One biodiversity hotspot to rule them all: southwestern Australia—an extraordinary evolutionary centre for plant functional and taxonomic diversity

MARK C. BRUNDRETT

School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.

✉ *mark.brundrett@uwa.edu.au*

Abstract

The Southwest Australian Floristic Region (SWAFR) is a global biodiversity hotspot with exceptional plant species richness, endemism and rarity linked to ancient landscapes, extremely infertile soils, complex habitats and a relatively stable climatic history. It contains about 9000 plant taxa (~8000 species), the majority of which are endemic. Key functional traits for nutrition, fire and pollination were assigned to 77% of taxa and extrapolated for all genera using existing data sources and new observations. Plants with complex mineral nutrition traits are 3–14 times more abundant than global averages, including 18% of all known ectomycorrhizal plants, 40% of nonmycorrhizal plants with cluster roots, 18% of carnivorous plants and most *Thysanotus* species with unique mycorrhizas. Many SWAFR plants also have complex pollination relationships with specific insects (30%), birds (12%), or non-flying mammals (2%). Most also have single (90%) or multiple (48%) traits that are important for fire survival and recovery, such as soil seed banks (70%), canopy-stored seed (20%), resprouting (24%), fire-promoted germination (56%), enhanced flowering (33%), or fire avoidance (14%). Despite these adaptations, fire impacts can cause substantially altered plant diversity and dominance, loss of species, seed banks that take decades to recover, and increased presence of weeds. Most SWAFR plants have adaptive traits for nutrition, pollination and fire, with the most complex trait combinations in specific families and genera that also are the most taxonomically diverse in this biome. Trait variability within genera or even species reveals that strong selective pressures are still driving local adaptation. Species richness patterns of highly diverse trait-complex clades extend the SWAFR boundary into the interzone where ironstone ranges, shrublands and eucalypt woodlands include additional local hotspots for plant diversity and endemism.

The SWAFR is globally unique due to the high proportion of plants with exceptionally complex functional traits that have evolved over long periods in response to adverse conditions, thereby making this region a key plant diversity hotspot for trait evolution. The SWAFR is the best location globally for studying long-term impacts of climate and soil conditions on plant functional and taxonomic diversity, and provides a preview of future conditions elsewhere. However, plants in this region now face even more severe fires, droughts, pollinator shortages and declining soil health. This greatly increases the need for well-resourced and science-based adaptive approaches for ecosystem management and rare flora conservation.

Keywords: southwestern Australia, biodiversity hotspot, mycorrhizas, plant nutrition, pollination, adaptation to fire, trait evolution

INTRODUCTION

The Southwest Australian Floristic Region (SWAFR) encompasses an area with a predominantly Mediterranean climate bounded by semiarid regions. It is one of the 25 original biodiversity hotspots for species richness and endemism (Myers *et al*. 2000). Using its original boundaries, the region contains over 7000 plant species of which 52% are endemic, whereas a similar sized area in eastern Australia contained 4810 species, but only 14% were endemic to that region (Thiele & Prober 2014). Within the SWAFR there are 363 threatened, six presumed extinct and 2074 apparently rare (priority flora) plants (florabase.dpaw.wa.gov.au, accessed 30-

4-21) and landscape age is positively correlated with the local diversity of rare flora species (Gosper *et al.* 2021a). Smaller biodiversity hotspots for specific groups of organisms have also been recognised in Australia for *Acacia* (González-Orozco *et al*. 2013), eucalypts (González-Orozco *et al*. 2014) and orchids (Phillips *et al*. 2011). The SWAFR contains five of the 15 recognised national biodiversity hotspots (www.wildlifelandtrust. org.au, accessed 30-4-21), as well as 14 additional areas of exceptionally high plant endemism and species richness missing from the national list (Hammer *et al*. 2018). Important threats to plant diversity in this region include vegetation clearing and fragmentation, substantial declines and fluctuations in rainfall, contraction of the Mediterranean climate zone, increasing frequency and severity of fires, *Phytophthora* dieback disease,

weed invasion and feral animals (O'Donnell *et al*. 2018; Hoffmann *et al*. 2019; Cross *et al*. 2020; Bergstrom *et al*. 2021; Ritchie *et al*. 2021; Gosper *et al*. 2021b).

The most important factors regulating global plant diversity include the size of bioregions, dominance by intermediate sized plants, complex environmental gradients and moderate disturbance regimes (Keddy 2005). In addition, ancient landscapes with relatively stable climates (OCBILs) and long periods without major disturbance can provide the opportunity for plants to maintain exceptionally high diversity (Cowling *et al*. 1994; Hopper & Gioia 2004; Mucina & Wardell-Johnson *et al*. 2007). In these areas weathering and erosion increase soil and regolith complexity, whereas prolonged leaching leads to extremely low soil fertility (Verboom & Pate 2015; Zemunik *et al*. 2016). Studies in Australia and elsewhere have confirmed that species richness is typically greatest at nutrient poor sites (Beadle 1954; Specht & Rundel 1990; Lambers *et al*. 2010). For example, shrublands and woodlands in southwestern Australia have more plant species in a 100 m^2 plot compared to soils with higher levels of phosphorus and nitrogen (Gibson *et al*. 2004; Zemunik *et al*. 2016). The SWAFR has a large proportion of species that are specialized and adapted to the low-nutrient soils that predominate in this highly weathered landscape (Hopper & Gioia 2004; Lambers *et al*. 2010). Even areas with redistributed substrates are comparatively ancient by global standards (Brundrett *et al*. 2017).

In Australia, vegetation patterns are also strongly driven by landform complexity and hydrology (Fordyce *et al*. 2007; Cardillo & Pratt 2013; Reyes *et al*. 2015; Brundrett *et al*. 2017). This complexity may be partly driven by the plants themselves, because cumulative long-term effects of root exudates on soil minerals are linked to laterite or clay formation (Pate & Verboom 2009). Complex landscapes also lead to edaphic specialisation by plants and provide refugia against extinction (Verboom & Pate 2015; Brundrett *et al*. 2017). These specialised habitats include saline areas, rock outcrops, banded ironstone ranges and wetlands (Mucina & Wardell-Johnson 2007; Pate & Verboom 2009; Macintyre & Mucina 2021). High species richness in this region is also linked to steep climatic gradients (Bui *et al*. 2014; Cook *et al*. 2015; Jones *et al*. 2016) and effective adaptations to survive severe droughts and fires (Orians & Milewski 2007; Carpenter *et al*. 2015; Groom & Lamont 2015). Thus, vegetation patterns, which are complex in areas of high plant diversity in Australia, are the product of the feedback processes shown in Figure 1 in addition to plant competition over evolutionary timescales.

Although the nature of trait evolution can be controversial in some cases (e.g. Bradshaw *et al*. 2011), there is compelling evidence that the evolution of traits for nutrition, fire and pollination have been driven by strong habitat specific selective pressures in the SWAFR. For nutrition traits this evidence includes strong correlations between soil nutrient status and the dominance and diversity of more specialised plants, as explained below in **Pollination traits**. There also are many SWAFR plant clades with advanced pollination strategies that have relatively specific pollen vectors and complex floral structures, which are also known as syndromes (e.g. Keighery 1980; Brown *et al*. 1997;
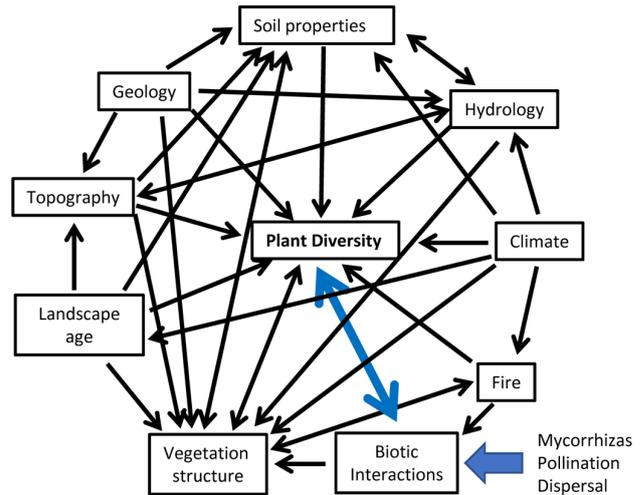
Figure 1. Interacting environmental actors that act as selective pressures in the SWAFR (after Brundrett *et al*. 2017).

Toon *et al*. 2014). For fire traits this evidence includes many plants, descended from fire intolerant ancestors, which have acquired traits that enhance fire survival. These include members of the Proteaceae, Myrtaceae, Restionaceae and Fabaceae, for which increased dominance of fire tolerant species over time in Australia is well documented in the fossil record and phylogenetic studies (Lamont *et al*. 2019). The fire intolerance of many rainforest plants limits the extent of this vegetation type in Australia, yielding 'islands of green in a sea of fire' (Bowman 2000). Lamont *et al*. (2019) identify fire as an important evolutionary trigger that led to multiple fire traits, some of which evolved as early as the Cretaceous in response to increased fire intensity or frequency and others that arose later to enhance the post-fire success of plants.

Mycorrhizal association types are normally consistent within plant families (Trappe 1987; Brundrett & Tedersoo 2018; Brundrett 2021). Most of the globe is dominated by families that have consistent arbuscular mycorrhizas (AM), an association that arose with the first land plants, along with ectomycorrhizal (EM) and nonmycorrhizal (NM) plants that diverged from AM plants in the Cretaceous (Brundrett & Tedersoo 2018; Soudzilovskaia *et al*. 2019). Australia also has many plant families in which ancestral traits have remained consistent, but a global comparison of mycorrhizal associations reveals that exceptions to this are more common in Australia, and are especially prevalent in the southwest of Western Australia (Brundrett 2017a). This is largely due to two large plant families—the Fabaceae and Myrtaceae—that have exceptionally variable root traits, (AM, EM and AM, or cluster roots with or without loss of mycorrhizas). The SWAFR is a globally significant region for root evolution, and also has many carnivorous plants and nitrogen fixing species (Lambers *et al*. 2010; Brundrett & Tedersoo 2018; Cross 2020). Species that grow in this region are also exceptionally efficient at utilising and recycling nutrients (Hayes *et al*. 2014). Furthermore, this area has an exceptional diversity of plants with complex

floral traits linked to relatively specific or extremely specific pollinators (Brown *et al.* 1997; Brundrett, Ladd & Keighery unpublished data).

Bushfires in Australia have substantiality increased in frequency, intensity and size in recent years (Godfree *et al.* 2021), with the Southwest being burnt more often than arid areas (Miller & Murphy 2017). Traits that lead to increased survival or reproduction of plants after severe fire have been important in Australia and globally since the Cretaceous (Pausas *et al.* 2004; Crisp *et al.* 2011; Lamont & He 2017; Bond 2015). The most common fire traits in Western Australia are canopy-stored seed (serotiny), vigorous resprouting, long-lived soil seed banks and promotion of seed germination by fire (Miller & Dixon 2014; Groom & Lamont 2015; Brundrett & Longman 2016; Ald & Ooi 2017; Pausas *et al.* 2018). Other plant traits common in the SWAFR flora include xerophily, assisted seed dispersal and groundwater dependence (Zencich *et al.* 2002; Groom & Lamont 2015). However, these traits are globally widespread, so are less useful for designating hotspots of plant evolution.

This paper summarises knowledge of nutrition, pollination and fire traits of plants in the southwest Australian biodiversity hotspot by addressing the following objectives:

1. Compile data on relatively specialised traits for mineral nutrition, pollination and fire for SWAFR plant species.

2. Compare the taxonomic diversity of plants with specific traits or combinations of traits in the region to global averages.

3. Identify families and genera which exhibit exceptional trait variability and/or have the most highly specialised combinations of traits in multiple categories.

4. For clades identified in objective 3, compare their taxonomic diversity and taxonomic complexity (unnamed or subspecies taxa) relative to other clades.

5. Compare geographic diversity patterns of selected highly specialised clades to existing or proposed boundaries to the SWAFR bioregion.

METHODS

Study area and species

The Southwest Australian Floristic Region boundary used here is loosely based on the southwest phytogeographical region, as defined by Ebach *et al.* (2015), which is substantially larger than the original SWAFR boundary (Gioia & Hopper 2017), but generally corresponds to the boundary between the Eremaean Province and the South-Western Interzone on the vegetation map of Western Australia (Beard *et al.* 2013). As defined here SWAFR includes nine IBRA7 regions—Avon Wheatbelt, Coolgardie, Esperance Plains, Geraldton Sandplains, Jarrah Forest, Mallee, Swan Coastal Plain, Warren and Yalgoo—totalling about 480 000 km², (Fig. 2). Species occurrence data for these bioregions was obtained from the Australian Virtual Herbarium for the SWAFR and the entire State (avh.chah.org.au, accessed 21-1-2021). The West Australian Herbarium database (florabase. dpaw.wa.gov.au) was subsequently used to check and update these lists, which were edited to remove records of weeds, cultivated native plants, non-terminal taxa, hybrids and invalid names. Taxonomic complexity was calculated using subspecies (including varieties or forma) and informal phrase names within families (Appendix 1).

Definition and quantification of traits

In this study specialised traits were defined as those absent from the ancestors of plants and also missing, or substantially less frequent, in plants from most other biomes. Plants were allocated to mineral nutritional trait categories by compiling lists of host and non-host plants using the data sources listed in Table 1. These categories include nutritional traits that were variable within families, as well as carnivorous, parasitic and nitrogen
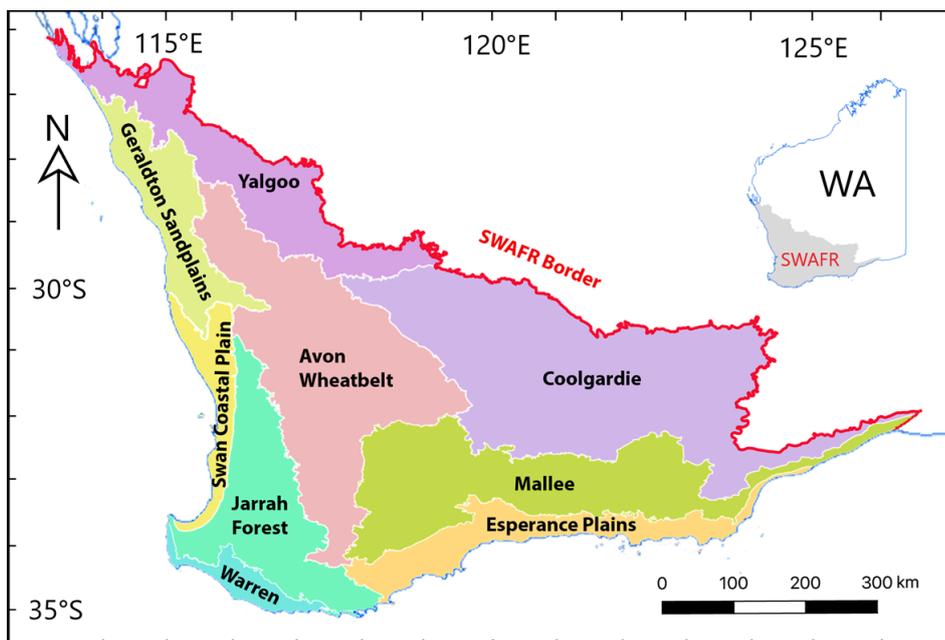
Figure 2. The Southwest Australian Floristic Region as defined here relative to IBRA regions in Western Australia (www.environment.gov.au/land/nrs/science/ibra).

fixing plants. This modified dataset for the SWAFR (Fig. 2) was also compared with state-wide, Australian and global totals for the same traits calculated by Brundrett (2017a, b) and Brundrett & Tedersoo (2018). These records are available in the FungalRoot database (Soudzilovskaia *et al.* 2020).

Data from a separate project that compiled existing data for SWAFR plants, provided the diversity of plants with specialised pollination mechanisms and/ or extremely specific pollinators (Brundrett, Ladd & Keighery unpublished data). These syndromes, which are defined by flower forms and pollinator records, include bird or animal pollination, secondary pollen presentation, deception and specific associations with insects, are listed along with key references in Table 1.

Records of fire traits such as lignotuber presence, resprouting capacity and canopy stored seed are available for many Western Australian species within species descriptions in the taxonomic literature (Table 1), including the Flora of Australia online (www.ausflora. org.au). Taxon-specific data were also obtained from 52 other studies (Table 1), including earlier compilations by Bell *et al.* (1993), Burrows *et al.* (2008), Enright *et al.* (2014), Clarke *et al.* (2015) and Tsakalos *et al.* (2019).

Table 1. Trait types, abbreviations and major sources of information.

Abbreviation	Trait type	Key references
Plant nutrition, root types and habitats		
AM	Arbuscular mycorrhizas	Australian data: updated from Brundrett (2008, 2017a);
EM	Ectomycorrhizas (primarily)	Ectomycorrhizal hosts: Tedersoo & Brundrett (2017);
EM-AM, etc.	Dual mycorrhizas (2 types)	Global data: Brundrett (2017b);
Eric	Mycorrhizas in Ericaceae	Flowering plant species: Christenhusz & Byng (2016);
Orchid	Mycorrhizas in Orchidaceae	Parasitic plants: Nickrent (2020);
Thys	Mycorrhizas in Thysanotus spp.	Carnivorous plants: Cross *et al.* (2020);
NM	Nonmycorrhizal	Australian Orchidaceae: Backhouse *et al.* (2019);
N2F	Nitrogen Fixation	Cyperaceae: Barrett (2013);
Carn	Carnivorous plant	Dauciform roots: Shane *et al.* (2005);
Para	Parasitic plant	Nitrogen fixing symbioses: Tedersoo *et al.* (2018)
CR	Cluster Roots	
DR	Dauciform Roots	
LRH	Long Root Hairs	
SBR	Sand Binding Roots	
Marine	Marine aquatic plant	
Aqua	Aquatic plant (freshwater)	
ASD	Arid, Saline and Disturbed habitats	
Pollination		
Bird	Bird Pollination	Brown *et al.* (1997);
BPB	Buzz Pollination by Bees	Brundrett (2014);
GIP	General Insect Pollination	Brundrett & Keighery unpublished data;
NFM	Non-Flying Mammal pollination	Chinnock (2007);
SD	Sexual Deception	French (2012);
SIP	Specialised Insect Pollination	French & Nicolle (2019);
SP	Self-Pollination	George (1999);
SPP	Secondary Pollen Presentation	George & Pieroni (2002);
VD	Visual Deception	Groom & Lamont (2015);
Water, Wind	Non biotic	Hopper (1993);
		Keighery (1980);
		Olde & Marriott (1995)
Fire survival or propagation		
CSB	Canopy Seed Bank	Baker *et al.* (2005); Barrett & Dixon (2001); Bell (2001); Bell *et al.*
FAA	Fire Avoidance by Annual growth	(1984, 1993, 1996); Bell & Pate (1996); BGPA (2016); Bellairs & Bell
FE	Fire Ephemeral	(1990); Brown *et al.* (1998); Brundrett (2014); Brundrett *et al.* (2018,
FPF	Fire Promoted Flowering	2019, 2020); Burrows *et al.* (2008); Chinnock (2007); Clarke *et al.*
GDP	Groundwater Dependant Plant	(2007); Cochrane *et al.* (2001, 2002); Collette & Ooi ((2020);
GPF	Germination Promoted by Fire	Commander *et al.* (2009); Crisp & Cook (2003); Cross *et al.* (2020);
NSH	Non-Susceptible Habitat (e.g. halophyte, aquatic)	Enright *et al.* (2007, 2014); French (2012); French & Nicolle (2019);
RAG	Resprouts Above Ground	Froend & Sommer (2010); George (1999); George & Pieroni (2002);
RCB	Resprouting from Corm or Bulb	Gosper *et al.* (2019); Grant & Koch (1997); Groom & Lamont
RLR	Resprouts from Lignotubers, roots, or Rhizomes	(2015); Hidayati *et al.* (2012); Hopper (1993); Lamont & Downes
SAF	Short-lived After Fire	(2011); Meney *et al.* (1994); Meney & Pate (1999); Olde & Marriott
SGP	Seed Germination Promoted by fire	(1995); Pate & Dixon (1982); Pate *et al.* (1985, 1991); Roche *et al.*
SIm	Severely Impacted by fire	(1997); Rokich *et al.* (2000); Stevens *et al.* (2016); Tieu *et al.* (2001);
SSB	Soil Seed Bank	Tsakalos *et al.* (2019); van der Moezel *et al.* (1987); Ward *et al.*
VFF	Highly Flammable Foliage	(1997); Wardell-Johnson *et al.* (2007); Zenich *et al.* (2002); Zhao &
WDS	Wind-Dispersed Seed (or spores)	Ladd (2014)

Data on seed banks were also obtained from restoration projects using respread topsoil in banksia woodland and kwongan (sclerophyllous shrubland) ecosystems (Table 1). By combining data sources and personal observations, the majority of plants (77%) could be directly assigned to all fire traits, or had data for some of these traits (92% in total). In cases where different trait states are reported within taxa both records are included and noted in the trait variability field. The fire-trait categories used in Table 1 are based on Groom & Lamont (2015) with additional categories for species with substantially enhanced flowering in the first 1–5 years post-fire, are short lived after fire (one year to several decades), or have topsoil-stored seed. Two categories were split (fire-enhanced seed germination and resprouting) between reported totals for traits and extrapolated totals for genera (proportion of sampled taxa with trait X total taxa in genus). Most traits were highly consistent within genera and between different data sources. Additional traits that are important in Western Australia were also noted, such as high flammability of leaves, thick bark, post-fire seed dispersal by wind and phreatophytes (plants utilising groundwater). All data are available from the author or the AusTraits database.

The taxonomic diversity of plants with different combinations of acquired traits for nutrition, pollination and fire were also determined (Appendices 1, 2). Trait complexity was assigned to a scale from zero, for ancestral states, to six, for the most advanced state. Trait categories were averaged for genera and weighted averages were calculated for families (Appendix 1). Trait variability was ranked as (1) basal traits that are highly consistent within families, (2) more variable traits that are usually consistent within genera and (3) highly variable traits that vary considerably within genera or even within species (Appendix 1). Ratios of the taxonomic diversity of plants with one or more complex traits were used to compare the SWAFR to global averages where comparable data exists. Linear regressions fit the comparative data best, explaining 24% of the variability between traits and species richness in families.

Diversity patterns for taxa with complex traits

Diversity maps were used to investigate spatial patterns in plant traits. Datasets for selected plant families or genera were analysed with Biodiverse software (Laffan *et al.* 2010) using the moving window method with 0.5° cells with and an 1° neighbouring area. Results of different diversity and endemism metrics produced similar results, so only a species richness map is presented.

