

# Pollination strategies are exceptionally complex in southwestern Australia – a globally significant ancient biodiversity hotspot

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## ABSTRACT

**Context.** The Southwest Australian Floristic Region has exceptional plant evolutionary complexity for fire, nutrition and pollination traits. **Aims.** Our aim was to allocate pollination strategies to all vascular plants in this biodiversity hotspot by analysing existing and new data. **Methods.** Here we assigned a flower syndrome to ~8800 plants in this region, using floral traits and visitation records for insects, birds or mammals, which were well correlated. **Key results.** Specific insect relationships were most common (3383), especially with native bees (2410), including buzz pollination (450). Others were pollinated by wind (1054 plants), water (35) or had relatively unspecialised flowers visited by diverse insects (3026). Specific associations with flies (588) or butterflies and moths (165) were less common. Approximately 14% were primarily pollinated by birds (601) or birds and insects (583) – with much larger flowers (corresponding with bird bill lengths), and less insect-attracting colours (e.g. red or green). Non-flying mammals, especially honey possums, visit certain flowers along with birds. Pollination complexity peaked in the Myrtaceae (11% bird, 25% bird and insect), Fabaceae (2% bird, 46% bee, 2% buzz pollination) and Proteaceae (40% birds, 31% specific insects). Bird pollination also has multiple origins in the Ericaceae (8%), Haemodoraceae (20%), Rutaceae (16%), Pittosporaceae (14%) and *Eremophila* (45%). Extreme specialisations included secondary pollen presentation (1231), post-pollination colour change (72), mobile columns (310), explosive pollen release (137) and visual (209) or sexual (171) deception in orchids. Pollination trait complexity included >275 evolutionary transitions, especially from insects to birds (130), more specific insects (100), or wind (15). These followed similar morphological pathways within families but differed between them. **Conclusions.** This complexity appears to be globally unique, and peaks in highly speciose plant families with diversity centred in the region. **Implications.** This has ecological and genetic consequences, especially for rare flora management, ecosystem restoration and assessing plant vulnerability to habitat degradation, fire and climate change.

**Keywords:** bees, bird pollination, floral evolution, mammal pollination, Myrtaceae, pollination ecology, Proteaceae, Southwest Australian Floristic Region, wind pollination.

## Introduction

Pollen transfer between individuals, especially between separate populations, is particularly important for maintaining the genetic integrity and diversity of plant species (Yates *et al.* 2007; Krauss *et al.* 2017; Eakin-Busher *et al.* 2020; Prendergast and Ollerton 2021). Although abiotic pollen transport (wind, water) is important in some plant families (e.g. Poaceae, Restionaceae, Cyperaceae), it is estimated that 88% of flowering plants are animal pollinated and the majority of these are served by insects (Ollerton *et al.* 2011). To ensure adequate pollination, flowers require effective visual and chemical attractants and must also provide (or appear to provide) adequate rewards to visitors (Woodcock *et al.* 2014). Although pollen and nectar food rewards primarily drive flower visits, there also are important non-nutritive rewards for insects (Woodcock *et al.* 2014). Apparent rewards are virtual food, virtual sex or a virtual place for their reproduction. Other attractions include places of congregation and shelter, and some flowers also become brood sites (see section *Pollinator attraction to flowers and food rewards*). However, effective pollination does not result from all flower visitors because some are resource robbers (e.g. Fenster *et al.* 2004).

Plant–animal interactions linked to pollination are categorised using standard floral syndromes based on floral traits and constancy in visitor data (Table 1). These include the size, structure, colour and arrangement of flowers that are linked to specific functional groups of pollinators (Ollerton *et al.* 2009; Willmer 2011; Groom and Lamont 2015; Dellinger 2020). Despite some variations in the consistency of pollination syndromes (Willmer 2011; Dellinger 2020; Scaccabarozzi *et al.* 2020a; Chmel *et al.* 2021; van der Niet

2021), these have been shown to be highly correlated with pollinator data by many studies across the globe (e.g. Kingston and Mc Quillan 2000; Johnson 2013; Rosas-Guerrero *et al.* 2014; Johnson and Wester 2017). Thus, assigning pollination syndromes to plants is a powerful tool for pollination research, provided they are backed up by evidence such as floral visitor consistency and pollen transfer.

Major groups of insect pollinators in Western Australia include indigenous (native) bee species (Houston 2000,

**Table 1.** Morphological and ecological syndrome definitions we used to allocate plant taxa by examining data, images and specimens.

Syndrome	Primary definition	Supporting evidence	References
Wind	<ol style="list-style-type: none"> <li>1. Flowers small, numerous, dull</li> <li>2. Poor visual display (e.g. no corolla)</li> <li>3. Nectarless</li> <li>4. Relatively large and/or numerous anthers clustered or pendulous on long filaments</li> <li>5. Pollen dispersible (relatively dry and not sticky)</li> <li>6. Exposed stigma is often very long, branched and/or hairy</li> </ol>	<ol style="list-style-type: none"> <li>1. Often dioecious</li> <li>2. Often in open vegetation, disturbed or harsh habitats</li> <li>3. Often growing in windy situations</li> <li>4. Few or no records of potential pollinators</li> <li>5. Massed synchronous flowering</li> <li>6. Abundant part of pollen rain</li> </ol>	Regal (1982), Newsome (1999) and van der Kaars and De Deckker (2003)
Water	<ol style="list-style-type: none"> <li>1. Small dull coloured flowers (as above)</li> <li>2. Submerged or on surface of water</li> <li>3. Highly specialised pollen and stigma</li> </ol>	<ol style="list-style-type: none"> <li>1. Often dioecious</li> <li>2. Flowering infrequent and may be synchronised</li> </ol>	Cox (1988), Ackerman (2007) and Van Tussenbroek <i>et al.</i> (2009)
General insects (GIP)	<ol style="list-style-type: none"> <li>1. Basic flower structures – usually radially symmetrical</li> <li>2. In part defined by absence of specialised features</li> <li>3. Nectar usually present and readily accessible</li> </ol>	<ol style="list-style-type: none"> <li>1. Relatively small and brightly coloured</li> <li>2. Often in massed displays, opening sequentially</li> </ol>	Proctor <i>et al.</i> (1996), Armstrong (1979), Eakin-Busher <i>et al.</i> (2020) and Macgregor and Scott-Brown (2020)
Native bees	<ol style="list-style-type: none"> <li>1. Pollen protected within flower</li> <li>2. Pollen inaccessible to other insects or oily</li> <li>3. Flowers more likely to be blue or yellow</li> </ol>	<ol style="list-style-type: none"> <li>1. Nectar may be absent or in small quantities</li> <li>2. Nectaries may be hidden from other insects</li> </ol>	Holm (1988), Proctor <i>et al.</i> (1996), Willmer (2011) and Houston (2000, 2018)
Buzz pollinated by bees (BPB)	<ol style="list-style-type: none"> <li>1. Closed anthers (indehiscent) with small openings as pores or slits</li> <li>2. Nectar usually lacking</li> <li>3. Pollen released by vibration</li> </ol>	<ol style="list-style-type: none"> <li>1. Flowers relatively small, but coloured to attract bees</li> <li>2. Flowers often blue with contrasting yellow anthers</li> <li>3. Anthers often adpressed</li> </ol>	Proença (1992), Houston (2018), Houston and Ladd (2002) and Keighery (2017)
Butterfly or moth	<ol style="list-style-type: none"> <li>1. Long floral tube with nectar at base</li> <li>2. Pale coloured and night scented (moth)</li> </ol>	<ol style="list-style-type: none"> <li>1. Abundant nectar</li> <li>2. More nectar or scent at night (moths)</li> </ol>	Holm (1988) and Proctor <i>et al.</i> (1996)
Fly	<ol style="list-style-type: none"> <li>1. Strongly scented like carrion</li> <li>2. Nectar present</li> </ol>	<ol style="list-style-type: none"> <li>1. Relatively dull colours or resembling flesh</li> </ol>	Willmer (2011)
Very small flowers	<ol style="list-style-type: none"> <li>1. Individual flowers minute – several mm wide</li> <li>2. Inflorescence small 2–10 mm?</li> </ol>	<ol style="list-style-type: none"> <li>1. Very crowded flowers</li> <li>2. Not normally recognised</li> </ol>	See text
Birds	<ol style="list-style-type: none"> <li>1. Flowers substantially larger than related species</li> <li>2. Abundant nectar</li> <li>3. Flowers trumpet, tubular bell or fan shaped or aggregated to form a brush</li> <li>4. Stigma and anthers project out of flower or inflorescence bracts</li> </ol>	<ol style="list-style-type: none"> <li>1. Flowers often bright red, orange or green</li> <li>2. Massed floral displays above foliage on sturdy stems</li> <li>3. More frequent visits by birds</li> <li>4. Secondary pollen presentation (SPP) more likely</li> </ol>	Proctor <i>et al.</i> (1996), Ford <i>et al.</i> (1979), Brown <i>et al.</i> (1997), Saffer (2004) and Johnson (2013)
Non-flying mammals (NFM)	<ol style="list-style-type: none"> <li>1. Large, sturdy, dull coloured inflorescences</li> <li>2. Musty odour and abundant nectar – high sugar concentration</li> </ol>	<ol style="list-style-type: none"> <li>1. Flowers hidden in foliage and/or close to ground</li> <li>2. SPP common</li> </ol>	Lynn Carpenter (1978), Holm (1988), Bradshaw (2014) and Saffer (2004)
Autogamous or high self-pollination	<ol style="list-style-type: none"> <li>1. Flowers small or very small</li> <li>2. Often in dense inflorescence</li> <li>3. Green or dull coloured</li> </ol>	<ol style="list-style-type: none"> <li>1. Most flowers set seed even when pollinators excluded</li> </ol>	Lloyd and Schoen (1992)

These are primarily based on standard definitions provided by the listed references.

2018), flies, especially bee flies (Bombyliidae), and hoverflies (Syrphidae) (Houston 2014; Inouye *et al.* 2015; Doyle *et al.* 2020), wasps (Brown and Phillips 2014; Houston 2014) and beetles (Bernhardt 2000). Introduced European honeybees (*Apis mellifera*) are now very common in flowers (van der Moezel *et al.* 1987; Prendergast *et al.* 2021). Native insects often have relatively specific relationships with flowers linked to specific pollination syndromes (Johnson 2013; Houston 2014; Dellinger 2020). Examples of highly specialised pollination syndromes in the region include secondary pollen presentation and buzz-pollination (Armstrong 1979; Keighery 1980, 1982, 1996; Proença 1992; Ladd 1994; Houston and Ladd 2002; De Luca and Vallejo-Marin 2013; Erbar and Leins 2015). It is important to study pollination strategies and their effectiveness, especially since animal vectors can be subject to declines both globally and locally (Hallmann *et al.* 2017; Sands 2018; Sánchez-Bayo and Wyckhuys 2019). It is also important to understand vegetation and plant traits required to support pollinator networks (Breeze *et al.* 2021; Prendergast and Ollerton 2021).

Bird pollination involves at least 560 species of plants in 16 families in Western Australia (Keighery 1980). Mammal pollinators in Australia include at least 10 genera and 20 species of small marsupials and at least 10 species of bats (Armstrong 1979), but the latter are not relevant in southwestern Australia (Holm 1988). Pollination by nectar-feeding non-flying mammals, especially honey possums, can be important in Western Australia (Hopper 1980; Saffer 2004). There are specialised floral features in both bird and mammal pollinated plant species, but many of these flowers also attract insects (Johnson 2013; Groom and Lamont 2015; Dellinger 2020).

Our study concerns the Southwest Australian Floristic Region (SWAFR), an area of exceptional plant species richness and endemism related to highly infertile soils and a long, relatively stable geological history and one of the original 25 global biodiversity hotspots (Myers *et al.* 2000; Hopper and Gioia 2004; Diels 2007). Soil and landform complexity and lower extinction rates may be equally important contributors to diversity (Cowling *et al.* 2017; Brundrett 2021). The SWAFR also has exceptional numbers of plants with complex functional traits, especially for mineral nutrition, fire recovery and pollination (see Brundrett 2021). The radiation of species in particular families may be pollinator driven as emphasised by radiations in the South African Cape Floristic Region for families such as the Iridaceae (Niet and Johnson 2009; Johnson 2010) and this may also be the situation in SWAFR for very diverse groups such as the Proteaceae, Myrtaceae and Fabaceae.

Bird or mammal pollination syndromes of Western Australian plants were summarised by Keighery (1980, 2017), Houston (2014) and Bradshaw (2014), but there was no synthesis of data for other syndromes. Thus, our first objective was to thoroughly review existing knowledge about pollination of all plants present in the SWAFR region, along with our own observations and floral trait data, to make a comprehensive

database of pollination syndromes and related floral traits for all SWAFR plants. Our second objective was to compare floral traits, such as size, shape and colour, with floral visitation data to test the reliability of syndrome allocations. We also compared pollination syndrome complexity within SWAFR plants to their global importance. Finally, we identify clades where syndrome switching has occurred and discuss ecological, genetic and evolutionary consequences of this in the bioregion. We believe this is the first attempt to assign pollination traits to the entire flora of a floristic region, which also is a global biodiversity hotspot.

## Methods and data sources

### Study area and species

The study area is limited to the Southwest Australian Floristic Region (SWAFR) as defined by Brundrett (2021). This 480,000 km<sup>2</sup> area, which is similar to the boundary in the Western Australian vegetation map by Beard *et al.* (2013), consists of nine contiguous IBRA (Interim Biogeographic Regionalisation for Australia) regions. These are the Avon Wheatbelt, Coolgardie, Esperance Plains, Geraldton Sandplains, Jarrah Forest, Mallee, Swan Coastal Plain, Warren and Yalgoo ([www.environment.gov.au/land/nrs/science/ibra](http://www.environment.gov.au/land/nrs/science/ibra)). Lists of all plant species in these areas were downloaded from the Australian Virtual Herbarium ([avh.chah.org.au](http://avh.chah.org.au), accessed 21 January 2021). The West Australian Flora Census ([florabase.dpaw.wa.gov.au](http://florabase.dpaw.wa.gov.au)) was used to update this list by adding recently described species and removing exotic taxa (Brundrett 2021).

### Definition and quantification of floral syndromes

As explained in the introduction, flowers are assigned to syndromes that categorise interactions between flowers and their vectors and mechanisms of pollination by biotic or abiotic means. The definitions and evidence we used to assign each taxon to a syndrome are provided in Table 1, with supporting references. These allocations are summarised in Table 4 for all genera of SWAFR plants; using a consistent approach and multiple evidence for syndrome allocations:

1. Scientific studies that confirm pollen vectors in SWAFR plants and some closely related taxa in eastern Australia (Table 5).
2. Animal associations with flowers from museum records, recorded images and our own observations.
3. Floral trait data from taxonomic sources or measured from herbarium specimens.
4. Where supported by agreement between floral traits and visitor records, syndrome allocations were extended to closely related species.

Data on features known to be associated with specific pollination syndromes such as flower size, structure and colour (Table 1) were obtained by consulting numerous images of flowers from online sources or wildflower guides and many taxonomic works (only references that concern pollination are listed here). Flower data were also available from the Western Australian Herbarium (<https://florabase.dpaw.wa.gov.au/>), the Flora of Australia (<https://profiles.ala.org.au/opus/foa>) and electronic keys (<https://florabase.dpaw.wa.gov.au/keys>). We also examined and measured flowers from representative specimens in the Western Australian Herbarium, especially in families with suspected wind or bird pollination (>3700 taxa). The average lengths of the pistil, anther and corolla or bracts in bird- or insect-pollinated flowers in the same genus were analysed by calculating averages and 95% confidence intervals. Floral size, colour and visitor data were complimentary so were summarised together for plant families in Figs 16–19. Comparison between floral length data and the size of nectar-feeding birds utilised bill length data for 140 specimens (83 species) of honeyeaters from Paton and Collins (1989). Data were also compiled for important floral features such as secondary pollen presentation, post pollination colour changes, dioecy, suspected autogamy, etc.

A conservative approach was used to assign syndromes, so data deficient plants were allocated to the most unspecialised applicable syndrome that was also considered typical or ancestral for given plant families, provided that floral morphology was similar. Thus, the number of plants with relatively complex or specific pollination syndromes is more likely to be underestimated here. However, there was sufficient evidence to allocate most SWAFR plant species to syndromes (Tables 4 and 2), with only 318 taxa listed as data deficient in Table 4.

## Floral visitation records

The SWAFR contains many plant species that lack detailed pollination studies, so we used data from well-studied plants as models to inform hypotheses about the pollination systems of close relatives that have similar floral morphologies. Lists of observed pollinators or flower visitors that could reasonably be assumed to be pollinators, compiled by Keighery (1980, 2017), Brown *et al.* (1997), Houston (2000) and many others, were used. Brown *et al.* (1997) had 255 sources including 86 detailed scientific studies, and 41 more from the past 25 years are cited in Table 2. Brown *et al.* (1997) collated 4093 records for animals visiting flowers of 744 plant species in 66 families. Recorded pollinators included 57 birds, 11 mammals and thousands of insects, some of which occur outside the SWAFR. Houston (2000) includes numerous records on interactions between bees and flowers and describes many highly specific syndromes. These datasets include numerous independent observations and many scientific studies, especially for large plant families. There

are some biases in these records, especially for birds and mammals over insects and for dominant plants in ecosystems (Brown *et al.* 1997). Some poorly studied groups remain, especially in the Apiaceae, Ericaceae, Lamiaceae, Malvaceae and Rhamnaceae.

We also relied on our own observations and photos of potential pollinators, some of which are illustrated here in Figs 2–15, or in online resources (Table 3). For author MCB these include 10 years of research focusing on banksia woodland restoration and 30 years of orchid ecology research (e.g. Brundrett 2016, 2019; Brundrett *et al.* 2018). For GJK these include 50 years of field ecological research as a biosystematist and biogeographer, pollination studies of *Thysanotus*, Ericaceae, *Boronia*, etc., and earlier compilations for buzz pollination and bird pollination (e.g. Keighery 1980, 1982, 2017). For PGL these include detailed studies of pollination especially concerning buzz pollination and pollen presentation in the Ericaceae, Malvaceae, Proteaceae, Myrtaceae and *Thysanotus* (e.g. Ladd 1994; Ladd *et al.* 1999; Ladd and Bowen 2020). We also provide >3000 supplemental images and 40 videos supporting pollination syndrome allocations (Table 3).

Animal visitor data were plotted against pollination syndromes to validate allocations in Table 4. As explained above, these data provided good coverage for most large families. Table 5 summarises data for Western Australian or closely related eastern Australian species where scientific studies have confirmed pollination vectors. This table includes 354 species (5% of the flora), including most of the largest plant families (26) and genera (66), as well as many keystone species; and 80% were studied in the SWAFR. Estimated numbers of clades where pollination syndrome switching has occurred in the SWAFR are provided in Supplementary Table S1.

## Pollination syndromes

Specialisation of floral morphology can be considered to involve changes towards pollination by fewer functional groups, use of fewer or less disparate pollinators, or changes in the intensity of use of a subset of pollinators (Fenster *et al.* 2004). Specialisation of flowers is common in the SWAFR, especially for bird and/or mammal pollination, or specific types of insects (Fig. 1). Traits were allocated to individual species in genera where pollination data support multiple trait categories (Table 4). Here is a continuum of flower types on a spectrum from highly specialised, to very generalist in some plant families in WA. However, syndromes were consistent at the genus level in many cases, allowing their records to be amalgamated in Table 4. In cases where flower structure and visitor data supports both birds and insects as major pollinators, species were designated to the bird and insect syndrome and some were also assigned to non-flying mammals and birds in Table 4.

**Table 2.** Pollination trait importance in southwestern Australia relative to global importance (data from Table 4).

Pollination syndrome	Major families in SWAFR (Total number of families)	Southwestern Australia	Global total species (%)	References for global importance
1. Wind	All Cyperaceae, Poaceae, Chenopodiaceae, Restionaceae, Casuarinaceae, Centrolepidaceae, Gyrostemonaceae, Juncaginaceae, Anarthriaceae, Cupressaceae, many Euphorbiaceae, Haloragaceae, some in other families and 685 gymnosperms (29)	1054 (12%)	~46,000–55,000 (14–18%)	Ackerman (2000), van der Kaars and De Deckker (2003), Ollerton <i>et al.</i> (2011) and Ollerton (2017)
2. Water	Marine or aquatic plants (7)	35 (0.39%)	~150 (0.05%)	Cox (1988) <sup>A</sup> and Du and Wang (2014)
3.0. All insects	See categories 3.1 to 4 below	6472 (74%)	~215,000 (70%)	Estimated here by subtracting categories above
3.1. General insects (GIP)	Non-specific invertebrates – bees, wasps, flies, beetles, etc. (81)	3026 (34%)	~150,000 (48%)	Ollerton (2017)
3.2. All specific insect pollination (SIP)	All specific syndromes (includes relatively specific syndromes)	3389 (38%)	~118,000 (38%)	See subcategories below
3.2. Native bees total	See below	2402 (27%)	~57,000 (19%)	Ollerton (2017)
3.2.1. Buzz-pollination	Asparagaceae ( <i>Thysanotus</i> ), Hemerocallidaceae, Boraginaceae, Elaeocarpaceae, Fabaceae, Solanaceae, Malvaceae, <i>Hibbertia</i> , etc. (16)	450 (5.2%)	~20,000 (6%)	Buchmann (1983) and Faegri (1986)
3.2.2. Bee SIP – other	Myrtaceae, <i>Haemodorum</i> , Rutaceae, Malvaceae, Stylidiaceae, etc. (15)	1355 (15%)	~37,000 (10%)	Calculated from 3.2 and 3.2.1
3.3. Fly or gnat SIP	Stylidiaceae, Orchidaceae, Proteaceae, etc. (4)	662 (7.5%)	~45,000 (15%)	Lloyd and Schoen (1992)
3.4. Moth and butterfly SIP	Some Capparaceae, Ericaceae, Goodeniaceae, Proteaceae, Rutaceae (5)	165 (1.9%)	~6000 (2%)	Ollerton (2017)
3.5. Beetle SIP	<i>Macrozamia</i> cycads (1)	3 (0.034%)	8000 (2.5%)	Ollerton (2017)
3.6. Wasp SIP	Orchidaceae, etc.	194 (2.2%)	~2000 (1%)	Ollerton (2017)
4. Deception in orchids <sup>B</sup>	Orchidaceae visual, sexual or brood site deception (1)	388 (3.8%)	~8000 (3%)	Ackerman (1986), Jersáková <i>et al.</i> (2009) and Gaskett (2011) (~30% of Orchidaceae)
5. Birds	See below (14)	1184 (13%)	7000–15,000 (2–5%)	Anderson <i>et al.</i> (2016), Ollerton (2017) and Abrahamczyk (2019)
5.1. Birds primarily	Myrtaceae, Proteaceae, Fabaceae, Haemodoraceae, Loranthaceae, etc. (11)	601 (6.8%)		Global split between 5.1 and 5.2 unclear
5.2. Birds and insects	Xanthorrhoeaceae, Ericaceae, Proteaceae, Scrophulariaceae, Myrtaceae (5)	583 (6.6%)		
6. Bats	Not relevant in region (Holm 1988)	0	528–1100 <sup>A</sup> (0.2–0.4%)	Kunz <i>et al.</i> (2011) and Ollerton (2017)
7. Non-flying mammals (NFM)	Some Proteaceae, Myrtaceae, Fabaceae (3)	36 <sup>A</sup> (0.41%)	~100 <sup>A</sup> (0.03%)	Carthew and Goldingay (1997) (85 sp., 43 genera, 19 families)
8. Self-pollination (autogamy)	Orchidaceae, Apiaceae, Araliaceae, Asteraceae, etc. (underestimated)	70 (0.79%)	~22,000 (5–10%)	Lloyd and Schoen (1992) and Ollerton <i>et al.</i> (2011)
9. Ferns	Non-flowering plants with motile gametes and wind-dispersed spores (18)	44 (0.50)	10,560	Christenhusz and Byng (2016)
Total	All vascular plants	8832	308,000	Christenhusz and Byng (2016)

Global estimates are from cited references and are extrapolated using the estimated number of species of vascular plants.

<sup>A</sup>Probably a substantial underestimate.

<sup>B</sup>Data also included in another category.

## Abiotic pollination

The proportion of plants with abiotic pollination (pollen moved by wind or water) worldwide is ~18% (Regal 1982; Ackerman 2000), compared with 11% in the SWAFR that

are primarily pollinated by wind (Fig. 1). Wind pollination is expected to be most dominant in areas where climatic conditions during flowering would be inimical to pollinator activity and this is not the case for most parts of the SWAFR. Wind pollination is also more important in colder

**Table 3.** Online resources

URL	Title
<a href="https://www.flickr.com/photos/rhizanthella/collections/72157721332055961">https://www.flickr.com/photos/rhizanthella/collections/72157721332055961</a>	Pollination in Western Australia (images organised in categories using Flickr)
<a href="http://www.flickr.com/groups/perth_banksia_invert">http://www.flickr.com/groups/perth_banksia_invert</a>	Images of banksia woodland insects and other invertebrates (Flickr Group)
<a href="http://www.youtube.com/channel/UCw3FAqI4-PXG8MxKhFYCwNQ">www.youtube.com/channel/UCw3FAqI4-PXG8MxKhFYCwNQ</a>	West Australian Orchid Pollination Channel (YouTube videos)

biomes than in the tropics and linked to increasing aridity (Regal 1982).

### Wind

Wind-pollinated plants occur in most SWAFR ecosystems, including over 1000 taxa in 30 families (Table 2). Wind pollination is the ancestral state for gymnosperms and is well studied globally (Lu *et al.* 2011). This includes the Cupressaceae (*Callitris*) and Podocarpaceae in the SWAFR region and exotic *Pinus* species, which are now widely planted and established. Wind pollination is very important in monocots with 638 taxa, in 111 genera from 11 families, which tend to have consistent floral traits (Table 4). Many of these species are dioecious (e.g. Anarthriaceae, Dioscoreaceae and Restionaceae) but some are not (Centrolepidaceae). Wind-pollinated dicots (406 taxa, 55 genera, 16 families) occur, as expected, in the Casuarinaceae, Chenopodiaceae (Amaranthaceae), Gyrostemonaceae, Haloragaceae, Hydatellaceae, Plantaginaceae, Polygonaceae, Rosaceae (*Acaena*), Sapindaceae and Urticaceae. Unexpected cases of wind pollination occur in the Euphorbiaceae s. l. (*Adriana*, *Amperea*, *Beyeria*, *Calycopeplus*, *Pseudanthus* and *Stachystemon*), Malvaceae (*Lawrencia*), Proteaceae (*Stirlingia latifolia*), Rubiaceae (*Opercularia*) and Surianaceae (*Stylobasium*), many of which are reported here for the first time.

Adaptation for wind pollination usually involved substantial reduction of perianth parts (Table 1, Fig. 2). Additionally, anthers are well exposed to the air stream as are the often densely papillate stigmas (e.g. Poaceae, Cyperaceae, Restionaceae) (Fig. 2). For example, the stigma of *S. latifolia* (the only specifically wind-pollinated Australian Proteaceae) is enlarged (Fig. 2v–x) compared with those of its sister species, and pollen is explosively released (Ladd and Bowen 2020). Wind-pollinated species tend to be dioecious (Table 4). Species in the Echeiocolaceae produce male or female flowers at different times on the same spikes (Fig. 1a) and this sexual dimorphism is synchronised across local areas (Briggs and Tinker 2014).

