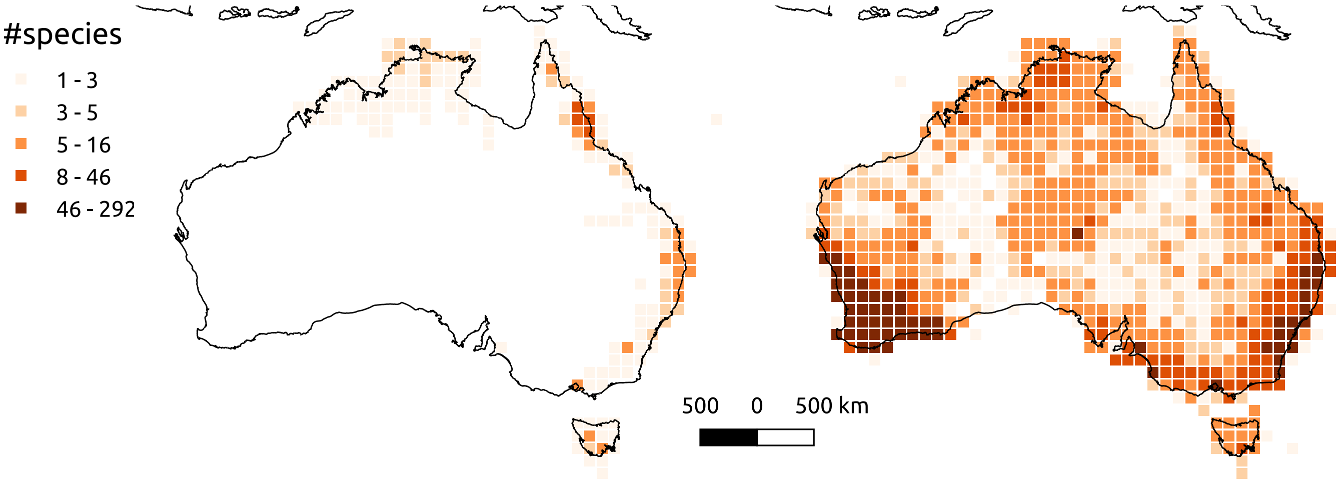

FIGURE 3 Proteaceae species richness in Australia by cells of 1 degree. Left: genera in non-fire-prone vegetation (rain forest and vine forest). Right: genera in fire-prone vegetation (savanna grassland and sclerophyll shrubland, woodland and forest). Note the concentration of records in SW and lesser extent SE Australia. Prepared from 218.322 records obtained from the Global Biodiversity Information Facility (gbif.org; accessed 16 May 2017, https://doi.org/10.15468/dl.9a0rtx). The continent is 3,500 km at its widest [Colour figure can be viewed at wileyonlinelibrary.com]

Bradstock, 2000; Pausas, Lamont, Paula, Appezzato-da-Glória, & Fidelis, 2018). None of these fire-related traits are ancestral for the family but each appeared in specific lineages and at different times in response to changing fire regimes (Lamont & He, 2012; Lamont, He, & Downes, 2013; Pausas et al., 2018).

2.3 | Biotic interactions

Many Proteaceae species are renowned for their conspicuous inflorescences that are pollinated by a wide range of day- and night-active insects, but also, more notably and recently in evolutionary time, by marsupials and nectar-feeding birds (Figure 4; Myerscough et al., 2000); some genera, e.g. *Telopea*, have become solely bird-pollinated. Seed dispersers and granivores are also diverse, from ants to strong-billed cockatoos, emus and other vertebrates (Figure 4; Hanley, Lamont, & Armbruster, 2009; Lamont, He, et al., 2016; Lamont, Hanley, et al., 2016). The Proteaceae also includes many wind-dispersed species, universally so among serotinous species (Figure 4).