RESULTS AND DISCUSSION

Overall plant diversity

An updated list of plant species for the larger SWAFR area (Fig. 2) contains 7883 species (including unnamed species with informal names) and 8703 taxa (including subspecies, varieties and forma). The overall diversity of vascular plants in all of Western Australia in January 2021 according to the data sources used was 11 415 species (12 666 taxa). Totals for families of plants in the Southwest (Appendix 1)s are substantially higher than previous estimates of the southwest floristic region (Gioia

& Hopper 2017) due to recent taxonomic work (e.g. Wege & Shepherd 2020) and a 34% increase in the area now included in the region.

Despite species being named at a steady rate, over 1000 known unnamed species remain in Western Australia (Wege & Shepherd 2020). Conversations with botanists also revealed that there still are many unnamed and unlisted plants, and that many existing species encompass much wider morphological or genetic variation than would normally be accepted. Thus, the diversity of SWAFR plants is likely to exceed 10 000, about twice that estimated when the area was first recognised as a major global biodiversity hotspot (Myers *et al.* 2000).

Plant nutrition

Nutritional complexity is exceptionally high in Australia relative to global averages (Brundrett 2017a) and in the SWAFR more so than the rest of the continent (Fig. 3). There are ~1600 taxa with cluster or dauciform roots and ~2000 with EM or EM-AM roots, as well as ~3000 other NM plants. Furthermore, plants in the SWAFR show unique levels of complexity due to variability within families or even genera for some traits (see text box, *Nutritional trait complexity*). Other distinct trends include exceptional numbers of carnivorous plants (127) and marine plants (19), as well as many parasitic plants (69), all of which have NM roots (Fig. 4). The diversity of parasitic plants is relatively high for a temperate region and the presence of widespread parasitic trees such as *Nuytsia floribunda* and four species of *Santalum* is also exceptional.

Plants in families reported to have nitrogen fixing associations, which also have one or more other nutritional traits, are also highly diverse (1270) relative to global totals (~20 000, Tedersoo *et al.* 2018). Nitrogen fixation has been confirmed for some *Acacia* spp. and other Fabaceae (e.g. Hansen *et al.* 1987), *Allocasuarina*
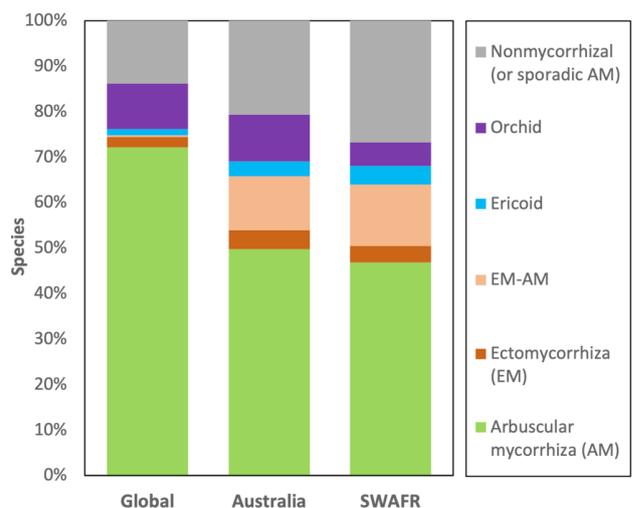
Figure 3. Relative proportions of species with different mycorrhizal association types or nonmycorrhizal roots globally, in Australia and in the Southwest. See Table 1 for data sources.
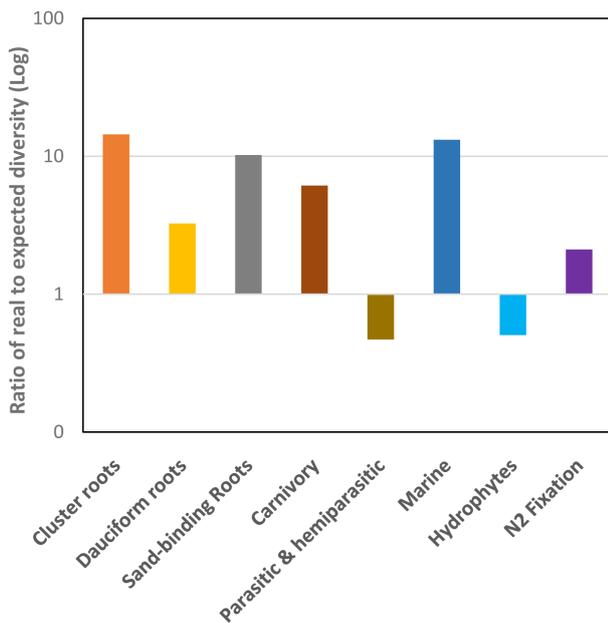
Figure 4. Relative proportions of highly specialised nonmycorrhizal, parasitic and nitrogen fixing plants in southwestern Australian taxa relative to global averages. See Table 1 for data sources.

spp. (Dawson *et al.* 1989) and coralloid roots (Fig. 5I) of the cycad *Macrozamia riedlei* (Grove *et al.* 1980). It has been assumed that all members of these families can fix nitrogen when required (Appendix 1), but it is common to find non-nodulated individuals. Members of the Zygophyllaceae have been reported to fix nitrogen (Tedersoo *et al.* 2018), but information on Australian species is lacking.

Further research is required to resolve trait complexity (see text box, *Nutritional trait complexity*). Both EM and cluster roots are considered to be more energy intensive than AM roots to produce, but these costs are compensated for by improved nutrition in highly infertile soils where phosphorus is tightly captured (Shane *et al.* 2005; Lambers *et al.* 2018). NM monocot species in certain families commonly have dauciform roots, which function like cluster roots, and sand binding roots that have less studied roles (Shane *et al.* 2005; Smith *et al.* 2011). Ectomycorrhizal roots typically also require more energy than AM roots, but are also believed to be more efficient, especially in soils high in organic matter (Raven *et al.* 2018; Soudzilovskaia *et al.* 2019; Li *et al.* 2020). Plants with advanced nutritional specialisations are typically most successful on the least fertile soils in Western Australia (Lambers *et al.* 2010; Zemunik *et al.* 2016; Brundrett *et al.* 2017a).

Australian habitats also contain an exceptionally high diversity of hypogeal (truffle-like) EM fungi (Fig. 5K), whose spores are dispersed by larger animals and insects (Bougher & Lebel 2001; Houston & Bougher 2010; Sheedy *et al.* 2016). SWAFR plant lineages with EM, including some shrubs in the Fabaceae and Myrtaceae, are keystone species for fungus feeding animals such as Gilbert's potoroo, bandicoots and woylies, as well as geotrupid beetles (Bougher & Lebel 2001; Houston & Bougher

2010; Nuske *et al.* 2017). Fungi that fruit underground in relatively dry habitats have undergone convergent evolution resulting in larger digestion-resistant spores and stronger scents to attract animals (Sheedy *et al.* 2016). Thus, animal dispersal is required for many essential symbiotic fungi, adding another layer of complexity to SWAFR ecosystems.

Nutritional trait complexity

Examples of plant clades with complex nutrition include dual AM-EM associations, cluster roots and invertebrate trapping structures (Fig. 5). The data reveals multiple switching events from arbuscular mycorrhizas (AM) to ectomycorrhizas (EM), or from AM to cluster roots, especially in the Myrtaceae and Fabaceae (Fig. 6). These represent clades with Newly acquired Complex Roots (NCR), most of which have diversified rapidly in the past 30 Ma (Brundrett 2017a; Brundrett & Tedersoo 2018). NCR genera are most common in two large families, the Myrtaceae and the Fabaceae:

1. The Myrtaceae includes (i) large shrubs or small trees like *Agonis, Kunzea* and *Eremaea*, in which EM roots are scarce and appear dysfunctional, (ii) shrubs and trees in *Melaleuca* in which species are either AM or EM-AM (Fig. 5BC) and (iii) *Eucalyptus*, *Corymbia* and other related trees whose roots primarily are EM, with occasional AM.

2. In the Fabaceae genus *Acacia* about half of the examined Australian species have EM (with AM) and the rest had only AM (Brundrett 2017a). Traits are correlated with plant size as EM are most common in trees and large shrubs. There are EM in at least four other Fabaceae genera (Appendix 1). *Daviesia* includes species with nonmycorrhizal cluster roots, as well as mycorrhizal species and a few that have both (Brundrett 2008, 2017a; Nge *et al.* 2020b). Several Fabaceae genera have cluster roots that are not always present (Appendix 1).

Compiling plant nutrition data for regions is usually straightforward because these traits are highly conserved within most plant lineages (Brundrett 2021). The SWAFR includes plant families for which data are complex due to highly variable or contradictory information. These primarily include the Fabaceae and Myrtaceae as explained above, but has also been reported in the Cyperaceae and Restionaceae. Nutritional trait innovation complexity in the SWAFR includes many more than expected clades with multiple traits that have overlapping functions, so some may be relic and redundant (Fig. 6, Appendix 1). These root trait gradients extend from AM only to AM (EM), AM-EM, EM-AM and EM (AM). These trait combinations, which list the dominant trait first and intermittent traits that may no longer be functional in brackets, form evolutionary sequences concluding in EM, or fully NM cluster roots. It has not been determined how habitat and climatic conditions and phylogeny interact to regulate nutrient trait switching, or if there also are instances of reversion back towards AM only roots (Brundrett 2017a). Many more plants belong to clades with a complex mycorrhizal status in the SWAFR than anywhere else, strongly suggesting that trait evolution is currently underway and may even be accelerating there (Brundrett 2017a; Brundrett & Tedersoo 2018).
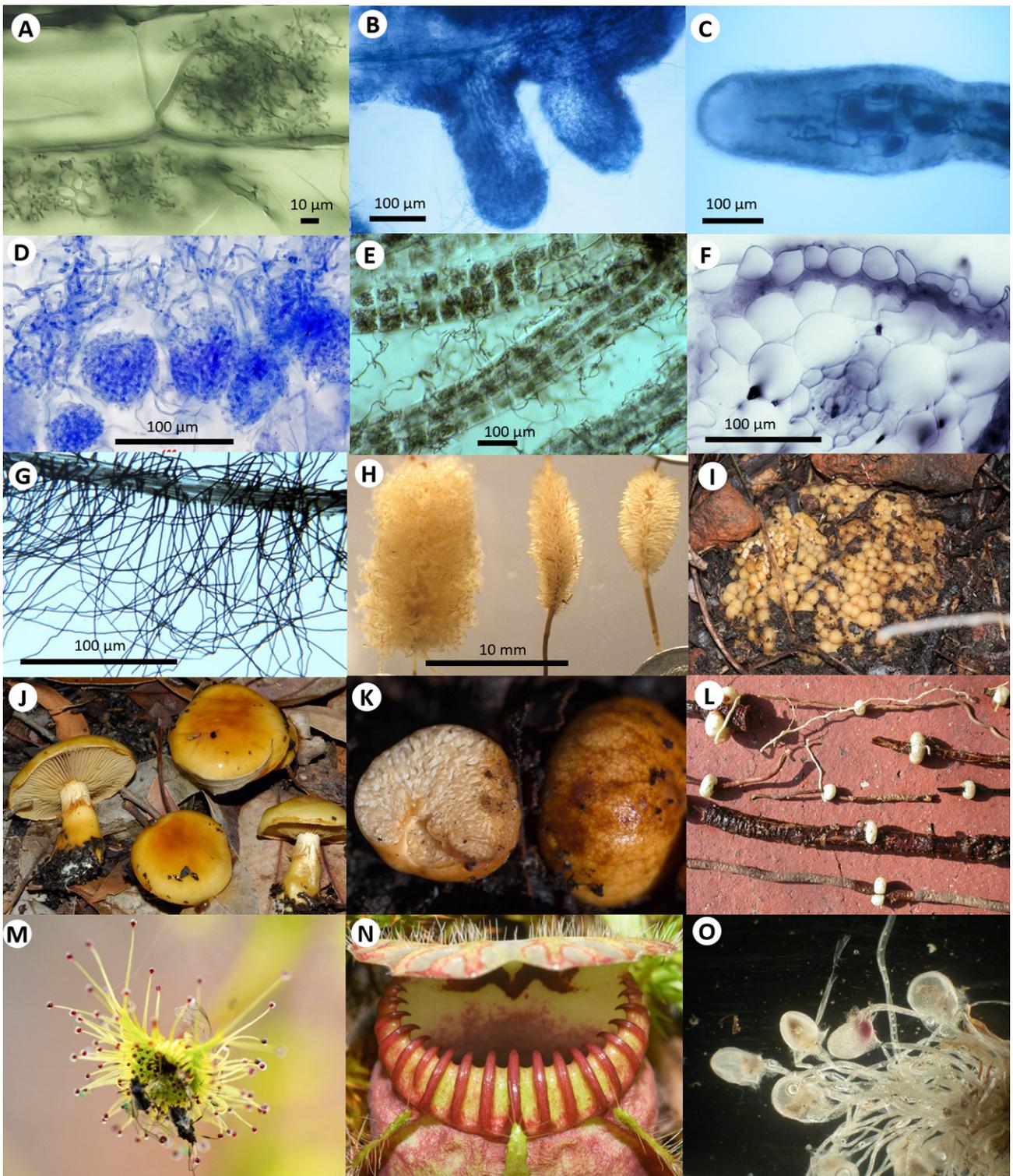
Figure 5. Examples of southwestern Australia plants with mycorrhizal root types and other highly specialised nutrient uptake mechanisms. These include: A) arbuscular mycorrhizas, B) ectomycorrhizas, or C) dual arbuscular mycorrhizas and ectomycorrhizas in *Melaleuca hamata*; D) orchid mycorrhizas in *Pterostylis sanguinea*; E) ericoid mycorrhizas in *Leucopogon verticillatus*; F) unique sub-epidermal associations of *Thysanotus*; G) long root hairs of a nonmycorrhizal carnivorous plant *Drosera erythrorhiza*; H) nonmycorrhizal cluster roots of *Hakea prostrata*; I) coralloid nitrogen-fixing roots of *Macrozamia riedlei*; J) ectomycorrhizal fungus *Cortinarius sinapicolor*; K) animal dispersed truffle-like ectomycorrhizal fungus *Zelleromyces*; L) parasitic root haustoria of *Nuytsia floribunda*; M) glandular leaf invertebrate traps of *Drosera menziesii*; N) leaf pitcher invertebrate traps of *Cephalotus follicularis*; and O) suction invertebrate traps of *Utricularia multifida*.

A. Myrtaceae

EM-AM or AM 17%

AM 47%

EM (AM) 27%

AM-EM 2%

AM (EM) 7%

B. Fabaceae

NM or AM 9%

EM (AM) 13%

AM 29%

AM (EM) 5%

AM-EM 44%
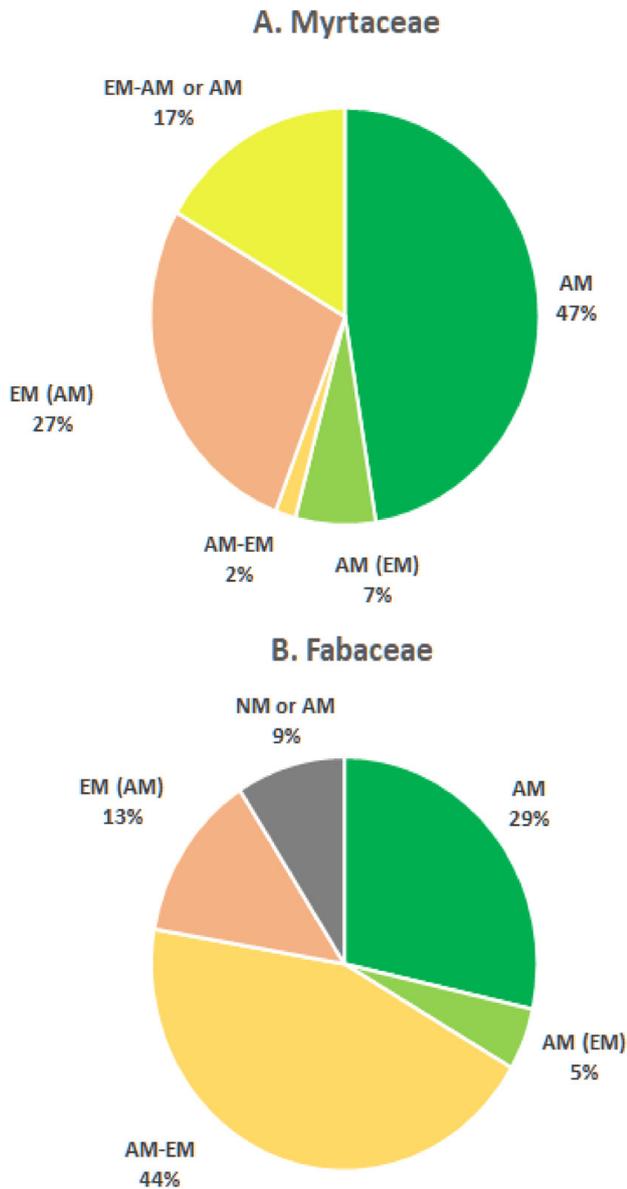
Figure 6. Case studies of families or genera with exceptionally complex nutritional traits within southwestern Australia for A) the Myrtaceae and B) Fabaceae. AM = arbuscular mycorrhizas, EM = ectomycorrhizas, NM = nonmycorrhizal.

Pollination traits

West Australian plants typically have specialised mechanisms that increase pollination efficiency and improve outcrossing (Brown *et al.* 1997; Groom & Lamont 2015; Brundrett, Ladd & Keighery unpublished). These include relatively or extremely complex interactions with specific insects, birds and non-flying mammals (Fig. 7) such as:

1 Non-biotic pollination in 993 wind pollinated and 35 water pollinated taxa (marine plants or hydrophytes).

2 Flowers primarily or partly bird pollinated in over 1000 taxa, much more than global averages. Flowers in these plants have been modified to be more attractive and accessible to birds such as honeyeaters.

3 At least 130 taxa are pollinated by non-flying mammals, especially honey possums, which also visit many other flowers.

4 There are very specific relationships with insects in over 3500 plants that have complex flower structures including secondary pollen presentation, buzz pollination and post-pollination colour changes.

5 The most complex families include the Myrtaceae with ~130 species with bee pollinated flowers and ~100 that are primarily bird pollinated. The Fabaceae includes ~20 bird-pollinated species and ~600 with specific insect visitors (Appendix 1).

6 Extreme pollination specialisation occurs in the Orchidaceae, including >200 taxa with visually deceptive flowers that lack rewards for pollinators and >170 with highly specific insects attracted by sexual deception (Brundrett 2014).

Responses for fire

The majority of SWAFR plants (90%) have at least one acquired fire-response trait (Fig. 8), including most trees, many shrubs and other long-lived perennials with rhizomes, bulbs or corms (Appendix 1). Overall, 48% of taxa have multiple fire traits, such as enhanced seed germination along with promoted flowering and/or resprouting (Fig. 8). The data in Figure 8 includes both conservative values based on documented responses only, as well as estimates of all species likely to have such traits. Fire-response traits are highly variable in some families and genera (see text box, *Fire trait complexity*).

RESPROUTING

At least 1500 species in 67 families resprout after fire (Appendix 1). Resprouting from enlarged subterranean stem bases (lignotubers) occurs in over 1000 dicot taxa and there are 616 monocots with rhizomes that normally resprout after fire. A further 69 rhizomatous hydrophytes or marine plants avoid fire. Many trees have lignotubers, as do shrubs in the Myrtaceae and Proteaceae, but some also or only resprout from epicormic buds in their trunk and branches (Figs 9, 10). Lignotubers, stems and rhizomes are combined, as many reports do not specify how resprouting occurs (Appendix 1). Subterranean bud protection is coupled with storage organs to fuel rapid regrowth after fire (Paula *et al.* 2016). Resprouting in *Daviesia* spp. is driven by a unique type of storage roots (Pate & Dixon 1982; Crisp & Cook 2003).