Pollen deposited in traps, wetlands, or recent offshore deposits is dominated by plant families known to be wind pollinated in Western Australia (Newsome 1999; Ackerman 2000; van der Kaars and De Deckker 2003; Semeniuk *et al.* 2006). Pollen rain also includes non-indigenous Pinaceae in recent sediments and fern spores in northern samples, as well as pollen from species not expected to be wind pollinated such as the Asteraceae, *Eucalyptus* and *Acacia*. This raises the possibility that these species may be partially pollinated by

wind, which could be very important for genetic continuity of widespread species, but this requires investigation. For example, *Acacia* is primarily animal pollinated, but some long-distance wind pollen dispersal also occurs (Macphail and Hill 2001), and eucalyptus pollen is often present in wetland sediments (e.g. Semeniuk *et al.* 2006).

Many Euphorbiaceae species have general insect pollination elsewhere (Willmer 2011), but not in the SWAFR where wind pollination is more prevalent (Table 4). *Beyeria* species, which have flowers characteristic of wind pollination, are also reported to be pollinated by a Miridae bug (Vincent *et al.* 2015), or by moths in eastern Australia (Finch *et al.* 2021), but this genus has flowers that are optimised for wind pollination. Wind pollination may not have been considered as a possibility in these studies, since ants and bugs may just be opportunistic herbivores. Honeybees visit wind-pollinated flowers such as *Beyeria viscosa* and *Tersonia cyathiflora* (Brown *et al.* 1997) and we commonly see them in the male flowers of sedges, but not female ones. Native bees (e.g. *Leioproctus* sp.) also visit *Allocasuarina*, *Gyrostemon* and *Suaeda* and the Haloragaceae (Orchard 1975; Keighery 1979a; Houston 2014). Insects collect pollen from wind-pollinated plants globally (Saunders 2018) but are presumably only stealing pollen since they generally avoid the inconspicuous female flowers.

### Water

Globally there are approximately 160 species of water-pollinated plants in 18 genera (Cox 1988; Du and Wang 2014). Western Australia is a global centre of diversity for marine plants (Carruthers *et al.* 2007) with 14 species in the Cymodoceaceae, Posidoniaceae and Zosteraceae present in the southwest region (Table 4). Seagrasses have extremely specialised pollen and flowers that can bloom synchronously in local areas (van Tussenbroek *et al.* 2009). There are also 16 other water-pollinated hydrophytes in the Araceae, Hydrocharitaceae, Potamogetonaceae and Ruppiaceae present in non-saline water. Hydrophily has evolved multiple times in submerged aquatic plants (Du and Wang 2014), but emergent hydrophytes are often insect or wind pollinated (Cook 1988). The SWAFR also has 44 taxa of terrestrial ferns or fern allies with water-mobile sperm that fertilise gametophytes, but only aquatic ferns (*Marsilea* and *Azolla* species) have dispersible gametes that function in a similar manner to the pollen of hydrophilus angiosperms.

**Table 4.** Summary of pollination trait data for all plant families in southwestern Australia with current numbers of taxa and species.

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references and GIP
Ferns																			
13	18	41	44		*														*Motile gametes on gametophytes
Gymnosperms																			
Cupressaceae	<i>Callitris</i>	9	9	9															Fig. 2g
Podocarpaceae	<i>Podocarpus</i>	1	1	1															Fig. 2h
Zamiaceae	<i>Macrozamia</i>	3	3					3	Weevil										Fig. 2f
Monocots																			
Alismataceae	<i>Damasonium</i>	1	1			1													
Anarthriaceae	3	11	11	11															Fig. 2a
Aponogetonaceae	<i>Aponogeton</i>	1	1					1	Small flies										Hydrophyte
Araceae	<i>Landoltia</i>	1	1		1														Hydrophyte
Araceae	<i>Lemna</i>	1	1		1														Hydrophyte
Asparagaceae	<i>Acanthocarpus</i>	8	8			8													Nectar/scent
Asparagaceae	<i>Arthropodium</i>	4	4					4	Bees			4							
Asparagaceae	<i>Chamaescilla</i>	4	5			5													Some nectar
Asparagaceae	<i>Chamaexeros</i>	4	4					4	Bees										
Asparagaceae	<i>Dichopogon</i>	3	3					3	Bees			3							
Asparagaceae	<i>Laxmannia</i>	10	15			15													Nectar
Asparagaceae	<i>Lomandra</i>	27	29			29													
Asparagaceae	<i>Sowerbaea</i>	2	2					2	Bees			2							Fig. 10h
Asparagaceae	<i>Thysanotus</i>	52	52					51	Bees			52					1		Figs 7m and 10a–c
Asparagaceae	<i>Xerolirion</i>	1	1			1													
Asphodelaceae	<i>Bulbine</i>	1	1			1													
Boryaceae	<i>Borya</i>	7	7			7													Floral tube
Centrolepidaceae	<i>Aphelia</i>	4	5	5															Very small flowers
Centrolepidaceae	<i>Centrolepis</i>	15	18	18															Very small flowers
Colchicaceae	<i>Burchardia</i>	5	5			5													Fig. 4f, g
Colchicaceae	<i>Wurmbea</i>	14	21			21			Flies, etc.										Fig. 4e, some dioecy (Case and Barrett 2004)
Commelinaceae	<i>Cartonema</i>	1	1					1	Bees			1							

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Cymodoceaceae		4	5		5														Marine
Cyperaceae		24	193	268	268														Fig. 2b, c
Dasypogonaceae	<i>Baxteria</i>	1	1					1	Unknown										Carrion smell
Dasypogonaceae	<i>Calectasia</i>	14	14					14	Bees				14		12				Figs 8i, j and 10d, pollen only
Dasypogonaceae	<i>Dasypogon</i>	3	3			3													Fig. 4h-m
Dasypogonaceae	<i>Kingia</i>	1	1			1													Insects and birds Powell (2009)
Dioscoreaceae	<i>Dioscorea</i>	1	1	1															Fig. 2t, u, dioecious
Ecdeiocoleaceae	<i>Ecdeiocolea</i>	2	2	2															
Ecdeiocoleaceae	<i>Georgeantha</i>	1	1	1															
Haemodoraceae	<i>Anigozanthos</i>	9	19							18							1		
Haemodoraceae	<i>Blancoa</i>	1	1							1									Fig. 14aa
Haemodoraceae	<i>Conostylis</i>	38	68			64				4					2				Figs. 4a–d and 14ab
Haemodoraceae	<i>Haemodorum</i>	10	11					11	Bees										Fig. 7f–k, open or closed corolla
Haemodoraceae	<i>Macropidia</i>	1	1							1									Fig. 14z
Haemodoraceae	<i>Phlebocarya</i>	3	4				4		Bees, etc.				4?					4	Fig. 10f, BPB?
Haemodoraceae	<i>Tribonanthes</i>	14	14				14		Unknown									14	Fig. 7d
Hemerocallidaceae	<i>Agrostocrinum</i>	2	2					2	Bees				2						Fig. 10e
Hemerocallidaceae	<i>Arnocrinum</i>	3	3					3	Bees				3						
Hemerocallidaceae	<i>Caesia</i>	3	8				7	1	Bees				1						Nectar
Hemerocallidaceae	<i>Corynotheca</i>	1	6			6			Bees, flies										
Hemerocallidaceae	<i>Dianella</i>	2	3					3	Bees				3						Fig. 10j, k
Hemerocallidaceae	<i>Hensmania</i>	3	3					3	Unknown										Fig. 7e, nectar
Hemerocallidaceae	<i>Hodgsoniola</i>	1	1					1	Bees				1						Nectar
Hemerocallidaceae	<i>Johnsonia</i>	5	6					6	Bees				6						Fig. 10g
Hemerocallidaceae	<i>Stawellia</i>	2	2					2	Bees				2						
Hemerocallidaceae	<i>Stypandra</i>	2	2					2	Bees				2						Fig. 10i
Hemerocallidaceae	<i>Tricoryne</i>	5	11					11	Bees										Fig. 7n, o, nectar, complex anthers
Hydrocharitaceae	<i>Halophila</i>	4	4		4														Marine
Hydrocharitaceae	<i>Hydrilla</i>	1	1		1														Hydrophyte
Hydrocharitaceae	<i>Najas</i>	1	1		1														Hydrophyte

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Hydrocharitaceae	<i>Ottelia</i>	1	1			1													Hydrophyte
Hydrocharitaceae	<i>Vallisneria</i>	1	1		1														Hydrophyte
Hypoxidaceae	<i>Pauridia</i>	5	8			8													
Iridaceae	<i>Orthrosanthus</i>	4	5					5	Bees										Fig. 7a, pollen only, flowers live ½ day
Iridaceae	<i>Patersonia</i>	14	20					20	Bees										As above
Juncaceae	<i>Juncus</i>	13	14	14															
Juncaceae	<i>Luzula</i>	1	1	1															
Juncaginaceae	<i>Cycnogeton</i>	2	2	2															
Juncaginaceae	<i>Triglochin</i>	12	14	14															Fig. 2o
Orchidaceae	<i>Caladenia</i>	125	162			108		54	Wasp or GIP							2			Fig. 13a, b, l, very complex
Orchidaceae	<i>Calochilus</i>	3	4					3	Scolid wasps								1		SD (Kuitert 2015)
Orchidaceae	<i>Corunastylis</i>	1	1					1	Small flies										Nectar
Orchidaceae	<i>Corybas</i>	5	5					5	Fungus gnats										Fig. 13e, fungus mimicry
Orchidaceae	<i>Cryptostylis</i>	1	1					1	Wasp										Fig. 13d, SD
Orchidaceae	<i>Cyanicula</i>	9	12				12		Bees or beetles										VD, bees primarily?
Orchidaceae	<i>Cyrtostylis</i>	3	3					3	Gnats										Nectar
Orchidaceae	<i>Diuris</i>	44	45				45		Bees										Fig. 13j, VD, pea mimicry
Orchidaceae	<i>Drakaea</i>	10	10					10	Wasp							10			SD lip mobile
Orchidaceae	<i>Elythranthera</i>	3	3				3		Flies or bees										Fig. 13m, VD
Orchidaceae	<i>Epiblema</i>	1	1				1		Bees?										VD
Orchidaceae	<i>Ericksonella</i>	1	1				1		Bees, etc.										VD
Orchidaceae	<i>Eriochilus</i>	6	12					12	Bees										Nectar
Orchidaceae	<i>Gastrodia</i>	1	1					1	Bees										Bees (Kuitert 2015)
Orchidaceae	<i>Leporella</i>	1	1					1	Ant										Fig. 13c, SD
Orchidaceae	<i>Leptoceras</i>	1	1				1		Flies, bees										VD
Orchidaceae	<i>Lyperanthus</i>	1	1					1	Bees										Some nectar?
Orchidaceae	<i>Microtis</i>	14	15			5		3	Small flies, ants								7		Scent, nectar
Orchidaceae	<i>Paracaleana</i>	12	13					13	Wasp							10			SD lip trigger
Orchidaceae	<i>Pheladenia</i>	1	1				1		Bees or flies										VD, bees?
Orchidaceae	<i>Praecoxanthus</i>	1	1				1		Unknown								1		VD, bees?

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**Table 4.** (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Orchidaceae	<i>Prasophyllum</i>	23	26			26			Beetles, flies, bees, wasps										Fig. 13g, nectar
Orchidaceae	<i>Pterostylis</i>	55	66					66	Fungus gnats							66			Fig. 13e, SD lip trigger
Orchidaceae	<i>Pyrorchis</i>	2	2				2		Bees										Some nectar?
Orchidaceae	<i>Rhizanthella</i>	2	2					2	Phorid fly										Fungus mimicry suspected
Orchidaceae	<i>Spiculaea</i>	1	1					1	Wasp							1			SD lip mobile
Orchidaceae	<i>Thelymitra</i>	36	38				33		Bees, flies, beetles								5		Fig. 13h, i, VD
Philydraceae	<i>Philydrella</i>	2	4					4	Bees								?		Fig. 7l, self-pollination also?
Poaceae	53	164	182	182															Well studied
Posidoniaceae	<i>Posidonia</i>	7	7		7														Marine
Potamogetonaceae	<i>Lepilaena</i>	6	7		7														Hydrophyte
Potamogetonaceae	<i>Potamogeton</i>	6	6	6															Hydrophyte
Potamogetonaceae	<i>Stuckenia</i>	1	1		1														Hydrophyte
Restionaceae	20	107	111	111															Fig. 2d, e
Ruppiaceae	<i>Ruppia</i>	4	4		4														Hydrophyte
Typhaceae	<i>Typha</i>	2	2	2															Hydrophyte
Xanthorrhoeaceae	<i>Chamaescilla</i>	1	1					1	Bees, etc.										Some nectar
Xanthorrhoeaceae	<i>Xanthorrhoea</i>	9	11			11													Fig. 4n–q, diverse insects, and birds (Powell 2009)
Xyridaceae	<i>Xyris</i>	11	11					11	Bees										Fig. 7b, c, pollen only
Zosteraceae	<i>Zostera</i>	1	1		1														Marine
Zosteraceae	<i>Heterozostera</i>	1	1		1														Marine
Dicots																			
Acanthaceae	<i>Avicennia</i>	1	1			1			Diverse										Many insects
Aizoaceae	6	26	27			27													Dioecious
Amaranthaceae	<i>Alternanthera</i>	2	2	2															
Amaranthaceae	<i>Amaranthus</i>	2	2	2															
Amaranthaceae	<i>Hemichroa</i>	1	1			1													
Amaranthaceae	<i>Ptilotus</i>	44	53				53		Bees, etc.										Most in arid zone
Amaranthaceae	<i>Surreya</i>	1	1	1															

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references	
Aphanopetalaceae	<i>Aphanopetalum</i>	1	1			1														
Apiaceae	3	3	3														3		Fig. 8v, w, very small flowers	
Apiaceae	10	54	60			60			Flies, etc.										Fig. 3q, x, y, small flowers	
Apocynaceae	<i>Alyxia</i>	2	2			2														
Apocynaceae	<i>Cynanchum</i>	2	2			2														
Apocynaceae	<i>Marsdenia</i>	2	2			2														
Apocynaceae	<i>Parsonsia</i>	1	1						1	Butterfly									Brown et al. (1997)	
Apodanthaceae	<i>Pilostyles</i>	2	2						2	Wasp									Small flowers	
Araliaceae	<i>Hydrocotyle</i>	27	27						Selfing								27	27	Very small flowers	
Araliaceae	<i>Trachymene</i>	10	12			8			Flies, etc								4	4	Very small flowers	
Asteraceae	13	45	45				41											?	41	Fig. 8y, very small inflorescences
Asteraceae	79	325	328			327	4													Fig. 3p, w
Bignoniaceae	<i>Pandorea</i>	1	1			1			Butterflies											
Boraginaceae	<i>Cynoglossum</i>	1	1			1														
Boraginaceae	<i>Halgania</i>	14	19						19	Bees			19							
Boraginaceae	<i>Heliotropium</i>	3	3			3														
Boraginaceae	<i>Myosotis</i>	1	1			1														
Boraginaceae	<i>Omphalolappula</i>	1	1			1														
Boraginaceae	<i>Plagiobothrys</i>	1	1			1														
Boraginaceae	<i>Trichodesma</i>	1	2						2	Bees			2							
Brassicaceae	11	40	41			38													3	
Byblidaceae	<i>Byblis</i>	2	2						2	Bees			2							Fig. 10p
Campanulaceae	<i>Isotoma</i>	4	4						4	Butterflies				4						Fig. 6n, o, nectary
Campanulaceae	<i>Lobelia</i>	12	14				13		Bees, etc.										1	
Campanulaceae	<i>Wahlenbergia</i>	7	7				5		Bees, etc.					7					2	
Capparaceae	<i>Capparis</i>	1	1						1	Butterflies and moths										Nocturnal
Caryophyllaceae	<i>Gypsophila</i>	1	1			1														
Caryophyllaceae	<i>Spergularia</i>	5	5			5														
Caryophyllaceae	<i>Stellaria</i>	2	2			2														

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**Table 4.** (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Casuarinaceae	<i>Allocasuarina</i>	27	31	31															Fig. 2i, j
Casuarinaceae	<i>Casuarina</i>	2	2	2															
Celastraceae	<i>Psammomoya</i>	4	4			4													
Celastraceae	<i>Stackhousia</i>	11	21					21	Butterflies and moths										Nectar tube
Celastraceae	<i>Tripterococcus</i>	1	1					1											
Cephalotaceae	<i>Cephalotus</i>	1	1			1			Bees, wasps, etc.										Wasp seen MCB
Chenopodiaceae	20	148	180	180															Fig. 2n
Convolvulaceae	8	15	16			16													
Crassulaceae	<i>Crassula</i>	8	11			11												11	
Dilleniaceae	<i>Hibbertia</i>	99	114					114	Bees (beetles)				114						Fig. 5l and 10r, s
Droseraceae	<i>Aldrovanda</i>	1	1			1													
Droseraceae	<i>Drosera</i>	93	108			108													Fig. 3o, pollen only
Elaeocarpaceae	<i>Platytheca</i>	3	4					4	Bees				4						Fig. 10l
Elaeocarpaceae	<i>Tetratheca</i>	30	33					33	Bees				33						
Elaeocarpaceae	<i>Tremandra</i>	2	2					2	Bees				2						
Elatinaceae	<i>Bergia</i>	3	3			3													
Elatinaceae	<i>Elatine</i>	2	2			2													
Emblingiaceae	<i>Emblingia</i>	1	1			1													
Eremosynaceae	<i>Eremosyne</i>	1	1			1													
Ericaceae	<i>Acrotriche</i>	7	8				8		Ants?									8	
Ericaceae	<i>Andersonia</i>	27	46				43	1	Bees, moths, etc.	2									Bee, fly, HP, butterfly Brown <i>et al.</i> (1997)
Ericaceae	<i>Brachyloma</i>	11	11				9			2									
Ericaceae	<i>Conostephium</i>	12	12					12	Bees				12						Fig. 10n
Ericaceae	<i>Cosmelia</i>	1	1							1									Bird
Ericaceae	<i>Dielsiodoxa</i>	5	6				5	1										5	Very small flowers
Ericaceae	<i>Leucopogon</i>	96	158				154	1	Bees, etc.	3									Fig. 6l
Ericaceae	<i>Lissanthe</i>	5	5				5		Bees, etc.									5	

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Ericaceae	<i>Lysinema</i>	6	6				5	1	Butterflies and moths										Nectar in tube
Ericaceae	<i>Melichrus</i>		3				3		Butterflies and moths										Nectar in tube
Ericaceae	<i>Monotoca</i>	1	1					1	Butterflies and moths										Nectar in tube
Ericaceae	<i>Needhamiella</i>	1	1					1	Moths, etc?										
Ericaceae	<i>Oligarrhena</i>	1	1				1											1	Very small flowers
Ericaceae	<i>Sphenotoma</i>	6	7					7	Butterflies and moths										Nectar in tube
Ericaceae	<i>Stenantha</i>	2	2							2									Bird in eastern Australia
Ericaceae	<i>Styphelia</i>	92	105				84	2	Butterflies (2), bees, etc.	19									Fig. 14w, in former genus <i>Astroloma</i>
Euphorbiaceae	<i>Adriana</i>	2	3	3															Fig. 2l, dioecious
Euphorbiaceae	<i>Amperea</i>	6	6	6															Dioecious
Euphorbiaceae	<i>Bertya</i>	2	2	2															Dioecious
Euphorbiaceae	<i>Beyeria</i>	20	24	24															Fig. 2k, dioecious
Euphorbiaceae	<i>Calycopeplus</i>	3	3	3															Dioecious
Euphorbiaceae	<i>Euphorbia</i>	10	11				11												
Euphorbiaceae	<i>Homalanthus</i>	1	1				1												
Euphorbiaceae	<i>Monotaxis</i>	5	6				6												
Euphorbiaceae	<i>Ricinocarpos</i>	13	13	3			10												nectar in some
Euphorbiaceae s. l.	<i>Stachystemon</i>	9	10	10															Fig. 2m, dioecious
Fabaceae	<i>Acacia</i>	451	571				571												Fig. 3s
Fabaceae	<i>Aotus</i>	12	20					20	Bees										
Fabaceae	<i>Bossiaea</i>	34	40					37	Bees	3									Fig. 14p
Fabaceae	<i>Callistachys</i>	1	2					2	Bees										
Fabaceae	<i>Chorizema</i>	24	24					24	Bees										
Fabaceae	<i>Cristonia</i>	2	3				3												
Fabaceae	<i>Cullen</i>	4	4				4												
Fabaceae	<i>Daviesia</i>	94	104					102	Bees	2									Fig. 9e–g, k–n
Fabaceae	<i>Dillwynia</i>	6	10					10	Bees										

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Fabaceae	<i>Erichsenia</i>	1	1					1	Bees										
Fabaceae	<i>Euchilopsis</i>	1	1					1	Bees										Fig. 9a
Fabaceae	<i>Eutaxia</i>	20	24					24	Bees										
Fabaceae	<i>Gastrolobium</i>	107	111					100	Bees	11									Fig. 9d
Fabaceae	<i>Glycine</i>	3	3			3													
Fabaceae	<i>Glycyrrhiza</i>	1	1			1													
Fabaceae	<i>Gompholobium</i>	27	28					28	Bees										
Fabaceae	<i>Goodia</i>	2	2					2	Bees										
Fabaceae	<i>Hardenbergia</i>	1	1					1	Bees										
Fabaceae	<i>Hovea</i>	6	7					7	Bees										
Fabaceae	<i>Indigofera</i>	8	8			8													
Fabaceae	<i>Isotropis</i>	4	5					5	Bees										
Fabaceae	<i>Jacksonia</i>	50	50					50	Bees										Fig. 9b, c, h–j
Fabaceae	<i>Kennedia</i>	10	13					9	Bees	4									Fig. 14n
Fabaceae	<i>Labichea</i>	7	9					9	Bees				9						Fig. 10q
Fabaceae	<i>Latrobea</i>	8	9					9	Bees										
Fabaceae	<i>Leptosema</i>	7	7							7									
Fabaceae	<i>Lotus</i>	2	2			2													
Fabaceae	<i>Mirbelia</i>	19	27					27	Bees										
Fabaceae	<i>Paragoodia</i>	1	1					1	Bees										
Fabaceae	<i>Paraserianthes</i>	1	1							1									Fig. 14m
Fabaceae	<i>Petalostylis</i>	2	2					2	Bees				2						
Fabaceae	<i>Phyllota</i>	4	4					4	Bees										
Fabaceae	<i>Ptychosema</i>	1	1					1	Bees										
Fabaceae	<i>Pultenaea</i>	27	32					32	Bees										
Fabaceae	<i>Senna</i>	9	12					12	Bees				12						
Fabaceae	<i>Sesbania</i>	1	1			1													
Fabaceae	<i>Sphaerolobium</i>	20	20					20	Bees										
Fabaceae	<i>Swainsona</i>	27	27					26	Bees	1									
Fabaceae	<i>Templetonia</i>	11	11					10	Bees	1									Fig. 14o

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Fabaceae	<i>Trigonella</i>	1	1					1	Bees										
Fabaceae	<i>Urodon</i>	2	2					2	Bees										
Fabaceae	<i>Viminaria</i>	1	1					1	Bees										
Frankeniaceae	<i>Frankenia</i>	21	24			24													
Gentianaceae	<i>Schenkia</i>	2	2			2													
Gentianaceae	<i>Sebaea</i>	1	1			1													
Geraniaceae	<i>Erodium</i>	2	2			2													
Geraniaceae	<i>Geranium</i>	2	2			2													
Geraniaceae	<i>Pelargonium</i>	4	4			4													
Goodeniaceae	<i>Anthotium</i>	4	6				5		Bees	1				6				5	Nectar in tube
Goodeniaceae	<i>Brunonia</i>	1	2			2								2					See text
Goodeniaceae	<i>Cooperhooia</i>	3	3				3							3				3	Nectar in tube
Goodeniaceae	<i>Dampiera</i>	47	55				55		Bees, etc.					55					Nectar in tube
Goodeniaceae	<i>Diaspasis</i>	1	1					1	Butterflies and moths					1					Nectar in long tube
Goodeniaceae	<i>Goodenia</i>	68	76				73	1	Bees, moth (l)					74			2		Fig. 6m, nectar (some selfing)
Goodeniaceae	<i>Lechenaultia</i>	23	24				13		Bees	11				24	4				Figs 3j–n, r, 8e, t and 14v, nectar – bird only
Goodeniaceae	<i>Scaevola</i>	53	61			60			Bees, wasps, etc.	1				61					Fig. 8c, nectar in tube
Goodeniaceae	<i>Selliera</i>	1	1			1								1					Nectar in tube
Goodeniaceae	<i>Velleia</i>	11	11				10		Bees, etc.					11			1		Some selfing
Goodeniaceae	<i>Verreauxia</i>	3	3					3	Bees, etc.					3					
Gyrostemonaceae	<i>Codonocarpus</i>	1	1	1															Mono or dioecious
Gyrostemonaceae	<i>Cypselocarpus</i>	1	1	1															Mono or dioecious
Gyrostemonaceae	<i>Gyrostemon</i>	10	13	13															Fig. 2r, s, dioecious
Gyrostemonaceae	<i>Tersonia</i>	1	1	1															Dioecious
Gyrostemonaceae	<i>Walteranthus</i>	1	1	1															Dioecious
Haloragaceae	<i>Glischrocaryon</i>	4	4			4													Likely reversion from wind
Haloragaceae	<i>Gonocarpus</i>	16	18	17													1		Typical for syndrome
Haloragaceae	<i>Haloragis</i>	13	17	17															

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Haloragaceae	<i>Haloragodendron</i>	2	2	2															
Haloragaceae	<i>Meionectes</i>	2	2	2															
Haloragaceae	<i>Myriophyllum</i>	13	14	14															
Haloragaceae	<i>Trihaloragis</i>	1	3	3															
Hydatellaceae	<i>Trithuria</i>	5	5	5															Taylor et al. (2010)
Hypericaceae	<i>Hypericum</i>	2	2			2													
Lamiaceae	<i>Brachysola</i>	2	2						2	Bees									
Lamiaceae	<i>Chloanthes</i>	1	1								1								Fig. 14r
Lamiaceae	<i>Cyanostegia</i>	4	4						4	Bees									Fig. 6k
Lamiaceae	<i>Dasymalla</i>	4	4						1	Bees	3								Fig. 6w
Lamiaceae	<i>Dicrastylis</i>	20	20						20	Bees									
Lamiaceae	<i>Hemiandra</i>	9	14						8	Bees	6								Fig. 6r
Lamiaceae	<i>Hemigenia</i>	43	50						48	Bees	2								
Lamiaceae	<i>Hemiphora</i>	5	5						1	Bees	4								
Lamiaceae	<i>Lachnostachys</i>	6	7						7	Bees									
Lamiaceae	<i>Mentha</i>	1	1			1	1												
Lamiaceae	<i>Microcorys</i>	17	26						23	Bees	3								
Lamiaceae	<i>Newcastelia</i>	2	2						2	Bees									
Lamiaceae	<i>Physopsis</i>	4	4						4	Bees									
Lamiaceae	<i>Pityrodia</i>	5	5						5	Bees									
Lamiaceae	<i>Prostanthera</i>	22	23						14	Bees	9								
Lamiaceae	<i>Quoya</i>	6	6						5	Bees	1								
Lamiaceae	<i>Teucrium</i>	6	10						10	Bees									
Lamiaceae	<i>Westringia</i>	8	9						9	Bees									
Lauraceae	<i>Cassytha</i>	8	13						13									13	Very small flowers
Lentibulariaceae	<i>Utricularia</i>	15	15						14	Bees, etc.	1							1	Fig. 14y, nectar in tube, bird (Cross 2019)
Linaceae	<i>Linum</i>	1	1			1													
Loganiaceae	<i>Adelphacme</i>	1	1			1													
Loganiaceae	<i>Logania</i>	10	10			10				Bees, flies, etc									Powell (2009), Brown et al. (1997), MCB