Thus, the wealth of knowledge about the natural history of the Proteaceae suggests that demographic processes (Figure 2) and the diversification of this family have been promoted by a long history of harsh environments, recurrent disturbances and a plethora of

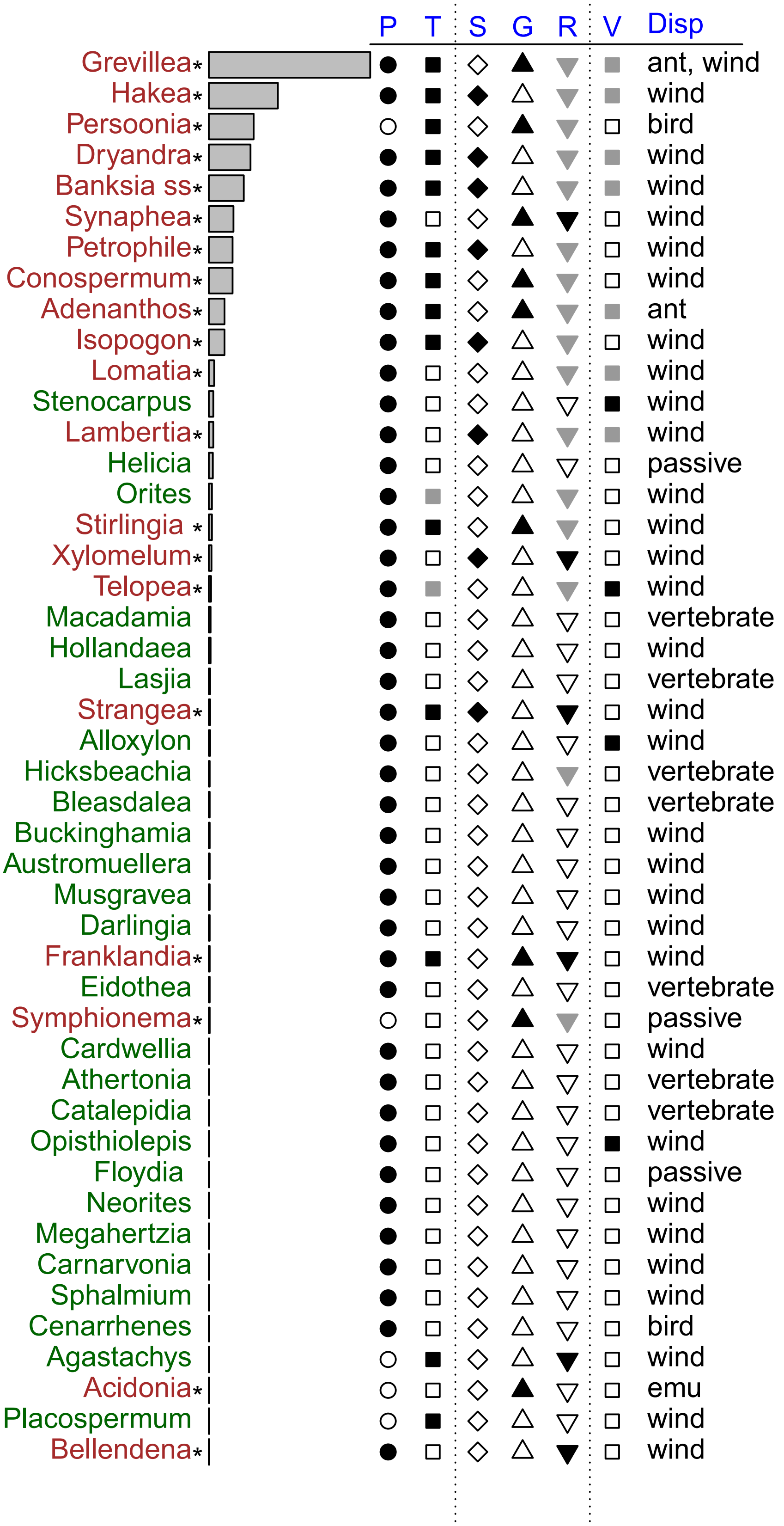

FIGURE 4 Summary of traits associated with environment, disturbance and biotic interactions, for all Proteaceae genera in Australia. Genera with an asterisk (text in reddish) occur in sclerophyll vegetation, otherwise (text in green) in rain forests. Histogram indicates the number of species (maximum = 360 in *Grevillea*). Variables are: presence of proteoid roots (P), thick leaves (including ericoid leaves; T), serotiny (S), fire-stimulated germination (G), resprouting (R), vertebrate pollination (V) and main dispersal vector (Disp). Black symbols = yes (most species); grey symbols = some species; white symbols = no (or rarely). For more details, see Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