Increased foliage flammability due to essential oil accumulation occurs in at least 900 resprouter species in the Myrtaceae, Rutaceae and Xanthorrhoeaceae (Fig. 9J). This trait increases local fire intensity resulting in a competitive advantage over plants that lack rapid regrowth after fires (Bond & Midgely 1995; Bowman *et al.* 2014), but can also lead to high mortality after extreme fires.
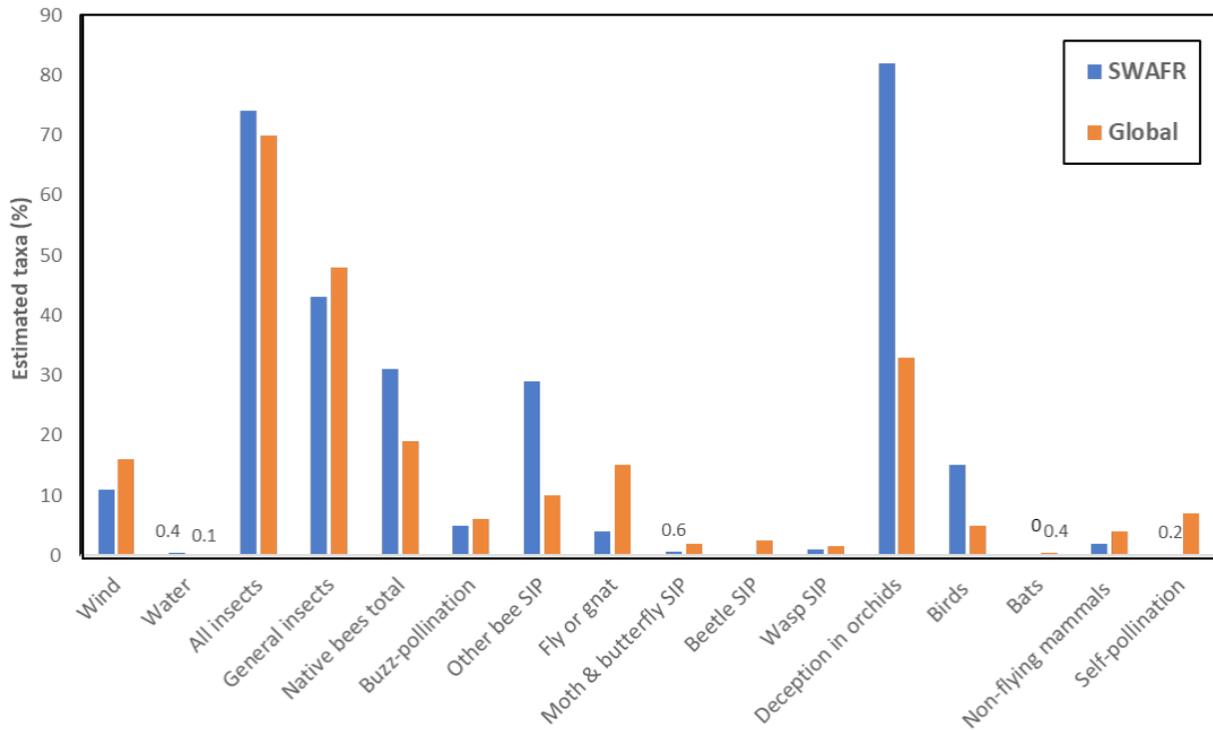
Figure 7. Summary of pollination traits in southwestern Australian plants relative to published estimates of global averages, with ferns included for comparison (SIP = specialised insect pollination). Only values <1 are provided. See Table 1 for data sources.
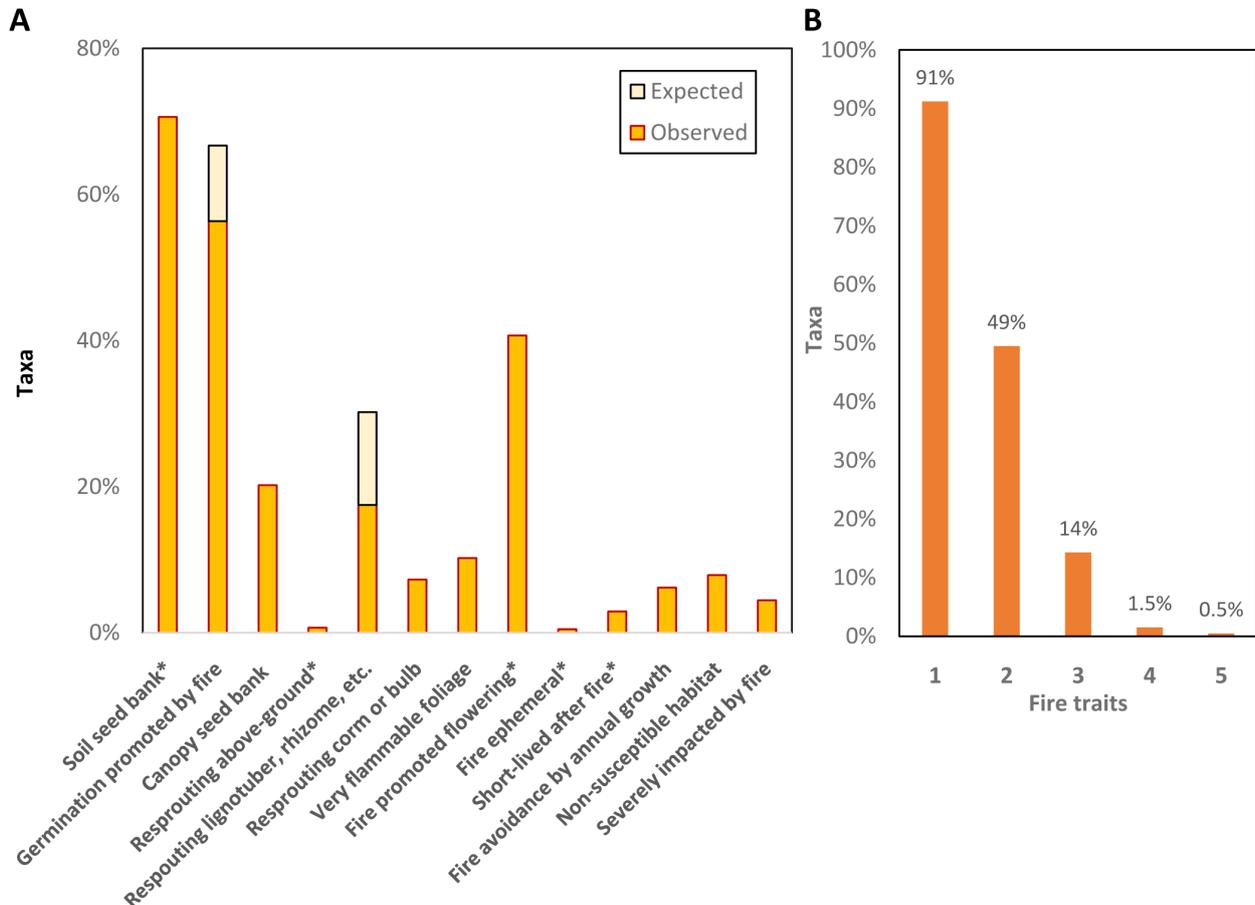
Figure 8. A. Summary of data on fire trait allocations for plant taxa in southwestern Western Australia (see Appendix 1; * indicates not a discrete category). B. The proportion of these taxa with single or multiple fire traits. Two traits with less data include extrapolated values for all taxa.

Resprouting plants are important in Mediterranean ecosystems, savannahs and prairies and can also be found in tropical or temperate forests after storm damage (Vesk & Westoby 2004; Maurin *et al.* 2014; Charles-Dominique *et al.* 2015; Pausas *et al.* 2016; Paula *et al.* 2016). The global distribution of tropical forests and savannas is strongly regulated by both rainfall and fire, as rainforests species tend to be fire intolerant (Bowman 2000; Murphy & Bowman 2012). Overall, the diversity of resprouting plants is much higher in the SWAFR than expected in most other regions. This strategy has originated many times within some genera and can even vary within species (see text box, *Fire trait complexity*). The nature of resprouting in SWAFR plants also differs from that in many other regions due to the importance of subterranean woody structures such as lignotubers and modified roots.

There are 543 geophytic species with corms or bulbs in the region (Fig. 8, Appendix 1). Many of these have vigorous growth and enhanced flowering after fire (Fig. 9O). There are at least 13 000 geophytic plants with corms, bulbs or rhizomes globally (Howard *et al.* 2019). They are common in all areas with seasonal climates, especially those classified as Mediterranean (Parsons & Hopper 2003).

SOIL SEED BANKS

About 70% of SWAFR plants recruit from soil or canopy-stored seed as a primary or secondary means of recovery after fire (Appendix 1). These include about 6200 taxa with topsoil-stored seed, of which at least 5000 germinate most abundantly after fire. Inclusion of plants in this category does not imply germination is specifically promoted by heat and/or smoke, but these traits are especially common in the region (Roche *et al.* 1997; Cochrane *et al.* 2002; Merritt *et al.* 2007). Heat promotion of seed germination occurs in hard seeded Fabaceae, with over 1000 species in the Southwest and many species in this family globally (de Casas *et al.* 2017). Other plants that primarily regenerate from seed include 75% of studied Ericaceae species (Bell & Pate 1996) and many others in at least 59 families (Appendix 1).

In the SWAFR, soil seed banks include species with a wide diversity of dormancy mechanisms that commonly occur in combination (Roche *et al.* 1997; Cochrane *et al.* 2002; Merritt *et al.* 2007; Koch *et al.* 2009; Zirondi *et al.* 2019). This results in a continuum of seed types extending from those that are primarily optimised for short-term dormancy (to bypass adverse growing conditions), but germinate more abundantly after fire, to those where germination is primarily, or only, after fire. This evolutionary trend leads to long-term seed dormancy in many SWAFR species and culminates in obligate fire ephemerals. Some hard-seeded species can also germinate in response to extreme summer heat, a factor that could undermine soil seedbank sustainability in the future (Cochrane 2017).

Soil seed banks are important in both Mediterranean and arid environments in Western Australia and it would be expected that the seed remains viable for many years in both systems. However, the importance of seed germination promotion by fire is likely to be much greater in the Southwest where fire is much more frequent (Miller & Murphy 2017; Shedley *et al.* 2018).

These traits are also important for restoration ecology, as the same species tend to emerge in severely disturbed topsoil (Rokich *et al.* 2000; Koch *et al.* 2009; Brundrett *et al.* 2020). For example, the majority of species present in a banksia woodland plant community (115 out of 160) recruited primarily from topsoil transferred to a new site (Fig. 11B), but this did not include trees or the majority of large shrubs that have canopy-stored seed (Brundrett *et al.* 2020). Many arid zone plants also have substantial fire adaptions such as topsoil- or canopy-stored seed (Commander *et al.* 2009; Erickson *et al.* 2018). Global data on species with persistent soil seed banks is limited. This trait is known from at least 15 plant families and 2566 species globally, but many of them have seeds that are viable for less than one year (Baskin *et al.* 2000; Gioria *et al.* 2019). In contrast, the majority of SWAFR plants have seeds that remain viable for decades in soil, particularly fire ephemerals that must survive long periods between fires.

CANOPY-STORED SEED

Storage of seeds for multiple years in the canopy is called serotiny, or bradyspory, but the former term is preferred (Lamont 1991). There are 1765 species with canopy-stored seed in five families in the SWAFR (Fig. 8, Appendix 1). This trait is most prevalent in the Myrtaceae (1143 taxa) and Proteaceae (448 taxa), but is also present in *Allocasuarina*, *Callitris* and samphires (Chenopodiaceae). About 420 serotinous species have seeds that are dispersed by wind after fire. Some Western Australia plants have extreme serotiny, such as the thick woody fruit that protects seed in hakeas and banksias. However, these structures also defend seed from granivorous birds, especially black cockatoos (Valentine *et al.* 2014; Groom & Lamont 2015). Only about 170 serotinous species are documented from outside Australia, including ~50 northern hemisphere conifers and 87 South African Proteaceae, but this is likely to be an underestimate (Lamont *et al.* 1991). At the other extreme it has been estimated that 8–20% of all plants globally have desiccation intolerant seed (Wyse & Dickie 2017), a trait that is rare in the SWAFR.

EXTREME FIRE SPECIALISTS

These plants are abundant by global standards in the SWAFR. These include fire ephemerals and orchid species that only flower after fire (Appendix 1). Some fire ephemerals also respond to soil disturbance so are not restricted to post-fire situations (Bell *et al.* 1984). Plants that are highly dependent on fire for growth or reproduction include:

1 At least 43 species of fire-ephemeral plants including annuals only found the first year after fire or perennials that persist for a few years after fire (Fig. 8, Appendix 1). These include most Gyrostemonaceae, *Brachyscias* (Fig. 9S) and some other Apiaceae, and members of 10 other families (Pate *et al.* 1985; Groom & Lamont 2015). Some of these annual species also have populations that germinate without fire (e.g. *Trachymene* spp.).

2 There also are at least 230 species with peak growth and reproduction after fire, followed by gradual attrition over several decades (Appendix 1). These include species of *Gompholobium*, *Bossiaea*, *Kennedia*
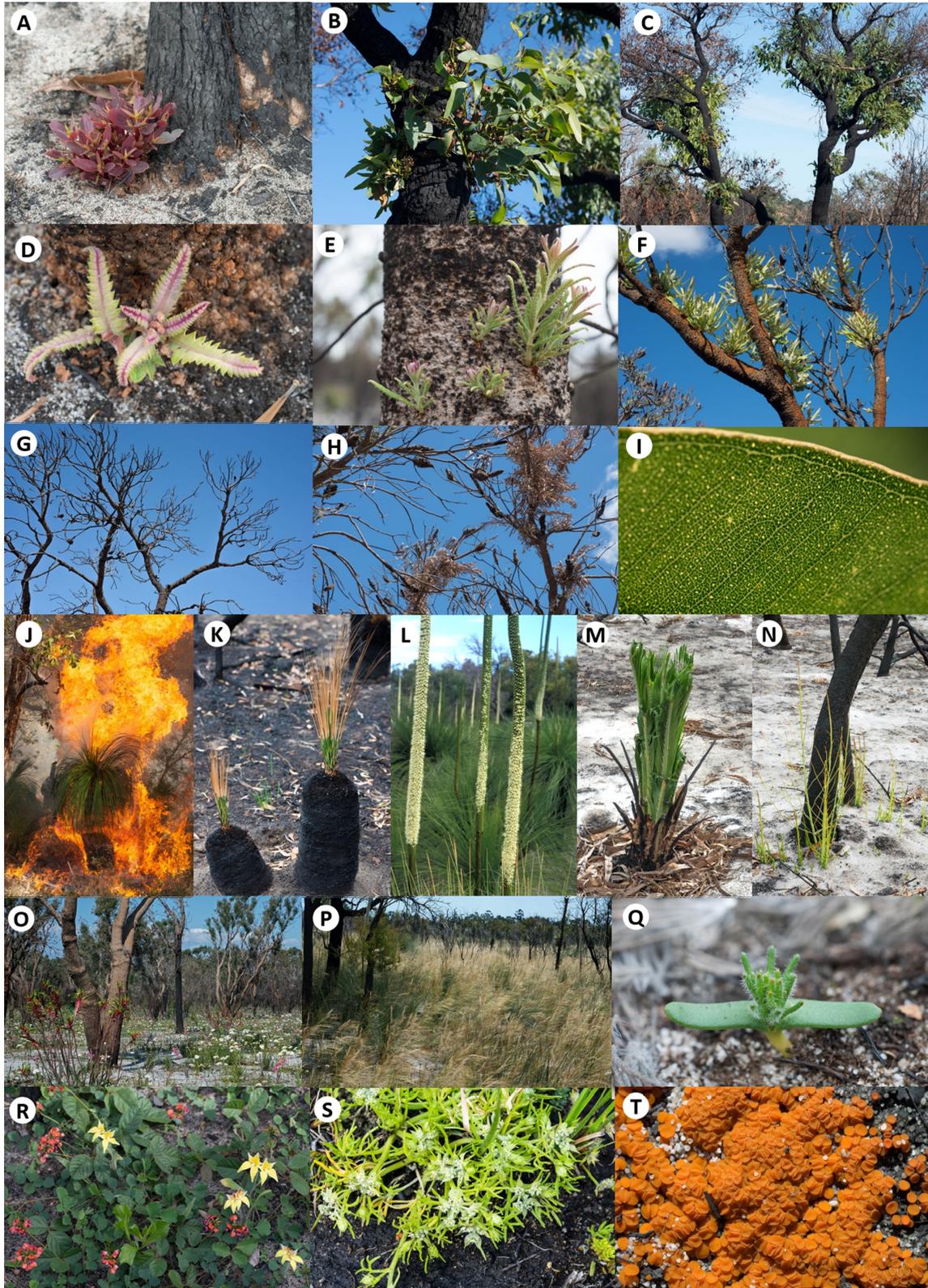
Figure 9. Illustrations of fire traits for selected southwestern Australian plants. Resprouting in *Eucalyptus todtiana* from A) the basal lignotuber, B) trunk, and C) crown; D) resprouting in *Banksia menziesii* from the lignotuber; resprouting in *B. attenuata* from E) the trunk or F) branches; G) *B. menziesii* killed at the time of thefire, or H) after resprouting; I) oil glands in leaf of *Eucalyptus tetraptera*; J) extremely flammable leaves of *Xanthorrhoea preissii*, but K) rapid regrow after fire, followed by L) abundant flowering; M) resprouting *Macrozamia riedlei*; N) *Nuytsia floribunda* resprouting from roots; O) temporary post-fire dominance by geophytes or P) the annual native grass *Austrostipa flavescens*; Q) germinating *Adenanthos cygnorum*; R) flowering promoted in *Caladenia flava* and *Kennedia coccinea*; S) the fire ephemeral *Brachyscias verecundus*; and T) the ash bed fungus *Anthracobia* sp.

A. Myrtaceae
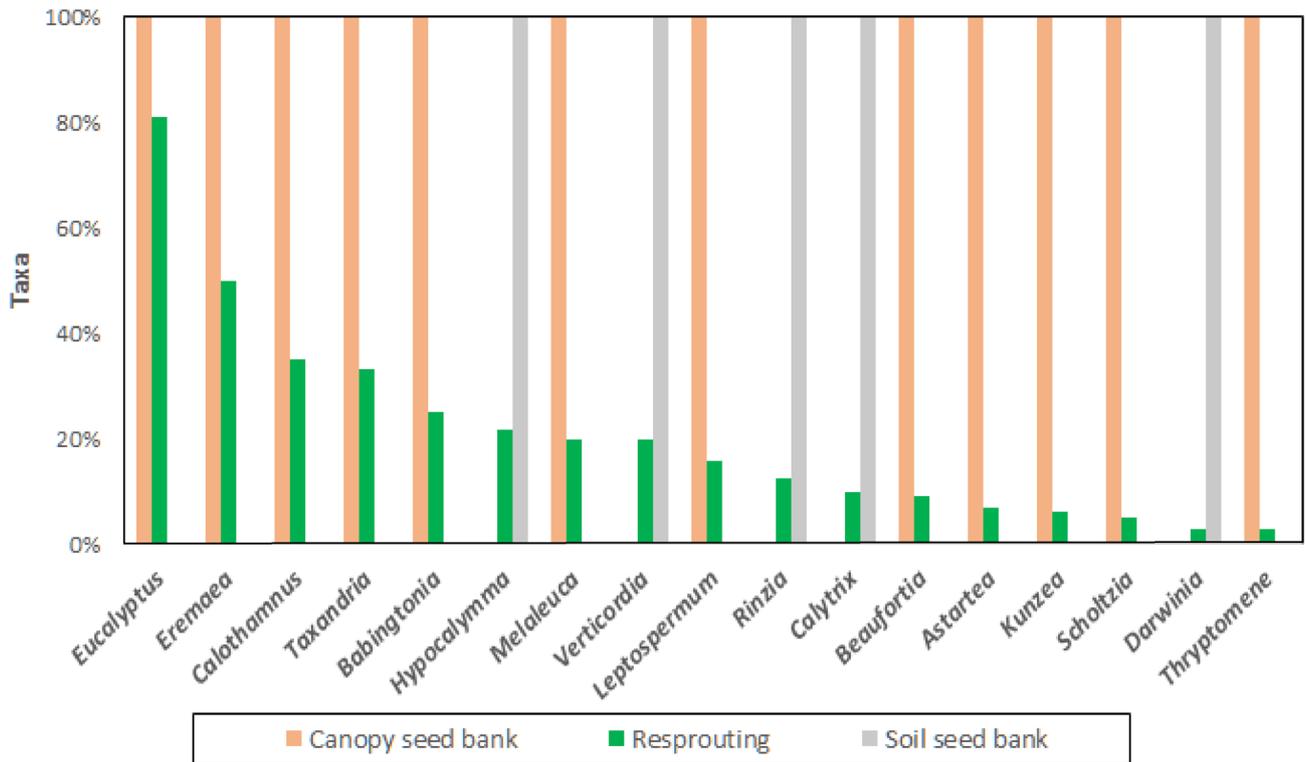
B. Proteaceae
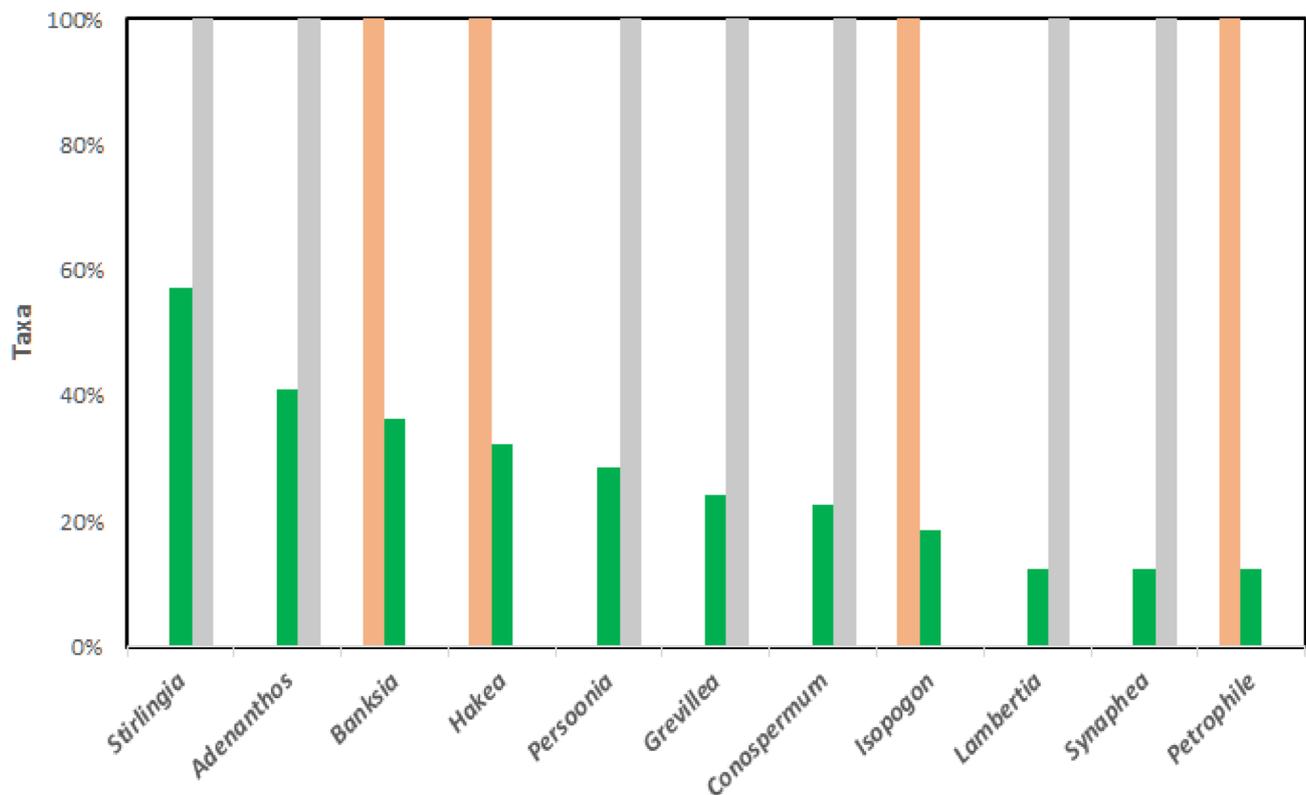
Figure 10. Case studies showing proportions of species with different fire trait specialisations in the largest genera within the plant families A) Myrtaceae and B) Proteaceae.

and *Viminaria* in the Fabaceae, as well as *Actinotus*, *Anthocercis*, *Macarthuria* and *Platysace*.

3 Fire promoted flowering occurs at least to some degree in over 3000 SWAFR species including many geophytes, resprouting and reseeding plants (Fig. 9R). This trait is also relatively common in the South African Mediterranean climate zone, but not elsewhere (Lamont & Downes 2011).