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Loganiaceae	<i>Orianthera</i>	11	12			12													
Loganiaceae	<i>Phyllangium</i>	4	4			3											1	3	Small flowers
Loranthaceae	<i>Amyema</i>	11	13							13									Fig. 14u
Loranthaceae	<i>Lysiana</i>	3	3							3									Brown <i>et al.</i> (1997)
Loranthaceae	<i>Nuytsia</i>	1	1								1								Diverse insects and birds
Lythraceae	<i>Lythrum</i>	1	1			1													Nectar
Malvaceae	<i>Abutilon</i>	9	9			9													
Malvaceae	<i>Alyogyne</i>	4	11						Bees		11								
Malvaceae	<i>Androcalva</i>	15	15				15		Bees									15	Fig. 8s, complex flowers
Malvaceae	<i>Brachychiton</i>	1	1								1								
Malvaceae	<i>Commersonia</i>	12	12				12		Bees									12	Complex flowers
Malvaceae	<i>Corchorus</i>	1	1				1											1	
Malvaceae	<i>Guichenotia</i>	17	17					17	Bees				17						Nectar
Malvaceae	<i>Hannafordia</i>	2	2				2											2	
Malvaceae	<i>Hibiscus</i>	3	4						Bees, etc.		4								
Malvaceae	<i>Lasiopetalum</i>	39	49					49	Bees				49						Fig. 10o
Malvaceae	<i>Lawrencia</i>	10	11	4		7													Dioecious
Malvaceae	<i>Lysiosepalum</i>	5	5					5	Bees				5						
Malvaceae	<i>Malva</i>	3	3			3													
Malvaceae	<i>Radyera</i>	1	1				1											1	
Malvaceae	<i>Seringia</i>	8	8					8	Bees				8						Closed anthers
Malvaceae	<i>Sida</i>	13	13			13													
Malvaceae	<i>Thomasia</i>	29	38					38	Bees				38						
Malvaceae	<i>Waltheria</i>	1	1			1													
Meliaceae	<i>Melia</i>	1	1			1													
Menyanthaceae	<i>Liparophyllum</i>	5	5			5													
Menyanthaceae	<i>Ornduffia</i>	5	5			5													
Molluginaceae	<i>Glinus</i>	2	2			2													
Molluginaceae	<i>Hypertelis</i>	1	1			1													
Molluginaceae	<i>Macarthuria</i>	5	5			5			Diverse										Fig. 3t, u

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Myrtaceae	<i>Actinodium</i>	1	2			2			Bees, etc.					2					Fig. 3f, oily pollen
Myrtaceae	<i>Agonis</i>	4	5			5													
Myrtaceae	<i>Aluta</i>	2	2			2													
Myrtaceae	<i>Anticoryne</i>	3	3			3													
Myrtaceae	<i>Astartea</i>	24	28			28													
Myrtaceae	<i>Astus</i>	4	4			4													
Myrtaceae	<i>Babingtonia</i>	11	11			11													
Myrtaceae	<i>Baeckea</i>	18	105			105													
Myrtaceae	<i>Balaustion</i>	1	1							1									Fig. 14h
Myrtaceae	<i>Beaufortia</i>	22	22							22					1				
Myrtaceae	<i>Callistemon</i>	2	2							2									
Myrtaceae	<i>Calothamnus</i>	44	52							52									Figs 8h and 14a
Myrtaceae	<i>Calytrix</i>	66	70				70		Bees, etc.						2				Fig. 6j, floral tube
Myrtaceae	<i>Chamelaucium</i>	12	50			46			Bees	4				50	6				Oily pollen
Myrtaceae	<i>Cheyniana</i>	2	2			1				1									Like <i>Balaustion</i>
Myrtaceae	<i>Conothamnus</i>	3	3			3													
Myrtaceae	<i>Corymbia</i>	4	4								4								
Myrtaceae	<i>Corynanthera</i>	1	1				1											1	Small flowers
Myrtaceae	<i>Cyathostemon</i>	7	24			24													
Myrtaceae	<i>Darwinia</i>	40	63			22				35	6			63					Figs 3b, c, 8d and 14e–g, oily pollen
Myrtaceae	<i>Enekbatus</i>	10	10			10													
Myrtaceae	<i>Eremaea</i>	16	26			26													
Myrtaceae	<i>Ericomyrtus</i>	4	5			5													
Myrtaceae	<i>Eucalyptus</i>	289	374							12	362								Fig. 14c
Myrtaceae	<i>Euryomyrtus</i>	4	4			4													
Myrtaceae	<i>Homalocalyx</i>	7	7			7													
Myrtaceae	<i>Homalospermum</i>	1	1			1													
Myrtaceae	<i>Hypocalymma</i>	26	36			36									1				
Myrtaceae	<i>Hysterobaeckea</i>	11	11			11													
Myrtaceae	<i>Kunzea</i>	26	32			30					2								

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Myrtaceae	<i>Lamarchea</i>	1	2							2									
Myrtaceae	<i>Leptospermum</i>	14	17			16				1									Fig. 3a
Myrtaceae	<i>Malleostemon</i>	17	18			18													
Myrtaceae	<i>Melaleuca</i>	176	192			176				16				7					Fig. 3e
Myrtaceae	<i>Micromyrtus</i>	28	31			31													
Myrtaceae	<i>Oxymyrrhine</i>	4	4			4													
Myrtaceae	<i>Paragonis</i>	1	1			1													
Myrtaceae	<i>Pericalymma</i>	4	5			5													
Myrtaceae	<i>Phymatocarpus</i>	3	3			3													
Myrtaceae	<i>Pileanthus</i>	8	9					9	Bees										Fig. 8r
Myrtaceae	<i>Regelia</i>	5	5			4				1									Fig. 3c
Myrtaceae	<i>Rinzia</i>	16	16			16													
Myrtaceae	<i>Scholtzia</i>	13	53			53													
Myrtaceae	<i>Seorsus</i>	1	1			1													
Myrtaceae	<i>Taxandria</i>	11	12			12													
Myrtaceae	<i>Tetrapora</i>	4	4			4													
Myrtaceae	<i>Thryptomene</i>	32	42			42													
Myrtaceae	<i>Verticordia</i>	95	144					131	Bees	13				97	21				Figs 8f, g and 14d, oily pollen
Nitrariaceae	<i>Nitraria</i>	1	1			1													Diocious?
Nyctaginaceae	<i>Boerhavia</i>	2	2			2													
Nyctaginaceae	<i>Commicarpus</i>	1	1			1													
Olacaceae	<i>Olax</i>	4	4			4													
Oleaceae	<i>Jasminum</i>	2	3			3													
Onagraceae	<i>Epilobium</i>	2	4			2											2		
Orobanchaceae	<i>Euphrasia</i>	1	1					1	Bees										Zygomorphic
Orobanchaceae	<i>Orobanche</i>		1			1													
Oxalidaceae	<i>Oxalis</i>	3	3			3													
Pedaliaceae	<i>Josephinia</i>	1	1			1													
Phrymaceae	<i>Elacholoma</i>	1	1			1													
Phrymaceae	<i>Glossostigma</i>	3	3			1											2		

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**Table 4.** (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Phrymaceae	<i>Peplidium</i>	2	2			2													
Phrymaceae	<i>Thyridia</i>	1	1			1													
Phyllanthaceae	<i>Phyllanthus</i>	4	4			4													
Phyllanthaceae	<i>Poranthera</i>	10	10			10													Small flowers
Phyllanthaceae	<i>Sauropus</i>	1	1			1													
Pittosporaceae	<i>Bentleya</i>	2	2							2									
Pittosporaceae	<i>Billardiera</i>	11	11			11													Nectar
Pittosporaceae	<i>Bursaria</i>	1	1			1													
Pittosporaceae	<i>Cheiranthra</i>	5	5					5	Bees				5						Fig. 10m
Pittosporaceae	<i>Marianthus</i>	14	14			11				3									Fig. 14r
Pittosporaceae	<i>Pittosporum</i>	3	3			3													Diverse insects and birds (Powell 2009)
Plantaginaceae	<i>Gratiola</i>	2	2			2													
Plantaginaceae	<i>Plantago</i>	6	6	6															
Plantaginaceae	<i>Stemodia</i>	2	2			2													
Plantaginaceae	<i>Veronica</i>	3	3			3													
Plumbaginaceae	<i>Muellerolimon</i>	1	1			1													
Polygalaceae	<i>Comesperma</i>	17	17					17	Bees					17					Fig. 6u, (Houston 2000)
Polygonaceae	<i>Duma</i>	2	2			2													
Polygonaceae	<i>Muehlenbeckia</i>	3	3			3													
Polygonaceae	<i>Persicaria</i>	3	3			3													
Polygonaceae	<i>Polygonum</i>	1	1			1													
Polygonaceae	<i>Rumex</i>	3	3	3															Well studied
Portulacaceae	<i>Calandrinia</i>	29	33			33													
Portulacaceae	<i>Montia</i>	1	1			1													
Portulacaceae	<i>Portulaca</i>	1	1			1													
Portulacaceae	<i>Rumicastrum</i>	1	1			1													
Primulaceae	<i>Samolus</i>	3	6			6													
Proteaceae	<i>Acidonia</i>	1	1					1	Bees					1					See Proteaceae
Proteaceae	<i>Adenanthos</i>	30	34							34				34					Fig. 14k
Proteaceae	<i>Banksia</i>	157	211							3	175	33		211	1				Figs 8b, 14i and 15

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Proteaceae	<i>Conospermum</i>	42	61				4	57	Bees							57	4		Fig. 6f, g, explosive
Proteaceae	<i>Franklandia</i>	2	2					2	Butterflies					2					Nectar in tube
Proteaceae	<i>Grevillea</i>	192	261			131				111	16	3		261	5				Figs 3g and 14j
Proteaceae	<i>Hakea</i>	98	112			82		6	Flies	24				112	6				Figs 3h, i and 6y (Barker <i>et al.</i> 1999)
Proteaceae	<i>Isopogon</i>	30	41					41	Bees					41	1				
Proteaceae	<i>Lambertia</i>	10	17							17				17					Fig. 14k
Proteaceae	<i>Persoonia</i>	44	44					44	Bees						1				Fig. 6b
Proteaceae	<i>Petrophile</i>	60	67					67	Bees					67	1				Figs 6c and 8k
Proteaceae	<i>Stirlingia</i>	7	7	1		6			Bees?							7			Fig. 2v–x, explosive (Ladd and Bowen 2020)
Proteaceae	<i>Strangea</i>	2	2			2								2					
Proteaceae	<i>Synaphea</i>	56	73					73	Bees							73			Fig. 6h–i, explosive
Proteaceae	<i>Xylomelum</i>	2	2			2								2					
Ranunculaceae	<i>Clematis</i>	3	3			3													
Ranunculaceae	<i>Myosurus</i>	1	1			1													
Ranunculaceae	<i>Ranunculus</i>	6	9			7											2		
Rhamnaceae	11	98	115				115											115	Fig. 8u, small complex flowers
Rosaceae	<i>Acaena</i>	1	1	1															
Rubiaceae	<i>Galium</i>	1	1			1													
Rubiaceae	<i>Opercularia</i>	10	11	11															Dioecious, Fig. 2p, q
Rubiaceae	<i>Psydrax</i>	3	3			3													
Rubiaceae	<i>Synaptantha</i>	1	1			1													
Rutaceae	<i>Asterolasia</i>	5	5			5													
Rutaceae	<i>Boronia</i>	51	76				70	6	Bees (70), moths (6)										Fig. 6e, s, q, complex flowers
Rutaceae	<i>Chorilaena</i>	1	1							1									Brown <i>et al.</i> (1997)
Rutaceae	<i>Correa</i>	1	1							1									
Rutaceae	<i>Crowea</i>	1	2				2		Bees									2	Probably SIP
Rutaceae	<i>Diplolaena</i>	15	15							15									Fig. 14q
Rutaceae	<i>Drummondita</i>	7	8							8									

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**Table 4.** (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird and GIP	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references
Rutaceae	<i>Geijera</i>	1	1				1											1	
Rutaceae	<i>Geleznowia</i>	1	4					4	Bees				4		1			4	
Rutaceae	<i>Microcybe</i>	4	9			9													
Rutaceae	<i>Muiriantha</i>	1	1							1									
Rutaceae	<i>Nematolepis</i>	1	1							1									
Rutaceae	<i>Phebalium</i>	14	15			15													Pollen only?
Rutaceae	<i>Philotheca</i>	23	33				31		Bees	2									Fig. 6d, nectar
Rutaceae	<i>Rhadinothamnus</i>	3	5			5													
Santalaceae	<i>Anthobolus</i>	1	1			1													
Santalaceae	<i>Choretrum</i>	4	4			4													
Santalaceae	<i>Exocarpos</i>	3	3			3			Bees, etc.										
Santalaceae	<i>Korthalsella</i>	2	2			2													
Santalaceae	<i>Leptomeria</i>	13	13				13		Bees, etc.									13	Fig. 6v, very small flowers
Santalaceae	<i>Santalum</i>	4	4					4	Flies or bees										Fig. 6x
Santalaceae	<i>Spirogardnera</i>	1	1			1													
Sapindaceae	<i>Alectryon</i>	1	1	1															Abundant exposed anthers
Sapindaceae	<i>Diplopeltis</i>	3	7			7													Likely reversion from wind
Sapindaceae	<i>Dodonaea</i>	24	28	28															
Scrophulariaceae	<i>Calamphoreus</i>	1	1			1													
Scrophulariaceae	<i>Diocirea</i>	4	4			4													
Scrophulariaceae	<i>Eremophila</i>	118	165				91		Bees, etc.	74									Fig. 14s
Scrophulariaceae	<i>Glycocystis</i>	1	1			1													
Scrophulariaceae	<i>Limosella</i>	2	2			2													
Scrophulariaceae	<i>Myoporum</i>	9	9			9													Brown <i>et al.</i> (1997)
Solanaceae	<i>Anthocercis</i>	10	12			12			Flies, etc.										GJK
Solanaceae	<i>Anthotroche</i>	3	3			3													
Solanaceae	<i>Crenidium</i>	1	1			1													Dioecious
Solanaceae	<i>Cyphanthera</i>	3	3			3													
Solanaceae	<i>Duboisia</i>	1	1			1													
Solanaceae	<i>Grammosolen</i>	1	1			1													

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Table 4. (Continued).

Family	Genus	Sp.	Taxa	Wind	Water	GIP	RSIP	SIP	Insects	Bird	Bird	NFM	BPB	SPP	PPCC	EAP	SP	DD	Figures, notes and references and GIP
Solanaceae	<i>Lycium</i>	1	1			1													
Solanaceae	<i>Nicotiana</i>	6	9			9													Knapp (2010)
Solanaceae	<i>Solanum</i>	16	16					16	Bees				16						Fig. 10t, u, blue-yellow flowers
Solanaceae	<i>Symonanthus</i>	2	2			2												2	Small flowers sweet scent, dioecious
Stylidiaceae	<i>Levenhookia</i>	9	9					6	Beeflies							9	3		Fig. 6t, very small flowers
Stylidiaceae	<i>Stylidium</i>	194	212					212	Beeflies or bees							212			Fig. 8l–q, column trigger
Surianaceae	<i>Stylobasium</i>	2	2	2															
Thymelaeaceae	<i>Pimelea</i>	46	56				55		Butterfly, etc.	1									Figs 6p, 8x and 14x, nectar, scent (dioecious 5)
Urticaceae	<i>Parietaria</i>	2	2	2															
Urticaceae	<i>Urtica</i>	1	1	1															
Violaceae	<i>Hybanthus</i>	6	10					10	Bees										Nectar
Vitaceae	<i>Clematicissus</i>	1	1			1													
Zygophyllaceae	<i>Tribulus</i>	3	3			3													Dioecious (!)
Zygophyllaceae	<i>Zygophyllum</i>	19	19			19													
135	743	7262	8832	1054	35	3026	1228	2155		601	583	36	450	1231	72	447	70	318	Totals

Data are summarised for genera or families when traits are consistent. See abbreviations below. Many additional references are provided in the text.

Sp., species, Taxa includes subspecies and phrase names; GIP, general insect pollination; RSIP, relatively specialised insect pollination; SIP, specialised insect pollination; SPP, secondary pollen presentation; BPB, buzz pollination by bees; Bird, bird pollination; Water, Wind, non-biotic pollination; NFM, non-flying mammal pollination; SD, sexual deception (orchids); VD, visual deception (orchids); SP, selfing, self-pollination; EAP, explosive or active pollen release; PPCC, post pollination colour change; DD, data deficient taxa.

**Table 5.** Scientific studies of plants from southwestern Australia (and closely related species from eastern Australia) that provide concrete evidence of animal-mediated pollen transfer between flowers.

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Davila and Wardle (2008)	Apiaceae	<i>Trachymene</i>	<i>incisa</i>	1	Honeybees, flies, bees, ants, etc.	Pollen transfer by insects required for seed set	Self-pollination reduces seed set	Annual herb	Pollen transfer by insects required for seed set
Eakin-Busher <i>et al.</i> (2016)	Asparagaceae	<i>Thysanotus</i>	spp.	4	Bee ( <i>Amegilla</i> sp.)	Buzz pollination observed	Outcrossing differences	<i>Thysanotus</i> species differ	Small beetles not effective
Loy <i>et al.</i> (2015)	Asteraceae	<i>Podolepis</i> , <i>Podotheca</i> , <i>Waitzia</i>	spp.	3	Flies, etc.	Pollen transport between flowers		Competition with weeds for pollinators	Arid eucalypt woodland annuals
Llorens <i>et al.</i> (2017)	Casuarinaceae	<i>Allocasuarina</i>	<i>humilis</i>	1	Wind	No pollen vector required	Population genetic structure confirms long-range dispersal	Shrub	High population connectedness and genetic diversity linked to wind pollination, dioecy and long life span
Holm (1988)	Celestraceae	<i>Stackhousia</i>	<i>monogyna</i>	1	<i>Pollanisus</i> sp. (forester moth)	Pollen carried between flowers		Small shrub	
Case and Barrett (2004)	Colchicaceae	<i>Wurmbea</i>	<i>dioica</i>	1	Flies	Pollen removal and deposition	Variable gender ratios	Small geophytes	Small geophytes
Keighery (1991) and Schatral (1996)	Dilleniaceae	<i>Hibbertia</i>	spp.	3	Bees, buzz pollination	Pollen carried and deposited on stigma by bees		Bee visits often rare, beetles carry very little pollen	Vibration causes pollen release from anther pores or slits
Tucker and Bernhardt (2000)	Dilleniaceae	<i>Hibbertia</i>	spp.	10	Bees (flies and beetles also visit)	Pollen carried between flowers and deposited on stigma		Four separate floral syndromes for buzz pollination	Detailed study on anther morphology and function
Briggs and Tinker (2014)	Ecdeiocoleaceae	<i>Ecdeiocolea</i> , <i>Georgeantha</i>	spp.	3	Wind	Pistillate and staminate flowers usually not present together	Self-pollination of clonal plants restricted by 'temporal dioecy'	Synchronous flowering of male or female flowers in zones	Wind pollination well established for family
Ladd <i>et al.</i> (2019)	Elaeocarpaceae	<i>Tetralochea</i>	<i>paynterae</i>	1	Bees	Pollen carried between flowers		Specific bee pollination	Rare flora on banded ironstone range
Houston (1991)	Ericaceae	<i>Astroloma</i>	<i>xerophyllum</i>	1	Bee ( <i>Leioproctus macmillani</i> )	Carried by specific bee		Monoleptic bee?	Highly specific feeding by bees
Houston and Ladd (2002)	Ericaceae	<i>Conostephium</i>	<i>pendulum</i>	2	Bees	Pollen carried between flowers		Buzz-pollination syndrome	Novel form of buzz pollination

*(Continued on next page)*

Table 5. (Continued).

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Bernhardt (1987)	Fabaceae	<i>Acacia</i>	spp.	8	Bees, wasps	Pollen carried between flowers		Bees are dominant pollinators	
Scaccabarozzi <i>et al.</i> (2020a)	Fabaceae	<i>Bossiaea</i> , <i>Daviesia</i> , <i>Hovea</i> , etc.	spp.	15	Bees, honeybees, beetles	Pollen carried between flowers		Dominated by bees, but complex	Co-flowering pea species
Keighery (1984b)	Fabaceae	<i>Gastrolobium</i>	<i>formosus</i>	1	Birds	Pollen carried and deposited on stigma		Bird pollination well documented	Flowers typical of syndrome – red with long pistil and anthers
Eakin-Busher <i>et al.</i> (2020)	Fabaceae	<i>Jacksonia</i>	<i>sericea</i>	1	Bees	Pollen carried between flowers	Reliant on insects for outcross pollination	Shrub, banksia woodland near Perth	
Mackay and Whalen (2009)	Frankeniaceae	<i>Frankenia</i>	<i>pauciflora</i>	1	Flies, bees, wasps, ants, etc.	Pollen carried between flowers	Bees and wasps carried more <i>Frankenia</i> pollen	Salt marsh species	South Australia
Kestel <i>et al.</i> (2021)	Haemodoraceae	<i>Anigozanthos</i>	<i>humilis</i>	1	Birds	Pollen carried between flowers	Low genetic diversity	Bird pollination well documented	
Van Der Kroft <i>et al.</i> (2019)	Haemodoraceae	<i>Anigozanthos</i>	<i>humilis</i>		Birds (honeyeaters)	Pollen carried between flowers	Self-pollination also occurs	Herb, banksia woodland near Perth	
Mees (1967)	Haemodoraceae	<i>Anigozanthos</i>	spp.	2	Birds (honeyeaters)	Pollen carried and deposited on stigmas		Pollen carried on back or head, silveryeyes steal nectar by piercing flowers	Reviews early records
Keighery (1981)	Haemodoraceae	<i>Blanchoa</i>	<i>canescens</i>	1	Birds	Pollen transport between flowers		Bird pollination well documented	Flowers typical of syndrome
Eakin-Busher <i>et al.</i> (2020)	Hemerocallidaceae	<i>Dianella</i>	<i>revoluta</i> var. <i>divaricata</i>	1	Bee	Pollen transport between flowers	Reliant on insects for outcross pollination	Herb, banksia woodland near Perth	Buzz-pollination
Duncan <i>et al.</i> (2004)	Hemerocallidaceae	<i>Dianella</i>	<i>revoluta</i> var. <i>revoluta</i>	1	Bees, buzz pollination	Pollen carried and deposited on stigma	Partly self-incompatible	Self-pollen transfer leads to low fruit set	Buzz-pollination, eastern Australia
Sokoloff <i>et al.</i> (2019)	Hydatellaceae	<i>Hydatella</i>	spp.	2	Self-pollination	No pollen vector required	Un-named cryptic species included in SWAFR taxa	Miniature wetland annual plant	Includes multiple ploidy levels and species defined by genetics only
Taylor <i>et al.</i> (2010)	Hydatellaceae	<i>Trithuria</i>	<i>submersa</i>	1	Wind	Wind pollination confirmed	Outcrossing low	Aquatic annual	

(Continued on next page)

**Table 5.** (Continued).

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Eakin-Busher <i>et al.</i> (2020)	Iridaceae	<i>Patersonia</i>	<i>occidentalis</i>	1	Honeybees	Pollen transport between flowers	Insects contributed significantly to reproduction	Herb, banksia woodland near Perth	
Eakin-Busher <i>et al.</i> (2020)	Lamiaceae	<i>Hemiandra</i>	<i>pungens</i>	1	Honeybees	Pollen transport between flowers	Insects contribute significantly to reproduction	Shrub, banksia woodland near Perth	Native bees also expected to be pollinators
Guerin (2005)	Lamiaceae	<i>Hemigenia</i> , <i>Microrcorys</i>	spp.	11	Bees, or flies	Pollen transport between flowers		Some nectar thieves	Eastern Australia
Wilson <i>et al.</i> (2017)	Lamiaceae	<i>Prostanthera</i>	spp.	17	Birds or diverse insects	Pollen transport between flowers	Floral mechanisms limit selfing	Most species are visited primarily by birds or insects	Eastern Australia
Plachno <i>et al.</i> (2019), G. J. Keighery unpublished	Lentibulariaceae	<i>Utricularia</i>	<i>menziesii</i>	1	Birds (honeyeaters)	Pollen transport between flowers			Typical bird syndrome flowers, pollination observations – GJK
Bernhardt and Knox (1983), Watson (2019)	Loranthaceae	<i>Amyema</i>	spp.	4	Birds (honeyeaters)	Pollen transport between flowers		Epiphytic haustorial parasites	Typical bird syndrome flowers
Hawkeswood (1981)	Loranthaceae	<i>Nuytsia</i>	<i>floribunda</i>	1	Beetles, flies, honeybees, birds	Pollen transport between flowers		Widespread parasitic tree with root haustoria	Birds also visit flowers, but insects carry most of the pollen
Gilpin <i>et al.</i> (2019)	Myrtaceae	<i>Backhousia</i>	<i>myrtifolia</i>	1	Honeybees, bees, etc.	Pollen transport between flowers		Areas dominated by weeds or tree crops	Honeybees were dominant
Hopper (1980)	Myrtaceae	<i>Beaufortia</i> , <i>Calothamnus</i>	spp.	2	Birds, NFM	Pollen transport between flowers		Bird pollination well documented	Focus on animals
Collins <i>et al.</i> (1984) and Byrne <i>et al.</i> (2007)	Myrtaceae	<i>Calothamnus</i>	<i>quadrifidus</i>	1	Birds	Pollen carried and deposited on stigma	Local genetic transfer tracked, outcrossing up to 5 km away	Bird foraging nectar dependant	Honeybees less effective for pollen transfer
Hawkeswood (1993)	Myrtaceae	<i>Calytrix</i>	<i>fraseri</i>	1	Bee	Pollen transport between flowers			Visits to flowers very brief
Bezemer <i>et al.</i> (2016)	Myrtaceae	<i>Eucalyptus</i>	<i>caesia</i>	1	Birds	Local genetic transfer tracked	Population genetics	Isolated populations	
Griffin <i>et al.</i> (2009)	Myrtaceae	<i>Eucalyptus</i>	<i>regnans</i>	1	Flies, etc.	Pollen carried between flowers		Dominant canopy tree	Eastern Australia
Hopper and Moran (1981)	Myrtaceae	<i>Eucalyptus</i>	<i>stoatei</i>	1	Honeyeaters	Transfer inferred from bird actions		Bird pollination well documented	
Byrne <i>et al.</i> (2008)	Myrtaceae	<i>Eucalyptus</i>	<i>wandoo</i>	1	Insects primarily	Inferred from genetics	Pollen dispersal up to 1 km	Widespread species	

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Table 5. (Continued).