interactions with fauna. Key remaining questions include estimating the time of origin of each adaptation in relation to the temporal order of inauguration of the different evolutionary pressures (Lamont, He, & Pausas, 2017). Current evidence indicates that many fire-related traits in the Proteaceae originated during the high oxygen atmosphere of the fiery Cretaceous (Carpenter, Holman, Abell, & Grice, 2016; Lamont & He, 2017b), and seasonality (and drought-resistance traits) came much later (Lamont & He, 2017a). Once the fire-adapted trait evolved, it set the stage for the diversification of the lineage in the presence of the vast range of habitats with different fire ages and fire regimes now available to it. Then, the lineage could respond positively to the appearance of other agents of selection, such as changing climates, advent of new types of pollinators (birds) and herbivores (cockatoos), and further changes in the fire regime. However, the extent of phenotypic and genotypic variability explained by each constraint remains to be studied in detail.

Another topic for further research is the interactions between these pressures, as they do not act in isolation. For instance, the instigation of bird pollination (exposed inflorescences) among *Hakea* species left the subsequent fruits vulnerable to granivorous insects and birds (especially black cockatoos). Spiny foliage and cryptic fruits that can be employed against granivores by insect-pollinated species (with hidden flowers and fruits) cannot be used by the exposed fruits of bird-pollinated species. As serotiny is of general benefit among hakeas in their nutrient-poor soils (Keeley et al., 2011), the adaptive solution is to produce exceptionally large woody fruits that far exceed their initial role in insulating the seeds against fire heat but now also deter cockatoos from reaching the protein-rich seeds (Lamont, He, et al., 2016; Lamont, Hanley, et al., 2016).

Recently, Onstein et al. (2016) reported on the causes of diversification in the Proteaceae using cutting-edge phylogenetic methods. They concluded that radiations in this family were associated with just one of the three possible dimensions, the seasonal climate of open mediterranean-type vegetation. Similarly, Prentice et al. (2017) explained the spatial distribution of Proteaceae in Australia as a function of the prevailing environment, climate and soils, and Mitchell, Carlson, and Holsinger (2018) only considered climatic parameters in searching for the drivers of *Protea* radiation in the Cape Floristic Region. Given that the vast majority of Proteaceae lives in fire-prone ecosystems (>90% of the Australian species, Figure 4), and many of them have fire-related traits (Figures 3 and 4, Table S1), it is difficult to understand the life cycle of most Proteaceae without also considering the role of fire (Figure 2). As both Australia and the Cape Region are among the most flammable regions on Earth, and have a long history of recurrent fires (Lamont & He, 2012; Lamont et al., 2017), one might question to what extent these studies have missed one of the key evolutionary dimensions, disturbance by fire.

Instead, Onstein et al. (2016) used “open” versus “closed” vegetation as a species trait, and found an increase in diversification rate of lineages with small, sclerophyllous leaves in open vegetation, under seasonally dry/warm climates. In fact, fire-prone Proteaceae occur in both dense shrublands and in the understorey of eucalypt forests (Australia's Virtual Herbarium, https://avh.chah.org.au), and in both cases, light is strongly reduced at ground level. These sclerophyll vegetation types are often limited by recruitment, and recurrent fires open the vegetation and select for species with traits for quick recruitment under open post-fire conditions; having a persistent seed bank (in the soil or crown) enables such a strategy to be effective among most Proteaceae (Figure 4). Furthermore, the ancestral reconstruction of the trait “open shrubland” by Onstein et al. (2016) suggests that it appeared in the Cretaceous, but this matches better with the age of fire as a selective process than with the likely Neogene age of the highly seasonal conditions that they considered responsible for scleromorphic leaves (Carpenter et al., 2016; Lamont & He, 2012, 2017a).

In addition, geographical variability in climate seasonality is strongly linked to variability in the fire regime, and thus some distribution patterns apparently due to climate could in fact be driven by fire. By looking at plant traits, it is possible to disentangle whether fire or seasonality is the actual constraint shaping those species; serotiny and fire-stimulated germination are good indicators of the former. Thus, traits related to the environment and traits related to fire explain similar levels of deviance in accounting for the number of Proteaceae species per genus, such that a model including both traits makes little further improvement to explaining variance (Figure 5), suggesting that they are strongly correlated. Overall, we suggest that fire is the most likely mechanism behind the pattern observed by Onstein et al. (2016) and Prentice et al. (2017).