4 Pyrogenic flowering occurs in the Colchicaceae, Haemodoraceae, Orchidaceae and Droseraceae, etc. (Lamont *et al*. 2019). Their flowers are highly visible to pollinators, or have less competition for them, than many other plants that require years to begin flowering after fire (Burrows *et al*. 2008). Whereas many orchids flower prolifically after fire, some flower primarily (27 species) or only (10 species) after fire (Brundrett 2014). However, others are likely to be harmed by fire, as explained below.

FIRE AVOIDANCE

There are 1175 geophyte or annual taxa that can avoid fire through summer dormancy or as seed (Appendix 1). Others grow in habitats where fire is unlikely or impossible. These include aquatic and marine plants as well as arid zone plants or halophytes which have succulent foliage or grow in areas with sparse vegetation (Appendix 1). These may still have fire adapted traits but are not as well studied as plants in more fire prone areas. Annuals are expected to be able to avoid fire and/ or recolonise sites due to wind-dispersed seeds, but some fail to reappear after severe fires (see **Winners and losers after fire**).

Fire trait complexity

1. There are 375 eucalypt taxa (*Eucalyptus* and *Corymbia*) in the region. These have variable fire traits, with 76% resprouting from lignotubers only, 1% resprouting from epicormic buds only and 6% resprouting from both (Fig. 9A–C). All species have canopy-stored seed so can germinate prolifically after fire (McCaw & Middleton 2015), but 18% lack resprouting capacity so only reseed (Appendix 1). Species with epicormic sprouting but no lignotubers may also primarily reseed after severe fires. Over 400 *Eucalyptus* species have lignotubers (Nicolle 2006; Clarke *et al*. 2015). Eucalypts also have highly flammable foliage (Bowman *et al*. 2014) due to oil storage in modified leaf cells called punctate glands (Fig. 9I). Their bark is either thick enough to protect trunks, or thin and frequently shedding, so contributes to the fuel load accumulating around tree bases (Grootemaat *et al*. 2017).

2. Fire-response complexity in myrtaceous shrubs such as *Melaleuca* includes canopy-stored seed in all species and about 25% of species that resprout from lignotubers (Fig. 10A, Appendix 1). In contrast, *Verticordia* is predominantly a reseeding genus of 94 species, but includes 14 resprouting species, including four with this trait in one subspecies but not in others (George & Pieroni 2002). Overall, there are >450 reported resprouters in 16 genera in the Myrtaceae (Fig. 10A), but the actual number would likely be over 700 when extrapolated to include data-deficient species. Many of these shrubs also have prominent oil storage glands in leaves or stems that increase their flammability.

3. There is similarly complex variability in resprouting capacity in Proteaceae taxa with canopy-stored seed or soil seed banks with fire-promoted germination, as well as >250 resprouters that also reseed (Appendix 1). There is a similar diversity of plants with canopy-stored (5 genera, 432 taxa), or topsoil-stored seed (9 genera, 487 taxa). These strategies are consistent within genera (Fig. 10B), but also help to define them. For example, *Hakea* is a monophyletic serotinous clade nested within *Grevillea* which are generally not serotinous (Mast *et al*. 2015). In contrast there are many separate origins of resprouting in the Proteaceae, which varies from none to all species in a genus (Fig. 10B). At least 11 *Banksia* or *Grevillea* species have resprouting ability that varies between subspecies. Variations in resprouting capacity and post-fire survival of banksias are linked to tree size and fire intensity (Figs 9D–H), but also vary over geographic ranges of species (Cowling & Lamont 1985).

4. Resprouting occurs in 10 Fabaceae genera, listed in decreasing sprouting frequency: *Hardenbergia, Hovea, Isotropis, Daviesia, Acacia, Bossiaea, Chorizema, Kennedia, Sphaerolobium Gastrolobium* and *Jacksonia*, but not in 31 others (Appendix 1). Resprouting occurs in 9 out of 60 species of *Acacia* examined (Burrows *et al*. 2008), but varies due to fire severity and bud depth (Wright & Clarke 2007). Overall, 6% of taxa in the Fabaceae resprout, with an extrapolated total of 18% of SWAFR species (Appendix 1).

5. Vigorous resprouting occurs from the stem and base of the arborescent monocots *Xanthorrhoea* spp., *Kingia australis* and *Dasypogon hookeri* (Lamont & Downes 1979; Staff & Waterhouse 1981). Growing points of these plants are protected by non-flammable leaf bases, but *Xanthorrhoea* leaves are extremely flammable overall (Figs 9J, K). These plants also flower most prolifically after fire (Fig. 9L).

6. Other examples of extreme fire recovery traits include anomalous wood in *Nuytsia floribunda* that allows resprouting from deep within its branches, but this tree also resprouts vigorously from roots (Fig. 9N). The cycad *Macrozamia riedlei* resprouts vigorously from its buried trunk (Fig. 9M). Resprouting from relatively fine roots also occurs in shrubs that 'sucker' such as species of *Lechenaultia* and *Isotropis*. These plants are virtually unkillable and flower most abundantly after fire. A similar strategy occurs in long-lived clonal plants including *Stirlingia latifolia* and *Hibbertia hypericoides*. The latter are two of the most dominant understory plants in banksia woodland, but may be non-clonal in other habitats.

7. Resprouting also occurs in over 1500 geophytes and at least 500 rhizomatous species (Appendix 1) that can flower prolifically after fire. Fire ephemeral grasses such as *Austrostipa* spp. that reseed also flower abundantly (Figs 9O, P).

103

FIRE INTOLERANCE

Plants that are killed by fire and lack a soil seed bank are less common than other categories (Fig. 8), but many plants become less dominant after fire. Mistletoes, which are killed when trees burn, can be dispersed by birds over moderate distances, but are lost from regions after large fires (Gosper & Prober 2020). Orchids such as *Pterostylis* and *Corybas* species are less likely to be seen after hot fires (166 taxa). These have relatively shallow tubers and prefer to grow in accumulated litter. The underground orchids (*Rhizanthella* spp.) should also be highly vulnerable to fire because they are fully reliant on mature plants of certain *Melaleuca* spp. for sustenance (Bougoure *et al*. 2010). The mycorrhizal fungi that orchids require to germinate and grow are most active in coarse soil organic matter (Brundrett *et al*. 2003), so frequent fires may indirectly impact on the abundance, diversity and vitality of all terrestrial orchids.

OTHER IMPORTANT TRAITS FOR SURVIVAL AND SPREAD

Many plants with canopy-stored seeds are dispersed by wind or animals after fire (Auld & Ooi 2017; Keith *et al*. 2020), including at least 1266 wind-dispersed plants (Appendix 1). Seed dispersal mechanisms involving birds, insects or other animals are also common for plants in the soil seed bank (Groom & Lamont 2015). Xerophytic plant traits occur in the majority of SWAFR perennial non-geophytic species and these traits are also common in other biomes. Reliance on intermediate or deep stored groundwater is important for trees and large shrubs that grow in summer (Zencich *et al*. 2002; Froend & Sommer 2010), including some banksias and many eucalypts. Many of these also flower in summer so have key roles supporting pollinators.

WINNERS AND LOSERS AFTER FIRE

SWAFR plants have a wide spectrum of inbuilt fire responses, but their survival is also regulated by fire intensity, frequency and seasonality (Godfree *et al*. 2021). Most habitats include fire ephemerals and fire intolerant species (Fig. 11A). Fire can also cause the loss of native annuals presumably because their seed was consumed with the litter (Bell *et al*. 1984; Brundrett & Longman 2016). Changes to vegetation structure last for years after fire and are primarily due to the altered dominance of plants, which is related to their fire traits (Hobbs & Atkins 1990; Burrows *et al*. 2008; Gosper *et al*. 2012; McCaw & Middleton 2015; Brundrett & Longman 2016; Etchells *et al*. 2020). Some reseeding native plants become much more dominant after fire in ecosystems and also tend to dominate young revegetation sites (Fig. 11B; Grant & Koch 1997; Brundrett *et al*. 2020). Disturbance opportunists such as species of *Gompholobium, Kunzea, Jacksonia, Acacia, Anthocercis, Kennedia* and *Adenanthos* (Fig. 9Q) can be abundant after fire but are relatively short lived. These include nodulated species of Fabaceae that help replace nitrogen, along with increased nodulation by *Allocasuarina* and *Macrozamia* (Hansen *et al*. 1987; Grove *et al*. 1980).

Fully aquatic and marine plants are fire avoiders, but plants in seasonal wetlands can be severely impacted. Peatlands are vulnerable to fire throughout Australia (Whinam & Hope 2005) and can be severely impacted
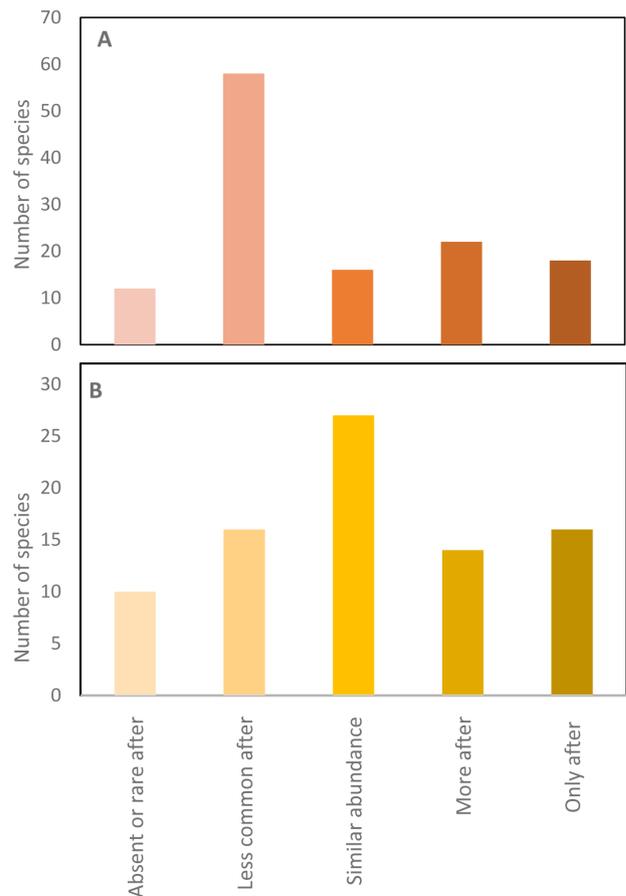
Figure 11. Responses of banksia woodland species to A) fire, or B) severe soil disturbance caused by topsoil transfer. Rankings are based on changes in the relative dominance of all plant species present (Brundrett *et al*. 2018, 2020).
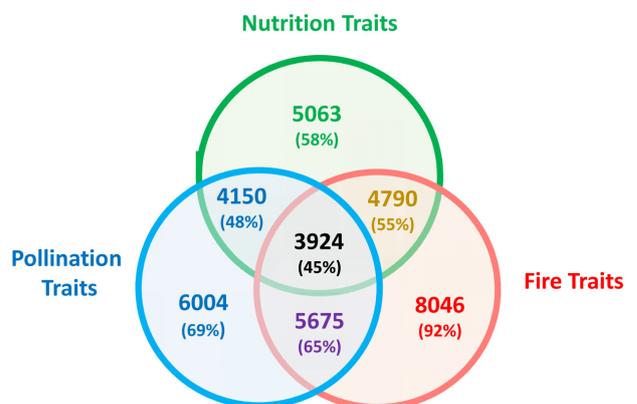
Figure 12. Venn diagram showing overlap in numbers of southwest Australian plants with relatively advanced nutrition, fire or pollination trait specialisations alone or in combination.

in the SWAFR (e.g. www.abc.net.au/news, accessed 19-2-2021). Ground fires can eliminate seed banks and resprouting structures when soil with high organic matter combusts (Bradshaw *et al*. 2018). Another commonly observed fire-response trend is for the dominance of weeds, especially grasses, exotic trees and annuals, to substantially increase at the expense of native plants (Hobbs & Atkins 1990; Milberg & Lamont 1995; Van Etten 1995; Fisher *et al*. 2009; Brundrett & Longman 2016). Common fire-promoted weeds include veldt grass (*Ehrharta calycina*), *Pelargonium capitatum*, pigface (*Carpobrotus edulis*) and weedy trees, especially exotic acacias and eucalypts. For example, one recent fire resulted in thousands of seedlings of *Acacia trigonophylla*, a non-local shrub uncommon before the fire (Keighery *et al*. 2017). Veldt grass alters the fuel composition potentially increasing the rate of spread of fires (Van Etten 1995).

Species that normally resprout strongly can be killed if severely burnt. For example, 51% of banksia trees died after an intense fire in Kings Park in 1989 (Bell *et al*. 1992) and 40% were killed by another in Banjup in 2014 (Brundrett & Longman 2016). Banksias can respond to fire by vigorously resprouting and reseeding (Fig. 9), but canopy structure requires years to recover (Brundrett *et al*. 2018), as is also the case in eucalypt forests (Wardell-Johnson *et al*. 2018a). Banksia seeds are also shed during drought providing some annual recruitment, but this increases dramatically after fire, resulting in thousands of seedlings per ha (McCaw & Middleton 2015; Brundrett *et al*. 2018). Most eucalypt species resprout and germinate from canopy-stored seed after fire, but 64 lack resprouting capacity so can only reseed (see text box, *Fire trait complexity*). Examples include *Eucalyptus salubris* (gimlet) and 43 relatively small trees (mallets). Species with epicormic buds but no lignotubers usually resprout, but may reseed only after extreme fires. These include *E. diversicolor* (karri), (Etchells *et al*. 2020), *E. salmonophloia* (salmon gum; Gosper *et al*. 2018) and *E. gomphocephala* (tuart). Overall, kwongan species with canopy-stored seed are less resilient than those with soil seed banks, or species which also resprout; however, even strong resprouters require some seedling recruitment to maintain populations (Enright *et al*. 2014). Impacts due to changes the fire severity or frequency, land clearing, as well as unsustainable timber harvesting, or grazing on SWAFR forests are of major concern due to their outstanding natural and cultural heritage values (Yates *et al*. 2017; Wardell-Johnson *et al*. 2018b). About half of the threatened flora species in the SWAFR are reseeders that are expected to be sensitive to increasing fire frequencies (Shedley *et al*. 2018).

Perennial plants have post-fire juvenile periods and most flower by year three, but trees can take more than seven to do so (Burrows *et al*. 2008; Brundrett *et al*. 2020; Wajon 2020). Soil seed banks may also be affected by long intervals between fires due to gradual declines in seed viability, as well as effective seed dispersal and seed predation. The longevity of seed in topsoil is largely unknown, but there are cases where plants may have persisted by this means for many decades and possibly centuries. Fire recovery requires at least 15–20 years in kwongan habitats, 25–30 years in sheoak or banksia woodland and up to a century to replace canopy seed

stores in arid woodlands (Enright *et al*. 2011; Harvey *et al*. 2017; Valentine *et al*. 2014; Gosper *et al*. 2018). Resprouters also require time for storage reserves in lignotubers or rhizomes to build up, making them vulnerability to frequent fires (Enright *et al*. 2011). Furthermore, reduction in rainfall due to climate change is predicted to increase the minimum inter-fire interval required for self-replacement, placing many species at risk of decline (Enright *et al*. 2014).

Plants with multiple specialised traits

Trait complexity and transition frequency data (Fig. 13, Appendices 1, 2) suggest the following for plants in the SWAFR:

1 Relative to global averages, plants with advanced nutritional traits are substantially overrepresented (3–14 times greater than expected), many plants have highly specialised pollination syndromes with insects or birds (e.g. 2.5 times more than expected for birds) and an exceptionally high proportion of plants have complex acquired fire traits. For example, serotiny, soil seed banks and resprouting are orders of magnitude more common in the SWAFR than expected from global data.

2 Fire traits are highly variable and can differ between subspecies or even between populations of species, pointing to ongoing evolution in response to strong selective pressures (see text box, *Fire trait complexity*).

3 Pollination traits are also evolving relatively rapidly, as some vary within genera, especially due to switches to pollination by birds or specific insects.

4 Nutrition traits have switched the least frequently and are consistent in most families. However, variability is common in the three largest SWAFR families, where evolution is ongoing (see text box, *Nutritional trait complexity*).

5 Trait transitions are more complex for fire and pollination than nutrition, leading to more trait types and intermediate trait states.

6 Many SWAFR species have complex traits for nutrition, pollination and fire (Figs 3–10). Overlap between these trait categories shows that overall, 58% of taxa have at least one trait category, whereas 47–65% have advanced traits in two categories and 45% are advanced in all three (Fig. 12). Overall, plants with advanced traits for nutrition are also more likely to also have traits for fire and pollination, which appear to be increasing in complexity in parallel (Fig. 13, Appendix 2). Most SWAFR plants also have efficient traits for surviving severe drought, seed dispersal, resistance to grazing, etc., as is common in other biomes.

7 There are 14 plant families with a combined trait index of 10 or higher (Appendix 1). These include many endemic species in the SWAFR and their diversity patterns help define the regional boundary (Fig. 14).

Revising the SWAFR Boundary

Despite the well-recognised significance of the Southwest Australian Floristic Region (Diels 2007; Myers *et al*. 2000;
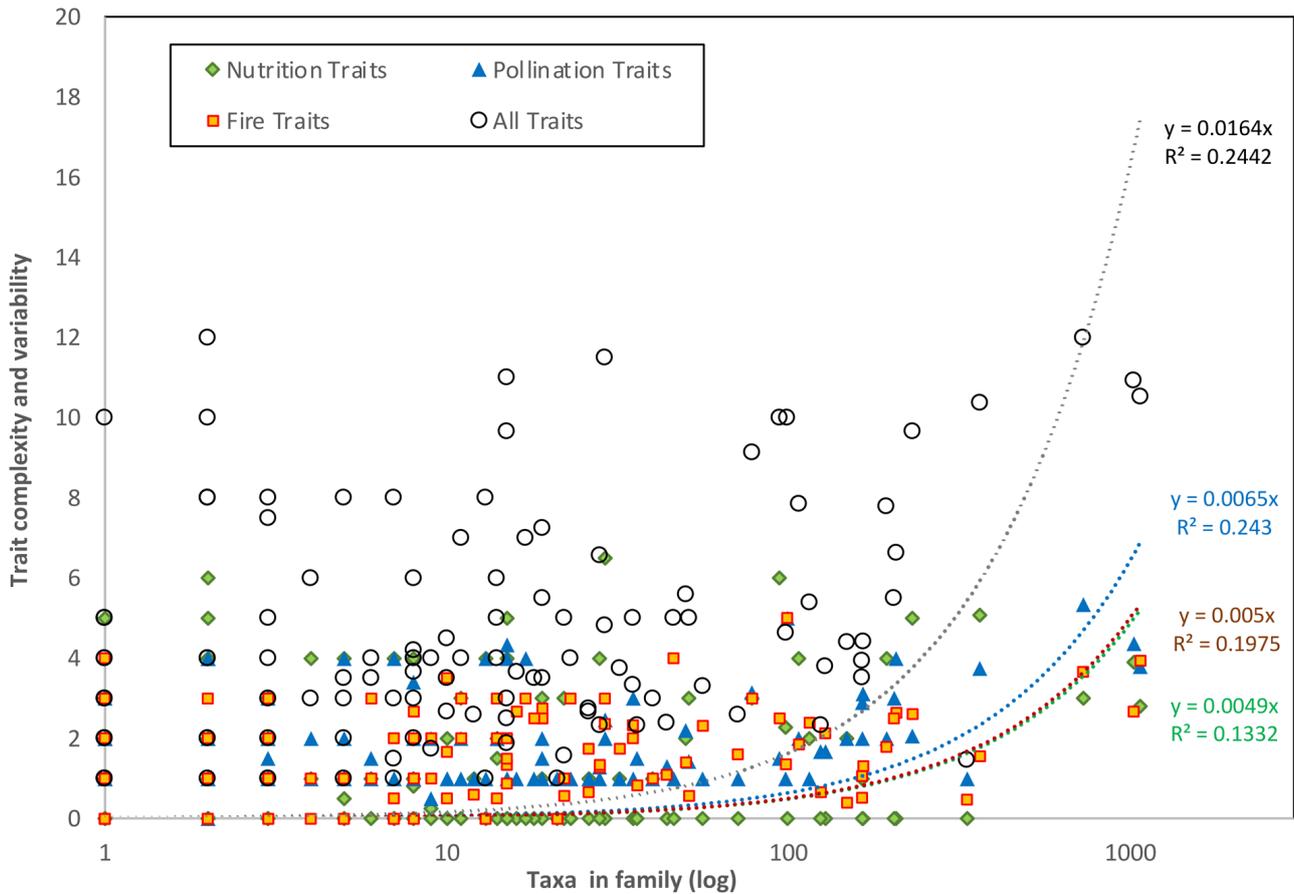
Figure 13. Comparison of the species richness of families of southwest Australian plants relative to complexity of their nutrition, fire and pollination traits, alone or in combination. Trait rankings are based on both the complexity and variability of traits for all taxa within families.

Hopper & Gioia 2004) defined regional boundaries for this region and methods used to define them differ considerably. Gioia & Hopper (2017) used plant species richness patterns and rainfall to define the SWAFR, but their plant diversity data did not extend far beyond their previously delineated boundary. Ebach *et al.* (2015) used the distributions and turnover for about 6000 plant species from nine widespread plant groups to demarcate a larger southwestern phytogeographical region. However, the extent of regions was not precisely determined in their analysis. Verboom & Pate (2015) used a combined analysis of soil and vegetation patterns to determine regional boundaries that were also similar to other studies. Long-term climatic fluctuations in the region (O'Donnell *et al.* 2018) and the recent contraction of the Mediterranean climate zone (Cross *et al.* 2020; grdc.com.au, accessed 3-3-2021) suggests that rainfall patterns cannot be used to define biogeographic regions. Vegetation patterns are strongly regulated by soils, landforms and hydrology (Fig. 1) and these remain much more stable over time.

The expanded SWAFR region boundary proposed here (Fig. 2) is more clearly demarcated than earlier proposed boundaries, as it corresponds with major discontinuities in the vegetation types mapped across Western Australia (Beard *et al.* 2013). Its boundary follows the inland margins of the Coolgardie and Yalgoo IBRA regions. The expanded bioregion includes three highly significant centres of plant diversity, rarity and endemism in the Coolgardie interzone: all of Forrestiana, the Mount Manning Region and the Great Western Woodlands (EPA 2007; Gibson *et al.* 2010; Harvey 2014; Hammer *et al.* 2018). For example, there are at least 1000 plant species including 9 rare, 72 priority and 32 endemic species in the Mount Manning Region (EPA 2007). The expanded bioregion also fully encompasses peak diversity hotspots for acacias (Hnatiuk & Maslin 1988; Bui *et al.* 2014) and eucalypts (Yates *et al.* 2017), the two most important genera in the region (Fig. 14). In addition, this results in a substantial increase of species endemism in the SWAFR (Fig. 14).