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Baskorowati <i>et al.</i> (2010)	Myrtaceae	<i>Melaleuca</i>	<i>alternifolia</i>	1	Flies, bees, wasps, thrips, beetles	Insect exclusion prevent seed set		Shrub	Small flies and thrips also important, eastern Australia
Beardsell <i>et al.</i> (1993a)	Myrtaceae	<i>Tryptomyne</i>	<i>calycina</i>	1	Bees, flies, etc.	Pollen carried between flowers		Pollen on insects identified	Eastern Australia
Houston <i>et al.</i> (1993)	Myrtaceae	<i>Verticordia</i>	spp.	2	Oil bees	Pollen carried between flowers		Bee behaviour	Highly specific feeding by bees
Erickson (1951)	Orchidaceae	<i>Caladenia</i>	<i>flava</i>	1	Bee ( <i>Paracolletes</i> )	Pollen deposition on stigma		Very widespread clonal orchid	Most flowers received pollen (pre-1949)
Brundrett (2016, 2019)	Orchidaceae	<i>Caladenia</i>	spp.	2	Thynnine wasps	Pollinia removal and transfer to stigma		Sexual deception	Confirmed by video footage (Table 3)
Phillips <i>et al.</i> (2009, 2017)	Orchidaceae	<i>Caladenia</i>	spp.	45	Thynnine wasps	Pollinia removal and transport	Phylogenetic comparison	Sexual deception	WA and eastern species
Brundrett (YouTube video Table 3)	Orchidaceae	<i>Cryptostylis</i>	<i>ovata</i>	1	Ichneumon wasp	Pollinia removal and transfer to stigma, capsule formation		Sexual deception in shade tolerant, clonal sp.	Confirmed by video footage
Scaccabarozzi <i>et al.</i> (2018)	Orchidaceae	<i>Diuris</i>	<i>brumalis</i>	1	Bees	Pollen carried between flowers		Visual deception by pea flower mimicry	Pollination mechanics and ecology
Phillips <i>et al.</i> (2014)	Orchidaceae	<i>Drakaea</i>	spp.	10	Thynnine wasps	Pollinia removal and transport		Sexual deception	Orchid flower baiting studies
Erickson (1981)	Orchidaceae	<i>Eriochilus</i>	sp.	1	Bee	Pollen deposition on stigma		Wheatbelt woodland	Most flowers received pollen (95%)
Peakall and James (1989) and Brundrett (2019, YouTube video Table 3)	Orchidaceae	<i>Leporella</i>	<i>fimbriata</i>	1	Male ant	Pollinia removal and transfer to stigma	Pollen transfer mostly within colonies	Sexual deception	Confirmed by video footage
Elliott and Ladd (2002)	Orchidaceae	<i>Prasophyllum</i>	spp.	2	Diverse insects	Pollinia removal and transport to flowers	Self-pollination limits seed set	Nectar or sexual deception	Pollination success determined by syndrome
Elliott and Ladd (2002) and Brundrett (2019, YouTube video Table 3)	Orchidaceae	<i>Pterostylis</i>	<i>orbiculata</i>	2	Fungus gnats	Pollinia removal and transport to flowers		Insects present in reserve and garden	Confirmed by video footage
Brundrett (2019, unpublished)	Orchidaceae	<i>Thelymitra</i>	<i>benthamiana</i> , <i>vulgaris</i>	2	Self-pollination	Pollinator exclusion (seed bag over flower buds)	Species may not be monophyletic	Geophytes	84–100% of flowers produce seed

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Table 5. (Continued).

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Cropper and Calder (1990)	Orchidaceae	<i>Thelymitra</i>	<i>epactoides</i>	1	Bee ( <i>Nomatia</i> )	Pollen carried between flowers		Bees feeding on co-flowering plants are deceived	Eastern Australia
Edens-Meier and Bernhardt (2014)	Orchidaceae	<i>Thelymitra</i>	spp.	3	Self-pollination	No pollen vector required	Inbreeding	Relatively small flowers	Pollination mechanics and ecology
Edens-Meier <i>et al.</i> (2013)	Orchidaceae	<i>Thelymitra</i>	spp.	3	Bees	Pollen carried and deposited on stigma	Interspecific pollen transfer (hybrids occur)	Pollinator visits measured	Pollination mechanics and ecology
Wiens <i>et al.</i> (1979)	Proteaceae	<i>Adenanthos</i>	<i>cuneatus</i>	1	Birds, NFM	Pollinia removal and transport		Shrub, kwongan shrubland	Both honey possums and honeyeaters are important pollen vectors
Collins and Rebelo (1987)	Proteaceae	<i>Adenanthos</i> , <i>Banksia</i> , <i>Grevillea</i> , <i>Hakea</i> , <i>Isopogon</i> , <i>Lambertia</i>	spp.	48	Birds, NFM	Pollen carried between flowers (48 sp.), deposited on stigmas (7 sp.)		Bird pollination very well documented for these genera	Review using data from west and east Australian species
Wiens <i>et al.</i> (1979)	Proteaceae	<i>Banksia</i>	<i>attenuata</i> , <i>coccinea</i> , <i>grandis</i>	3	NFM, birds	Pollen carried between flowers		Tree	NFM may be more effective than birds for <i>B. attenuata</i> and <i>B. grandis</i>
Lynn Carpenter (1978)	Proteaceae	<i>Banksia</i>	<i>ericifolia</i> , <i>spinulosa</i>	2	NFM, birds, bees, honeybees	Pollen carried between flowers		Birds poor pollen carriers for <i>B. ericifolia</i>	Hooked stigma linked to NFM
Krauss <i>et al.</i> (2009)	Proteaceae	<i>Banksia</i>	<i>hookeriana</i>	1	Birds (honeyeaters)	Pollen carried between flowers	Consequences of bird pollination and seed dispersal identified	Kwongan shrub	Pollinator visits by white-cheeked honeyeaters ( <i>Phylidonyris nigra</i> )
Millar <i>et al.</i> (2020)	Proteaceae	<i>Banksia</i>	<i>media</i>	1	Birds, NFM, insects	Pollen transport between flowers up to hundreds of m	Pollen dispersal determined by genetics		
Ramsey (1988) and Frick <i>et al.</i> (2014)	Proteaceae	<i>Banksia</i>	<i>menziesii</i>	1	Primarily birds	Pollen carried between flowers	Pollen dispersal also confirmed by genetics	Bird pollination well documented	Honeybees rarely contact stigma
Thavornkanlapachai <i>et al.</i> (2018)	Proteaceae	<i>Banksia</i>	<i>nivea</i>	1	NFM, birds	Pollinator exclusion prevents seed set		NFM more important than birds?	No pollinator observations
Wooller and Wooller (2003)	Proteaceae	<i>Banksia</i>	<i>nutans</i>	1	NFM (honey Possums) and birds (honeyeaters)	Substantial amounts of pollen carried between flowers	Self-pollination also occurs	Flying animal exclusion also reduces seed set considerably	Honey possums are important pollinators

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Table 5. (Continued).

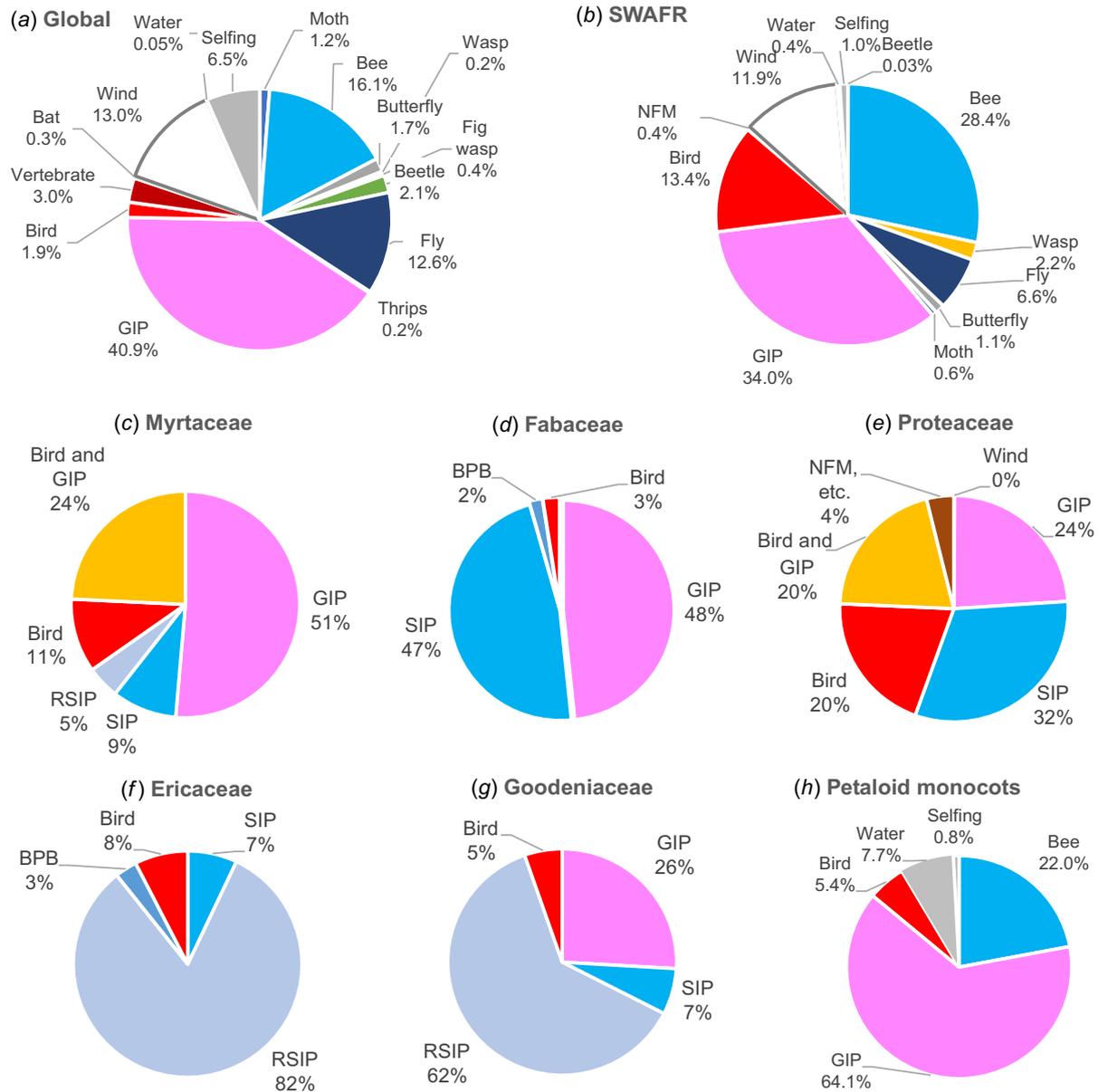
Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Collins and Spice (1986)	Proteaceae	<i>Banksia</i>	<i>prionotes</i>	1	Birds	Pollen carried and deposited on stigmas	Limited outcrossing	Insect also visit	Self incompatible
Hackett and Goldingay (2001)	Proteaceae	<i>Banksia</i>	spp.	4	NFM	Pollen carried between flowers		Other vectors not studied	Eastern Australia
Whelan and Burbidge (1980)	Proteaceae	<i>Banksia</i>	spp.	5	Birds	Pollen carried between flowers		Tree, banksia woodland near Perth	Insects and NFM not studied
Hopper (1980)	Proteaceae	<i>Banksia</i> , <i>Adenanthos</i> , <i>Lambertia</i> ,	spp.	6	Birds, NFM	Pollen carried between flowers		Bird pollination well documented	Flowers typical of syndrome
Saffer (1998)	Proteaceae	<i>Banksia</i> , <i>Lambertia</i> , <i>Adenanthos</i>	spp.	8	NFM, birds	Pollen carried between flowers by NFM		Bird pollination well documented	Primarily bird pollinated
Houston (1989)	Proteaceae	<i>Conospermum</i>	spp.	6	Specific bees	Pollen carried between flowers		Pollen inaccessible to most animals	Explosive pollination syndrome
Delnevo <i>et al.</i> (2020a)	Proteaceae	<i>Conospermum</i>	<i>undulatum</i>	1	Bees	Specific bee required		Bees rare in small reserves	Major pollinator limitations
Collins <i>et al.</i> (2008a)	Proteaceae	<i>Dryandra</i> ( <i>Banksia</i> )	<i>sessilis</i>	1	Birds	Pollen carried and deposited on stigmas quantified	Pollination behaviour leads to outcrossing	Large shrub	Often occurs in dense stands
Burne <i>et al.</i> (2003)	Proteaceae	<i>Grevillea</i>	spp.	3		Inferred from genetics	<i>G. althoferorum</i> clonal	Rare species	
Richardson <i>et al.</i> (2000b)	Proteaceae	<i>Grevillea</i>	spp.	2	Birds	Pollen carried and deposited on stigmas		Honeybees visit but fail to transfer pollen	Eastern Australia
Collins <i>et al.</i> (2008a)	Proteaceae	<i>Grevillea</i>	<i>wilsonii</i>	1	Birds	Pollen carried and deposited on stigmas quantified	Self-pollination is common	Small shrub	Typical bird syndrome flowers
Bernhardt <i>et al.</i> (2019)	Proteaceae	<i>Isopogon</i>	<i>anemonifolius</i>	1	Bees	Pollen carried between flowers		Most pollen transfer is within species	Eastern Australia
Holm (1988)	Proteaceae	<i>Lambertia</i>	<i>ericifolia</i> , <i>inermis</i>	2	Birds	Pollen carried between flowers		Bird pollination well documented	Flowers typical of syndrome
Bernhardt and Weston (1996)	Proteaceae	<i>Persoonia</i>	spp.	20	Bees	Pollen carried between flowers		Shrubs	Eastern Australia
Rymer <i>et al.</i> (2005)	Proteaceae	<i>Persoonia</i>	spp.	4	Bees, honeybees	Pollen transfer to stigma		Honeybees rarely contact stigma	Eastern Australia

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**Table 5.** (Continued).

Citation	Family	Genus	Species	No.	Pollinators	Pollen transport or transfer confirmed	Genetics	Ecology	Notes
Wallace <i>et al.</i> (2002)	Proteaceae	<i>Persoonia</i>	<i>virgata</i>	1	Bees	Pollinator exclusion prevents seed set	Self incompatible	Highly specialised for bees	Eastern Australia
Keighery (1976)	Rutaceae	<i>Diplolaena</i> , <i>Chorilaena</i>	spp.	6	Birds (honeyeaters)	Pollen carried between flowers		Bird pollination well documented	Flowers typical of syndrome – brush shaped very long pistils
Keighery (1979a)	Rutaceae	<i>Nematolepis</i>	<i>phebaloides</i>	1	Birds	Pollen carried and deposited on stigma		Bird pollination well documented	Flowers typical of syndrome – red tubular
Houston and Ladd (2002)	Rutaceae	<i>Philotheca</i>	<i>spicata</i>	2	Bees	Pollen carried between flowers		Buzz-pollination syndrome	Unusual floral form
Stace (1995)	Solanaceae	<i>Anthocercis</i>	<i>gracilis</i>	1	Unknown insects	Pollen vectors required for seed set	Protogyny and strong self-incompatibility	Fire responsive species	
Anderson and Symon (1988)	Solanaceae	<i>Solanum</i>	spp.	16	Bees, buzz pollination	Pollen carried between flowers		Some bees have high fidelity for <i>Solanum</i>	Most bees collected in arid areas
Armbruster <i>et al.</i> (1994)	Stylidiaceae	<i>Stylidium</i>	spp.	11	Bees, flies	Pollen placement and collection by column	Pollen placement location on insect is specific to plant species	Pollination by mechanical force (sensitive column)	Most use bees or flies, but some attract both
Terry <i>et al.</i> (2005)	Zamiaceae	<i>Macrozamia</i>	spp.	2	Beetles	Pollen carried between flowers	Separate male and female plants	Male cones are more common (see text)	Queensland species, same syndrome occurs in WA
Totals	26	66		354					

NFM, non-flying mammals.



**Fig. 1.** The relative importance of pollination strategies globally (a) and in southwestern Australia (SWAFR) (b) using data in Tables 2 and 4. Separate data for important families in southwestern WA and the petaloid monocots are also provided (c–h). GIP, general insect pollination; RSIP, relatively specialised insect pollination; Bee, specialised native bee; NFM, non flying mammals.

## Insects

It is estimated that approximately 87.5% of flowering plants are animal pollinated globally (Asar *et al.* 2022, Table 2). Although generalist-pollinated plants are also important, many southwestern Australian plants have relatively specific pollination strategies with insect groups (Fig. 1b), as explained in greater detail in case studies in *Case studies in pollination syndrome consistency and variability*.

### General insect pollination

Generalised insect pollination, where floral visitors are not from a narrow group of related species, is the most common

strategy both in WA and globally (Fig. 1, Waser *et al.* 1996). This syndrome has relatively small and morphologically simple flowers with conspicuous visual displays that are easily seen by insects and have readily accessible nectar and pollen (Figs 3 and 4). They attract a wide range of insects (and may also be visited by birds and mammals) that seek nectar, pollen or both. As shown in Fig. 1a, which is based on Ollerton (2017) and other sources in Table 1, pollination by invertebrates globally involves many hymenopterans (especially bees and wasps – 16.7%), 51% of dipteran (fly) families, 23% of coleopterans (beetles) and many lepidopterans (butterflies and moths). In the SWAFR many insects that are common in



**Fig. 2.** Wind-pollinated flowers of *Ecdeiocolea monostachya* with male (left) and female (right) phases (a). *Morelotia octandra* male (b) and female (c) flowers highly magnified. *Lyginia imberbis* male (d) and female (e) flowers. Abundant pollen shed from male cones on *Macrozamia riedlei* (f) which are primarily pollinated by *Tranes vigorsi* weevils (g). Male cones of *Callitris preissii* with dispersing pollen (h). *Allocasuarina humilis* male (i) and female (j) flowers. Male flowers of the Euphorbiaceae members *Beyeria viscosa* (k), *Adriana quadripartita* (l) and *Stachystemon polyandrus* (m). Male flowers on a samphire *Halosarcia* sp. (n). *Triglochin* sp. female (o), and *Opercularia hispidula* male (p) and female (q) flowers. *Gyrostemon subnudus* male (r) and *Tersonia cyathiflora* female (s) flowers (Gyrostemonaceae). *Dioscorea hastifolia* female (t) and male flowers (u). *Stirlingia latifolia* flowers (v) *S. latifolia* microscopic views of anthers before (w) and after (x) explosive pollen release (after Ladd and Bowen (2020), scale bars = 1 mm).

flowers do not have unique interactions with plants since they often co-occur (Table 2, Figs 3 and 4). Flies, bees and feral honeybees are especially common. Wasps in the families Scoliidae and Thynnidae (Brown and Phillips 2014; Brock *et al.* 2021) and beetles in the Buprestidae, Cleridae, Lycidae, Meloidae and Scarabaeidae are also often observed. We have designated 3028 taxa in 309 genera and 75 families with no known specific insect–flower association in the SWAFR (Table 2), but this would be an overestimate since

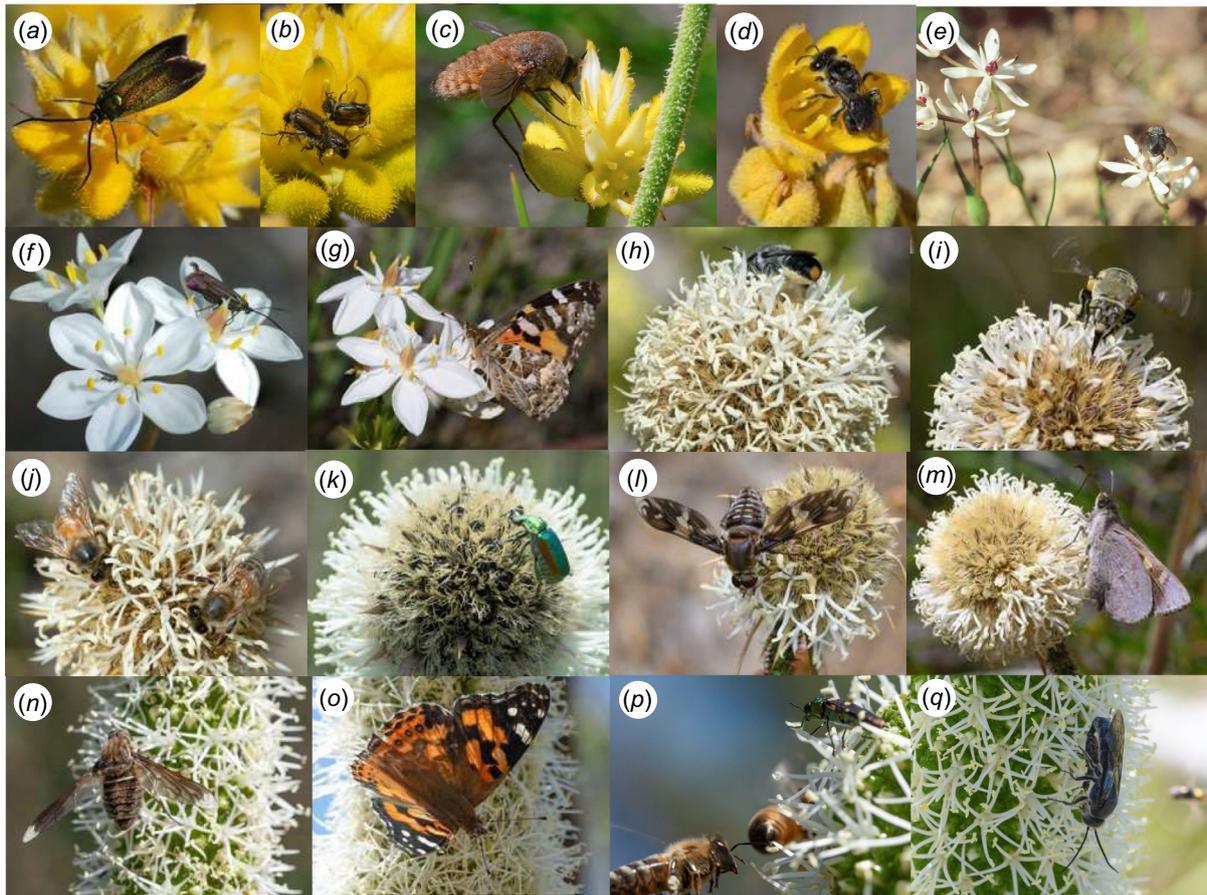
we did not assign specific syndromes to poorly studied plants that lack complex flower morphology.

#### Other visitors and predators

Not all common floral visitors are pollinators, because some are the wrong size or shape or have behaviours that prevent successful pollen transfer. Insects that graze on flowers or steal pollen may also sometimes pollinate flowers despite damaging them (Fig. 5). These include many beetles



**Fig. 3.** Examples of dicotyledons with general insect pollinators. *Leptospermum* sp. with jewel beetles and native bee (a), *Darwinia diosmoides* with fly (b) or Jewel beetle (c), *Regelia ciliata* with *Bembix* wasp (d), *Melaleuca subfalcata* with scolid wasp (e), *Actinodium cunninghamii* with native bee (f), *Grevillea uniformis* with native bee (g), *Hakea psilorrhyncha* with thynnid wasp mating pair (h), *Hakea ruscifolia* with fly (i), *Eucalyptus marginata* with bee fly (j), *Eucalyptus todtiana* with wanderer butterfly (k) and diverse insects (l), *Nuytsia floribunda* with very large fly (m), *Lechenaultia biloba* with forester moth (*Pollanisia* sp.) (n), *Calandrinia* sp. with fly and small native bee (o), *Rhodanthe chlorocephala* with flies (p), *Eryngium pinnatifidum* with a net-winged beetle (*Porrostoma* sp.) (q), *Lechenaultia linarioides* with butterfly (r), *Acacia pulchella* with green spring beetles (*Diphucephala edwardsii*) (s), *Macarthuria australis* with bee fly (t), and scolid wasp (u). *Olearia* sp. with forester moth (v), *Hyalosperma cotula* with nectar scarabs (*Phyllotocus* sp.) (w), *Trachymene coerulea* with hoverfly (x) and sun moth (y).



**Fig. 4.** Monocotyledons with general insect pollinators. *Conostylis aurea* with forester moth (a). *Conostylis aculeata* with nectar scarabs (b), bee fly (c), and native bee (d). *Wurmbea dioica* and fly (e). *Burchardia congesta* with forester moth (f) and painted lady butterfly (g). *Dasypogon bromeliifolius* with native bee (h), blue-banded bee (i), honeybees (j), green spring beetle (k), a bee fly (l) or iris skipper butterfly (m). *Xanthorrhoea preissii* with large bee fly (n), painted lady butterfly (o), honeybees and jewel beetle (p) or thynnine wasp mating pair (q).

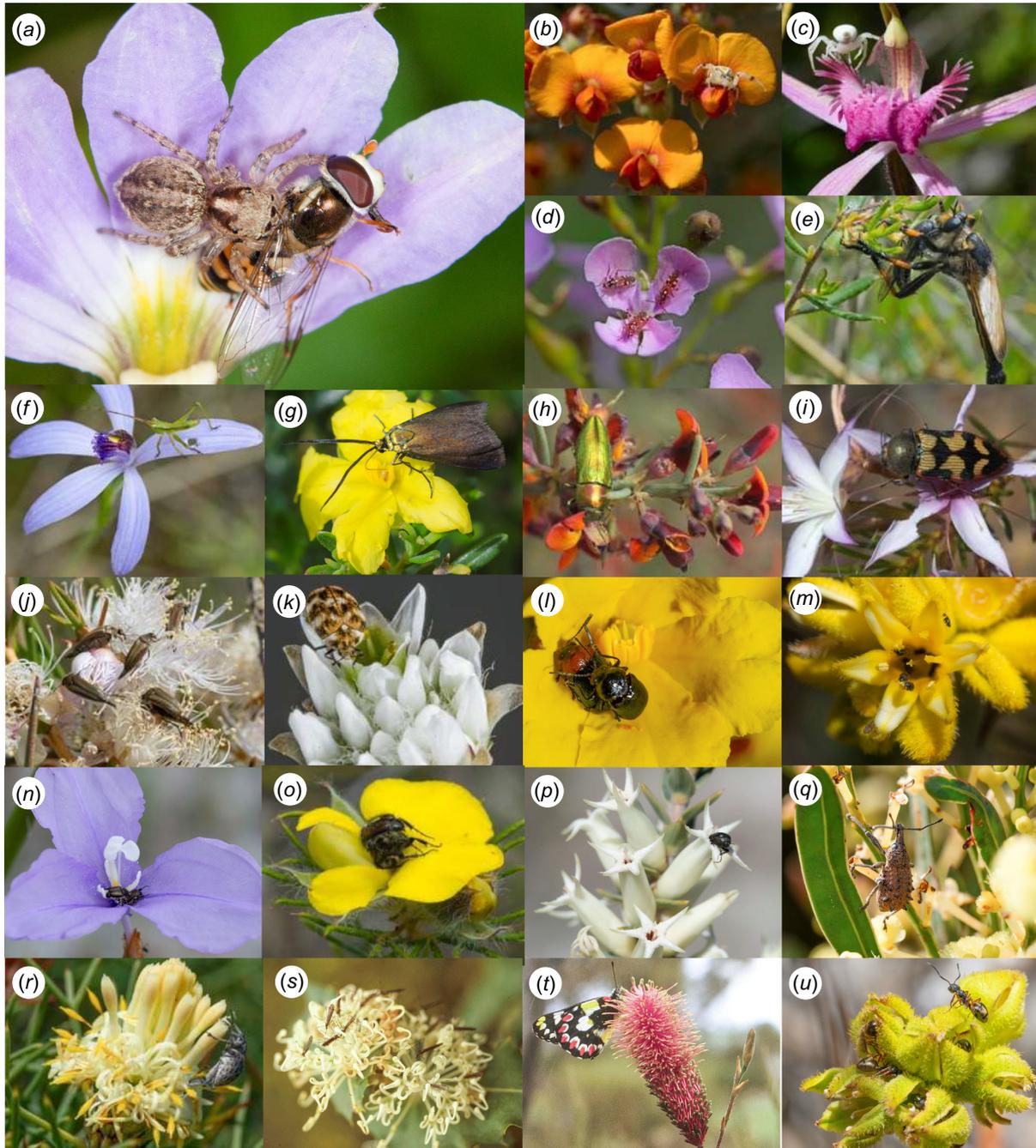
that feed on pollen, nectar or other flower parts (see *Beetles*). Various insects visit wind-pollinated flowers but major roles in pollen transport are unlikely in most cases (see *Wind Pollination*). Worker ants are often observed in flowers but are rarely considered to be effective pollinators (e.g. Fig. 5u). However, they have been suggested to be important in *Acrotriche*, *Conospermum* (one species), *Beyeria* and *Microtis*, (Peakall and Beattie 1989; Schneemilch *et al.* 2011; Delnevo *et al.* 2020a). Predators that ambush pollinating insects, including crab spiders, assassin bugs and robber-flies, also frequent flowers (Fig. 5).