There are numerous independent sources of evidence for the long history of fire in Australia, including phylogenetic studies (Crisp,

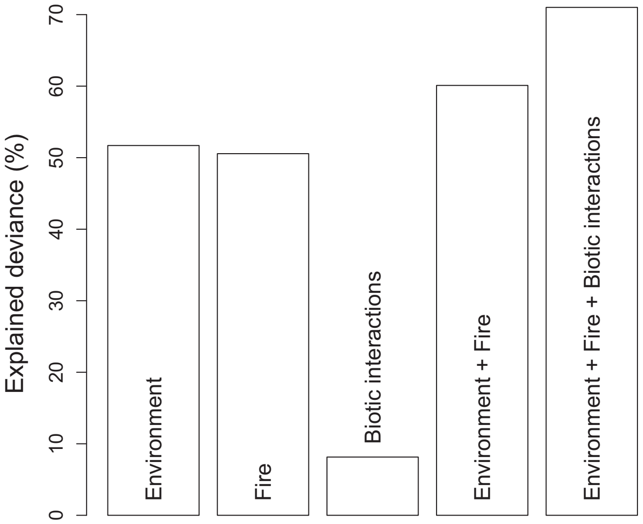

FIGURE 5 Proportion of deviance in species richness per genus of the Proteaceae listed in Figure 3 and Table S1 explained by five models combining the different dimensions: Environment only (proteoid roots + thick leaves), fire only (serotiny + fire-stimulated germination), biotic interactions only (vertebrate pollination + animal dispersal), environment + fire and all three dimensions. Models were fitted with a GLM and a quasipoisson link function, using binary traits from Figure 3 (most species versus few or none)

TABLE 1 Main plant traits that are under selection by the three types of evolutionary pressures

Environment	Disturbance	Biotic interactions
Leaf traits (photosynthetic and water-use efficiency, heat load control)	Bud bank size, location and protection	Flower traits and pollination syndrome
Root system traits (spread and depth)	Resource storage (resprouting)	Fruit and seed traits, seed protection and dispersal syndrome
Nutrient-uptake strategies (fine root development and location)	Seed release and germination cues	Leaf traits (herbivory resistance)
Seed traits (including dormancy and germination, nutrient storage)	Stem protection (bark thickness)	Volatile organic compounds
Root:shoot ratio	Root:shoot ratio	Spinescence
Leaf area:sapwood area	Volatile organic compounds (flammability)	Stem and root traits (parasitism resistance)
Leaf and flowering phenology	Age to maturity, plant longevity Flowering phenology (post-disturbance) Fruit/infructescence traits (seed release cue, flammability) Branching pattern, dead foliage retention (flammability)	Nutrient uptake symbioses with microorganisms

Burrows, Cook, Thornhill, & Bowman, 2011; He et al., 2011; Rundel et al., 2016) and fossil records (Carpenter, Macphail, Jordan, & Hill, 2015; Macphail & Stone, 2004; Pole & Douglas, 1999). These suggest that fire was sufficiently frequent and predictable to act as a selective agent by the mid-upper Cretaceous, essentially due to the high atmospheric oxygen levels in that period; seasonality (summer drought) is a more recent Neogene phenomenon (Lamont & He, 2012, 2017a). Thus, the diversification and distribution of Proteaceae are likely to be strongly linked to the long history of fire in its habitats, not just by the climate and soil characteristics. In the next section, we specifically show how fire may have driven this diversification.