The addition of the two interzones into the SWAFR is justified because they contain vegetation that is more similar to the wheatbelt bioregion of the southwest botanical province than to the adjacent Eremaean or Nullarbor regions (Beard *et al.* 2013). Overall, there are six major vegetation types common to both the Coolgardie and wheatbelt regions, out of 13 overall. There is a gradual transition from the wheatbelt to the Coolgardie interzone, but the interzone–Eremaean transition encompasses abrupt changes from eucalypt- to acacia-dominated woodlands to the north and to chenopod-
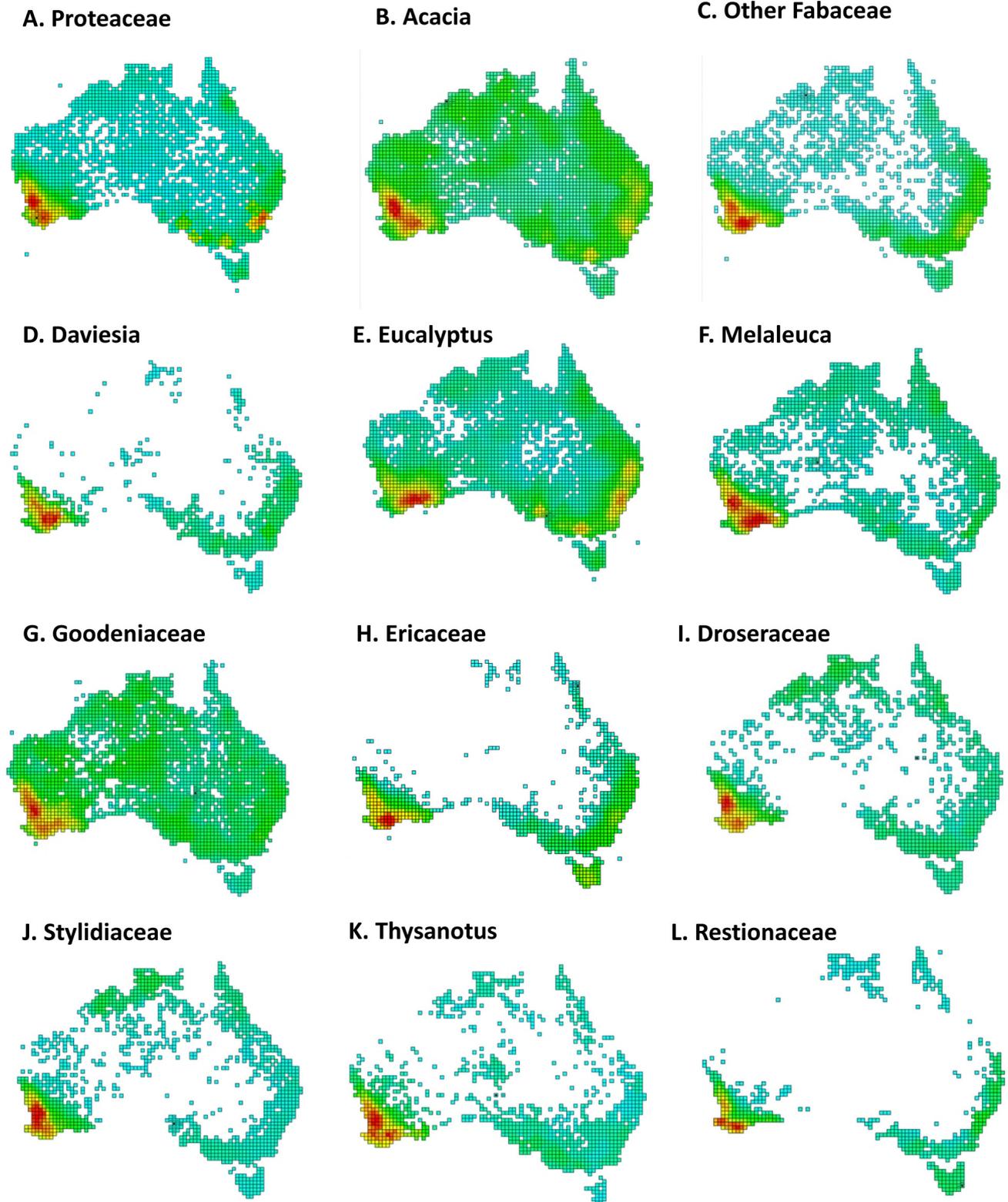
Figure 14. Spatial diversity patterns for selected clades of Australian plants with advanced traits for mineral nutrition, pollination and fire. Collections and observations data are plotted as a species richness index (ABC) using a moving window method, 1° cells and a 3° neighbouring area with Biodiverse software (Laffan *et al*. 2010).

dominated shrublands on alkaline soils across the Nullarbor to the east (Beard 2015). The narrow northern interzone (Yalgoo bioregion) has a mixture of vegetation types that are structurally more similar to wheatbelt than Eremaean vegetation (Beard *et al.* 2013). Both interzones include many poorly known species, especially where plant occurrence data is sparse (Gioia & Hopper 2017), but there is also limited data from the wheatbelt where extensive areas are largely cleared. Some habitat types typical of the SWAFR occur as localised patches in the Eremaean zone (Beard *et al.* 2013; Macintyre & Mucina 2021) and as far north as Cape Range next to Exmouth Gulf (Keighery & Gibson 1993). Specialised vegetation types like salt lakes and rock outcrops are important on both sides of the new SWAFR boundary but occupy relatively small areas.

An alternative designation for the biodiverse region in the Southwest is the Southwest Australian Trait Evolution Region (SWATER), given that it can be defined by the relative diversity of plants with extremely complex adaptations to local conditions (Fig. 14). This approach to defining regional boundaries utilises plant diversity to integrate all the complex interactions that regulate vegetation (Fig. 1) and plant trait complexity patterns to represent the evolutionary history of the region.

Trait evolution

Trait data was available for the majority of SWAFR plants (Appendix 1), but data availability varies between plant families and genera because some taxonomists are unconcerned about key functional attributes of plants whereas others use them to help define taxa. SWAFR plant diversity comparisons are also complicated by families or genera that include many unnamed species (Wege & Shepherd 2020), or apparent hybrids named as species (French & Nicole 2019). There are also many species complexes (closely related taxa that may intergrade) in the SWAFR where taxonomic variability can be overlooked (resulting in massive genetic divergence in ecotypes/provenances within species), assigned to subspecies, varieties or forma (e.g. Proteaceae), or divided into numerous similar species which cannot be readily identified (e.g. Orchidaceae). There are also major taxonomic issues, especially in the Proteaceae, Myrtaceae and Fabaceae, due to non-monophyletic genera (Orthia *et al.* 2005; Edwards *et al.* 2010).

Nutritional trait innovation complexity in the SWAFR includes many more clades than expected that include species with differing traits with overlapping functions (see text box, *Nutritional trait complexity*). clades represent a new wave of mycorrhizal evolution (Brundrett & Tedersoo 2018) which peaks in the SWAFR, as shown by the higher diversity of plants with advanced traits relative to other bioregions (Fig. 3). This strongly suggests that trait evolution is currently underway in the SWAFR and may even be accelerating (Brundrett 2017a; Brundrett & Tedersoo 2018). The highly infertile soil could explain why so many plants have switched from their ancestral AM symbiosis to EM or cluster roots, both of which are considered to be more energy intensive but also more effective at nutrient uptake when soil conditions are suitable (see text box, *Nutritional trait complexity*). Australia also is the source of a structurally

unique mycorrhizal associations in the Asparagaceae (*Thysanotus* only) and the Rhamnaceae—a family that has EM associations here but not on other continents. Nitrogen fixation in the Fabaceae and Casuarinaceae may have caused a predisposition for acquisition of other nutritional traits (EM and cluster roots).

Key trends in pollination specialisation in the SWAFR involve the increased importance of birds and ground-dwelling animals, as well as specific interactions with insects, especially native bees, which are exceptionally diverse and specialised in the region (Keighery 1980; Brown *et al.* 1997; Houston 2018). These trends suggest that strong competition for general insect pollinators caused switching to more specific pollinators. However, pollinator declines and climatic impacts on pollination rates for plants in the region require further investigation (see text box, *Multidimensional interactions between fire, nutrition and pollination traits*).

The majority of Western Australian plant have one or more highly effective mechanism for fire recovery or avoidance that would not have been present in their distant ancestors. The most common strategy is for plants to rely on seed stored in topsoil for survival after being killed by fire. Fire responsive seeds have complex dormancy mechanisms that allow them to persist in soil for many years, followed by germination in response to cues such as heat or smoke. The second most common strategy is for plants to be partly consumed by fire but reuse part of their existing structure by resprouting. This strategy requires plants to store sufficient energy to support rapid regrowth and provides a considerable competitive advantage, especially for trees and large shrubs. The third common strategy is for plants to retain seed within protective structures for years, before their thick woody fruit or cones open for dispersal after fire (serotiny). Other common strategies include fire avoidance by summer dormancy in geophytes or as seeds for annual plants and post-fire flowering promotion (Appendix 1). Secondary traits that are also important in the SWAFR include efficient seed dispersal and long-term vegetative persistence, as well as tolerance to soil, climate or hydrology conditions (e.g. phreatophytic, xerophytic). There also can be an increased dominance of nitrogen fixing plants, which tend to produce more nodules after fire (Hansen *et al.* 1987; Grove *et al.* 1980).

In plant families with the most complex fire traits, such as the Proteaceae, Myrtaceae and Fabaceae, fire responses seem to be progressing from soil to canopy seed storage with fire-enhanced germination, to reseeding with some resprouting, then to primarily resprouting with some reseeding (Fig. 10). Resprouting capacity is gradually increasing in these families due to multiple origins of lignotubers and other subterranean storage organs. This trend is accompanied by increased importance of canopy seed protection, lignotubers and epicormic buds (Groom & Lamont 2015). Other fire traits that may occur in combination with these traits include thicker bark, wind dispersed seeds and fire-enhanced germination. Evolution in these families is complex and ongoing with some traits varying within species (see text box, *Fire trait complexity*). Resprouting also tends be more common in relatively large plants, which have invested more energy in persistent structures. This is best studied for *Banksia* species, which are more

serotinous in semiarid shrublands on highly infertile soils (kwongan) than in woodlands on the Swan Coastal Plain (Cowling & Lamont 1985). In contrast, traits that originate infrequently, such as canopy or topsoil-stored seed are usually consistent within genera (Fig. 10).

Fire traits can also arise by modification of existing structures that initially increased survival in seasonally dry climates, such as resprouting from corms, bulbs or rhizomes. These plants presumably adapt to fire by increasing dormant bud protection by placement deeper in the soil or accumulation greater storage reserves. There also are examples of long-lived clonal forms of plants within otherwise non-clonal species (see text box, *Fire trait complexity*). Most rhizomatous species are monocots (Litsios *et al*. 2014; Howard *et al*. 2019), but some dicots have acquired modified woody roots with similar functions (Pate & Dixon 1982).

Variations in serotiny within families of SWAFR plants suggests that evolution of these traits must be ongoing (Lamont 2021). This incorporates multiple separate origins in the Proteaceae, which includes two species with a unique form of serotiny in *Conospermum* (Zhao & Ladd 2014). The evolution of persistent soil seed banks is more complex as this trait is also beneficial in areas where rainfall is highly seasonal or unreliable (de Casas *et al*. 2017). This includes hard seeded species, especially the Fabaceae, which can also be stimulated to germinate by mechanical scarification or fluctuations in heat without fire (Cochrane 2017). Extended seed dormancy can also result from increased apoplastic lipid barriers in seed coats (Renard *et al*. 2021). *Eremophila* fruit have a complex dormancy, which causes sporadic germination in arid regions but switches to fire-promoted germination in the Southwest (Richmond & Ghisalberti 1994; Chinnock 2007).

Seed germination that is enhanced by smoke has multiple origins in 58 separate SWAFR families and commonly occurs in combination with other seed dormancy mechanisms, so the role of seed ageing or priming is also important (Roche *et al*. 1997; Cochrane *et al*. 2002; Merritt *et al*. 2007; Koch *et al*. 2009; Zirondi *et al*. 2019). Fire-promoted seed germination can vary within species and smoke-responsive species can also germinate in response to severe soil disturbance, and perhaps could have been activated by digging native animals in the past. The final stage of this evolutionary trend leads to long-term persistence of seeds for fire-ephemeral plants, which are otherwise only present briefly after fire. One example of this is the annual herb *Brachyscias verecundus*, a rare annual Apiaceae species, which was considered to be almost extinct but reappeared in abundance after a recent fire (Fig. 9S).

The earliest angiosperms were likely to be disturbance opportunists that were much less competitive than the dominant gymnosperm trees (Wing & Boucher 1998) and were probably already responding to and benefiting from fire in the Cretaceous (Crisp *et al*. 2011; Carpenter *et al*. 2015). SWAFR plants have evolved to survive in a regime with infrequent hot fire and some have flammable leaves that can increase fire severity (Crisp *et al*. 2011). The high frequency of multiple fire traits in SWAFR plants suggests that one trait alone may not be sufficient to ensure the survival of species.

The changing nature of fire regimes in the 'Anthropocene' also need to be considered, as species that have survived infrequent hot fires for millennia may not be resilient to more frequent fires, even if they have relatively low intensity. As explained above, substantial intervals between fires are critical to the survival of many species, whereas others are only present briefly after fires (Fig. 11). Thus, maximising plants (and animal) diversity in ecosystems will require a mosaic that includes substantial areas of long-unburnt vegetation, as well as areas that have been burnt relatively recently. However, the optimal proportion of recently burnt areas may be much less than that of long-unburnt areas in many habitats due to the ability of plants that benefit from fires to persist for many decades in soil seed banks (see above). Most of what we know about fire ecology in Australia is based on unplanned hot fires in relatively undisturbed habitats. Much less is known about the long-term impacts of more frequent, relatively cool, fuel reduction burns early or late in the growing season, but these now traverse large areas each year (Bradshaw *et al*. 2018). Interactions between fire frequency and increased weed dominance also need to be considered.

As explained above, complex combinations of nutrition, pollination and fire traits are predominant in SWAFR plant species, especially in highly speciose and taxonomically complex clades (Appendix 2) Some of these clades are known to have relatively fast rates of evolution and/or low rates of extinction relative to other Australian plants and diversified rapidly in parallel with the aridification of Australia in the past 25–30 Ma (Crisp & Cook 2013; Toon *et al*. 2014; Cook *et al*. 2015; Groom & Lamont 2015; Cardillo *et al*. 2017; Mast *et al*. 2015). However, interactions between net diversification and extinction rates vary considerably between taxa and regions, and over time (Cook *et al*. 2015; Cardillo *et al*. 2017; Nge *et al*. 2020a). Plants that migrated into arid regions such as the Amaranthaceae have also become successful in the SWAFR (Hammer *et al*. 2019).

Australian temperate plants (and their associated fungi) are being dispersed globally by humans and can become major weeds elsewhere. These include highly invasive members of the Myrtaceae (*Eucalyptus* and *Melaleuca*), as well as *Acacia* and *Casuarina* species (Richardson & Rejmánek 2011). In addition to leaving most pests and diseases behind, SWAFR plants with several of the following traits are likely to be highly successful invaders in exotic locations:

1 Rapid growth, efficient dispersal and drought tolerance.

2 Rapid recovery and/or enhanced dispersal after fire due to multiple fire traits.

3 Nutritional trait flexibility such as dual mycorrhizal associations or the capacity to form cluster roots.

4 Nitrogen fixation (Casuarinaceae and Fabaceae).

5 General insect or wind pollination.

Factors that lead to highly successful invasions of exotic plants in Australia also include many of these traits. For example, many weeds have wind or general insect pollination and benefit from fire in the SWAFR.

Trait data in Figure 13 shows that the most successful and diverse SWAFR plant clades also tend to be the

most specialised. Cowling *et al.* (1994) determined Mediterranean climate diversity hotspots contained many edaphic specialists, especially members of the Fabaceae, Proteaceae, Cyperaceae, Ericaceae, Myrtaceae, Restionaceae and Asteraceae. Selection pressures that drive trait evolution are similar in many regions, but plants have had less time for extreme specialisation to appear in most of them. For example, tropical ecosystems include many species with highly specialised pollination and seed dispersal syndromes (Willmer 2011; Wenny *et al.* 2016) but tend to have fewer specialised traits for nutrition or fire. Fire is also important in savannah and prairie grasslands (Maurin *et al.* 2014), but there is less evidence of extreme nutrition and pollination specialisation. The South African Floristic Region may well be the second-most trait complex flora globally, due to many species with complex fire and pollination traits (Cowling *et al.* 1994; Johnson & Steiner 2003), but it has fewer clades with nutrient trait switching than the SWAFR (Brundrett 2017a). Thus, the extreme nature of selective pressures for multiple trait categories seems to be unique to the SWAFR, which may have the most specialised flora on earth.

Multidimensional interactions between fire, nutrition and pollination traits

A. Fire–Nutrition

i. Fire responses and nutrient strategies are linked, with EM, cluster root and nitrogen fixing species more dominant in fire-prone habitats (Pekin *et al.* 2012).

ii. Fire causes major losses of volatile nutrients such as nitrogen, and other nutrients are redistributed or lost to wind and water erosion of damaged soils (Grove *et al.* 1986).

iii. Increased nutrient availability (except for nitrogen) at the soil surface promotes rapid growth of reseeders (Grove *et al.* 1986).

iv. Nitrogen deficits post-fire are redressed by abundant nitrogen fixing plants such as acacias and peas, cycads and *Allocasuarina* spp. (Hansen *et al.* 1987; Grove *et al.* 1980).

v. Fire ephemeral fungi such as *Anthracobia* sp. (Fig. 9T) and bryophytes seem to have major roles in initial soil and nutrient stabilisation (McMullan-Fisher *et al.* 2011).

vi. Some reseeders and resprouters take advantage of increased soil fertility post-fire, but become less common in long inter-fire periods (Grove *et al.* 1986; Brundrett *et al.* 2018).

vii. Mycorrhizal associations are likely to be suspended after fire as defoliated trees can lack the energy to support mutualists. Mycorrhizal fungus diversity substantially declines when trees are severely damaged (Robinson & Bougher 2003; Anderson *et al.* 2010).

viii. The nutrient cycling system for litter and wood could take years to recover after fire due to impacts on saprophytic fungi, invertebrates and digging mammals.

B. Fire–Pollination

i. Flowering abundance increases briefly after fire for some insect pollinated plants.

ii. Resources for nectivorous birds could be scarce for several years due to the slow recovery of large shrubs and trees.

i. Many native bees that nest in holes in dead wood (Houston 2018) would perish, potentially leading to pollination shortages, especially for sort-lived reseeders after fire.

iii. Long-term reductions in pollination efficiency due to insect decline (Sánchez-Bayo & Wyckhuys 2019) could have a major impact on seed bank restocking after fire. This would reduce the competitive advantage of reseeders and extend safe inter-fire intervals.

iv. Non-flying mammal pollinators are likely to be rare or missing after fire (Bradshaw 2014).

v. Some wind pollinated plants grow primarily after fire (e.g. Gyrostemonaceae).

C. Pollination and other animal roles–Nutrition

i. Excess energy in plants with slow growth in highly infertile soils can lead to increased switching from insect to bird or animal pollination (Orians & Milewski 2007).

ii. Seed accumulation in canopy and soil seed banks would lead to declining overall available nutrient stocks with time since fire in fire prone ecosystems.

iii. Seed eating birds such as black cockatoos are likely have an important role to redistributing nutrients tied up in seeds in these ecosystems.

iv. Impacts on soil digging animals such as bandicoots on nutrient cycling can be severely interrupted by fire (Fleming *et al.* 2014).

v. Animal species that formerly dispersed hypogeal mycorrhizal fungi are now absent in most parts of the SWAFR.

D. Interactions altered by severe climatic conditions

i. Seedlings can perish post-fire due to severe drought.

ii. Severe drought also reduces the capacity for plants to resprout or restock seed banks.

iii. Severe drought can reduce flowering and seed production (e.g. Brundrett 2019).

iv. Recently burnt ecosystems may have greater supplies of water in the short term due to greatly reduced transpiration (Mappin *et al.* 2003).

SWAFR plants have evolved a three-way combination of acquired traits for (1) nutrition, (2) fire and (3) pollination (Fig. 12). It seems that these three opposing drivers of evolution are generally not in conflict, or do not greatly reduce competitive ability, due to their combined costs. Evolution of these traits would be driven by highly infertile soils, fires, as well as drier and more variable climates, all of which have all increased in severity and

in parallel since the Cretaceous (Lamont *et al.* 2011; Gosper *et al.* 2019). For example, Orians & Milewski (2007) noted that both bird pollination, which requires abundant nectar in flowers, and increased flammability of plants likely result from slow plant growth in extremely infertile soils leading to surplus energy stored in Australian plants. Pausas & Lamont (2018) also noted the 3-dimensional nature of trait evolution, but they assigned broader trait categories to major axes (environment, disturbance and biotic interactions). Thus, there are more than three important interacting axes that drive plant evolution overall. However, triangular (or 3D) conceptual models are especially useful for illustrating the complexity of trait-species interactions. The text box '*Multidimensional interactions between fire, nutrition and pollination traits'* provides examples of these interactions that impact on the management of ecosystems and threatened species.

The unique nature of SWAFR plant trait specialisations leads to a number of key unanswered questions:

1 Why are some traits consistent within families (or orders) whereas others vary within species?

2 Why are plants with complex traits so prevalent in this region?

3 Why do new traits arise more often within clades that already have complex acquired traits?

4 Can traits be classified as fundamental (required to avoid extinction), or adaptive (acquired to increase competitive ability)?

5 Is extreme trait specialisation risky for plants and thus linked to the abundance of rare plants?

CONCLUSIONS

Diversity maps show that the majority of Australian plants in trait-complex clades, which are also highly speciose and taxonomically complex, have distributions centred in the SWAFR. These plants tend to be exceptionally well adapted to infertile soils, have relatively advanced pollination strategies and also have one or more acquired fire recovery traits. These traits evolved over long periods due to intense competition for soil nutrients and pollinators and the need to survive fires. Similar evolutionary trends also apply to a lesser degree in the rest of Australia and other regions with a Mediterranean climate.