### Beetles

Jurado-Rivera *et al.* (2009) used DNA barcoding to confirm that 76 species of Chrysomelinae beetles are pollen vectors for members of 13 plant families, with preferences for Australian Myrtaceae (eucalypts) and Fabaceae (acacias). Most beetles that visit flowers in the SWAFL (Table 2) are not specialised to the flowers they visit, but some have relatively specific associations with plants (Keighery 1975; Armstrong 1979;

Bernhardt 2000; Hangay and Zborowski 2010). The small black beetle *Notobrachypterus* sp. uses the flowers of *Thysanotus patersonii* and *Thysanotus manglesianus* for feeding and mating and its larvae eat the seeds of some flowers (Ladd and Eakin-Busher 2023). In *T. patersonii* this seems mainly a parasitic relationship, as the species is autogamous, but in *T. manglesianus* it may be a nursery pollinator relationship, as if bees are absent in flowers with beetles approximately 53% of stigmas bore pollen of *Thysanotus*.

Specialist nectar and pollen feeding beetles include members of the Buprestidae (jewel beetles), Scarabaeidae (scarabs), Dermestidae, Meloidae, Mordellidae (tumbling flower beetles) and Cleridae (Fig. 5). The most commonly observed are scarabs, especially *Neophyllotocus* and *Diphucephala* species. The former often frequent yellow flowers such as *Hibbertia* spp., *Caladenia flava* and the Asteraceae, whereas the latter seem to prefer acacias (Fig. 13). *Neophyllotocus* sp. beetles were the most frequent visitors to *Isotropis cuneifolia* and it was hypothesised they were the primary pollinator of the species (Scaccabarozzi *et al.* 2020b). The role of nectar



**Fig. 5.** Floral visitors that are predators of pollinators or have opportunistic roles. A jumping spider with captured hoverfly (a). Crab spider on *Gastrolobium capitatum* (b). Crab spider hunting on *Caladenia startiorum* (c). Assassin bugs on *Stylidium affine* (d). Robber fly with captured thynnine wasp (e). Grasshopper feeding on *Pheladenia deformis* flower (f). Forester moth on *Hibbertia hypericoides*, a species on which its larvae feed (g). Jewel beetles on *Daviesia incrassata* (h) and *Calytrix glutinosa* (i). Tumbling flower beetles (Mordellidae) swarming on *Melaleuca radula* (j). *Laxmannia squarrosa* with dermestid beetle (k). Beetles feeding on *Hibbertia hypericoides* anthers (l). Very small beetles on *Conostylis aculeata* (m). Nectar scarabs (*Neophyllotocus* sp.) feeding on *Patersonia occidentalis* pollen (n), *Gompholobium capitatum* (o), and *Croninia kingiana* (p). Weevils feeding on *Acacia myrtifolia* (q), and *Petrophile drummondii* (r). Crane flies swarming on *Hakea amplexicaulis* (s). Wood white Jezebel butterfly on *Grevillea petrophiloides*, which is primarily bird pollinated (t). Ants feeding inside *Conostylis aculeata* subsp. *cygnorum* flowers (u).

scarabs as pollinators has been questioned in some cases since they also feed on flowers (Hawkeswood 1989). *Grevillea leucopteris* is pollinated at night by giant scarabs (*Pachytricha* sp. – Groom and Lamont 2015), but other diurnal visitors are common (Brown *et al.* 1997). Jewel beetles are very common in large flowers of Myrtaceae species in the genera *Eucalyptus*, *Melaleuca*, *Leptospermum* and *Agonis*, but they also visit smaller-flowered Myrtaceae species and members of other families including *Myoporum insulare*, *Nuytsia floribunda* and *Xanthorrhoea* spp. (Brown *et al.* 1997).

Eastern Australian cycads in the genus *Macrozamia* are specifically pollinated by oligolectic weevils (*Tranes* spp.) and thrips (Terry *et al.* 2005). Weevils and beetles also occupy cones of SWAFR species (Ornduff 1991, Fig. 2g). Some cycads have been beetle pollinated since the Mesozoic (Cai *et al.* 2018). However, male cones also release abundant wind-blown pollen (Fig. 2f), which may not all be wasted. These cycads often have substantially more male than female plants producing cones, which is inconsistent with insect pollination, but could also reflect the cost of producing very large seeds (Ornduff 1985). The role of cycad specialist weevils and thrips in pollen transfer from male to female flowers was established experimentally for two *Macrozamia* species from Queensland (Terry *et al.* 2005).

### Flies

The global importance of fly pollination is well documented (Woodcock *et al.* 2014; Inouye *et al.* 2015; Shrestha *et al.* 2019; Raguso 2020). Many types of flies contribute to pollination, but syrphid hoverflies and bee flies are especially important (Kastinger and Weber 2001; Orford *et al.* 2015; Dunn *et al.* 2020). Pollinating flies often have specialised mouthparts (Larson *et al.* 2001), such as a long proboscis on some bee flies (Fig. 6v). Australia is a biodiversity hotspot for flies with an estimate of 30,000 species, the majority of which are undescribed (Yeates *et al.* 2009).

Flies associate with many plants that attract generalist pollinators in the SWAFR but have relatively specific pollination associations with at least 588 taxa, as explained below. They are as common as bees in images of wildflowers, but many of these images are of flowers with generalist pollination (see Jean and Fred Hort's images on Flickr). Bee flies are commonly observed visiting *Stylidium* species but some primarily attract bees (see *Stylidiaceae*). They also have relatively specific associations with some Asteraceae, Apiaceae and Ericaceae, especially those with small flowers (see *Case studies in pollination syndrome consistency and variability*). Foul-smelling hakeas as well as two of the three *Santalum* species primarily attract flies and other insects (Fig. 6x, y). This includes the economically significant *Santalum spicatum* that especially attracts Calliphoridae (blow flies), whereas *Santalum acuminatum* attracts many bees (T. Houston, pers. comm.). The importance of fly pollination in SWAFR plants is likely to be currently underestimated.

### Butterflies and moths

At least 165 species have flowers with attributes that would attract butterflies and moths, but other insect types such as bee flies also visit them (Holm 1988, Brown *et al.* 1997, G. J. Keighery, unpubl. data). These flowers typically have nectar located at the base of the corolla tube, most suitable to pollination by insects with a long proboscis, and include species in the genera *Calytrix*, *Franklandia*, *Isotoma*, *Pimelea*, *Lysinema*, *Stackhousia* and *Sphenotoma*. Butterflies and sun moths often visit *Isotoma hypocrateriformis* (Fig. 6n, o). *Stackhousia* (Celastraceae) includes five species with scented flowers and long nectar tubes expected to be primarily pollinated by butterflies and moths, as well as at least four with shorter tubes that lack pollination records. Holm (1988) confirmed *Stackhousia* pollination by a forester moth (*Pollanisia* sp.). *Calytrix* flowers were designated as butterfly pollinated by Groom and Lamont (2015), but also attract bees, beetles and rarely also birds or honey possums (Brown *et al.* 1997; Houston 2000). Some Ericaceae species in *Leucopogon*, *Styphelia*, *Andersonia*, *Lysinema* and *Sphenotoma* also attract moths (Table 4). *Parsonia diaphanophleba*, in a family rare in the SWAFR (Apocynaceae), only has butterflies listed as visitors (Brown *et al.* 1997).

### Relatively specific insect pollination

Without detailed studies it is only possible to propose hypotheses about the pollination mechanisms for some species in the SWAFR flora, especially those with structurally complex or very small flowers. Here these are assigned to the category of Relatively Specific Insect Pollination (RSIP). RSIP include approximately 75 species that are predominantly pollinated by butterflies and moths (see above), but also attract other insects. There are also species that attract both bees and flies. Pollen transfer data are required to resolve syndromes for some members of the Haemodoraceae, Dasypogonaceae (*Baxteria*), Aizoaceae, Pittosporaceae, Rutaceae, Solanaceae and *Cassytha* (Lauraceae). There are 1220 taxa (14%) allocated to RSIP in Table 4, of which 287 (3%) require further investigation and the rest are known to have structurally complex flowers with a low diversity of pollinators.

There has been almost no study of pollination in species with very small flowers, which include some Asteraceae (15 genera, 58 sp.), Apiaceae (six genera, 14 sp.) and Araliaceae (two genera, 31 sp.), as well as Crassulaceae, *Levenhookia* (Stylidiaceae) and a few monocots. Some of these have inflorescences only a few mm wide (Fig. 8u–w, y). It is expected that only small insects would be effective pollinators of these flowers. *Trachymene incisa*, an Apiaceae member from eastern Australia, is primarily pollinated by bees but flies and ants also visit its flowers (Davila and Wardle 2008). Flies and bees were the most common floral visitors for annual Asteraceae species in SWAFR eucalypt woodlands (Loy *et al.* 2015). In Israel small



**Fig. 6.** Dicotyledons with relatively specialised insect pollination. Native bee (*Megachile* sp.) after emerging from a nest hole in wood (a). Native bee pollinating *Persoonia longifolia* (b), *Petrophile drummondii* (c), *Philotheca spicata* (d), *Boronia spathulata* and native bee (e). *Conospermum huegelii* (f). *Conospermum amoenum* microscopic view of flower with anthers exploded (g). *Synaphea spinulosa* (h). *Synaphea favosa* flower in microscopic view with exploded anthers (i). (g) and (i) are after Ladd and Bowen 2020, scale bars = 1 mm. Blue banded bee on *Calytrix fraseri* (j). *Cyanostegia angustifolia* with native bee (k). Native bee on *Leucopogon* sp. (l). *Scaevola crassifolia* (Goodeniaceae) with native bee aligned under column (m). *Isotoma hypocrateriformis* with blue iris skipper butterfly (n) and sun moth (o). Skipper butterfly on *Pimelea* sp. (p). *Boronia megastigma* with heliozid moth – arrow (q). Forester moth (*Pollanispus* sp.) with *Stackhousia monogyna* (r). Other complex flowers associated with relatively specific pollinators include *Hemianthra pungens* (s), *Boronia cymosa* (t), *Levenhookia leptantha* (u), *Comesperma confertum* (v), and *Leptomeria empetriformis* (w). *Santalum acuminatum* (quandong) has fly pollinated flowers (x). *Hakea trifurcata* flowers attract flies (y).

bees, medium-sized bees and syrphid flies were listed as pollinators of relatively small flowers (Dafni and Kevan 1997).

The miniature flower syndrome has multiple separate origins in families that include very small plants with short lifecycles that grow in soils scarce in mineral resources and brief periods with adequate soil moisture (Short 1996). Many of these are likely to be self-pollinating as a primary or back-up mechanism (Keighery 1982). Some very small flowers occur in dense clusters, increasing their attractiveness and available rewards to insects. These include *Trymalium* and *Cryptandra* in the Rhamnaceae (Fig. 8u) and *Poranthera* in the Euphorbiaceae, where observed visitors include flies, bees, beetles and ants.

### Flowers with complex morphology

Secondary pollen presentation is a form of protandry where pollen is transferred to part of the gynoecium before flowers open and the stigma is initially unreceptive (Fig. 8a, c, t). This strategy has evolved independently at least once in over 24 plant families globally (Howell *et al.* 1993; Yeo 2012) and is exceptionally important in WA (1231 taxa – 14%). The most common examples occur in the species-diverse families Asteraceae, Proteaceae, Myrtaceae and Goodeniaceae (Holm 1988; Ladd 1994; Groom and Lamont 2015). In the Myrtaceae this trait occurs in *Darwinia*, all *Actinodium*, *Chamelaucium*, *Homoranthus* and most *Verticordia* species (see *Myrtaceae*).

Flowers that become more colourful after pollination are rare globally, since most fade as they age. Post-pollination colour intensification usually involves rapidly increasing red pigmentation in tepals or anthers that are not senescing. This is expected to reduce their visibility to insects, which in many cases are bees, to help direct them to receptive flowers of the same species (see Fig. 8). Weiss and Lamont (1997) recognised such colour change in 456 species in 253 families globally, including at least 100 in Australia. Our revised list includes 72 known species in the SWAFR, including iconic wildflowers such as feather flowers (*Verticordia* spp.), *Banksia ilicifolia* and the wreath flower (*Lechenaultia macrantha*). This trait is most striking in the Myrtaceae for at least 13 *Verticordia* and 7 *Melaleuca* species. Tinsel lilies (*Calectasia* sp.) include six species with anthers that turn from bright yellow to red or orange, six others with tepals that become reddish and two that do not change colour (Barrett and Dixon 2001; Barrett and Barrett 2015).

Other examples of exceptional floral specialisations in the SWAFR include:

1. Extreme colour variability within species, which is especially common in visually deceptive orchids, as well as species of *Lechenaultia*, *Gompholobium*, *Verticordia*, *Chamelaucium* and *Stylidium* (e.g. *S. dichotomum*).
2. Attraction to flowers primarily via brightly coloured leaves occurs in some *Adenanthos* and *Hakea* species. One iconic example is *H. victoriae*, where leaves are the

primary attractants. Their colour intensifies from pale yellow to red with age and marks the location of open flowers. Another striking contrast in colour occurs in *Eucalyptus erythrocorys* where flowers shed bright red bud caps to reveal bright yellow anthers.

3. Extrafloral nectaries occur in some species in nine genera and six families, including *Adenanthos* and *Acacia*, but these often attract ants for defence (Groom and Lamont 2015).
4. Pollen application by force (ballistic pollination) occurs in triggerplants and explosive dispersal in the Proteaceae genera *Conospermum*, *Synaphea* and *Stirlingia* (Fig. 8). Floral spring-traps occur in the orchid genera *Paracaleana* and *Pterostylis* and a hinged labellum also occurs in *Drakaea*, *Spiculaea* and some *Caladenia* species.
5. Pollen in some flowers is coloured, scented or coated in oil and the latter is often linked to specialised bee pollinators (see *Bee-pollination in dicots*).
6. Toxic floral defences against grazing such as cyanide occur in the Proteaceae and probably other families (Groom and Lamont 2015).
7. We have observed strictly diurnal flowers in some Iridaceae and buzz-pollinated Fabaceae and Asparagaceae (*Thysanotus*). Some everlastings (Asteraceae) and sundew (Droseraceae) flowers last for longer but close each night and offer protection for pollinators. Others such as the Stylidiaceae, Proteaceae, Rutaceae and Orchidaceae have relatively long-lived flowers.
8. Temporal flowering variability between species in plant communities may support bird pollinators in the SWAFR, especially in the Myrtaceae and Proteaceae. Members of these families often also have very large and colourful floral displays, which provide extended flowering times and long-range attraction of nomadic birds (Main 1981). There also is a staggered schedule of flowering of *Banksia* species through the year (Collins *et al.* 2008b).
9. Flowering and pollination occur primarily after fire in at least 43 species and 230 more are obligate post-fire flowering ephemerals (Lamont and Downes 2011; Brundrett 2021).

## Highly specialised insect pollination

### Petaloid monocots

Specialised insect pollination, especially by bees, is common in this group (Fig. 7). There are also several switches to bird pollination in Haemodoraceae (Table S1). Members of the Dasypogonaceae and Xanthorrhoeaceae have nectaries in *Xanthorrhoea*, *Baxteria*, *Dasypogon* and *Kingia*, but these are absent in *Calectasia*, which is buzz pollinated (Keighery 1983; Clifford *et al.* 1998; Rudall and Conran 2012). The others attract generalist insects (*Dasypogon* and *Kingia*) or have carrion-scented flowers (*Baxteria*). As shown in Fig. 7, an unusual bee pollination syndrome occurs in *Haemodorum*



**Fig. 7.** Petaloid monocots with relatively specialised insects or complex flowers. *Orthrosanthus laxus* with native bee (a). Complex flowers of *Xyris lanata* (b), *Xyris lacera* with native bee (c). *Tribonanthes violacea* (d), *Hensmania turbinata* (e). Pollination sequence for closed flowers of *Haemodorum spicatum* with native bees (f–h), internal flower structure (i) and damage caused by honeybees (j, k), *Philydrella pygmaea* (l) *Thysanotus patersonii*, which has autogamous flowers (m). *Tricoryne elatior* with native bee (n) and hoverfly (*Melangyna* sp., Syrphidae) (o).

(Houston 2014), where closed dark-coloured flowers need to be forced open by bees (Fig. 7f–h). Genera that are primarily bee pollinated (but not buzz pollinated) include *Caesia* and *Corynotheca* (Barrett *et al.* 2021), *Chamaescilla* (Cropper and Calder (1990), *Xyris* (Wall *et al.* 2002), as well as many Iridaceae and the Asparagaceae (Table 4). *Phlebocarya*, *Tribonanthes* and *Hensmania* have complex flower structures (Fig. 7d, e). The latter are visited by small flies, such as *Pollenia* sp., but this requires further study.

### Bee pollination in dicots

There is a high degree of specialisation and speciation both in bees and the flowers they pollinate in the SWAFR (Figs 6–10). There are many native bees in WA that feed from plants in specific families or genera (oligolectic) and some specialise on a single plant species (Houston 1989, 2000, 2018; Houston *et al.* 1993; Wallace *et al.* 2002; Stone *et al.* 2006).

Oligolectic bees are generally only common in areas with a high diversity of bees, such as other mediterranean-climate regions (Michener 1979; Kuhlmann 2009). Bees specialised to match a particular flower form are especially common in the SWAFR, as listed below. Western Australia includes an exceptionally high diversity of bees, including endemic species and highly specialised bees, with many unnamed and over 800 in total (Houston 2000; Batley and Hogendoorn 2009). This contrasts with some other biomes where insect pollination is often dominated by generalist social bees (Michener 1979). In total there are approximately 2400 plants in the SWAFR that may have highly specific associations with bees (Table 2). However, some native bee species primarily feed on plants that also attract a diversity of other pollinators, such as keystone species of acacias, eucalypts and banksias. For example, Cropper and Calder (1990) found bees that pollinated an orchid also carried pollen from seven different plant families.



**Fig. 8.** Complex dicotyledon flowers. Flowers with secondary pollen presentation include *Petrophile linearis* with jewel beetles (a), *Banksia prionotes* (b), *Scaevola nitens* (c) and *Darwinia chapmanii*, which also has oily pollen on the papillate pollen presenter at the end of the style (d). *Lechenaultia macrantha* (e), *Verticordia chrysantha*, which does not have a pollen presenter (f), *Verticordia huegelii* with native bee (g), *Chamelaucium megalopetalum* (h). *Calectasia demarzii* (i) have flowers that become redder after pollination. *Calectasia narragara* anthers turn orange (j). Pollen presenter colour change with age in *Petrophile linearis* (k). *Stylidium schoenoides* with column set (l), sprung, female phase with papillate stigma at end of column (m) and with trapped hover fly (n). *Stylidium petiolare* with Bombyliidae bee fly (o) and *S. recurvum* with native bee (p). Hoverfly on *Stylidium caespitosum* (q). *Pileanthus peduncularis* (r). *Androcalva pulchella* with bee fly (s). Pollen deposition on nectar scarab from column of *Lechenaultia floribunda* (t). *Stenanthemum notiale* subsp. *chamelum* has very small flowers (u). Other very small flowers include *Actinotus leucocephalus* (v), *Trachymene pilosa* (w), *Pimelea argentea* (x) and *Myriocephalus gueriniae* with small bees (y).



**Fig. 9.** Fabaceae pollination by native bees. *Euchilopsis linearis* with stigma and styles released from keel (a). *Jacksonia spinosa* with native bee (b). *Jacksonia hakeoides* with honeybee (c). Native bee on *Gastrolobium capitatum* (d). *Daviesia divaricata* primarily attracts bees including species of *Megachile* (e), *Exoneura* (f) and *Trichocolletes* (g). *Jacksonia sternbergiana* pollination sequence with *Exoneura* sp. (h, i) and with blue-banded bee (j). Other visitors to *Daviesia divaricata* flowers that are unlikely to be effective pollinators include a long-nosed fly (k), forester moth (l), skipper butterfly (m) and twin spotted line blue butterfly (n).

Examples of associations between oligolectic native bees and flowers are summarised below using information primarily from [Houston \(2000, 2018\)](#).

1. The Myrtaceae is the most important family overall for bees, due to high plant diversity and dominance plus abundant pollen and nectar in flowers, but also has many other syndromes (see *Myrtaceae*). Most *Darwinia*, *Chamelaucium*, *Verticordia* and *Pileanthus* species have oily pollen and narrowly specialised bee species that are structurally modified to collect it (e.g. [Houston et al. 1993](#), see also *Myrtaceae*). *Verticordia* hosts an exceptionally diverse array of specific bee species and other floral visitors are less likely to be effective pollinators. Small-flowered genera such as *Baeckea*, *Calytrix* and *Scholtzia* also seem to be primarily specialised for bee pollination.
2. In the Proteaceae highly specialised bee-pollinated flowers include *Conospermum* and all *Synaphea* species that have explosive pollen release when flowers are triggered by small bees ([Houston 1989](#); [Stone et al. 2006](#)), including 122 taxa in total (see *Proteaceae*). Pollination by specialised bees is also known for *Isopogon* and *Petrophile*, but other insects also visit their flowers. *Persoonia* ([Fig. 6b](#)) has a pollination syndrome with specific structurally specialised bees in eastern ([Bernhardt and Weston 1996](#); [Wallace et al. 2002](#); [Rymer et al. 2005](#)) and western Australia ([Houston 2000](#)). *Persoonia* bees must be strong enough to force tepals apart and *Xylomelum* flowers also attract specific bee species. All banksias are visited by bees and these seem to pollinate *Banksia menziesii* ([Ramsey 1988](#)), but bees seem to be less efficient pollinators than birds for most other species ([Table 5](#)).

3. The Fabaceae has specialised bee associations in *Daviesia*, *Jacksonia*, *Gompholobium* (Scaccabarozzi *et al.* 2020b) and 29 other genera, including buzz pollination in some (Fig. 9, see Fabaceae). *Acacia* species (Mimosoideae) are presumed to be pollinated by generalists but also support highly specific bee species.
4. *Comesperma* (Polygalaceae) and *Hybanthus* (Violaceae) species are expected to be bee pollinated due to zygomorphic flowers very similar to the Fabaceae (Holm 1988).
5. The flowers of most Goodeniaceae are linked to structural specialisations for more efficient pollen gathering by particular bees (Haviland 1915, see Goodeniaceae).
6. In Lamiaceae, bee pollination is dominant in *Dicrastylis*, *Hemiantra*, *Hemigenia*, *Microcorys*, *Pityrodia*, *Prostanthera*, *Westringia* and 10 other genera with zygomorphic flowers (see Lamiaceae).
7. Malvaceae members that are primarily bee pollinated include *Androcalva*, *Guichenotia*, *Lasiopetalum*, *Lysiosepalum*, *Seringia* and *Thomasia*, but others that attract diverse pollinators such as *Alyogyne* are also very important food sources to bees (see Malvaceae).
8. *Eremophila* (Scrophulariaceae) supports relatively specific bee species, which are likely to be the main pollinators of species that are not primarily bird pollinated (see *Other large families with complex pollination*). Bees specialising on *Eremophila* flowers have acquired a longer tongue, palpi, or proboscis than other bees to access to nectar behind a constriction at the base of the floral tube (see Houston 2000).
9. *Solanum* (Solanaceae) is buzz pollinated by certain bee species, which is consistent globally, whereas most other genera in this family are pollinated by general insects (Knapp 2010).
10. Other dicots with reported bee associations where pollination is not well studied include some Asteraceae, *Frankenia* (Frankeniaceae) and *Ptilotus* (Amaranthaceae). *Frankenia* flowers attract bees, flies and butterflies (Mackay and Whalen 2009).
11. Monocots reported to attract specialised bees include *Conostylis*, which also attracts other pollinators (Fig. 4), *Haemodorum* (Haemodoraceae) and buzz-pollinated lilies (see below).

### Buzz pollination

The buzz-pollination syndrome usually involves female bees grasping the apically dehiscent anthers, hunching over the terminal pores and shivering their flight muscles, causing the vibrations to be transferred to the anthers and shaking out the dry pollen onto the hairs on the bee's body (Buchmann 1983; Vallejo-Marín 2019). Buzz flowers generally lack nectar and often have a strong colour contrast between bright yellow anthers and blue or purple petals. These are often clumped in a cone around the style on short filaments and held above radial petals (Fig. 10). This is exemplified by tomato plants leading to the common name 'solanum-type'

for some buzz-pollinated flowers (Anderson and Symon 1988; Houston 2014; Keighery 2017).

Buzz pollination is present in approximately 75 families and over 20,100 species of flowering plants globally (Buchmann 1983; Vallejo-Marín 2019). Lists of buzz-pollinated plants in West Australia based on floral morphology were provided by Faegri (1986), Furness *et al.* (2014) and Keighery (2017). The latter is updated here (Table 4) and now includes 456 plants, representing 5% of the SWAFR flora, which is similar to the global average (Table 2). There are also at least 169 species in the arid zone and 87 in the tropical north in West Australia with this syndrome (Keighery 2017).

Buzz pollination occurs in approximately 100 species of monocots in specific genera of the Asparagaceae, Commelinaceae, Dasygogonaceae and Hemerocallidaceae (Fig. 10a–k) where many of the flowers are strictly diurnal (only lasting from morning to mid-afternoon of a single day). The Hemerocallidaceae (hem.) and Asparagaceae (asp.) have genera with porose anthers and other genera with anthers that dehisce by slits. Buzz pollination is considered ancestral in the Hemerocallidaceae (Furness *et al.* 2014). There seems to have been convergent evolution in flower form within these two families. *Sowerbaea* (asp.) and *Arnocrinum* (hem.) have the solanum flower form, whereas *Arthropodium* (including *Dichopogon*, asp.), *Dianella* and *Stypantra* (hem.) have pendulous flowers with widely spread versatile anthers. *Agrostocrinum* (hem.) and *Thysanotus* (asp.) have upright flowers and anthers widely spread. One species of *Caesia* (Hemerocallidaceae) also has buzz pollination (Barrett *et al.* 2021), as do some species of *Cartonema* (Commelinaceae). Duncan *et al.* (2004) noted that high rates of self-pollen transfer can be linked to low fruit set in *Dianella revoluta*, but we have observed adequate pollination in local buzz-pollinated monocot species, including *Dianella* and *Thysanotus*.