3 | FIRE AND DIVERSIFICATION

Post-fire seeders delay their recruitment to the optimal conditions available post-fire. Many Proteaceae produce a persistent seed bank either in the canopy (serotiny) or in the soil, and fire stimulates seed release (in the former) or germination (in the latter) (Figure 4). Wells (1969) suggested that because seeders in fire-prone ecosystems have a high population turnover (recruiting after each fire), they have an increasing opportunity for natural selection to act, compared with species that do not recruit post-fire. Among seeders, recurrent post-fire recruitment events increases recombination-based mutations, but also, the fluctuations in population size under recurrent fire favour genetic drift processes (Engen, Lande, & Saether, 2005). In addition, the fact that seeders recruit from a multiaged seed bank promotes the generation of genetic novelty (Barrett, He, Lamont, & Krauss, 2005; Levin, 1990). These genetic effects are even stronger in obligate (non-resprouting, fire-killed) seeders as there is no overlap among generations (monopyric life cycle; Pausas & Keeley, 2014), so enhancing genetic differentiation and evolutionary changes among populations (Ellner & Hairston, 1994; Wade & McCauley, 1988). In addition, resprouters under recurrent fire and with large bud banks can also acquire genetic novelty through occasional somatic mutations (Lamont & Wiens, 2003) whose expression is promoted by fire through the production of new genetically altered seed-bearing stems (Lamont, Enright, & He, 2011). Furthermore, fire may also promote hybridization (Ortego, Gugger, & Sork, 2017). Attempts to quantify the relative diversification rates of seeders versus resprouters showed inconclusive results when resprouters were also facultative seeders (Litsios et al., 2014; Verdú, Pausas, Segarra-Moragues, & Ojeda, 2007), as post-fire seeding is likely a key trait for diversification. However, there is evidence of higher speciation rates among lineages associated with the seeder life history than those lineages associated with obligate resprouting (López-Villalta, 2014; Verdú & Pausas, 2013).

All genetic changes associated with the life history of species living in fire-prone ecosystems are the raw material for natural selection to act, and should enable the species to better fill new niches due to changes in the environment, the disturbance regime and the biotic interactions (Schwilk & Kerr, 2002), with consequent enhanced diversification. There is evidence that populations of the same species living under different fire regimes may diverge phenotypically and genetically (Pausas et al. 2012; Moreira, Castellanos, & Pausas, 2014; Pausas, 2015; Vandvik et al., 2014). As a consequence of all these processes, the richness of many fire-prone ecosystems can be explained by the high diversification rates associated with fire (Barraclough, 2006; Cowling & Pressey, 2001; Wisheu, Rosenzweig, Olsvig-Whittaker, & Shmida, 2000), and Proteaceae is a good example, as all the most species-rich genera (>35 species) are in fire-prone habitats (Figure 4). Overall, fire can be considered a strong driver of differentiation through promoting novelty, selection and stabilization processes (Lamont et al., 2013; He & Lamont 2018), and thus fire makes a major contribution to global plant diversity (Pausas & Ribeiro, 2017).

4 | CONCLUDING REMARKS

As the scope of ecological and biogeographical studies increases, it becomes more important to include multiple evolutionary dimensions in our analyses. Failure to recognize the prominent ecological and evolutionary roles of fire in fire-prone ecosystems ("*fire blindness*") is likely to result in a misunderstanding of the key evolutionary processes behind the ecological patterns. To make satisfactory progress in ecology and biogeography, we need to overcome the traditional view that vegetation patterns may be explained solely through climate and soils, and to acknowledge fire as a potent evolutionary force (Keeley et al., 2011; Lamont & He, 2017b; He & Lamont 2018) and a key factor in explaining the distribution and diversity of many ecosystems (Bond et al., 2005; He & Lamont, 2017; Keeley et al., 2012; Pausas & Keeley, 2009; Pausas & Ribeiro, 2017). This may be especially important in lineages from mid and low latitude environments where benign climatic conditions for plant growth and fuel build-up alternate with dry periods prone to fire that resets community dynamics. Specifically, Proteaceae without fire (Mitchell et al., 2018; Onstein et al., 2016; Prentice et al., 2017) would still be confined to the rain forest fringes (Figure 3) and depauperate in species instead of the dominant position it currently occupies throughout the Australian continent (Figure 4).

We live in a multidimensional world; failing to recognize the different dimensions leads to a biased view of nature. Ecological and biogeographical studies in fire-prone and seasonal ecosystems that focus on environmental correlates should also consider the evidence for plausible alternative hypotheses and possible mechanisms of adaptation.

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Australia, disturbance regimes, evolutionary pressures, fire ecology, plant traits, Proteaceae

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DATA AVAILABILITY

The data used in this paper are available in the Supplementary Material and at www.gbif.org.

BIOSKETCHES

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SUPPORTING INFORMATION

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

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