There is now evidence that the complex trait strategies of SWAFR plants are becoming less effective due to reduced beneficial fungal activity, pollinator decline and substantial increases in fire severity and frequency. Threats to biodiversity both locally and globally include accelerating habitat loss and degradation due to fire, weeds, drought and pollinator decline (Sánchez-Bayo & Wyckhuys 2019; Bell & Callow 2020; Godfree *et al.* 2021; Bergstrom *et al.* 2021). The SWAFR is now considered to be prone to ecosystem collapse due to climate change interacting with these factors (Bergstrom *et al.* 2021; Ritchie *et al.* 2021).

This paper amalgamates information from several disparate disciplines that study plant adaptations to environmental stresses in Australia. Experts in these disciplines (e.g. ecologists, entomologists, mycologists, restoration ecologists and seed biologists) all know of extreme cases of specialised plant traits and exceptionally complex interactions with fungi or animals, but this knowledge has to be combined to reveal how unique the SWAFR is. This broad-based knowledge is essential to conserve threatened species, restore habitats and sustainably manage ecological communities (see text box, *Multidimensional interactions between fire, nutrition and pollination traits*). However, caution is required when scaling trait data from individual plants up to ecosystems and avoid using simplified concepts in ecosystem management.

Globally, the southwest Australian biodiversity hotspot arguably has the most highly complex combination of plant traits that promote survival in fire-prone and infertile habitats, and efficient pollination. This assertion is supported by correlations between the taxonomic diversity of plant clades in the region and their trait complexity. The SWAFR should also be designated as an advanced trait evolution region (SWATER), because its boundaries can be defined by the relative diversity of the plants with highly complex functional traits, along with vegetation and soil patterns. This approach for defining bioregions integrates key trends in evolutionary history with interacting factors that currently regulate distributions of vegetation types and species. Due to the extreme complexity of interactions between plant functional traits and environmental stresses in the region, the SWAFR is the best location on earth for studying the long-term impacts of these factors on plant evolution, physiology, genomics and diversity. This bioregion also provides a preview of conditions elsewhere on earth in the future, when many plants will need to survive in more flammable habitats with fewer pollinators and less fertile soils.

ACKNOWLEDGEMENTS

REFERENCES

Anderson P, Brundrett M, Grierson P & Robinson R 2010. Impact of severe forest dieback caused by *Phytophthora cinnamomi* on macrofungal diversity in the northern jarrah forest of Western Australia. *Forest Ecology and Management* **259**, 1033–1040.

Auld T D & Ooi M K J 2017. Plant life cycles above-and below-ground. Pages 230–253 *in* D A Keith, editor, *Australian vegetation*. Cambridge University Press, Cambridge.

Backhouse G, Bates R J, Brown A P & Copeland L M 2019. *A Checklist of the orchids of Australia including its island territories*. Self-published, Melbourne, Australia. Available at: ISBN 978-0-9946489-3-8.

Baker K S, Steadman K J, Plummer J A & Dixon K W 2005. Seed dormancy and germination responses of nine Australian fire ephemerals. *Plant and Soil* **277**, 345–358.

Barrett R L 2013. Ecological importance of sedges: a survey of the Australasian Cyperaceae genus *Lepidosperma*. *Annals of Botany* **111**, 499–529.

Barrett R L & Dixon K W 2001. A revision of the genus *Calectasia* (Calectasiaceae) with eight new species described from south-west Western Australia. *Nuytsia* **13**, 1–44.

Baskin J M, Baskin C C & Li X 2000. Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* **15**, 139–152.

Beadle N C W 1954. Soil phosphate and the delimitation of plant communities in eastern Australia. *Ecology* **35**, 370–375.

Beard J S 2015. *Plant life of Western Australia*. A S George & N Gibson, editors, Rosenberg Publishing Pty Ltd, Dural NSW, Australia.

Beard J S, Beeston G R, Harvey J M, Hopkins A J M & Shepherd D P 2013. The vegetation of Western Australia at the 1: 3,000,000 scale. Explanatory memoir. Second edition. *Conservation Science Western Australia* **9**, 1–252.

Bell D T 2001. Ecological response syndromes in the flora of southwestern Western Australia: fire resprouters versus reseeders. *The Botanical Review* **67**, 417–440.

Bell D T, Hopkins A J M & Pate J S 1984. Fire in the Kwongan. Pages 178–204 *in* J S Pate & J S Beard, editors, *Kwongan: Plant life of the sandplain*. University of Western Australia Press, Nedlands, Western Australia.

Bell D T, Loneragan W A, Ridley W J, Dixon K W & Dixon I R 1992. Response of tree canopy species of Kings Park, Perth, Western Australia to the severe summer wildfire of January 1989. *Journal of the Royal Society of Western Australia* **75**, 35–40.

Bell D T, Plummer J A & Taylor S K 1993. Seed germination ecology in southwestern Western Australia. *The Botanical Review* **59**, 24–73.

Bell R-A & Callow J N 2020. Investigating *Banksia* coastal woodland decline using multi-temporal remote sensing and field-based monitoring techniques. *Remote Sensing* **12**, 669. doi: 10.3390/rs12040669.

Bell T L & Pate J S 1996. Growth and fire response of selected Epacridaceae of south-western Australia. *Australian Journal of Botany* **44**, 509–526.

Bellairs S M & Bell D T 1990. Canopy-borne seed store in three Western Australian plant communities. *Austral Ecology* **15**, 299–305.

Bergstrom D M, Wienecke B C, van den Hoff J, Hughes L, Lindenmayer D B, Ainsworth T D, Baker C M Bland L, Bowman D M & Brooks S T 2021. Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology* **27**, 1692–1703.

BGPA (Botanic Garden and Parks Authority) 2016. *The future keepers unlocking the secrets of seeds*. Botanic Garden and Parks Authority, Kings Park, WA.

Bond W J 2015. Fires in the Cenozoic: a late flowering of flammable ecosystems. *Frontiers in Plant Science* **5**, 749, 1–11.

Bond W J & Midgley J J 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. *Oikos* 79–85.

Bougher N L & Lebel T 2001. Sequestrate (truffle-like) fungi of Australia and New Zealand. *Australian Systematic Botany* **14**, 439–484.

Bougoure J J, Brundrett M C & Grierson P F 2010. Carbon and nitrogen supply to the underground orchid, *Rhizanthella gardneri*. *New Phytologist* **186**, 947–956.

Bowman D M 2000. *Australian rainforests: islands of green in a land of fire*. Cambridge University Press, Cambridge.

Bowman D M, French B J & Prior L D 2014. Have plants evolved to self-immolate? *Frontiers in plant science* **5**, Article 590, doi: 10.3389/fpls.2014.00590.

Bradshaw D 2014. The honey possum, *Tarsipes rostratus*, a keystone species the Kwongan. Pages 215–224 *in* H Lambers, editor, *Plant life on the sandplains in southwest Australia: a global biodiversity hotspot*. Kwongan Foundation, Perth, Western Australia.

Bradshaw S D, Dixon K W, Hopper S D, Lambers H & Turner S R 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends in Plant Science* **16**, 69–76.

Bradshaw S D, Dixon K W, Lambers H, Cross A T, Bailey J & Hopper S D 2018. Understanding the long-term impact of prescribed burning in Mediterranean-climate biodiversity hotspots, with a focus on south-western Australia. *International Journal of Wildland Fire* **27**, 643–657.

Brown A, Thomson-Dans C & Marchant N (editors) 1998. *Western Australia's threatened flora*. Department of Conservation and Land Management, Western Australia.

Brown E M, Burbidge A H, Dell J, Edinger D, Hopper S D & Wills R T 1997. *Pollination in Western Australia: a database of animals visiting flowers*. Handbook no. 15. Western Australian Naturalists Club: Perth, Western Australia.

Brundrett M C 2008. *Mycorrhizal associations: the web resource*. Available at: mycorrhizas.info.

Brundrett M 2014. *Identification and ecology of Southwest Australian orchids*. Western Australian Naturalists' Club Inc., Perth, Western Australia.

Brundrett M C 2017a. Distribution and evolution of mycorrhizal types and other specialised roots in Australia. Pages 361–394 *in* L Tedersoo, editor, *Biogeography of mycorrhizal symbiosis*. Springer, Cham, Switzerland.

Brundrett M C 2017b. Global diversity and importance of mycorrhizal and nonmycorrhizal plants. Pages 533–556 *in* L Tedersoo, editor, *Biogeography of mycorrhizal symbiosis*. Springer, Cham, Switzerland.

Brundrett M C 2019. A comprehensive study of orchid seed production relative to pollination traits, plant density and climate in an urban reserve in Western Australia. *Diversity* **11**, 123. doi: 10.3390/d11080123.

Brundrett M C 2021. Auditing mycorrhizal data reveals how diagnosis errors accumulate in databases and confirms mycorrhizal consistency for most genera and families of flowering plants. *Mycorrhiza* **31**, 671–683.

Brundrett M, Bennett L, Weston C & Grierson P 2017. Soils and below-ground interactions that shape Australian vegetation. Pages 156–181 *in* D A Keith, editor, *Australian vegetation*. Cambridge University Press, Cambridge.

Brundrett M & Longman V 2016. Recovery of *Banksia* woodland after fire. *Western Wildlife* **20**, 10–12.

Brundrett M, Longman V, Wisolith A, Jackson K, Collins M & Clarke K 2018. *Banksia Woodland Restoration Project Annual Report 6 January - December 2017*. Department of Biodiversity, Conservation and Attractions, Perth, WA.

Brundrett M, Scade A, Batty A, Dixon K & Sivasithamparam K 2003. Development of *in situ* and *ex situ* seed baiting techniques to detect mycorrhizal fungi from terrestrial orchid habitats. *Mycological Research* **107**, 1210–1220.

Brundrett M C & Tedersoo L 2018. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytologist* **220**, 1108–1115.

Brundrett M, van Dongen R, Huntley B, Tay N & Longman V 2019. A monitoring toolkit for banksia woodlands: comparison of different scale methods to measure recovery of vegetation after fire. *Remote Sensing in Ecology and Conservation* **5**, 33–54.

Brundrett M, Wisolith A, Collins M, Longman V & Clarke K 2020. Several complimentary methods of plant establishment are required for effective restoration of banksia woodland. *bioRxiv* doi: 10.1101/2020.07.09.195131 (Preprint).

Bui E N, González-Orozco C E & Miller J T 2014. *Acacia*, climate, and geochemistry in Australia. *Plant and Soil* **381**, 161–175.

Burrows N D, Wardell-Johnson G & Ward B 2008. Post-fire juvenile period of plants in south-west Australia forests and implications for fire management. *Journal of the Royal Society of Western Australia* **91**, 163–174.

Cardillo M & Pratt R 2013. Evolution of a hotspot genus: geographic variation in speciation and extinction rates in *Banksia* (Proteaceae). *BMC Evolutionary Biology* **13**, 155.

Cardillo M, Weston P H, Reynolds Z K, Olde P M, Mast A R, Lemmon E M, Lemmon A R & Bromham L 2017. The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. *Evolution* **71**, 1928–1943.

Carpenter R J, Macphail M K, Jordan G J & Hill R S 2015. Fossil evidence for open, Proteaceae-dominated heathlands and fire in the Late Cretaceous of Australia. *American Journal of Botany* **102**, 2092–2107

Charles-Dominique T, Beckett H, Midgley G F & Bond W J 2015. Bud protection: a key trait for species sorting in a forest–savanna mosaic. *New Phytologist* **207**, 1052–1060.

Chinnock R J 2007. Eremophila *and allied genera: a monograph of the plant family Myoporaceae*. Rosenberg Publishing Pty Ltd.

Christenhusz M J & Byng J W 2016. The number of known plants species in the world and its annual increase. *Phytotaxa* **261**, 201–217.

Clarke P J, Lawes M J, Murphy B P, Russell-Smith J, Nano C E M, Bradstock R, Enright N J, Fontaine J B, Gosper C R, Radford I, Midgley J J & Gunton R M 2015. A synthesis of postfire recovery traits of woody plants in Australian ecosystems. *Science of the Total Environment* **534**, 31–42.

Cochrane A 2017. Are we underestimating the impact of rising summer temperatures on dormancy loss in hard-seeded species? *Australian Journal of Botany* **65**, 248–256.

Cochrane A, Brown K, Cunneen S & Kelly A 2001. Variation in seed production and germination in 22 rare and threatened Western Australian Verticordia (Myrtaceae). *Journal of the Royal Society of Western Australia* **84**, 103–110.

Cochrane A, Kelly A, Brown K & Cunneen S 2002. Relationships between seed germination requirements and ecophysiological characteristics aid the recovery of threatened native plant species in Western Australia. *Ecological Management & Restoration* **3**, 47–60.

Collette J C & Ooi M K 2020. Distribution of seed dormancy classes across a fire-prone continent: effects of rainfall seasonality and temperature. *Annals of Botany* **127**, 613–620.

Commander L E, Merritt D J, Rokich D P & Dixon K W 2009. Seed biology of Australian arid zone species: Germination of 18 species used for rehabilitation. *Journal of Arid Environments* **73**, 617–625.

Cook L G, Hardy N B & Crisp M D 2015. Three explanations for biodiversity hotspots: small range size, geographical overlap and time for species accumulation. An Australian case study. *New Phytologist* **207**, 390–400.

Cowling R M & Lamont B B 1985. Variation in serotiny of three *Banksia* species along a climatic gradient. *Journal of Ecology* **10**, 345–350.

Cowling R M & Witkowski E T F 1994. Convergence and non-convergence of plant traits in climatically and edaphically matched sites in Mediterranean Australia and South Africa. *Austral Ecology* **19**, 220–232.

Cowling R M, Witkowski E T F, Milewski A V & Newbey K R 1994. Taxonomic, edaphic and biological aspects of narrow plant endemism on matched sites in Mediterranean South Africa and Australia. *Journal of Biogeography* 651–664.

Crisp M D & Cook L G 2003. Phylogeny and evolution of anomalous roots in *Daviesia* (Fabaceae: Mirbelieae). *International Journal of Plant Sciences* **164**, 603–612.

Crisp M D, Burrows G E, Cook L G, Thornhill A H & Bowman D M 2011. Flammable biomes dominated by eucalypts originated at the Cretaceous–Palaeogene boundary. *Nature Communications* **2:193** doi: 10.1038/ncomms1191.

Crisp M D & Cook L G 2013. How was the Australian flora assembled over the last 65 million years? A molecular phylogenetic perspective. *Annual Review of Ecology, Evolution, and Systematics* **44**, 303–324.

Cross A T, Krueger T A, Gonella P M, Robinson A S & Fleischmann A S 2020. Conservation of carnivorous plants in the age of extinction. *Global Ecology and Conservation* **24**, e01272 doi: 10.1016/j.gecco.2020.e01272.

Dawson J O, Kowalski D G & Dart P J 1989. Variation with soil depth, topographic position and host species in the capacity of soils from an Australian locale to nodulate *Casuarina* and *Allocasuarina* seedlings. *Plant and Soil* **118**, 1–11.

de Casas R R, Willis C G, Pearse W D, Baskin C C, Baskin J M & Cavender-Bares J 2017. Global biogeography of seed dormancy is determined by seasonality and seed size: a case study in the legumes. *New Phytologist* **214**, 1527–1536.

Diels L 2007. *The plant life of Western Australia-South of the Tropics (Diels 1906)*. Conservation Science Western Australia **6**, 1–373.

Ebach M C, González-Orozco C E, Miller J T & Murphy D J 2015. A revised area taxonomy of phytogeographical regions within the Australian Bioregionalisation Atlas. *Phytotaxa* **208**, 261–277.

Edwards R D, Craven L A, Crisp M D & Cook L G 2010. *Melaleuca* revisited: cpDNA and morphological data confirm that *Melaleuca* L. (Myrtaceae) is not monophyletic. *Taxon* **59**, 744–754.

Enright N J, Fontaine J B, Lamont B B, Miller B P & Westcott V C 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *Journal of Ecology* **102**, 1572–1581.

Enright N J, Fontaine J B, Westcott V C, Lade J C & Miller B P 2011. Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology* **212**, 2071–2083.

Enright N J, Mosner E, Miller B P, Johnson N & Lamont B B 2007. Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands. *Ecology* **88**, 2292–2304.

EPA (Environmental Protection Authority) 2007. Advice on areas of the highest conservation value in the proposed extensions to Mount Manning Nature Reserve. Environmental Protection Authority, Perth, Western Australia. 1256.

Erickson T E, Muñoz-Rojas M, Kildisheva O A, Stokes B A, White S A, Heyes J L, Dalziell E L, Lewandrowski W, James J J & Madsen M D 2018. Benefits of adopting seed-based technologies for rehabilitation in the mining sector: a Pilbara perspective. *Australian Journal of Botany* **65**, 646–660.

Etchells H, O'Donnell A J, McCaw W L & Grierson P F 2020. Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of southwest Australia. *Forest Ecology and Management* **459**, 117850.

Fisher J L, Loneragan W A, Dixon K, Delaney J & Veneklaas E J 2009. Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. *Biological Conservation* **142**, 2270–2281.

Fleming P A, Anderson H, Prendergast A S, Bretz M R, Valentine L E & Hardy G E S 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review* **44**, 94–108

Fordyce I R, Gilkes R J, Loneragan W A, Beale S & Middleton N 2007. Vegetation zoning in relation to site and soil properties: a case study in the Darling Range, south-western Australia. *Journal of the Royal Society of Western Australia* **90**, 1–14.

French M 2012. *Eucalypts of Western Australia's wheatbelt*. Malcolm French, Perth, Western Australia.

French M E & Nicolle D 2019. *Eucalypts of Western Australia: The south-west coast and ranges*. Malcolm French, Perth, Western Australia.

Froend R & Sommer B 2010. Phreatophytic vegetation response to climatic and abstraction-induced groundwater drawdown: Examples of long-term spatial and temporal variability in community response. *Ecological Engineering* **36**, 1191–1200.

George A S 1999. *Flora of Australia* Volume 17B, *Banksia, Dryandra*. ABRS/CSIRO Publishing, Melbourne, Australia.

George E A & Pieroni M 2002. *Verticordia: the turner of hearts*. University of Western Australia Press, Nedlands, Western Australia.

Gibson N, Keighery G J, Lyons M N & Webb A 2004. Terrestrial flora and vegetation of the Western Australian wheatbelt. *Records of the Western Australian Museum* **67**, 139–189.

Gibson N, Yates C J & Dillon R 2010. Plant communities of the ironstone ranges of South Western Australia: hotspots for plant diversity and mineral deposits. *Biodiversity and Conservation* **19**, 3951–3962.

Gioia P & Hopper S D 2017. A new phytogeographic map for the Southwest Australian Floristic Region after an exceptional decade of collection and discovery. *Botanical Journal of the Linnean Society* **184**, 1–15.

Gioria M, Le Roux J J, Hirsch H, Moravcová L & Pyšek P 2019. Characteristics of the soil seed bank of invasive and non-invasive plants in their native and alien distribution range. *Biological Invasions* **21**, 2313–2332.

Godfree R C, Knerr N, Encinas-Viso F, Albrecht D, Bush D, Cargill D C, Clements M Gueidan C, Guja L K & Harwood T 2021. Implications of the 2019–2020 megafires for the biogeography and conservation of Australian vegetation. *Nature Communications* **12**, 1–13.

González-Orozco C E, Laffan S W, Knerr N & Miller J T 2013. A biogeographical regionalization of Australian *Acacia* species. *Journal of Biogeography* **40**, 2156–2166.

González-Orozco C E, Thornhill A H, Knerr N, Laffan S & Miller J T 2014. Biogeographical regions and phytogeography of the eucalypts. *Diversity and Distributions* **20**, 46–58.

Gosper C R, Coates D J, Hopper S D, Byrne M & Yates C J 2021a. The role of landscape history in the distribution and conservation of threatened flora in the Southwest Australian Floristic Region. *Biological Journal of the Linnean Society* **133**, 394–410

Gosper C R, Hopley T, Byrne M, Hopper S D, Prober S M & Yates C J 2019. Phylogenomics shows lignotuber state is taxonomically informative in closely related eucalypts. *Molecular Phylogenetics and Evolution* **135**, 236–248.

Gosper C R, Kinloch J, Coates D J, Byrne M, Pitt G & Yates C J 2021b. Differential exposure and susceptibility to threats based on evolutionary history: how OCBIL theory informs flora conservation. *Biological Journal of the Linnean Society* **133**, 373–393.

Gosper C R & Prober S M 2020. Using a multi-century post-fire chronosequence to develop criteria to distinguish Prior and Bowman's (2020) post-fire obligate coloniser and fire-intolerant flora. *Fire* **3**, 48 doi: 10.3390/fire3030048.

Gosper C R, Yates C J, Cook G D, Harvey J M, Liedloff A C, McCaw W L, Thiele K R & Prober S M 2018. A conceptual model of vegetation dynamics for the unique obligate-seeder eucalypt woodlands of south-western Australia. *Austral Ecology* **43**, 681–695.

Gosper C R, Yates C J & Prober S M 2012. Changes in plant species and functional composition with time since fire in two Mediterranean climate plant communities. *Journal of Vegetation Science* **23**, 1071–1081.

Grant C D & Koch J M 1997. Ecological aspects of soil seed-banks in relation to bauxite mining. II. Twelve year old rehabilitated mines. *Austral Ecology* **22**, 177–184

Groom P K & Lamont B 2015. *Plant life of southwestern Australia: adaptations for survival*. Walter de Gruyter GmbH, Berlin.

Grootemaat S, Wright I J, van Bodegom P M, Cornelissen J H C & Shaw V 2017. Bark traits, decomposition and flammability of Australian forest trees. *Australian Journal of Botany* **65**, 327–338.

Grove T S, O'Connell A, Dimmock G M 1986. Nutrient changes in surface soils after an intense fire in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest. *Australian Journal of Ecology* **11**, 303–317.

Grove T S, O'Connell A M & Malajczuk N 1980. Effects of fire on the growth, nutrient content and rate of nitrogen fixation of the cycad *Macrozamia riedlei*. *Australian Journal of Botany* **28**, 271–281.

Hammer T A, Brundrett M C, Macintyre P D & Keighery G J 2018. Recognising biodiversity hotspots at multiple overlapping scales in Western Australia. The Royal Society of Western Australia Symposium: Landscapes, Seascapes & Biota: Unique WA — Past, Present & Future, 27–28 July 2018, Perth Western Australia. Available at www.researchgate.net/publication/326648134 (unpublished poster).