Fringe lilies in the genus *Thysanotus* (Asparagaceae) provide well documented case studies of buzz pollination where pollen transfer by bees has been confirmed (Eakin-Busher *et al.* 2016). Most *Thysanotus* species have anthers with terminal pores, but six species have narrow slits (Brittan 1981; Eakin-Busher *et al.* 2016). The latter can also be buzz pollinated since the anthers open from the tip and release pollen when vibrated. One species with slits (*T. patersonii*) seems to be self-pollinating and is closely related to a buzz-pollinated taxon (*T. manglesianus*, Sirisena 2010). Two species with anthers that open by slits that were formerly classified in the genus *Murchisonia* are now placed within *Thysanotus* (Sirisena *et al.* 2016). The former *Murchisonia* species grow in arid regions and may represent evolutionary reversions to general insect pollination.

Dicotyledons with buzz pollination in the SWAFR include three Fabaceae genera (*Labichea*, *Petalostylis*, *Senna*), a few *Solanum* species, *Tetratea* and *Platytheca* (Elaeocarpaceae), *Halgania* and *Trichodesma* (Boraginaceae, Dukas and Dafni 1990; Keighery 2017; Holstein and Gottschling 2018) and many *Lasiopetalum*, *Thomasia* and *Guichenotia* (Malvaceae), which have a similar flower form (Fig. 10). Most observations



**Fig. 10.** Buzz pollination by native bees. *Thysanotus sparteus* flowers (a). *Thysanotus manglesianus* with native bee and *Notobrachypterus* sp. to the right that can also pollinate (b). *Thysanotus sparteus* anthers have pores or narrow slits (c). *Calectasia narragara* anthers have small pores (d). Other petaloid monocots with this syndrome include *Agrostocrinum scabrum* (e), *Phlebocarya ciliata* – unconfirmed (f), *Johnsonia teretifolia* (g), *Sowerbaea laxiflora* (h), *Stypandra glauca* (i) and *Daniella revoluta* with a native bee (j). Details of *Dianella revoluta* var. *divaricata* flower structure (k). Dicotyledons with this syndrome include *Platytheca galioides* (l), *Cheiranthra filifolia* (m), *Conostephium pendulum* with two images of buzz pollination (n), *Lasiopetalum drummondii* (o), *Byblis gigantea* (p), *Labichea punctata* (q), *Hibbertia hypericoides* with bees (r, s), *Solanum orbiculatum* (t) and *Solanum* sp. with a blue-banded bee (u).

on *Solanum* have been for arid species where three species of bee are dominant (Anderson and Symon 1988). *Tetratea* is visited by *Lasioglossum* bees (Ladd *et al.* 2019), and highly

specific bee species visit *Halgania* (Holstein and Gottschling 2018). In the Fabaceae (Caesalpinioideae), *Labichea* and *Senna* are also buzz pollinated, together with one genus

(*Cheiranthra*) in the Pittosporaceae (Cayzer *et al.* 2007) (Fig. 10l–q). The Pittosporaceae may include buzz pollination in several *Billardiera* and *Marianthus* species, but evidence is lacking. In the Ericaceae, *Conostephium* has anthers hidden in, but firmly attached to, the corolla tube that bees vibrate to release the pollen through the narrow corolla mouth (Houston and Ladd 2002, see Fig. 10n). In the same family *Styphelia coelophylla* may also be buzz pollinated. The genus *Geleznovia* (Rutaceae) also appears to be buzz pollinated (see Rutaceae).

The large genus *Hibbertia* (119 spp.) only has one species (*Hibbertia conspicua*) with the morphology of a typical buzzed flower (Keighery 1991), but all have clustered anthers with apical dehiscence and lack nectar (Fig. 5l). Buzz pollination is likely to be ancestral in *Hibbertia* as it also occurs in *Dillenia* species (Endress 1997). Buzz pollination and transfer of pollen by bees was confirmed for 10 Australian *Hibbertia* species by Tucker and Bernhardt (2000). Houston (1992) noted that *Hibbertia* flowers in Western Australia are often buzzed by females of the bee genus *Lestis* (Fig. 10r, s). Schatral (1996) found that nectar scarab beetles (*Neophyllotocus dispar*) were common on *Hibbertia* flowers near Perth but carry very little pollen, whereas bees were rarer but carried much more pollen. Nectar scarabs primarily feed on stamens and petals (see Fig. 5o). Forester moths also commonly visit *Hibbertia* flowers (Fig. 5g), but presumably for mating and egg laying since the larvae of the common Perth species (*Pollanisus cupreus*) feeds on *Hibbertia hypericoides* (Tarmann 2004).

### Orchid pollination

Orchids are treated separately from other petaloid monocots here due to their exceptionally complex pollination mechanisms, including many species that are visually or sexually deceptive. Renner (2006) estimate that approximately 8000 plant species have food deceptive pollination globally. The majority of these are orchids, where approximately 46% use sexual or visual deception (Ackerman *et al.* 2023). This is particularly common in Australian terrestrial orchids (Tremblay *et al.* 2005; Phillips *et al.* 2009, 2014, 2017; Gaskett 2011; Kuitert 2015; Brundrett 2019), including 84% of SWAFR orchids (Figs 11 and 13a–f). Case studies confirm pollination syndromes for 73 orchid species in Table 5. Probable pollinators have been documented by repeated observations in many other orchids in Victoria with close relatives in the SWAFR (e.g. Kuitert 2015). These include bees in *Gastrodia* sp., 5 *Diuris* sp., *Eriochilus*, *Caladenia* and 3 *Thelymitra* sp., ants and other insects visiting *Microtis*, diverse insects in *Prasophyllum*, fungus gnats in 35 *Pterostylis* sp., 3 *Corybas* sp. and *Cyrtostylis*, scolid wasps in *Calochilus*, as well as ichneumon wasps (*Lissopimpla* sp.) in 2 *Cryptostylis* sp.

Nectar is produced by *Prasophyllum* (Elliott and Ladd 2002, Fig. 13g), *Cyrtostylis*, *Eriochilus* and *Microtis*, and perhaps other genera that require further study. Deceptive pollination syndromes can result in low rates of seed

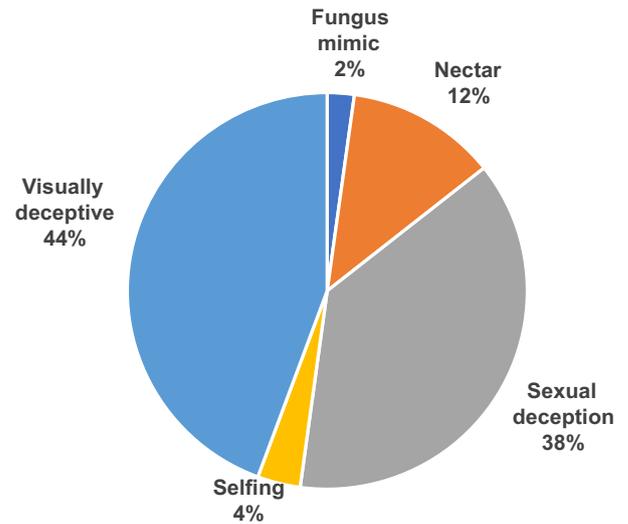
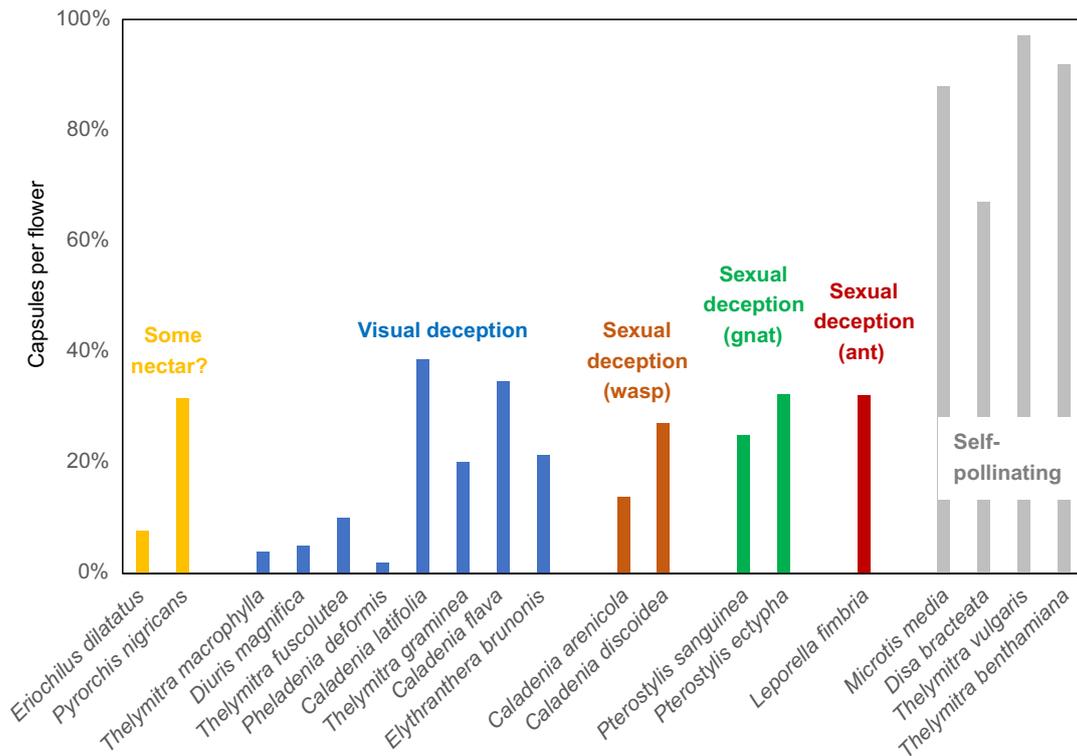


Fig. 11. The relative proportions of southwestern Australian terrestrial orchid species with different pollination strategies (data from Table 4).

production (Fig. 12), especially within large groups of plants (Brundrett 2019). Sexual deception is by emission of odour chemicals (pheromones) that attract male invertebrates, especially wasps or fungus gnats (Phillips *et al.* 2009; Gaskett 2011; Bohman *et al.* 2014). Visual deception includes *Diuris* and *Thelymitra* species (Fig. 13j–i), that utilise mimicry of specific native peas for donkey orchids (*Diuris* spp.), or irises for sun orchids (*Thelymitra* spp.) (Bernhardt and Burns-Balogh 1986; Edens-Meier *et al.* 2013; Scaccabarozzi *et al.* 2020b). Other orchids such as *Elythranthera*, *Epiblema* and some *Thelymitra* species have false anthers that mimic a buzzed flower but have no rewards for the bee, representing amazing cases of deception by floral mimesis (Bernhardt and Burns-Balogh 1986). Other complex orchid flowers have floral traps that spring shut (*Pterostylis* spp.) or remain open (*Corybas*, *Rhizanthella*). Fire promotion of flowering is very strong in many SWAFR orchids (263) and obligate in 10 species (Brundrett 2021).

### Pollination by birds

Globally, birds pollinate 4–6% of flowering plants in rainforests and fewer plants in most other regions (Table 2). These percentages are highest on some islands, in the neotropics (where hummingbirds occur), South Africa (due to sunbirds) and New Guinea – where 22% of tree species rely on birds (Brown and Hopkins 1995; Anderson *et al.* 2016). Bird pollination is important in the Cape of South Africa (Geerts *et al.* 2020) and is also very important in Australia, involving approximately 15% of flowering plants (Ford *et al.* 1979; Hopper 1980; Keighery 1980; Johnson 2013; Low 2014; Lamont *et al.* 2016). Detailed studies have shown that birds are key pollen vectors for many SWAFR plants in the Proteaceae, Myrtaceae, Fabaceae, Haemodoraceae,



**Fig. 12.** The relative effectiveness of different orchid pollination strategies in an urban nature reserve (data from Brundrett (2019) and M. C. Brundrett, unpubl. data).

etc. (Table 5). These include 14% of SWAFR plants, of which 601 are primarily bird pollinated and a similar number (577) are visited by both birds and insects (Table 2). The former include all mistletoes (Watson 2019) and some species in the Scrophulariaceae (*Eremophila*), Proteaceae, Fabaceae, Myrtaceae, Ericaceae, Goodeniaceae, Haemodoraceae, Lamiaceae, Rutaceae, Thymelaeaceae and Pittosporaceae (Table 4). For some species in Western Australia fruit set is low and pollen limited but is still dependent in birds (van der Kroft *et al.* 2019).

The bird-pollination syndrome is typically associated with large floral displays and red coloured, tubular or brush-type inflorescences or flowers, and in the SWAFR they often have secondary pollen presentation (see case studies below). These flowers are often substantially larger (Fig. 14) to match the size of bird beaks and tongues (Rodríguez-Gironés and Llandres 2008). Main (1981) summarises characteristics of bird-pollination floral syndromes associated with Australia honeyeaters. These include:

1. Specific visual attractants that work over large distances, especially large red flowers.
2. Abundant rewards in the form of nectar that is renewed to allow repeated visits to the same flower.
3. Exclusion of insects by cryptic colour, lack of odour, lack of landing platforms and/or hiding nectar at the base of long tubes.

4. Robust flowers and their supports to withstand more forceful contact by heavier animals.
5. Arrangement of reproductive structures for efficient contact with larger animals.

These observations are confirmed by significant differences in the floral data presented here (Figs 16–19).

The main bird pollinators in southwestern Australia are honeyeaters, silvereyes and lorikeets (Burbidge *et al.* 1979; Brown *et al.* 1997; Saffer 2004; Bradshaw 2014; Low 2014). In total, 57 bird species are reported to visit flowers in WA, but the records are dominated by 35 honeyeater species (Brown *et al.* 1997). The most reported is the New Holland honeyeater (*Phylidonyris novaehollandiae*) with 142 plant species. Honeyeaters have diverse foraging preferences and diets, and they can feed primarily on nectar or other foods depending on species, habitats and timing (Collins and Briffa 1982; Recher and Davis 2011; Low 2014) Nectar-feeding birds can be nomadic to exploit unreliable resources in dry areas (Main 1981). Some bird–flower associations are less specialised in Australia, because birds such as silvereyes and some parrots are casual pollinators and other birds that visit flowers may be feeding primarily on insects (Anderson *et al.* 2016). Other birds that occasionally feed on flowers include butcher birds and wood swallows, as well as black cockatoos and other parrots that frequent large floral displays in the Myrtaceae and Proteaceae (Brown *et al.* 1997). Most



**Fig. 13.** Orchid pollination syndromes. Sexual deception by pheromones where male thynnine wasps with pollinia are attracted to *Caladenia arenicola* (a) and *C. discoidea* (b). Similar interactions occur between male bull ants (*Myrmecia* sp.) and the hare orchid (*Leporella fimbria*) (c), the orchid dupe wasp (*Lissopimpla excelsa*) and slipper orchid (*Cryptostylis ovata*) (d) and a greenhood orchid (*Pterostylis* spp.) with dark wing fungus gnats (*Mycomya* spp.) (e). The helmet orchid (*Corybas recurvus*) also attracts fungus gnats, probably by fungal mimicry (f). A leek orchid (*Prasophyllum hians*) with native bee attracted by nectar (g). Deceptive orchids that use intense visual clues to attract pollinators include *Thelymitra apiculata* (h) and *T. graminea* with a visiting hoverfly (i). The pansy orchid *Diuris magnifica* (j) and enamel orchid *Elythranthera emarginata* (k) are also visually deceptive, as is *Caladenia longicauda* which has a native bee (*Leioproctus worsfoldii*) stuck to its stigma (l).

bird-pollinated flowers are also visited by insects, especially honeybees and other generalists (Houston 2014; Chmel *et al.* 2021). These may be nectar thieves, but oligolectic bees that target these flowers may also pollinate them (see *Bee-pollination in dicots*).

### Non-flying mammals

Bats can be important pollinators in tropical regions globally, but this syndrome is less important in Australia and unknown in the SWAFLR (Kunz *et al.* 2011; Bradshaw 2014). Plants known to be pollinated by non-flying vertebrate pollinators globally include at least 85 sp., 43 genera, 19 families (Carthew and Goldingay 1997). This is a substantial underestimate, since more species are visited by honey possums in WA

alone (Brown *et al.* 1997). Honey possums (*Tarsipes rostratus*) are the most frequently observed NFM, but mice, rats and six other small marsupials also feed in flowers (Armstrong 1979; Turner 1982; Wooller *et al.* 1983; Goldingay *et al.* 1991; Brown *et al.* 1997; Saffer 2004). Brown *et al.* (1997) list 93 species visited by honey possums, 4 by pygmy possums (*Cercartetus concinnus*), 7 by ash-grey mice (*Pseudomys albocinereus*), 11 by house mice (*Mus musculus*), 7 by bush rats (*Rattus fuscipes*), 1 by dibblers (*Parantechinus apicularis*), and 8 by dunnarts (*Smithopsis* spp.).

Non-flying mammal (NFM) pollination is substantially more important in the SWAFLR and South Africa than elsewhere (Rourke and Wiens 1977; Goldingay *et al.* 1991; Johnson *et al.* 2001; Turner *et al.* 2011; Bradshaw 2014).



**Fig. 14.** Examples of flowers pollinated primarily by birds. White-cheeked honeyeater on *Eucalyptus kruseana* (a). Other Myrtaceae examples include *Calothamnus sanguineus* (b), *Melaleuca fulgens* with singing honeyeater (c), *Verticordia grandis* (d), *Darwinia citriodora* (e), *Darwinia lejustyla* (f), *Darwinia chapmanii* with New Holland honeyeater (g) and *Balaustion pulcherrimum* (h). Proteaceae examples include *Banksia coccinea* (i), *Grevillea dielsiana* (j), *Lambertia multiflora* (k) and *Adenanthos strictus*, which has a very long pistil (l). Fabaceae examples include *Paraserianthes lophantha* (m), *Kennedia coccinea* (n), *Templetonia retusa* (o) and *Bossiaea dentata* (p). Other dicots include *Diplolaena dampieri*, which is a brush blossom with very long stamens and longer pistils (q), *Marianthus erubescens* (r), *Eremophila decipiens* (s), *Chloanthes coccinea* (t), *Amyema preissii* (u), *Lechenaultia formosa* (v), *Styphelia (Astroloma) stomarrhena* (w), *Pimelea physodes* (x) and *Utricularia menziesii* (y). Monocots in the Haemodoraceae include *Anigozanthos flavidus* with New Holland honeyeater with pollen deposited on its head (z), *Blancoa canescens* (aa) and *Conostylis androstemma* (ab).

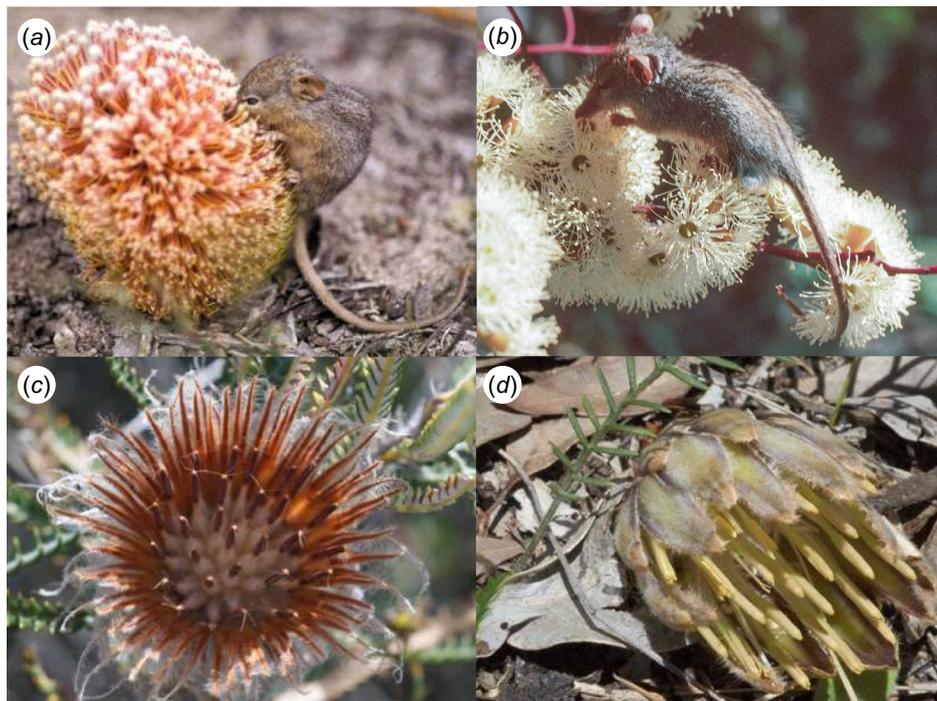
This is only allocated as a primary syndrome to 36 taxa in Table 2, because 85% of species on which NFM have been observed (Brown *et al.* 1997) are primarily visited by birds or insects, so this syndrome is less specific than others (Wiens *et al.* 1979; Wooller and Wooller 2003; Bradshaw 2014). However, honey possums are considered key pollinators of at least six *Banksia* species (Wooller *et al.* 1983) and Wiens *et al.* (1979) noted they were effective pollinators of *Banksia attenuata*, but also carried pollen from predominantly bird-pollinated species. Flower visitation by mammals in Brown *et al.* (1997) is dominated by banksias and dryandras, with 180 records from 44 species in the Proteaceae (see Proteaceae).

Saffer (1998, 2004) provides detailed comparisons of flowering phenology, nectar production and flower forms of bird or honey possum pollinated Myrtaceae and Proteaceae in Fitzgerald River National Park. Characteristic floral features of NFM plants are duller colours, a musky/mousey scent, proximity to the ground and flowers hidden within dense foliage (Table 1, Fig. 15), as well as large size (of the flowers or inflorescence), stiff styles, hooked pistils and highly concentrated nectar (Lynn Carpenter 1978; Holm 1988; Bradshaw 2014; Groom and Lamont 2015). Foraging NFM also visit flowers that lack nectar or accessible pollen (e.g. *Hibbertia*, *Patersonia*) and *Calectasia*, which is buzz pollinated (Brown *et al.* 1997). Overall, the NFM syndrome seems to be a subset of the bird-pollination syndrome, but with some relatively exclusive plant species and others

which are only visited opportunistically. There probably are many other SWAFR plant species that can be pollinated by NFM (especially in the Myrtaceae and Fabaceae) but these animals are now uncommon across most of their former ranges (Bradshaw 2014).

### Case studies in pollination syndrome consistency and variability

Floral morphology graphical comparisons, which included 1843 taxa in 18 genera in 8 families, found there were significant differences in flower sizes between bird- and insect-pollinated plants in all cases (Figs 16–19). There also typically were stark differences in flower colours between syndromes, as explained below. Two large databases of observations of floral visitors allowed us to test the reliability of syndrome allocations based on floral features. Comparative data were available for 179 taxa in the Proteaceae (19% of SWAFR taxa) and agreed with syndromes in 70% of cases (Fig. 17b). Despite some observational biases, syndrome allocations agree with records for the Proteaceae (44/46 taxa). In the Myrtaceae visitation data were available for 212 species (16%), of which 70% agree with floral syndromes and the rest lack sufficient data (Fig. 16b, c). Visitation data were available for 10% of Fabaceae species and agreed with syndromes for 90% of these (Fig. 18b). Overall, pollination syndrome



**Fig. 15.** Examples of flowers known to be or suspected to be pollinated by non-flying mammals, especially the honey possum (a, b). These include *Banksia blechnifolia* (a), *Eucalyptus marginata* (b), *Banksia shuttleworthiana* (c), and *Banksia bipinnatifida* (d).

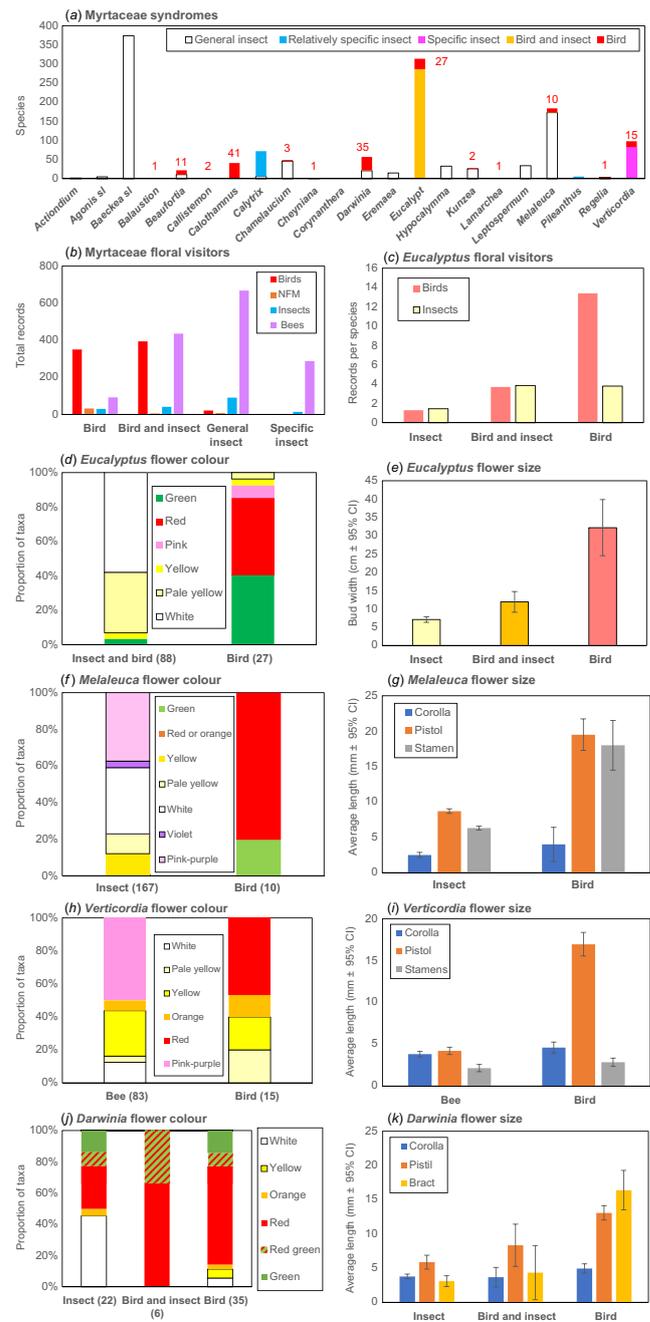
allocations based on consistent floral morphology were well supported by multiple independent records for pollinator visitor fidelity (Figs 16–19). Syndrome allocations used here (Table 2) were also in close agreement with the results of detailed pollination and genetic studies presented in Table 5. These studies included 125 species in the Proteaceae, 13 Myrtaceae, ~70 Orchidaceae, 25 Fabaceae and 116 species in 22 other families. These studies were primarily from the SWAFR (80%) and the rest were for southeastern Australian species with close SWAFR relatives.

### Myrtaceae

Generalist insect pollination occurs in 51% of the species in the family, specialised insects in 14%, birds, generalist insects in 24% and birds in 11% of taxa (Fig. 1c). General insect pollination is typical of genera with rather unspecialised flowers such as *Agonis*, *Eucalyptus*, *Taxandria* and *Melaleuca*, which often have bowl-shaped flowers that provide easy access to a nectar for diverse insects (Yates *et al.* 2005; Menz *et al.* 2015), but records of bees tend to be most frequent overall (Beardsell *et al.* 1993b). Four *Darwinia* species, several *Calothamnus* species and *Lamarchea hakeifolia* have inflorescences that may be pollinated, at least in part, by NFM, but this lacks confirmation (Table 4).

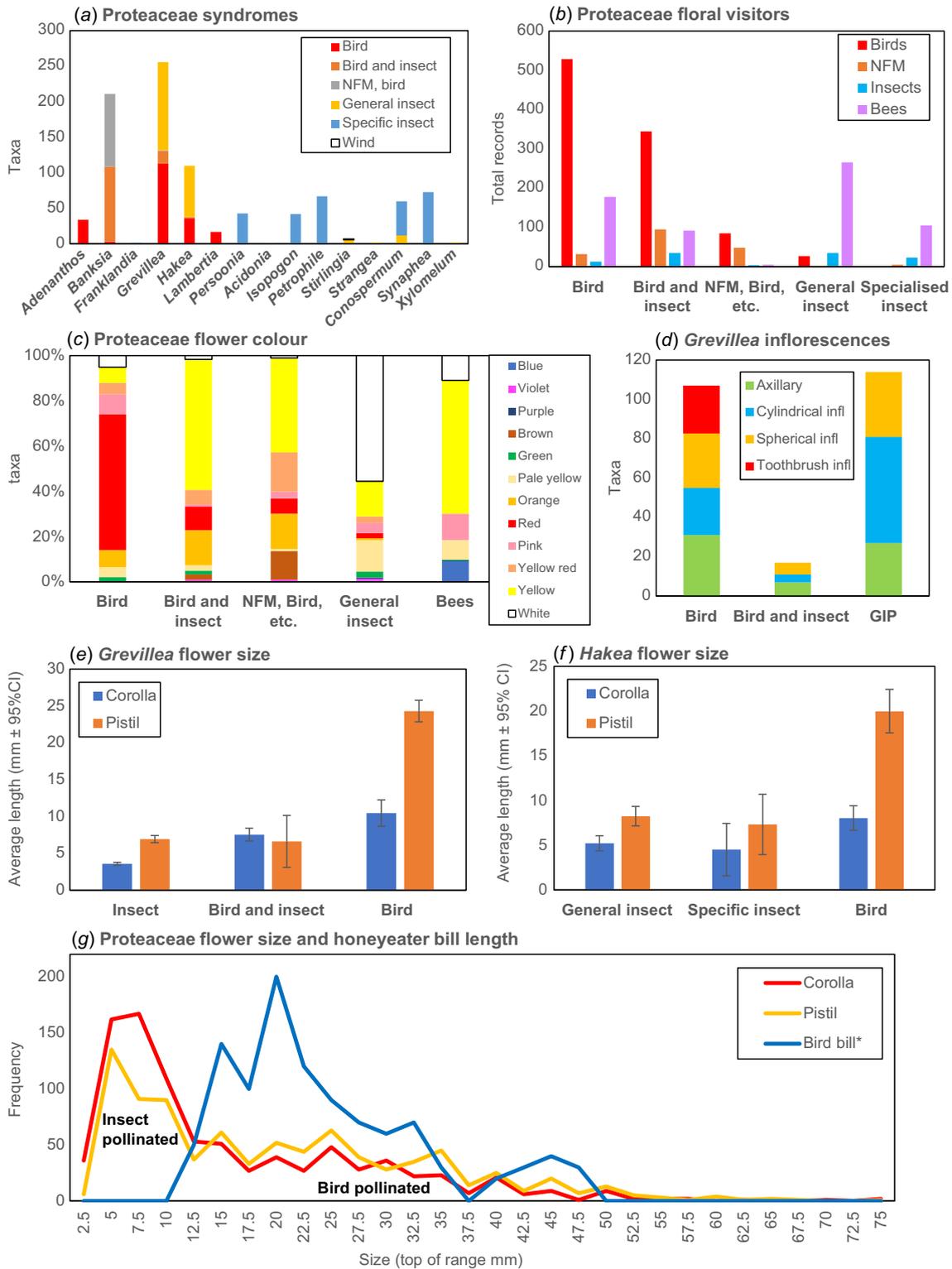
Pollination by birds occurs in *Balaustion* (1 species), *Beaufortia* (22), *Callistemon* (2), *Calothamnus* (52), *Chamelaucium* (4), *Cheyniana* (1), *Darwinia* (35, see Fig. 14g), *Eucalyptus* (12, see Fig. 14a), *Lamarchea* (2), *Kunzea* (2), *Melaleuca* (16), *Regelia* (1) and *Verticordia* (13). Bird pollination in *Calothamnus* results in efficient pollen dispersal within and between populations up to 5 km away (Byrne *et al.* 2007). As shown in Fig. 14, these species have specialised red tubular, brush, or bell-shaped inflorescences in the SWAFR, with another category with claw-shaped fused anthers (*Calothamnus* and *Lamarchea*). There are 35 taxa with bell-shaped inflorescence bracts in *Darwinia* with bird syndrome flowers (Fig. 14f, g), 22 species visited by diverse insects (Fig. 3b, c), six with intermediate floral features assigned as bird- and insect-pollinated and one (*Darwinia citriodora*) that includes separate forms optimised for birds or insects (Fig. 14e – bird form). Some Myrtaceae have flowers that fall on a continuum of features from those that primarily attract insects to those which are mostly visited by birds (Figs 3 and 14). These include many *Eucalyptus* species (see below).

Transition to bird pollination in the Myrtaceae is accompanied by consistent shifts in flower colours and larger sizes in *Eucalyptus*, *Melaleuca*, *Verticordia* and *Darwinia* (Fig. 16d, f, h, j). These transitions also result in extension of the pistil (all but *Eucalyptus*), hypanthium (*Eucalyptus*, *Balaustion*), anthers (*Melaleuca*, *Eucalyptus*, *Calothamnus*, *Callistemon*), or bracts (*Darwinia*), with consistent colour shifts away from white or yellow towards red or green (Figs 14a–h and 16e, g, i, k).

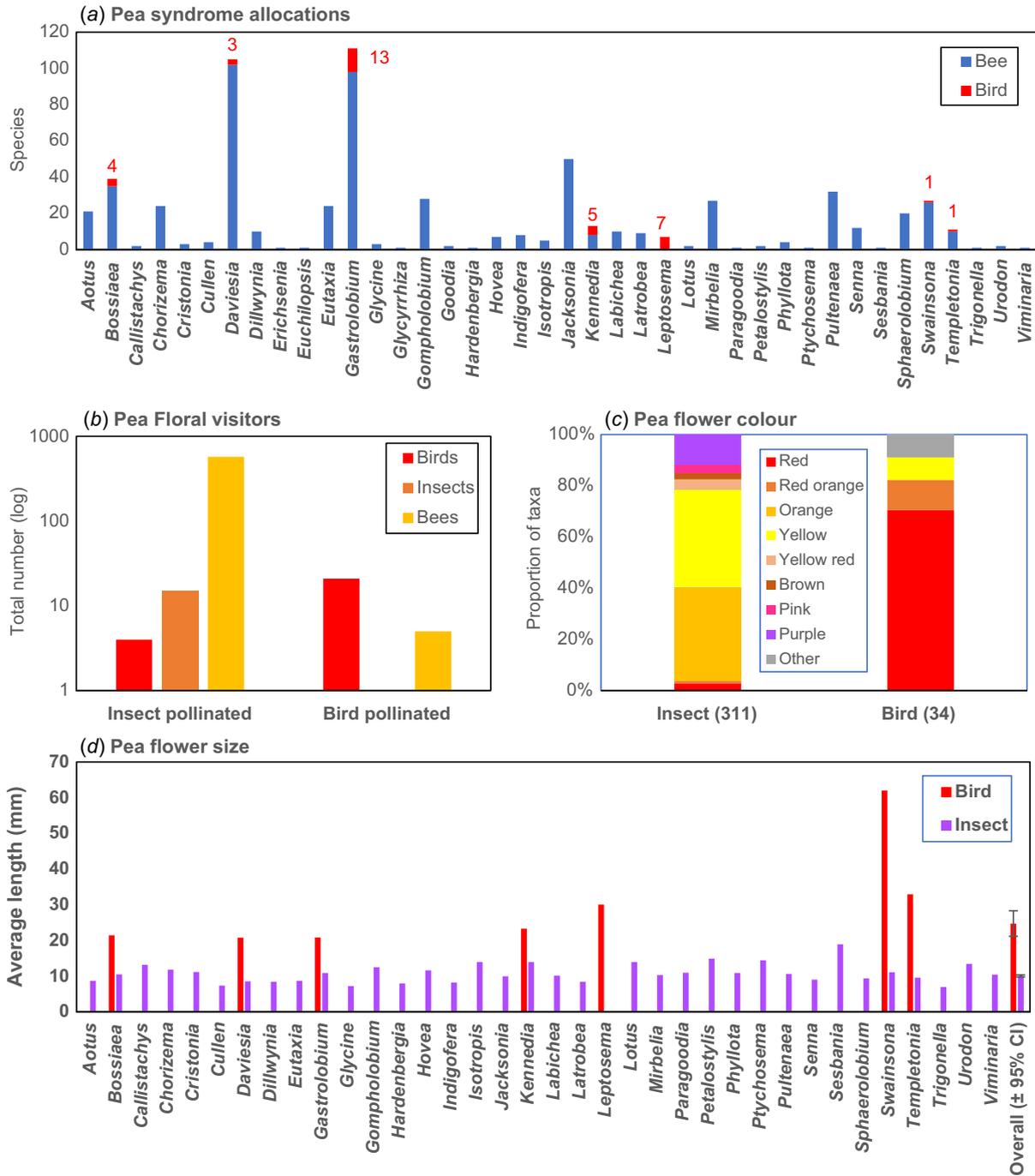


**Fig. 16.** Pollination syndrome complexity and consistency in the Myrtaceae. (a) Taxa with pollination syndromes for genera (red numbers are taxa with bird pollination). Genera with very similar flowers are combined. (b) Visits to flowers by birds or insects are correlated with pollination syndromes (1925 records for 225 taxa). (c) *Eucalyptus* species often support birds and insects. Flower colours are strongly linked to pollination syndromes in *Eucalyptus* (d), *Melaleuca* (f), *Verticordia* (h) and *Darwinia* (j). Numbers after syndrome names are taxa with flower data. Flower size is also strongly correlated with pollination in these genera (e, g, i, k).

The genus *Verticordia* has specific pollination syndromes with oil-attracted bees, and at least 18 taxa have flowers



**Fig. 17.** Pollination syndrome complexity and consistency in the Proteaceae. (a) Taxa with pollination syndromes for all genera. (b) Visits to flower by native bees, other insects or birds (2361 records for 189 taxa). Flower colours are strongly linked to pollination syndromes in *Eucalyptus* (c). *Grevillea* inflorescence shapes (d) and flower size (e) relative to syndromes. (f) *Hakea* flower size relative to syndromes. (g) Proteaceae flower size frequency histogram with superimposed honeyeater bill length frequency (\*data from Paton and Collins 1989).



**Fig. 18.** Pollination syndrome complexity and consistency in the Fabaceae excluding *Acacia*. (a) Taxa with pollination syndromes for all genera (numbers are taxa with bird pollination). (b) Visits to flowers by birds or insects by pollination syndrome (623 records for 63 taxa). (c) Flower colours are strongly linked to pollination syndromes. (d) Flower size is also strongly correlated with pollination in this family.

that change colour after pollination (Fig. 8f, g). For two yellow flowered species, pollination is primarily by oligolectic bees (especially *Euryglossa* spp. Houston *et al.* 1993) that collect oil, which is produced by apical anther glands and coats the pollen in these flowers. This specialisation is likely to extend to other yellow-flowered verticordias. Visits by other insects

that feed on nectar are also common. Pollen in many myrtaceous shrub species is extruded from the anthers as a viscous mixture of pollen and tapetal material and in some cases is mixed with oil from the anther glands e.g. in *Chamaelucium* and *Darwinia*, which also can have relatively specific insect pollinators (Slater and Beardsell 1991;



in *Grevillea* (Table S1). Many of these are members of the former genus *Dryandra* (now included in *Banksia*), as well as inflorescences on prostrate stems of several other *Banksia* species (Fig. 15).

There are consistent colour shifts away from yellows or white to red flowers in bird-pollinated Proteaceae (Fig. 17c). Inflorescence shapes are also important, especially the 'toothbrush'-shaped inflorescences and large inflorescences held above or below the leaves (Fig. 17d). As also observed by Hanley *et al.* (2009), pistil length was consistently several times longer in bird-pollinated flowers relative to insect-pollinated *Grevillea* and *Hakea* species (Fig. 17e, f). Comparison with Australian honeyeaters using data from Paton and Collins (1989) shows a consistent relationship between bill length and flower depth (Fig. 17g). Bird-pollinated flowers had several peaks in the 12–50 mm range, whereas insect-pollinated flowers were predominantly under 10 mm long. This demonstrates a threshold of 12 mm between flowers that are bird- or insect-pollinated, with even stronger evidence of bird-pollination for flowers over 20 mm long. Longer pistils and anthers in bird-pollinated flowers make sense, as they have much larger heads than insects and pollen transfer on head feathers rather than their beaks would be more reliable (see *Pollination by birds*).

The Proteaceae in Australia has developed unique insect-pollination syndromes, especially due to pollen release complexity (Carolin 1961; Holm 1988; Bernhardt *et al.* 2019; Ladd and Bowen 2020). *Banksias* have an open floral morphology that attracts insects, birds and mammals, and many are primarily pollinated by birds and mammals where the combination of a stiff style and plastic stylar tip only allows pollen from large pollinators to be inserted into a pollination chamber (Ladd *et al.* 1996; Thavornkanlapachai *et al.* 2019; Ladd and Bowen 2020). Secondary pollen presentation, which may have evolved as a response to larger vertebrate pollinators, occurs locally in 11 genera and 750 taxa (see Ladd and Bowen 2020, Table 4). Several *Adenanthos* species have extrafloral nectaries, but these primarily attract ants, which help defend plants (Groom and Lamont 2015).

As shown in Fig. 6g, i, *Conospermum* and *Synaphea* have explosively released pollen, which showers bees when flowers are triggered (Houston 1989; 2014; Ye *et al.* 2012). Most reports about *Conospermum* are of pollination by bees, especially *Leioproctus* spp. (Houston 1989; Delnevo *et al.* 2020b), but ants may also be important for one species (Delnevo *et al.* 2020a) and wasps visit another species. Delnevo *et al.* (2020b) found honeybees were ineffective for pollination of *Conospermum undulatum*, which requires a specific native bee to trigger its anthers. There is also one species (*S. latifolia*) with wind-pollination (see *Wind*), whereas others in this genus are insect-pollinated with explosive pollen release (Ladd and Wooller 1997; Ladd and Bowen 2020) and are primarily visited by bees (Houston 2000). Relatively specific pollination by bees (Fig. 6b, c) is also likely for *Isopogon*, *Petrophile* and *Persoonia*

(Houston 1989). In eastern Australia, bees are recorded as pollinators of *Persoonia* and *Isopogon* (Bernhardt and Weston 1996; Bernhardt *et al.* 2019) and are also likely to be very important for Western Australian species in these genera. Another specialist insect syndrome has been identified in at least six *Hakea* species (Fig. 6y) where flowers smell like carrion and strongly attract flies (Groom and Lamont 2015). *Hakea leucoptervis* is reported to be pollinated by nocturnal beetles (Groom and Lamont 2015), but also attracts birds and other insects (Holm 1988).

## Fabaceae

Overall, the 1203 taxa of Fabaceae in the SWAFR are almost equally split between general insect-pollination (49%) and relatively specific pollination by bees (46%), but most of the former are acacias (Table 4, Fig. 1f). Fabaceae with pea-shaped flowers are primarily pollinated by bees globally and in Australia (Proctor *et al.* 1996; Kingston and McQuillan 2000; Houston 2000; Scaccabarozzi *et al.* 2018, 2020b). Bees usually force the keel open to access stamens (Fig. 9a–j), but other floral visitors do not, so seem to be nectar thieves (Fig. 9k–n). The bee buzz-pollination syndrome occurs in 12 *Senna* (Caesalpinioideae), 9 *Labichea* (Fig. 10q) and 2 *Petalostylis* (Dialioideae) taxa (Table 4).

In the Fabaceae, bird-pollination occurs in eight genera (30 taxa), including multiple origins in *Bossiaea*, *Daviesia*, *Gastrolobium*, *Kennedia* and *Leptosema* (Toon *et al.* 2014, Fig. 18a). These flowers have fewer visits from bees and other insects and more from birds and some are also visited by honey possums (Fig. 18b). As with other bird-pollinated flowers there are consistent shifts in hues from lighter colours to dark red (Fig. 18c). This syndrome has consistently also resulted in larger flowers (Fig. 18d) and loss of a prominent floral display perpendicular to the floral axis (standard), which is replaced by elongation of the keel into a tubular, or sickle-shaped structure (Fig. 14).

By extension from the few studies that have been done, 571 SWAFR *Acacia* taxa should have relatively general insect-pollination (Fig. 3s). Acacias in the Phyllodinea generally lack nectar and attract pollen-feeding insects dominated by a specific suite of bees (Houston 2000), but also including wasps and flower beetles (Bernhardt 1987; Kenrick 2003; Stone *et al.* 2003). Honeyeaters also visit some acacias, especially in the north (Brown *et al.* 1997). Extrafloral nectaries are common in *Acacia* species and also reported in *Paraserianthes*, *Senna* and *Hardenbergia* (Groom and Lamont 2015). *Acacia* pollen is known to be dispersed by wind (Macphail and Hill 2001), but the relative importance of this requires investigation (Kenrick 2003).

## Goodeniaceae

This family primarily occurs in Australia and the Pacific islands (Jabaily *et al.* 2014) and most visitor records are of

bees (Brown *et al.* 1997). However, other insects visit flowers (Figs 3n, r and 8t) and there are transitions to birds for single *Anthotium* and *Scaevola* species and some *Lechenaultia* species (Figs 1g and 14v, Table 4). Flowers in this family have secondary pollen presentation from an indusium, which later becomes receptive through growth of the stigma from its base (Ladd 1994; Jabaily *et al.* 2014; Groom and Lamont 2015). Their zygomorphic flowers have an association with certain species in the Megachilidae and Colletidae bee families, which scrape pollen from the indusium using modified setae on their heads (Houston 2000). A detailed study of *Scaevola taccada* in India showed that bees and wasps were more effective pollinators than other visitors, which included ants and moths (Raju *et al.* 2019). Most Goodeniaceae are allocated to the relatively specialised insect syndrome, due to their complex flowers and the importance of bees.

Members of the taxonomic group *Lechenaultia* Section *Lechenaultia* have red, yellow or light green flowers with nectar, petals held erect to form a tube and a straight style and are considered to be bird pollinated, whereas those in other sections usually have blue flowers that lack nectar and are insect pollinated (Holm 1988; Morrison and George 2004). As in other families, the switch to bird pollination is supported by strong and consistent trends in flower colour and size (Fig. 19e, f), except for *Lechenaultia tubiflora*, which has smaller flowers and requires further investigation. Bird pollination also occurs in two *Scaevola* species in Hawaii (Abrahamczyk 2019). A few annual Goodeniaceae species are highly inbreeding (e.g. *Goodenia micrantha*). Another relatively common feature of this family is clonal propagation by underground stems, especially in *Lechenaultia* and *Scaevola*. This can lead to mass flowering (especially after fires) and intense competition for pollinators.

## Ericaceae

Pollination varies considerably between and within genera of this family (Keighery 1996; Brown *et al.* 1997; Houston and Ladd 2002; Johnson and McQuillan 2011; Johnson 2013). Johnson (2013) summarised pollination data for 87 Australian Ericaceae species (~15%) and found that the majority were insect pollinated, but approximately 30% of those studied were pollinated by birds. Based on floral morphology our current totals for the family in Western Australia include over 250 species in 11 genera that are likely to have relatively specific pollination by bees and 29 species pollinated by moths and butterflies, or small flies (Table 2, Fig. 1f). Buzz pollination occurs in 13 *Conostephium* species (Fig. 10n) and possibly one *Styphelia* species (see *Buzz pollination*). The taxa pollinated by insects have complex flowers that attract relatively specific pollinators, but further studies are required. Transitions to bird pollination have occurred for 20 species in *Andersonia* (2 sp.), *Brachyloma* (2), *Cosmelia* (1), *Leucopogon* (3) and *Styphelia* (20, especially in the former genus *Astroloma*). These typically have red tubular flowers with

longer anthers and pistils than others in the same genus (Fig. 14w).

## Lamiaceae

Flowers of insect-pollinated Australian species are structurally specialised for pollination by bees or flies (Guerin 2005) and such zygomorphic bilabiate flowers are associated with bee pollination globally (Westerkamp and Claßen-Bockhoff 2007). Over 15 genera of bees have been observed visiting flowers (Houston 2000). *Hemiandra pungens* is visited by feral and native bees but controlled pollinations identified that the species, at least in the studied population, was autogamous (Eakin-Busher *et al.* 2020) with delayed self-fertilisation (Lloyd and Schoen 1992). Considering the configuration of anthers and stigmas in many of the flowers in this group it is likely that autogamy may be common (P. G. Ladd, pers. obs.). *Lachnostachys* and *Dicrastylis* are very generalist-pollinated genera, mainly by Muscid and Calliphorid male flies (G. J. Keighery, pers. obs.). The mangrove genus *Avicennia* (Acanthaceae in the Lamiales) has generalist-pollinated flowers (flies, bees and wasps).

The Lamiaceae in Australia also has very complex transitions to the bird syndrome in eight genera, including one *Chloanthes*, three *Dasymalla*, six *Hemiandra*, two *Hemigenia*, four *Hemiphora*, three *Microcorys*, nine *Prostanthera* and one *Quoya* species in the SWAFLR (Figs 19a and 14t). Wilson *et al.* (2017) confirmed that syndrome allocations based on floral morphology are highly consistent with visitation records for birds or insects in *Prostanthera* species, but some species with intermediate floral morphology were visited by both birds and insects.

## Malvaceae

The Malvaceae is a clade where molecular based taxonomic classification has recently combined families that have flowers which are structurally and functionally very different. The family as defined earlier typically has relatively uncomplicated flowers suitable for both insect and bird pollination. In contrast, members of the former family Sterculiaceae typically have very complex flowers with specialised bee pollination (142 taxa in eight genera). These include 117 taxa with buzz pollination in *Guichenotia*, *Lysiosepalum*, *Lasiopetalum*, *Seringia* (*Keraudrenia*) and *Thomasia* (see *Buzz pollination*). The pollination method is less well known for the intricate flowers of *Androcalva* and *Commersonia* (Fig. 8s) but is likely to involve bees or flies.

## Rutaceae

General insect pollination is expected to occur in 29 species and 9 genera, which seems to be the ancestral condition for this family in Australia (Table 4). Specific insect pollination occurs in over 87 species in 5 genera where most floral visitors are bees. This is linked to complex anthers (Fig. 6d, e) in

*Boronia*, *Correa*, *Crowea*, *Geleznovia*, *Phebalium* and *Philotheca* (Armstrong 1979, Auld 2001). There are many collections of bees from *Boronia* and *Philotheca* species but fewer for other genera (Terry Houston, pers. comm.). Beetles and butterflies also visit these genera (Armstrong 1979). *Geleznovia* produces only pollen and attracts bees that vibrate the anthers. Pollination of four pink *Boronia* spp. in Queensland was primarily by bees (Shapcott *et al.* 2005).

The *Boronia megastigma* group of six species (*Boronia clavata*, *Boronia heterophylla*, *B. megastigma*, *Boronia molloyae*, *Boronia purdieana* and *Boronia tetrandra*) endemic to the SWAFL have greatly enlarged stigmas (Fig. 6q), on which female moths of the family Heliozelidae place eggs after picking up pollen from under the stigma from the small anthers (G. J. Keighery, unpubl. data). The caterpillars develop in the stigma and ovary. Male moths patrol the flowers but do not seem to pollinate. These species fail to set seed unless pollinated by these moths. The phylogeny of Heliozelidae moths in Australia show diversification and dispersal of these pollinators along with flowering plants since the Cretaceous (Milla *et al.* 2018).

The Rutaceae has bird pollination in 1 *Chorilaena*, 1 *Correa*, 15 *Diplolaena*, 8 *Drummondita*, 1 *Muiriantha* and 1 *Nematolepis* taxa (27 in total). Rutaceae bird-pollination syndromes are generally consistent with trends described above but take a very different form in *Diplolaena* and *Chorilaena* which have flowers aggregated into a brush inflorescence of red or green anthers surrounded by red, green, or straw-coloured bracts (see Fig. 14q).

## Stylidiaceae

As shown in Fig. 8, many triggerplants (*Stylidium* sp.) are pollinated by bee flies (Diptera: Bombyliidae), but other species are primarily visited by bees (Erickson 1981; Armbruster *et al.* 1994; Nge 2019). Different suites of pollinators are associated with nectar tube length and flowering times (Armbruster *et al.* 1994). *Stylidium* flowers have a unique column that when tripped springs forward to strike insects visiting flowers for nectar (Fig. 8l–n). The column bears the stigma and anthers, so the flowers are protandrous, and they also have pollen that has different colours in different species (Nge 2019). The column strikes insect visitors extremely rapidly (15 ms) and then resets after at least 5 min (Findlay 1978). Armbruster *et al.* (1994) observed variations in column orientation between co-occurring species that is postulated to reduce intraspecific pollination (by pollen placement location) and prevent visitors from learning how to avoid triggering flowers. *Levenhookia* flowers are similar in structure but extremely small (Fig. 6t). Most are visited primarily by woolly bee-flies, but three species have a column that only triggers once and probably self-pollinate (Erickson 1981).

## Other large families with complex pollination

The majority of petaloid monocots have relatively complex syndromes, whereas abiotic pollination occurs in families with reduced floral displays (see *Abiotic pollination*). The Haemodoraceae features several shifts from insect to bird pollination, which have been well studied (Table 5). These include four species of *Conostylis* (Fig. 14ab), as well as *Anigozanthos* (9 sp.), *Blancoa* (1) and *Macropidia* (1), whereas others in the family have general insect pollination. There are consistent floral colour and size differences between flowers with bird or insect pollination in this family (Figs 14z, ab and 19c, d).

The Pittosporaceae has bird pollination in *Bentleya* and *Marianthus*, associated with larger red or pale-yellow flowers (Figs 14r and 19b), contrasting with *Cheiranthra* which has five species with blue petals and yellow anthers that are buzz pollinated (Fig. 10m). The Thymelaeaceae has a single species with bird pollination (*Pimelea physodes*), which has a head of small flowers surrounded by long bracts like those of some *Darwinia* species (Fig. 14x).

*Eremophila* (Scrophulariaceae), which is almost fully endemic to Australia, includes at least 74 bird-pollinated taxa, of which 77% occur in WA. Most occur in arid regions, but 17 are in the SWAFL (Chinnock 2007). Flower colours are strongly linked to pollination in *Eremophila* with 81% of insect-pollinated flowers being violet or purple, whereas most red flowers are bird-pollinated (Fig. 19i). Floral syndrome allocations are also strongly supported by corolla tube length (Fig. 19j). As shown in Fig. 19k, bees often visit bird-pollinated species (Houston 2000), but birds only visited flowers with that syndrome (505 records for 25 *Eremophila* species).

Highly specialised insect pollination and complex floral forms occur in many other families, including buzz pollination in 39 genera within 16 families, other forms of specialised bee pollination in 122 genera within 18 families and associations with other insects in 26 genera within 13 families in total (Table 4).