Hammer T A, Zhong X, Colas des Francs-Small C, Nevill P G, Small I D & Thiele K R 2019. Resolving intergeneric relationships in the aervoid clade and the backbone of *Ptilotus* (Amaranthaceae): evidence from whole plastid genomes and morphology. *Taxon* **68**, 297–314.

Hansen A P, Pate J S, Hansen A & Bell D 1987. Nitrogen economy of post-fire stands of shrub legumes in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest of SW Australia. *Journal of Experimental Botany* **38**, 26–41.

Harvey J M 2014. *Regional variability in salmon gum (*Eucalyptus salmonophloia*) woodlands of south-western Australia, with particular focus on the great Western Woodlands*. PhD Thesis, Curtin University (unpublished).

Harvey J M, Hopkins A J M, Langley M A, Gosper C R, Williams M R & Yates C J 2017. Long-term studies of post-fire reproduction in an Australian shrubland and woodland. *Australian Journal of Botany* **65**, 339–347.

Hayes P, Turner B L, Lambers H & Laliberté E 2014. Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *Journal of Ecology* **102**, 396–410.

Hidayati S N, Walck J L, Merritt D J, Turner S R, Turner D W & Dixon K W 2012. Sympatric species of *Hibbertia* (Dilleniaceae) vary in dormancy break and germination requirements: implications for classifying morphophysiological dormancy in Mediterranean biomes. *Annals of Botany* **109**, 1111–1123.

Hnatiuk R J & Maslin B R 1988. Phytogeography of *Acacia* in Australia in relation to climate and species-richness. *Australian Journal of Botany* **36**, 361–383.

Hobbs R J & Atkins L 1990. Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97–110.

Hoffmann A A, Rymer P D, Byrne M, Ruthrof K X, Whinam J, McGeoch M, Bergstrom D M, Guerin G R, Sparrow B & Joseph L 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecology* **44**, 3–27.

Hopper S D 1993. *Kangaroo paws and catspaws*. Dept. of Conservation and Land Management, Kensington, Western Australia.

Hopper S D & Gioia P 2004. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology Evolution and Systematics* **35**, 623–650.

Houston T 2018. *A guide to native bees of Australia*. CSIRO Publishing, Melbourne, Australia.

Houston T F & Bougher N L 2010. Records of hypogeous mycorrhizal fungi in the diet of some Western Australian bolboceratine beetles (Coleoptera: Geotrupidae, Bolboceratinae). *Australian Journal of Entomology* **49**, 49–55.

Howard C C, Folk R A, Beaulieu J M & Cellinese N 2019. The monocotyledonous underground: global climatic and phylogenetic patterns of geophyte diversity. *American Journal of Botany* **106**, 850–863.

Johnson S D & Steiner K E 2003. Specialized pollination systems in southern Africa. *South African Journal of Science* **99**, 345–348.

Jones M M, Gibson N, Yates C, Ferrier S, Mokany K, Williams K J, Manion G & Svenning J-C 2016. Underestimated effects of climate on plant species turnover in the Southwest Australian Floristic Region. *Journal of Biogeography* **43**, 289–300.

Keddy P 2005. Putting the plants back into plant ecology: six pragmatic models for understanding and conserving plant diversity. *Annals of Botany* **96**, 177–189.

Keighery G J 1980. Bird pollination in south Western Australia: a checklist. *Plant Systematics and Evolution* **135**, 171–176.

Keighery G & Gibson N 1993. Biogeography and composition of the flora of the Cape Range peninsula, Western Australia. *Records of the Western Australian Museum* **45**, 51–85.

Keighery G, Longman V & Brundrett M 2017. Weedy and natural distribution of *Acacia trigonophylla* (Fabaceae). *The Western Australian Naturalist* **31**, 53–62.

Keith D A, Dunker B & Driscoll D A 2020. Dispersal: the eighth fire seasonality effect on plants. *Trends in Ecology & Evolution* **35**, 305–307.

Koch J M, Ruschmann A M & Morald T K 2009. Effect of time since burn on soil seedbanks in the jarrah forest of Western Australia. *Australian Journal of Botany* **57**, 647–660.

Laffan S W, Lubarsky E & Rosauer D F 2010. Biodiverse, a tool for the spatial analysis of biological and related diversity. *Ecography* **33**, 643–647.

Lambers H, Albornoz F, Kotula L, Laliberté E, Ranathunge K, Teste F P & Zemunik G 2018. How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impoverished hyperdiverse ecosystems. *Plant and Soil* **424**, 11–33.

Lambers H, Brundrett M C, Raven J A & Hopper S D 2010. Plant mineral nutrition in ancient landscapes: high plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil* **334**, 11–31.

Lamont B B 1991. Canopy seed storage and release: what's in a name? *Oikos* **60**, 266–268.

Lamont B B 2021. Evaluation of seven indices of on-plant seed storage (serotiny) shows that the linear slope is best. *Journal of Ecology* **109**, 4–18.

Lamont B B & Downes K S 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecology* **212**, 2111–2125.

Lamont B B & Downes S 1979. The longevity, flowering and fire history of the grasstrees *Xanthorrhoea preissii* and *Kingia australis*. *Journal of Applied Ecology* 893–899.

Lamont B B, Enright N J & He T 2011. Fitness and evolution of resprouters in relation to fire. *Plant Ecology* **212**, 1945–1957.

Lamont B B & He T 2017. Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends in Plant Science* **22**, 278–288.

Lamont B B, He T & Yan Z 2019. Fire as a pre-emptive evolutionary trigger among seed plants. *Perspectives in Plant Ecology, Evolution and Systematics* **36**, 13–23.

Lamont B B, Le Maitre D C, Cowling R M & Enright N J 1991. Canopy seed storage in woody plants. *The Botanical Review* **57**, 277–317.

Li J, Shangguan Z & Deng L 2020. Variations of belowground C and N cycling between arbuscular mycorrhizal and ectomycorrhizal forests across China. *Soil Research* **58**, 441–451.

Litsios G, Wüest R O, Kostikova A, Forest F, Lexer C, Linder H P, Pearman P B, Zimmermann N E & Salamin N 2014. Effects of a fire response trait on diversification in replicated radiations. *Evolution* **68**, 453–465.

Macintyre P D & Mucina L 2021. The biomes of Western Australia: a vegetation-based approach using the zonality/azonality conceptual framework. *New Zealand Journal of Botany* 1–23.

Mappin K A, Pate J S & Bell T L 2003. Productivity and water relations of burnt and long-unburnt semi-arid shrubland in Western Australia. *Plant and Soil* **257**, 321–340.

Mast A R, Olde P M, Makinson R O, Jones E, Kubes A, Miller E T & Weston P H 2015. Paraphyly changes understanding of timing and tempo of diversification in subtribe Hakeinae (Proteaceae), a giant Australian plant radiation. *American Journal of Botany* **102**, 1634–1646.

Maurin O, Davies T J, Burrows J E, Daru B H, Yessoufou K, Muasya A M, Van der Bank M & Bond W J 2014. Savanna fire and the origins of the 'underground forests' of Africa. *New Phytologist* **204**, 201–214.

McCaw L & Middleton T 2015. Recovery of tall open eucalypt forest in south-western Australia following complete crown scorch. *Fire Ecology* **11**, 95–107.

McMullan-Fisher S J, May T W, Robinson R M, Bell T L, Lebel T, Catcheside P & York A 2011. Fungi and fire in Australian ecosystems: a review of current knowledge, management implications and future directions. *Australian Journal of Botany* **59**, 70–90.

Meney K A & Pate J 1999. *Australian rushes: biology, identification and conservation of Restionaceae and allied families*. University of Western Australia Press, Nedlands, Western Australia.

Meney K A, Nielssen G M & Dixon K W 1994. Seed bank patterns in Restionaceae and Epacridaceae after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* **5**, 5–12.

Merritt D J, Turner S R, Clarke S & Dixon K W 2007. Seed dormancy and germination stimulation syndromes for Australian temperate species. *Australian Journal of Botany* **55**, 336–344.

Milberg P & Lamont B B 1995. Fire enhances weed invasion of roadside vegetation in southwestern Australia. *Biological Conservation* **73**, 45–49.

Miller B P & Dixon K W 2014. Plants and fire in kwongan vegetation. Pages 147–169 in H Lambers, editor, *Plant life on the sandplains in Southwest Australia: A global biodiversity hotspot*. UWA Publishing, Crawley, Western Australia.

Miller B P & Murphy B P 2017. Fire and Australian vegetation. Pages 113–134 in D A Keith, editor, *Australian vegetation*. Cambridge University Press, Cambridge.

Mucina L & Wardell-Johnson G W 2011. Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant and Soil* **341**, 1–23.

Murphy B P & Bowman D M 2012. What controls the distribution of tropical forest and savanna? *Ecology Letters* **15**, 748–758.

Myers N, Mittermeier R A, Mittermeier C G, Da Fonseca G A & Kent J 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Nge F J, Biffin E, Thiele K R & Waycott M 2020a. Extinction pulse at Eocene–Oligocene boundary drives diversification dynamics of two Australian temperate floras. *Proceedings of the Royal Society B* **287**, 20192546 doi: 10.1098/rspb.2019.2546.

Nge F J, Cambridge M L, Ellsworth D S, Zhong H & Lambers H 2020b. Cluster roots are common in *Daviesia* and allies (Mirbelioids; Fabaceae). *Journal of the Royal Society of Western Australia* **103**, 111–118.

Nickrent D L 2020. *The parasitic plant connection*. Department of Plant Biology, Southern Illinois University Carbondale. Available at: parasiticplants.siu.edu

Nicolle D 2006. A classification and census of regenerative strategies in the eucalypts (*Angophora*, *Corymbia* and *Eucalyptus*—Myrtaceae), with special reference to the obligate seeders. *Australian Journal of Botany* **54**, 391–407.

Nuske S J, Vernes K, May T W, Claridge A W, Congdon B C, Krockenberger A & Abell S E 2017. Redundancy among

mammalian fungal dispersers and the importance of declining specialists. *Fungal Ecology* **27**, 1–13.

O'Donnell A J, Cook E R, Palmer J G, Turney C S & Grierson P F 2018. Potential for tree rings to reveal spatial patterns of past drought variability across western Australia. *Environmental Research Letters* **13**, 024020 doi: 10.1088/1748-9326/aaa204.

Olde P M & Marriott N R 1995. *The Grevillea book*. Kangaroo Press, Kenthurst, NSW.

Orians G H & Milewski A V 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews* **82**, 393–423.

Orthia L A, Cook L G & Crisp M D 2005. Generic delimitation and phylogenetic uncertainty: an example from a group that has undergone an explosive radiation. *Australian Systematic Botany* **18**, 41–47.

Parsons R F & Hopper S D 2003. Monocotyledonous geophytes: comparison of south-western Australia with other areas of Mediterranean climate. *Australian Journal of Botany* **51**, 129–133.

Pate J S, Casson N E, Rullo J & Kuo J 1985. Biology of fire ephemerals of the sandplains of the kwongan of south-western Australia. *Functional Plant Biology* **12**, 641–655.

Pate J S & Dixon K 1982. *Tuberous, cormous and bulbous plants*. University of Western Australia Press, Nedlands, Western Australia.

Pate J S & Verboom W H 2009. Contemporary biogenic formation of clay pavements by eucalypts: further support for the phytotarium concept. *Annals of Botany* **103**, 673–685.

Paula S, Naulin P I, Arce C, Galaz C & Pausas J G 2016. Lignotubers in Mediterranean basin plants. *Plant Ecology* **217**, 661–676.

Pausas J G, Bradstock R A, Keith D A & Keeley J E 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85**, 1085–1100.

Pausas J G & Lamont B B 2018. Ecology and biogeography in 3D: The case of the Australian Proteaceae. *Journal of Biogeography* **45**, 1469–1477.

Pausas J G, Lamont B B, Paula S, Appezzato-da-Gloria B & Fidelis A 2018. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* **217**, 1435–1448.

Pausas J G, Pratt R B, Keeley J E, Jacobsen A L, Ramirez A R, Vilagrosa A, Paula S, Kaneakua-Pia I N & Davis S D 2016. Towards understanding resprouting at the global scale. *New Phytologist* **209**, 945-954.

Pekin B K, Wittkuhn R S, Boer M M, Macfarlane C & Grierson P F 2012. Response of plant species and life form diversity to variable fire histories and biomass in the jarrah forest of south-west Australia. *Austral Ecology* **37**, 330–338.

Phillips R D, Brown A P, Dixon K W & Hopper S D 2011. Orchid biogeography and factors associated with rarity in a biodiversity hotspot, the Southwest Australian Floristic Region. *Journal of Biogeography* **38**, 487–501.

Raven JA, Lambers H, Smith S E, Westoby M 2018. Costs of acquiring phosphorus by vascular land plants: patterns and implications for plant coexistence. *New Phytologist* **217**, 1420–1427.

Renard J, Martínez-Almonacid I, Queralta Castillo I, Sonntag A, Hashim A, Bissoli G, Campos L, Muñoz-Bertomeu J, Niñoles R & Roach T 2021. Apoplastic lipid barriers regulated by conserved homeobox transcription factors extend seed longevity in multiple plant species. *New Phytologist* **231**, 679–694.

Reyes E, Morlon H & Sauquet H 2015. Presence in Mediterranean hotspots and floral symmetry affect speciation and extinction rates in Proteaceae. *New Phytologist* **207**, 401–410.

Richardson D M & Rejmánek M 2011. Trees and shrubs as invasive alien species–a global review. *Diversity and Distributions* **17**, 788–809.

Richmond G S & Ghisalberti E L 1994. Seed dormancy and germination mechanisms in *Eremophila* (Myoporaceae). *Australian Journal of Botany* **42**, 705–715.

Ritchie A L, Svejcar L N, Ayre B M, Bolleter J, Brace A, Craig M D, Davis B, Davis R A, van Etten E J & Fontaine J B 2021. A threatened ecological community: research advances and priorities for *Banksia* woodlands. *Australian Journal of Botany* **69**, 53–84.

Robinson R M & Bougher N L 2003. The response of fungi to fire in jarrah (*Eucalyptus marginata*) and karri (*Eucalyptus diversicolor*) forests of south-west Western Australia. Pages 269–289 in I Abbott & N Burrows, editors, *Fire in ecosystems in south-west Western Australia: Impacts and management*. Backhuys Publishers, Leiden, The Netherlands.

Roche S, Dixon K W & Pate J S 1997. Seed ageing and smoke: Partner cues in the amelioration of seed dormancy in selected Australian native species. *Australian Journal of Botany* **45**, 783–815.

Rokich D P, Dixon K W, Sivasithamparam K & Meney K A 2000. Topsoil handling and storage effects on woodland restoration in Western Australia. *Restoration Ecology* **8**, 196–208.

Sánchez-Bayo F & Wyckhuys K A 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* **232**, 8–27.

Shane M W, Dixon K W & Lambers H 2005. The occurrence of dauciform roots amongst Western Australian reeds, rushes and sedges, and the impact of phosphorus supply on dauciform-root development in Schoenus unispiculatus (Cyperaceae). *New Phytologist* **165**, 887–898.

Shedley E, Burrows N, Yates C J & Coates D J 2018. Using bioregional variation in fire history and fire response attributes as a basis for managing threatened flora in a fire-prone Mediterranean climate biodiversity hotspot. *Australian Journal of Botany* **66**, 134–143

Sheedy E M, Ryberg M, Lebel T, May T W, Bougher N L & Matheny P B 2016. Dating the emergence of truffle-like fungi in Australia, by using an augmented meta-analysis. *Australian Systematic Botany* **29**, 284–302

Smith R J, Hopper S D & Shane M W 2011. Sand-binding roots in Haemodoraceae: global survey and morphology in a phylogenetic context. *Plant and Soil* **348**, 453–470.

Soudzilovskaia N A, van Bodegom P M, Terrer C, van't Zelfde M, McCallum I, McCormack M L, Fisher J B, Brundrett M C, de Sá N C & Tedersoo L 2019. Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* **10**, 1–10.

Soudzilovskaia N A, Vaessen S, Barcelo M, He J, Rahimlou S, Abarenkov K, Brundrett M C, Gomes S I, Merckx V & Tedersoo L 2020. FungalRoot: global online database of plant mycorrhizal associations. *New Phytologist* **227**, 955–966.

Specht R L & Rundel P W 1990. Sclerophylly and foliar nutrient status of Mediterranean-climate plant communities in southern Australia. *Australian Journal of Botany* **38**, 459–474.

Staff I A & Waterhouse J T 1981. The biology of arborescent monocotyledons, with special reference to Australian species. Pages 216-257 in J S Pate & A J McComb, editors, *The biology of Australian plants*. University of Western Australia Press, Nedlands, Western Australia.

Stevens J C, Rokich D P, Newton V J, Barrett R L & Dixon K W (editors) 2016. *Banksia woodlands: A restoration guide for the Swan Coastal Plain*. UWA Publishing, Crawley, Australia.

Tedersoo L & Brundrett M C 2017. Evolution of ectomycorrhizal symbiosis in plants. Pages 407–467 in L Tedersoo, editor, *Biogeography of Mycorrhizal Symbiosis*. Springer, Cham, Switzerland.

Tedersoo L, Laanisto L, Rahimlou S, Toussaint A, Hallikma T & Pärtel M 2018. Global database of plants with root-symbiotic nitrogen fixation: Nod DB. *Journal of Vegetation Science* **29**, 560–568.

Thiele K R & Prober S M 2014. Progress and prospects for understanding evolution and diversity in the southwest

Australian flora. *Journal of the Royal Society of Western Australia* **97**, 35–45.

Tieu A, Dixon K W, Meney K A & Sivasithamparam K 2001. The interaction of heat and smoke in the release of seed dormancy in seven species from southwestern Western Australia. *Annals of Botany* **88**, 259–265.

Toon A, Cook L G & Crisp M D 2014. Evolutionary consequences of shifts to bird-pollination in the Australian pea-flowered legumes (Mirbelieae and Bossiaeeae). *BMC Evolutionary Biology* **14**, 1–11.

Trappe J M 1987. Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. Pages 5–25 *in* G R Safir, editor, *Ecophysiology of VA mycorrhizal plants*. CRC Press, Boca Raton, Florida.

Tsakalos J L, Renton M, Riviera F, Veneklaas E J, Dobrowolski M P & Mucina L 2019. Trait-based formal definition of plant functional types and functional communities in the multi-species and multi-traits context. *Ecological Complexity* **40**, 100787.

Valentine L E, Fisher R, Wilson B A, Sonneman T, Stock W D, Fleming P A & Hobbs R J 2014. Time since fire influences food resources for an endangered species, Carnaby's cockatoo, in a fire-prone landscape. *Biological Conservation* **175**, 1-9.

van der Moezel P G, Loneragan W A & Bell D T 1987. Northern sandplain kwongan: regeneration following fire, juvenile period and flowering phenology. *Journal of the Royal Society of Western Australia* **69**, 123–132.

Van Etten E J 1995. The problem of weeds in bushland-implications for fire management. Pages 62–69 *in* J Harris, editor, *Burning our bushland. Proceedings of a conference on fire and urban bushland*. Urban Bushland Council (WA), West Perth WA.

Verboom W H & Pate J S 2015. An integrated approach to mapping and understanding of vegetation: soil systems. *Catena* **126**, 134–145.

Vesk P A & Westoby M 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* **92**, 310–320.

Wajon E 2020. Response of native vegetation in the Great Southern region of Western Australia to fire. *Australasian Plant Conservation: Journal of the Australian Network for Plant Conservation* **29**, 8–11.

Ward S C, Koch J M & Grant C D 1997. Ecological aspects of soil seed-banks in relation to bauxite mining. I. Unmined jarrah forest. *Austral Ecology* **22**, 169–176.

Wardell-Johnson G, Luxton S, Craig K, Brown V, Evans N & Kennedy S 2018a. Implications of floristic patterns, and changes in stand structure following a large-scale, intense fire across forested ecosystems in south-western Australia's high-rainfall zone. *Pacific Conservation Biology* **23**, 399–412.

Wardell-Johnson G, Wardell-Johnson A, Schultz B, Dortch J, Robinson T, Collard L & Calver M 2018b. The contest for the tall forests of south-western Australia and the discourses of advocates. *Pacific Conservation Biology* **25**, 50–71.

Wardell-Johnson G W, Williams M R, Mellican A E & Annells A 2007. Floristic patterns and disturbance history in karri (*Eucalyptus diversicolor*: Myrtaceae) forest, south-western Australia: 2. Origin, growth form and fire response. *Acta Oecologica* **31**, 137–150.

Wege J A & Shepherd K A 2020. 50 years of botanical discovery: a golden anniversary edition of Nuytsia, the journal of the Western Australian Herbarium. *Nuytsia* **31**, 1–7.

Wenny D G, Şekercioğlu Ç H, Cordeiro N J, Rogers H S & Kelly D 2016. Seed dispersal by fruit-eating birds. Pages 107–146 *in* C H Şekercioglu, D G Wenny & C J Whelan, editors, *Why birds matter*. University of Chicago Press, Chicago.

Whinam J & Hope G 2005. The peatlands of the Australasian region. *Stapfia* **85**, 397–433.

Willmer P 2011. *Pollination and floral ecology*. Princeton University Press, Princeton, New Jersey.

Wing S L & Boucher L D 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth and Planetary Sciences* **26**, 379–421.

Wright B R & Clarke P J 2007. Resprouting responses of *Acacia* shrubs in the Western Desert of Australia–fire severity, interval and season influence survival. *International Journal of Wildland Fire* **16**, 317–323.

Wyse S V & Dickie J B 2017. Predicting the global incidence of seed desiccation sensitivity. *Journal of Ecology* **105**, 1082–1093.

Yates C J, Gosper C R, Hopper S D, Keith D A, Prober S M & Tozer M G 2017. Mallee woodlands and shrublands–the mallee, muruk/muert and maalok vegetation of southern Australia. Pages 570–598 *in* D A Keith, editor, *Australian vegetation*. Cambridge University Press, Cambridge.

Zemunik G, Turner B L, Lambers H & Laliberté E 2016. Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot. *Journal of Ecology* **104**, 792–805.

Zencich S J, Froend R H, Turner J V & Gailitis V 2002. Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia* **131**, 8–19.

Zirondi H L, Silveira F A & Fidelis A 2019. Fire effects on seed germination: Heat shock and smoke on permeable vs impermeable seed coats. *Flora* **253**, 98–106.

Zhao X & Ladd P G 2014. Seed germination and unusual serotiny in two species of *Conospermum* from fire-prone vegetation in Western Australia. *Australian Journal of Botany* **62**, 511–517.

Appendix 1. Summary of acquired traits for nutrition, fire or pollination in plants from southwestern Western Australia. Trait categories, complexity and variability are summarised for families or genera when they vary within families (with number of taxa). See Table 1 for abbreviations (CV = complexity and variability index).

| Family | Genera | Species | Taxa | Plant Nutrition Traits | | | Pollination Traits | | Fire Response Traits | | | | CV sum |
				Nutrition	Habitat	CV	Syndrome	CV	Seed	Sprouting	Ecology	CV	
Ferns													
Aspleniaceae	2	5	6	AM		0	WDS	0	WDS	RLR		1	3.5
Dennstaedtiaceae	1	1	1	AM, LRH		1	WDS	0	WDS	RLR	FPF	2	5
Isoetaceae	1	8	9	AM, LRH		0	WDS	0	WDS	RCB (9)	NSH	1	4
Lindsaeaceae	1	1	1	AM, LRH		0	WDS	0	WDS	RLR		1	4
Lycopodiaceae	1	1	1	AM, LRH		2	GIP	2	WDS	RCB (1)		1	5
Marsileaceae	2	6	6	AM (NM), LRH		2	Water	3	WDS	RCB (5)	NSH	1	3.5
Ophioglossaceae	1	3	3	AM		2	GIP	0	WDS	RCB (3)	NSH	1	5
Psilotaceae	1	1	1	AM		2	WDS	2	WDS		SIm	1	5
Pteridaceae	4	9	10	AM, LRH		1	WDS	2	WDS	RLR	FPF	1	1.8
Salviniaceae	1	2	2	NM, no roots	Aqua	4	Water	0	WDS		NSH	0	8
Schizaeaceae	1	2	2	AM, LRH		0	WDS	0	WDS	RLR	SIm	1	4
Selaginellaceae	1	1	1	AM (NM)		0	WDS	0	WDS		SIm	0	3
Thelypteridaceae	1	1	1	AM, LRH		1	WDS	2	WDS	RLR		1	4
Gymnosperms													
Cupressaceae	1	9	9	AM		0	Wind	2	CSB	RLR (1)	SIm	2	4
Podocarpaceae	1	1	1	AM		0	GIP	3		RLR	FPF	2	5
Zamiaceae	1	3	3	AM, N2F		2	SIP	3		RLR	FPF	3	8
Monocots													
Acanthaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Aizoaceae	6	26	27	NM	ASD	1	GIP	1	SSB, GPF (4)	RCB (1)	FPF (4), NSH	0.7	2.7
Alismataceae	1	1	1	NM (AM)	Aqua	3	GIP	1			NSH	0	4
Amaranthaceae	5	50	59	NM, LRH	ASD	2	GIP, SIP	2.2	SSB, GPF?	RCB (3)	FPF (4), FAA (6), NSH (53)	1.4	5.6
Anarthriaceae	3	11	11	NM, SBR		3	Wind	2	SSB, GPF	RLR	FPF	2	7
Aphanopetalaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Apiaceae	13	56	61	AM		0	GIP	1	SSB, GPF	RLR (19)	FPF (59), FE (3), SAF (19)	2.3	3.3
Apocynaceae	4	7	7	AM		0	GIP	1	SSB, GPF	RLR (1)	SIm (5)	0.5	1.5
Apodanthaceae	1	2	2	NM, Para	Internal	6	SIP	4			SIm (2)	0	10
Aponogetonaceae	1	1	1	NM	Aqua	1	GIP	1			NSH	0	2
Araceae	2	2	2	NM	Aqua	4	Water	4			NSH	0	8
Araliaceae	3	35	37	AM		0	GIP	1	SSB, GPF (13)	RLR (1)	FPF (36), FE (4), FAA (13)	2.3	3.3
Asparagaceae	10	115	123	AM, or Thys (52)		2	GIP	1	SSB, GPF (102)	RLR (41), RCB (47)	FPF (104), SAF (15), SIm (18)	2.4	5.4
Asphodelaceae	1	1	1	AM		0	GIP	1	SSB, GPF	RCB (1)	FPF, FE	2	3
Asteraceae	92	332	368	AM		0	GIP	1	SSB, GPF (152)	RLR (8)	FPF (155), FE (5), FAA (260)	0.5	1.5
Boraginaceae	7	22	28	AM		0	GIP	1	SSB, GPF?		FPF (24), FAA (3), NSH (3)	0.6	1.6
Boryaceae	1	7	7	AM		0	GIP	1	SSB, GPF?	RLR	NSH	2	3
Brassicaceae	11	40	41	NM, LRH	ASD	1	GIP	1	SSB, GPF (1)		FPF, FAA	1	3
Burmanniaceae	1	1	1	AM (NM)	Aqua	2	GIP	1	SSB		NSH	0	2
Byblidaceae	1	2	2	NM, Carn		5	SIP	4	SSB, GPF		FPF, FE	3	12
Campanulaceae	3	23	25	AM		0	GIP	1	SSB, GPF (21)	RLR (1)	FPF (25), FAA (11)	3	4
Capparaceae	1	1	1	NM, LRH	ASD	2	GIP	1			NSH	0	3
Caryophyllaceae	3	8	8	NM, LRH	ASD	1	GIP	1	SSB, GPF?		FPF (2), FAA	1	3

Family	Genera	Sp	Sp2	Myc	Habitat	n1	Pollination	n2	Seed	Root codes	FPF codes	v1	v2
Casuarinaceae	2	29	33	EM-AM, CR AM, N2F,		6.5	Wind	2	CSB, WDS	RLR (450), RAG (7)	NSH (2)	3	11.5
Celastraceae	3	16	19	AM		0	GIP	1	SSB, GPF (15)	RLR (3)	FPF (19)	2.7	3.7
Centrolepidaceae	2	19	23	NM, LRH	Aqua	1	Wind	2	SSB, GPF?		FPF (18), FAA (23)	2.5	5.5
Cephalotaceae	1	1	1	NM, Carn		5	GIP	1	SSB, GPF	RLR (1)	FPF, FE	4	10
Chenopodiaceae	20	148	180	NM, LRH	ASD	2	Wind	2	SSB (80), CSB (134), WDS (38)		NSH (150)	0.4	4.4
Colchicaceae	2	19	26	AM		0	GIP	1	SSB, GPF (5)	RCB (26)	FPF (5)	2.5	3.5
Commelinaceae	1	1	1	NM, LRH	ASD	1	GIP	1	SSB, GPF	RCB	FPF, SAF	3	5
Convolvulaceae	8	15	16	AM		0	GIP	1	SSB, GPF?	RLR (9)	FPF (8), NSH	0.9	1.9
Crassulaceae	1	8	11	NM	ASD	1	GIP	1	SSB, GPF		FPF, FAA	2	4
Cymodoceaceae	4	5	5	NM	Marine	4	Water	4			NSH	0	8
Cyperaceae	24	193	268	NM (AM), DR		4	Wind	2	SSB, GPF (178)	RLR (195), RCB (2)	FPF (37), FAA (18), SIm (4)	1.8	7.8
Dasypogonaceae	4	19	19	NM, SBR		3	SIP, GIP	1.5	SSB, GPF	RLR (450), RAG (1)	FPF (19), SIm (1)	2.8	7.3

Dicots

Family	Genera	Sp	Sp2	Myc	Habitat	n1	Pollination	n2	Seed	Root codes	FPF codes	v1	v2
Dilleniaceae	1	99	114	AM		0	SIP, BP	5	SSB, GPF	RLR (17)	FPF (114), SAF (2)	3	10
Dioscoreaceae	1	1	1	AM		0	GIP	1	WDS	RLR	FPF	2	3
Droseraceae	2	94	109	NM, Carn, LRH		6	GIP	1.5	SSB, GPF	RCB (58)	FPF (108), NSH (1)	2.5	10
Ecdeiocoleaceae	2	3	3	NM, SBR		3	GIP	1.5	SSB, GPF	RLR	FPF	3	7.5
Elaeocarpaceae	3	35	39	AM		0	SIP	3	SSB, GPF	RLR (1)	FPF (39), NSH (6)	2	5
Elatinaceae	2	5	5	AM		0	GIP	1			SIm (5)	0	1
Emblingiaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Eremosynaceae	1	1	1	AM		0	GIP	1	SSB, GPF		FPF, SAF	2	3
Ericaceae	18	230	343	Eric		5	SIP, Bird, NFM	2	SSB, GPF	RLR (39)	FPF (19), SAF (11)	2.6	9.7
Euphorbiaceae	10	71	79	AM		0	GIP	1	SSB, GPF	RLR (3)	FPF (23), SAF (6), NSH (11)	1.6	2.6
Fabaceae	42	1021	1204	AM, EM-AM, NM, CR, N2F		3.9	GIP, SIP, Bird, BPB	3.1	SSB, GPF	RLR (86)	FPF (330), SAF (31), FAA (2), NSH (50)	2.7	10.9
Frankeniaceae	1	21	24	AM	ASD	0	GIP	1	SSB, GPF?		NSH	0	1
Gentianaceae	2	3	3	AM		0	GIP	1	SSB, GPF?		NSH	0	1
Geraniaceae	3	8	8	AM		0	GIP	1	SSB, GPF, WDS (4)	RLR (3)	FPF, FAA (2)	2.7	3.7
Goodeniaceae	11	206	236	AM		0	SIP	4	SSB, GPF (146)	RLR (35)	FPF (155), SAF (13)	2.6	6.6
Gyrostemonaceae	5	14	17	AM		0	Wind	2	SSB, GPF		FPF, FE	3	5
Haemodoraceae	7	78	109	NM, SBR		3	Bird, GIP, SIP	3.1	SSB, GPF (96)	RLR (27), RCB (16)	FPF (109), FE (5), SAF FAA (2)	3	9.1
Haloragaceae	7	51	60	AM, NM (AM)	Aqua (14)	3	GIP	1.4	SSB, GPF (18)	RLR (4)	FPF (22), SAF FAA (1), NSH (33)	0.6	5
Hemerocallidaceae	11	29	47	AM		0	GIP	2.4	SSB, GPF (34)	RLR (30), RCB 8	FPF (34), SAF (3), SIm (2)	2.4	4.8
Hydatellaceae	1	5	5	NM	Aqua	1	GIP	1	SSB		FPF, FAA, NSH	1	3
Hydrocharitaceae	5	8	8	NM	Marine	4	Water, GIP	3.4			NSH	0	4.2
Hypericaceae	1	2	2	AM		0	GIP	1	SSB, GPF?		FAA	1	2
Hypoxidaceae	1	5	8	AM		0	GIP	1	SSB, GPF?	RCB (8)	FPF	1	2
Iridaceae	2	18	25	AM		0	GIP	1	SSB, GPF	RLR (23), RCB (2)	FPF (20)	2.5	3.5
Juncaceae	2	14	15	NM, LRH		2	Wind	2	SSB, GPF?	RLR (10)	FPF FAA (1)	2	6
Juncaginaceae	2	14	16	NM	Aqua	1	Wind	2	SSB		FAA (4), NSH (2)	0.5	4
Lamiaceae	19	165	193	AM		0	SIP, GIP	3.1	SSB, GPF (52)	RLR (4)	FPF (21)	1.3	4.4
Lauraceae	1	8	13	NM, Para		4	GIP	1	SSB, GPF		SIm (13)	1	6
Lentibulariaceae	1	15	15	NM, Carn	Aqua	5	SIP	4	SSB, GPF?	RLR (1)	FPF, FAA	2	11
Linaceae	1	1	1	AM		0	GIP	1	SSB, GPF?		FAA (1)	1	2
Loganiaceae	4	26	27	AM		0	GIP	1	SSB, GPF (14)	RLR (3)	FPF (8), FAA (5)	1.8	2.8
Loranthaceae	3	15	18	NM, Para	Mistletoe (17)	4	Bird, GIP	4.3			FPF (1), SIm (17)	1.3	9.7

Appendix 1. (cont.).

Family	Genera	Species	Taxa	Plant Nutrition Traits			Pollination Traits			Fire Response Traits			CV
				Nutrition	Habitat	CV	Syndrome	CV	Seed	Sprouting	Ecology	CV	sum
Lythraceae	1	1	1	AM		0	GIP	1	SSB		FAA (1)	1	2
Malvaceae	18	164	191	AM		0	SIP, GIP	2.9	SSB, GPF (109)	RLR (5)	FPF (103), SAF (11), NSH (19)	1.1	3.9
Meliaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Menyanthaceae	2	10	10	NM	Aqua	2	GIP	1	SSB	RLR (2)	NSH	0.5	3.5
Molluginaceae	3	8	8	AM		0	GIP	1	SSB, GPF (5)	RLR (1)	FPF SAF (5), NSH (3)	1	2
Myrtaceae	48	1066	1510	AM, EM-AM, EM (AM)		2.8	GIP, SIP, Bird, NFM, SPP	2.4	SSB GPF (367), CSB (1143), WDS (210)	RLR (450), RAG (42)	FPF (218), SAF (64), SIm (27), VFF (834)	3.9	10.5
Nitrariaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Nyctaginaceae	2	3	3	AM		0	GIP	1			SIm (3)	0	1
Olacaceae	1	4	4	AM		4	GIP	1	SSB, GPF?		FPF SAF (1)	1	6
Oleaceae	1	2	3	AM		0	GIP	1	SSB			0	1
Onagraceae	1	2	4	AM		0	GIP	1	SSB, WDS, GPF?		FPF, FAA	1	2
Orchidaceae	27	362	428	Orchid		5.1	SIP, GIP, SD, VD	3.7	WDS (426)	RLR (1), RCB 427)	FPF (263), SIm (78),	1.6	10.4
Orobanchaceae	2	1	2	AM		0	GIP	1	SSB, GPF?		FAA	1	2
Oxalidaceae	1	3	3	AM		0	GIP	1		RCB (3)	FAA (3)	2	3
Pedaliaceae	1	1	1	AM		0	GIP	1	SSB, GPF		SIm (1)	0	1
Philydraceae	1	2	4	AM		1	GIP	1	SSB, GPF?	RCB (4)	FPF, FAA	2	4
Phrymaceae	4	7	7	AM		0	GIP	1	SSB, GPF?		FAA (1)	0	1
Phyllanthaceae	3	15	15	AM		0	GIP	1	SSB, GPF (14)	RLR (3)	FPF, SAF (4)	2	3
Pittosporaceae	6	36	36	AM		0	GIP	1.5	SSB, GPF (17)	RLR (19)	SIm (2), NSH (3)	0.8	2.3
Plantaginaceae	4	13	13	AM		0	GIP	1	SSB		FAA (6)	0	1
Plumbaginaceae	1	1	1	AM		0	GIP	1			NSH	0	1
Poaceae	53	164	182	AM, LRH		1	Wind	2	SSB, GPF (68)	RLR (15)	FPF (94), FAA (11), NSH (90)	0.5	3.5
Polygalaceae	1	17	17	AM		0	GIP	4	SSB, GPF	RLR (17)	FPF	3	7
Polygonaceae	5	12	12	NM, LRH	ASD	1	GIP	1	SSB, GPF (3)		FPF (3), FE (1), FAA (4), NSH (5)	0.6	2.6
Portulacaceae	4	32	36	NM	ASD	1	GIP	1	SSB, GPF (34)	RCB (8)	FPF (34), FE (1), FAA (1)	1.8	3.8
Posidoniaceae	1	7	7	NM	Marine	4	Water	4			NSH	0	8
Potamogetonaceae	4	13	14	NM	Aqua	4	Water, Wind	5			NSH	0	8
Primulaceae	1	3	6	AM		0	GIP	1	SSB, GPF?		FPF	1	2
Proteaceae	15	726	928	NM, CR		3	SIP, Bird, GIP, NFM, SPP	5.3	SSB GPF (565), CSB WDS (446)	RLR (450), RAG (10)	FPF (161)	3.7	12

Ranunculaceae	3	10	13	AM		0	GIP	1	SSB, GPF (9)	RLR (4)	FPF (4), FE FAA (1)	1.7	2.7
Restionaceae	20	107	111	NM (AM) DR, SBR		4	Wind	2	SSB, GPF	RLR (48)	SIm (61)	3	7.9
Rhamnaceae	11	98	115	EM-AM, AM		2.3	GIP	1	SSB, GPF (81)		FPF (106)	1.4	4.6
Rosaceae	1	1	1	AM		0	GIP	1			SIm (1)	0	1
Rubiaceae	4	15	16	AM		0	GIP	1	SSB, GPF (12)	RLR (3)	FPF, SAF FAA (1), NSH (4)	1.5	2.5
Ruppiaceae	1	4	4	NM	Aqua	4	Water	4			NSH	0	3
Rutaceae	15	128	176	AM		0	GIP, SIP	1.7	SSB, GPF (141)	RLR (18)	FPF (89), SAF (4), VFF	2.1	3.8
Santalaceae	7	28	28	NM, Para		4	GIP	1.3	SSB, GPF (15)	RLR (1)	SIm (27)	1.3	6.6
Sapindaceae	3	28	36	AM		0	GIP	1	SSB, WDS, GPF?	RLR (6)	FPF (7), SIm (1)	1.3	2.3
Scrophulariaceae	6	124	170	AM		0	GIP	1.7	SSB, GPF		SAF (30), NSH (8)	0.7	2.3
Solanaceae	10	44	49	AM		0	GIP, SIP, BPB	1.3	SSB, GPF (29)	RLR (1)	FPF (30), SAF (25), NSH (35)	1.1	2.4
Stylidiaceae	2	203	221	AM		0	SIP, GIP	3	SSB, GPF (212)	RLR (6)	FPF (15), FAA (33)	2.5	5.5
Surianaceae	1	2	2	AM		0	GIP	2	SSB, GPF		FPF, NSH	2	2
Thymelaeaceae	1	46	57	AM		0	GIP	1	SSB, GPF	RLR (6)	FPF (57)	3	5
Typhaceae	1	2	2	NM (AM)	Aqua	2	Wind	2	WDS	RLR	NSH	0	4
Urticaceae	2	3	3	NM		1	Wind	2	SSB, GPF?		FAA (3)	1	4
Violaceae	1	6	10	AM		0	GIP	1	SSB, GPF	RLR	FPF	3	4
Vitaceae	1	1	1	AM		0	GIP	1		RLR	NSH	1	2
Xanthorrhoeaceae	2	10	12	AM		0	GIP, Bird	1	SSB, GPF	RLR (11), RCB (1)	FPF, VFF	3.5	4.5
Xyridaceae	1	11	11	AM		0	GIP	1	SSB, GPF	RLR	FPF	3	4
Zosteraceae	2	2	2	NM	Marine	4	Water	4			NSH	0	8
Zygophyllaceae	2	22	22	NM, N2F?	ASD	3	GIP	1	SSB, WDS, GPF?		NSH	1	5

Appendix 2. Clades of southwestern Australian plants which have exceptional diversity and highly specialised nutrition, pollination or fire traits (see Table 1 for abbreviations).

Family or group	Genera	Species WA	Subspies WA	Informal names	Taxa WA	Taxa SWAFR	Australia species	Global species	Nutrition	Pollination	Fire, etc.
Casuarinaceae	*Casuarina, Allocasuarina*	29	4	0	33	32	69	91	AM-EM, AM, CR, N2F	Wind	CSB, RSA, RLR, WDS
Eucaylptineae (Myrtaceae) with EM	Trees—*Eucalyptus, Corymbia*, etc.	389	80	26	497	309	883	~860	EM (AM)	Bird, Insect GIP, NFM	CSB, RSA, RLR, REB, GDR
Melaleuceae (Myrtaceae)	Shrubs—*Melaleuca alliance*	281	39	3	324	570	453	~500	EM-AM, AM, AM-EM	Insect GIP & Bird	CSS, some RCL
Mimosoideae (Fabaceae)	*Acacia* only	641	93	67	801	571	1058	~1550	AM, AM-EM, EM (AM), N2F	Insect GIP, NFM	SSB, some RLR
Mirbelieae (Fabaceae)	*Gastrolobium, Gompholobium*, etc.	489	20	31	540	203	405	~700	EM-AM, AM, N2F, CR	Insect SIP & Bird	SSB, RLR, SGP
Mirbelieae in part	*Daviesia* only	103	12	0	115	117	130	130	NM-CR, AM, N2F	Insect SIP & Bird	SSB, RLR, SGP
Pomaderreae (Rhamnaceae)	Australian genera	112	15	1	128	115	251	~260	EM-AM or AM	Insect GIP	SSB, RLR, SGP
Proteaceae	*Banksia, Grevillea*, etc.	758	177	32	967	930	1176	~4000	NM-CR	Bird, NFM, SIP, GIP, SPP	CSB, SSB, RLR, REB, GDR, WDS
Cyperaceae	13 genera	351	14	96	461	268	882	~5500	NM-DR, SBR	Wind	RLR, RCB (FAA), SSB, SGP, LCP
Restionaceae	19 genera	102	5	1	108	111	181	485	NM-DR, SBR	Wind	SSB, RLR, SGP, LCP
Haemodoraceae	*Haemodorum, Anigozanthos*, etc.	94	27	3	124	110	131	131	NM, SBR	Bird, SIP, GIP	RCB, RLR, SSB, SGP, FPF, WDS
Dasypogonaceae	*Dasypogon, Kingia, Calectasia*	19	0	0	19	19	20	16	NM, SBR	Insect GIP, BPB	SSB, RLR, SGP, LCP
Carnivorous plants (3 families)	Drosera, Utricularia, etc.	150	14	2	167	127	251	860	NM carnivorous	Insect GIP (1 bird)	RCB, FAD, FAA, SGP, FPF
Parasitic plants (4 families)	*Amyema, Santalum, Nuytsia, Cuscuta*, etc.	111	11	1	123	69	190	4881	NM parasites with haustoria	Bird & insect	SIm (most), bird dispersed
Orchidaceae	Terrestrial genera (26)	398	38	24	460	440	1866	~28500	Orchid mycorrhizas	SIP (most are deceived)	RCB, many FPF, some SIm, WDS
Asparagaceae	*Thysanotus* only	49	0	10	59	53	64	64	Unique mycorrhiza type	SIP, BPB	RCB or RLR, SSB, SGP
Stylidiaceae	*Stylidium, Levenhookia*	254	12	9	275	221	300	~310	AM	SIP (trigger), SPP	SSB, SGP, some RLR or RRB