## Families with wind pollination

As explained earlier, we found newly discovered or unexpected origins of wind pollination in ~40 species of *Beyeria* and 2 or 3 other genera in the Euphorbiaceae, 10 of *Stachystemon* (Euphorbiaceae s. l.), 4 species of *Lawrencia* (Malvaceae) and a species of *Stirlingia* alone in the Australian Proteaceae (see *Wind*). Wind pollination makes sense for *Stirlingia* due to the very large scale of mass flowering after fire, which may overwhelm insects. *Lawrencia* species occur in arid habitats or near salt lakes along with wind-pollinated Amaranthaceae species. *Beyeria* and *Stachystemon* species occur in a wide variety of habitats, but can also be fire or disturbance responsive, as is the case for many Haloragaceae species (Orchard 1975).

*Lawrenzia* flowers lack nectar or attractive floral parts and are unusual in that when not dioecious (*Lawrenzia glomerata*, *Lawrenzia spicata*, *Lawrenzia repens* and *Lawrenzia squamata*) they are extremely protandrous (the stigmas mature when male flowers are present, so selfing is possible). Others are dioecious (*Lawrenzia chrysoderma*, *Lawrenzia cinerea*, *Lawrenzia densiflora*, *Lawrenzia helmsii* and *L. squamata*). They often grow in habitats that tend to be windy (salt lakes, coastal sites, post fire areas). Only one species *Lawrenzia berthae*, a post fire species, has scented attractive flowers that are visited by bees and wasps (observed south of Norseman).

All Haloragaceae in WA are wind pollinated, except for *Glischrocaryon* which has colourful flowers. *Haloragodendron* also includes several species with relatively colourful flowers (Orchard 1975), but all those in WA have flowers consistent with wind pollination. These taxa have small (~2 mm) dull coloured petals that just cover anthers in male flowers which contain non-sticky pollen. Tepals are also dull and small (~0.5 mm) or missing from female flowers, which have enlarged hairy stigmas. Most plants are dioecious, and some produce male flowers above female flowers that become dusted with their own pollen. Dispersed Haloragaceae pollen is present in sediment cores in WA (Newsome 1999; Atahan *et al.* 2004; van der Kaars and De Deckker 2003).

### Pollinator attraction to flowers and food rewards

Most flowering plants (~80%) utilise animals to complete sexual reproduction (Table 2). Animals will only participate in pollination if they are either offered or apparently offered a reward (see *Introduction*). Animals will learn to associate food with flowers once they find them, but they initially need to be attracted to the flower and subsequently use the advertisement to repeat visits. Advertisements are either visual or chemical (smell).

#### Visual signals

Visual signals are most useful in daylight. The optimal spectra of attractant colour signals differ for bees, butterflies and birds due to differing visual sensory receptors (Shrestha *et al.* 2019; Narbona *et al.* 2021). Visual attraction is mainly through the colour of petals or more rarely sepals. UV reflection is particularly important for insect attraction, especially for guiding pollinator interactions at close range (Lunau *et al.* 2021). Another potential attractant about which little is known is coloured nectar, present in only 67 species worldwide (Hansen *et al.* 2007). Coloured pollen is also found in some flowers (e.g. Nge 2019; Ladd and Bowen 2020). Visually deceptive pollination syndromes are particularly common in orchids (Fig. 11) where bees are attracted to orchid flowers that mimic a rewarding flower type, especially pea or iris species (Edens-Meier *et al.* 2013; Scaccabarozzi *et al.* 2018).

As explained above, floral shapes and colours such as red flowers, longer stigmas and brush-shaped or tubular flowers are consistently linked to bird pollination in the SWAFR and elsewhere. Research has shown that these flowers are more visually attractive to birds than bees (Burd *et al.* 2014; Bergamo *et al.* 2019; Coimbra *et al.* 2020). Coimbra *et al.* (2020) also found that flower visitor data was well correlated with syndrome morphotypes (colour and flower depth) for bird- vs bee-pollinated flowers in Brazil. As explained in *Non-flying mammals*, pollination by non-flying mammals, especially honey possums, is also linked to specific colours, scents and arrangements of flowers.

#### Chemical lures

Flowers produce small amounts of volatile organic compounds that often contain a complex mixture of compounds to attract pollinators (Proctor *et al.* 1996; Willmer 2011). Aromatic attraction is useful in daylight and even more so at night. There is a very wide range of chemicals used to attract insects and NFM but rarely birds (Table 1). Many white-flowered species have sweet or honey-like scents that are attractive to bees and fermentation odours attract beetles. Flowers attended by non-flying mammals, that in most cases are nocturnal, have mousey or musky scents (Table 1). Scented pollen occurs in some *Hibbertia* species. In sexually deceptive orchids male wasps are attracted by female pheromone chemicals that together with visual signals induce copulatory behaviour that results in the wasp transferring the orchid pollinarium from one flower to the next (Bohman *et al.* 2014; Weinstein *et al.* 2022; Table 5).

In a few species, carrion scents attract flies that hope to find a site for oviposition. Species with this adaptation in SWAFR include a few in the Proteaceae (see *Flies*), but it is likely others remain undocumented. *Baxteria australis* is the only monocot in SWAFR with a similar odour. Orchids in the genera *Corybas* and *Rhizanthella* seem to mimic fungal fruit bodies, as they attract small flies or gnats (Brundrett 2014; Han *et al.* 2022).

#### Pollinator food rewards and nutrition

The food rewards for pollinators are pollen or nectar. Insect pollinators need to obtain protein as well as sugars and there are usually only small amounts of amino acids in nectar (Gottsberger *et al.* 1984). Beetles may feed on flower parts and/or on pollen (see *Beetles*) whereas bees take nectar and need to collect pollen to feed their young (Houston 2018), but this seems rare in other insects. Not many vertebrates feed on pollen, but for honey possums it is their main source of protein (Wooller *et al.* 1988; Bradshaw 2014) and some birds take pollen as well as nectar (see *Pollination by birds*). However most take only nectar and obtain protein from insects, thus having key roles controlling pests (Gartrell 2000).

## Genetics

This topic is only briefly covered here, with a primary focus on genetic consequences of pollination syndromes. There are insufficient detailed studies of the breeding systems of Western Australian plants that allow the importance of inbreeding, dioecy or apomixis to be assigned to all relevant species. However, it is expected that most relatively long-lived trees and shrubs are either obligately or modally outbreeding due to their large conspicuous flowers. This is the case for most members of highly speciose families such as the Myrtaceae, Fabaceae, Ericaceae, Goodeniaceae and Lamiaceae that rely on biotic pollinators for seed set (Table 5).

### Genetic consequences of pollination syndromes

Bird pollination can lead to more effective pollen transfer between different individual plants and thus more outcrossing, which can also occur over larger distances (Table 5, Ford *et al.* 1979; Beardsell *et al.* 1993b; Frick *et al.* 2014; Krauss *et al.* 2017; Kestel *et al.* 2021). They have larger home ranges and visit more flowers because they require more nectar to support their metabolism than much smaller, cold-blooded insects (Sampson *et al.* 1989; Frick *et al.* 2014; Bezemer *et al.* 2016). Paternal diversity is relatively high in bird pollinated plants in the Proteaceae and Myrtaceae (Byrne *et al.* 2007; Frick *et al.* 2014; Bezemer *et al.* 2016). However, low paternal diversity was associated with bird pollination in *Anigozanthos humilis*, which is primarily pollinated by western spinebills and brown honeyeaters (van der Kroft *et al.* 2019; Kestel *et al.* 2021). Studies designed to guide seed collection found that wind-pollinated plants had a high degree of genetic continuity over broad (4 sp.) or intermediate (2 sp.) sized areas whereas insect-pollinated plants had continuity that was confined to narrow (5 spp.) or intermediate (9 spp.) zones (Krauss 2016). For example, *Allocasuarina humilis*, a common wind-pollinated shrub, had high population connectedness across its 900 km range (Llorens *et al.* 2017). Overall, evidence supports major differences in the spatial genetic variability of plants that can be partly explained by how far pollen is dispersed due to pollination syndromes.

### Plants with autogamy or high rates of inbreeding

These taxa are relatively uncommon in the SWAFR, since we only identified 84 species where this is known or strongly suspected (Table 4). Many of these are very small annual plants that grow in arid, disturbed or saline situations. When genetic data are missing, these have been designated by the presence of small inconspicuous flowers, with dull colours and little or no nectar, that also have high rates of seed set (e.g. 90–100% of fruits or seeds) even when they occur alone (see *Flowers with complex morphology*). Others are small plants that often grow in large numbers in ephemeral wetland habitats. These potentially include small wind-pollinated

sedges (as well as *Triglochin* and *Centrolepis*), which tend to be self-fertile and self-pollinate, but we suspect that genetics would show a mixed pollination system (see *Genetics*). We also expect that other widespread annual taxa have populations (or unrecognised taxa) that are largely autogamous, such as cleistogamous forms of *Ottelia ovalifolia*. Considerable variation in mating systems occurs in annual species, especially in the Asteraceae. Inbreeding species have been documented in species pairs of *Chthonocephalus*, viz. *C. pseudavax* (Short 1990), *Pogonolepis* (Short 1986) and *Angianthus* (Short 1981). *Thysanotus patersonii* and *T. tenellus* are autogamous and flower late in winter/early spring when pollinators are scarce (Eakin-Busher *et al.* 2016, Ladd and Eakin-Busher 2023). Self-pollinated species are likely to be underestimated in Table 2, since there are other plants with very small dull coloured flowers where pollination has not been investigated. Self-pollination or autogamy also occurs in some orchids (see *Orchid pollination*), especially in small green orchids in the genera *Microtis* and *Prasophyllum*, and there is a gradient from obligately insect-pollinated to self-pollinated flowers in *Thelymitra* (Edens-Meier and Bernhardt 2014).

Cleistogamy is comparatively rare (Culley and Klooster 2007), being recorded primarily in annual species of *Juncus*, *Wahlenbergia*, *Gomphrena*, *Orobanche* and a few orchids. Apomixis is also apparently rare, being documented or strongly suspected in *Tecticornia* (Wilson 1980), *Casuarina* (Barlow 1959) and by extension *Allocasuarina*, *Callistemon* and *Melaleuca*, where stable triploids have been reported in *Allocasuarina corniculata* and some *Melaleuca* species.

There are also shrubs that produce clones, especially in edaphically marginal sites/habitats, but these can be scattered amongst non-clonal populations of the same species. Examples of this include *Stypandra glauca*, *Acacia anomala* and *Grevillea pythara*, but there are probably others that await discovery. These examples of trait variability within species often seem to be driven by fire responses. In detailed population studies, mainly of rare taxa (*A. anomala*, *Grevillea althoferorum*), disjunct populations that propagate entirely from vegetative spread have been recorded (Burne *et al.* 2003).

### Overall importance and biogeography of pollination syndromes

Pollination syndrome complexity and specificity are exceptionally high relative to their global trends in the SWAFR (Table 2). It is unlikely that greater numbers of transitions to complex syndromes for pollination by bird, highly specific insects or wind occur at biome or continental scales elsewhere (>275, Table S1). We also found strong agreement between pollinator visitor record fidelity, outcomes of detailed pollination and genetic studies and specific traits for floral morphology and colour in the SWAFR (Figs 16–19, Table 5). However, our syndrome categories may not fully

agree with those used in other studies, especially when comparing relatively specific to highly specific plant–animal relationships, so further studies are required (Table 4). Despite an overall trend for increased pollination specificity, approximately 1/3 of SWAFR plants have retained relatively general pollination strategies, including highly successful genera such as *Eucalyptus*, *Banksia* and *Acacia*. Most cases where syndrome allocations are complicated result from plants with several categories of pollen vectors (insects and birds or birds and NFM) where both categories are well supported by data. However, for some of these plants, research has shown that one of these categories is more effective for pollination outcomes or genetic continuity than the other (Table 5).

Most SWAFR plants with well-resolved pollination syndromes are also visited by opportunistic animals that primarily steal pollen or nectar, but sometimes have more substantial roles (see *Beetles*). Interpretations of the roles of floral visitors are also complicated by variations in plant–animal fidelity and insects that will visit anything (e.g. honeybees and some flies). Birds often visit flowers that are not ornithophilous (Anderson *et al.* 2016). Consequences of these opportunistic visitors may not be significant in the short term but could provide the means for occasional evolutionary transitions to new syndromes.

Table 2 compares the relative importance of pollination syndromes in the SWAFR with global estimates primarily from Ollerton (2017), who summarised data from 33 pollination surveys at 65 locations in 16 countries for approximately 2000 species. Global estimates change as more data become available but allow overall comparisons with the SWAFR. The global data for wind, water, bird and mammal pollination is based on more comprehensive geographic coverage than that for categories of invertebrates, which are less reliable. Overall, there is a similar proportion of wind pollination, but substantially more bird, NFM or specific insect pollination in the SWAFR (Fig. 1, Table 2). Further research is required to determine how regional variations in climate and vegetation drive transitions in pollination syndrome complexity.

Despite many similarities in pollination complexity between eastern and western Australia there is clear evidence for substantially greater complexity in the SWAFR, especially for bird, bee, NFM and wind pollination. These include more plants with complex and specific bee or bird syndromes in the SWAFR than elsewhere in Australia. There are even more substantial differences between the SWAFR and Tasmania, where the majority of species have unspecialised floral morphology, so host a diverse array of visitors and only a few attract birds (Kingston and Mc Quillan 2000). Overall pollination syndrome complexity is also lower in tropical rainforests in Australia, but includes additional syndromes such as bat pollination and insect-pollinated sedges (Keighery 1984a; Williams and Adam 2010; Franklin and Noske 2000).

Global comparisons show that bird pollination is uncommon in most regions except for Australia, New Zealand and islands such as Hawaii (see *Pollination by birds*). South

Africa has at least 130 bird-pollinated flowers, including 46 *Erica* species and 69 species in the Proteaceae (Geerts and Pauw 2009; Geerts *et al.* 2020). Overall bird pollination is more common in southern mediterranean climatic regions than in adjacent temperate biomes. Abrahamczyk (2019) identified 19 phylogenetic lineages of bird-pollinated plants in Hawaii. These include 177 species in 11 plant families. An even more substantial number of transitions to bird pollination have occurred in the SWAFR than elsewhere (>130, see Table S1), resulting in 13% of the flora becoming fully or partly dependent on birds for reproduction (1184 taxa). There is a 50–50 split between highly specialised bird syndrome flowers and those with both birds and insects in the SWAFR (Table 4), but the latter category is not recognised in other regions. There also is a very high degree of pollination specificity, especially for complex insect syndromes in the Greater Cape Floristic Province in South Africa (Johnson 2010; Johnson and Steiner 2003), but there seem to be fewer cases of specific bee or bird pollination.

### Weeds that invade or originate in the SWAFR

Invasive plants have generalist insect pollination more than any other syndrome (Richardson *et al.* 2000a). Exceptions to this generalisation include many wind-pollinated, some bird-pollinated and a few water-pollinated weeds. Australian plants that are highly invasive overseas and pollinated by diverse insects include members of the Myrtaceae (*Eucalyptus* and *Melaleuca*), Proteaceae (*Hakea*) and *Acacia*, as well as *Casuarina*, which is wind pollinated (Richardson and Rejmánek 2011). These species are also less likely to be self-incompatible (Rambuda and Johnson 2004) and often also have complex nutritional strategies (Brundrett 2021). Australian *Banksia* species in South Africa are pollinated by birds (sunbirds replace honeyeaters) and insects, especially honeybees (Moodley *et al.* 2016). Thus, indigenous nectivorous birds may encourage invasion by these species.

We have observed that many alien invasive species in the SWAFR are visited by diverse insects, especially honeybees. Wind pollination is the second most common syndrome, found in amaranths, chenopods, grasses, rushes, sedges and pine trees. Some other weeds have relatively specific pollination, especially by bees in the Fabaceae, Lamiaceae, Scrophulariaceae, etc. Buzz-pollinated weeds include *Solanum* spp. and *Cyanella hyacinthoides* (Tecophyllaceae). Bird pollination is expected to occur in species of *Caesalpinia*, *Chasmanthe*, *Cotyledon*, *Fuchsia*, *Lachenalia* and *Leonotis*. *Nicotina glauca* has spread globally and is most invasive in areas with pollinating birds (Ollerton *et al.* 2012). It is now also established in the SWAFR.

### Invasive pollinators in the SWAFR

The ecology of honeybees is fundamentally different from native bees, which tend to be far more specialised and are

only active at the specific time of year when their preferred food is available (Houston 2000, 2018). In contrast, honeybees are active all year round and will visit any plant where pollen or nectar can be obtained. Furthermore, honeybees use effective communication and large colonies to obtain a larger proportion of resources than native insects or birds (Roubik *et al.* 1986; Hansen *et al.* 2002; Henry and Rodet 2018). These factors should result in a competitive imbalance between native bees and honeybees (Paini 2004; Prendergast *et al.* 2023) but impacts of honeybees on native pollinators have only been reported in a few SWAFR habitats (van der Moezel *et al.* 1987; Celebrezze and Paton 2004; Prendergast *et al.* 2021). Honeybees are also known to be ineffective pollinators of some plants because they fail to contact the stigma (Ramsey 1988; Rymer *et al.* 2005; Richardson *et al.* 2000b). Poor habitat quality, fragmentation and climatic extremes have also been linked to poor pollination outcomes, especially in small patches of urban vegetation (e.g. Phillips *et al.* 2010; Delnevo *et al.* 2020b; Eakin-Busher *et al.* 2020; Kestel *et al.* 2021; Prendergast and Ollerton 2021).

Rainbow lorikeets (*Trichoglossus haematodus*) are an eastern Australian bird that is now well established in the SWAFR after escaping from captivity approximately 55 years ago (Chapman 2005). They are commonly observed feeding on flowers of bird-pollinated eucalypts, banksias, melaleucas and bottlebrushes near Perth. Their significance is not known, as they may contribute to effective pollination but also strongly compete with indigenous nectivorous birds.

## Overall trends and consequences of pollination evolution

Except for wind pollination, evolutionary complexity is primarily due to switching to more specific associations with animals and usually involves increasing floral complexity in one of the oldest terrestrial biodiversity hotspots (Table S2). There also are a few notable exceptions where transitions occur in the reverse direction, such as from wind to insects or from buzz pollination to general insects. Thus, pollination evolution in SWAFR is driven by strong pressures to attract specific pollinators and transfer pollen over greater distances or more efficiently, as well as very long periods of time and fewer plant extinctions than have occurred elsewhere (see *Introduction*). This complexity is greatest in plant families that are the most taxonomically diverse and dominant in this biodiversity hotspot and the same families include complex nutritional and fire response traits (Brundrett 2021). Pollination complexity often also involves plant species complexes where taxonomy is not fully resolved.

For SWAFR plants, evolution of complex flower structures and more specific insect interactions is likely to result in more cross-pollination, but perhaps at the expense of overall pollination rates. Pollinators must also respond to brief

periods of flowering in seasonally unreliable semi-arid climates in WA. Thus, insect phenology must also be responsive enough to take advantage of brief very wet periods between extended droughts. Key groups of pollinators, especially native bees, which may have brief periods of activity so can be difficult to detect in habitats (Houston 2014), may be replaced by other insects. Potential secondary pollinators observed most often include bee flies, hoverflies, forester moths, nectar scarab beetles and honeybees (which may be a problem or a solution). In some cases, magnet plants are required to attract pollinators for other species (Gilpin *et al.* 2019; Scaccabarozzi *et al.* 2020b).

The occurrence of intermediate states suggests that changes to pollination syndromes typically progress in stages from general insects to mixed syndromes and more specific insect, bird or mammal syndromes resulting in characteristic changes to floral features (Wester and Claßen-Bockhoff 2007, see Table S2). The most common transition is from general to specific insect pollination. Transitions from specialised insect pollination to bird or large animal pollination are less common but has occurred in the Fabaceae, and reversion from bird to insects can also occur (Van der Niet *et al.* 2014). Flower structure trends linked to specific insect pollination can include anthers that require vibration, specific colour signals, or the absence of nectar. The most extreme flower structures occur in orchids with sexual or visual deception, but there are many other examples of SWAFR flowers (e.g. Proteaceae species with explosive pollen release and *Stylidium* species, Fig. 8). Pollination syndromes seem to be more consistent within families or genera globally than in Australia where at least 275 transitions occur within genera, and some also occur within species (Table S1).

Optimisation for a specific pollination guild typically leads to distinct and highly consistent flower size, shape and colour classes in SWAFR plants (Table 1) and this type of convergent evolution also arises elsewhere (Schiestl and Johnson 2013). Efficient bird pollination requires separation of pollen in anthers from the nectaries by a distance similar to the length of bird bills (see pictures in Wester and Claßen-Bockhoff 2007, Figs 14z and 18e). Overall, bird-pollinated SWAFR flowers are 2–4 times longer than closely related insect-pollinated flowers, due to elongation of pistils, anthers, corolla tubes, bracts, or a combination of these (Figs 16–19). Bird-pollinated flowers also require physical protection and support for heavier animals, accurate placement of pollen relative to the shape of pollen vectors and production of abundant dilute nectar (Holm 1988; Cronk and Ojeda 2008). In contrast, wind-pollinated flowers are reduced to the size required to effectively produce reproductive structures and lack prominent visual signals for insects.

The most common floral colour trends were red or green for birds, blue, yellow, white, for insects and dull coloured flowers for NFM. Pollination syndrome switching trends (Table S2) were generally consistent within families but often followed different specialisation pathways between them. For

example, transitions to bird pollination in the Myrtaceae lead to large claw-shaped multistamen anthers in clades related to *Melaleuca*, whereas claw-shaped corollas occur in the Haemodoraceae (*Anigozanthos*). The selection for specialisation improves the efficiency of pollen transfer (Johnson 2010). For example, anthers remain very small in Proteaceae genera such as *Grevillea* due to secondary pollen presentation. Finally, expanded bracts form the main display for birds in some species (e.g. *Darwinia* and *Pimelea*), or larger inflorescences are employed, especially in the Proteaceae and Myrtaceae. Thus, inherent properties of flowers result in a higher degree of convergent evolution for more closely related taxa. Other relatively common SWAFR floral evolution trends include post-pollination colour change in 72 taxa, spring-loaded (297) or mobile (12) columns in triggerplants and orchids, explosive pollen transfer in the Proteaceae (137) and extremely variable brightly coloured flowers in visually deceptive orchids (186).

Intermediate steps are required for transitions from insect to bird pollination (Table S2). Relatively short-billed birds that feed on nectar, such as silvereyes, may be important for initiating these transitions. The overlap between specialist and generalist bird pollinators is more pronounced in Australia than other areas (Abrahamczyk 2019). Mammals such as honey possums may also be involved. Birds or mammals visiting flowers primarily optimised for insects are common and honey possums in particular visit a wide diversity of flowers, some of which do not seem suitable due to their small size, poorly accessible anthers or lack of nectar. Relatively large animals visiting small flowers are unlikely to be effective pollinators since pollen would not remain on their tongue or bill long enough to be transferred to other plants and their fur or feathers would often remain too far away from anthers to receive pollen. Overall, Australia has much more pollination by larger animals, especially birds, than would be expected in comparison with other parts of the world (Armstrong 1979). The production of copious nectar that supports bird pollinators may be linked to plants growing in highly infertile soils but with abundant sunlight accumulating excess carbon that can be used to produce abundant nectar and larger floral displays (Orians and Milewski 2007). From an animal perspective, evolution probably progresses from birds that casually feed on nectar to specialised nectar-feeding birds and eventually to those that can also feed on pollen. As explained above, this can lead to characteristic structural specialisations such as a longer beak in birds or proboscis or tongue in insects. From a plant perspective, the persistence of clades with dual syndromes for bird and insects or NFM suggest that greater pollination flexibility can be beneficial, especially for trees that produce massed synchronised floral displays (eucalypts, banksias, melaleucas, *N. floribunda*, etc.), or plants with mass flowering after fire (e.g. *Xanthorrhoea* spp.).

Explanations for the diversity of plant species in the SWAFR has been examined in several studies (e.g. Cowling *et al.* 1994;

Hopper 2009) but pollination complexity has not previously been addressed in any detailed way. The closest environment to that of the SWAFR where this has been studied is the Cape of South Africa where there are similarities in biota, climate and geomorphology. These studies link high species richness to topographic complexity (van Mazijk *et al.* 2021), habitat variability (Goldblatt and Manning 2002), or soils and habitats (Petersen *et al.* 2020). In this region, sister species divergence was accompanied by more floral than vegetative diversification and therefore was also pollinator driven (Niet and Johnson 2009; Johnson 2010). The SWAFR landscape is less structurally diverse than the Cape but has very complex soils due to prolonged weathering and plant–soil feedback (Verboom and Pate 2006). Stable landscapes and the relatively stable climates in the SWAFR are linked to highly complex plant pollination, nutrition and fire traits (Brundrett 2021).

Flowering throughout the SWAFR varies throughout the year with a low proportion of species in flower in summer when dry conditions prevail (e.g. Barrett and Ladd 2021). As noted earlier, banksia species have a sequence of flowering through the year, as do eucalypts and other species, that makes it seem they are cooperating to keep pollinators with longer life spans fed all year round. However, this is likely to be a product of competition between plant species for pollinators. A similar situation occurs in southern Africa where *Erica* species share the orange breasted sunbird as their primary pollinator and also in South America where hummingbird pollinated plants have sequential flowering (Aizen and Vázquez 2006; Heystek and Pauw 2014). Sequential flowering over the seasons in the SWAFR is aided by phreatophytic plants in many communities (e.g. Tsakalos *et al.* 2019). These can flower at times when more shallow rooted species have ceased flowering due to drought stress. Impacts on pollination by increasing aridity and extremes in rainfall and temperatures also need to be considered (Hoffmann *et al.* 2019; <https://www.agric.wa.gov.au/climate-change/climate-projections-western-australia>).

Pollination strategies seemed to be linked to rarity of some plant species in the SWAFR. Overall pollination rates can be very low for orchids with sexually or visually deceptive pollination and can be even lower when plants occur in large groups (Elliott and Ladd 2002; Brundrett 2016, 2019). This strategy is risky because highly specific insect pollinators may be uncommon, have their own habitat requirements and only be active for a few weeks. Limited pollination is a major concern for other rare plants where it has been investigated (Lamont *et al.* 1993; Yates and Ladd 2004; Rymer *et al.* 2005; Ye *et al.* 2012; Phillips *et al.* 2015; Ladd *et al.* 2019; Delnevo *et al.* 2020b). Habitat disruption and pollinator decline has been documented globally and regionally (Hallmann *et al.* 2017; Sands 2018; Sánchez-Bayo and Wyckhuys 2019). These ecological trends and consequences can only be measured by effective monitoring of pollination in ecosystems (Thavornkanlapachai *et al.* 2018; Brundrett 2019; Oliveira *et al.* 2020; Breeze *et al.* 2021).

Our study resolves how most SWAFR plants are pollinated but many questions remain:

1. How have the interacting influences of long time periods, climatic history, habitat complexity, etc. contributed to extremely complex floral evolution?
2. Similar types of pollination syndrome transitions occur across Australia and elsewhere but why are they far more frequent and complex than expected in the SWAFR?
3. Have the same processes that cause higher plant diversity also resulted in greater pollination complexity, or is the reverse true, or does a feedback loop drive complexity in both?
4. Do improved genetic outcomes and/or greater reproductive success of plants explain the many cases of pollination syndrome switching and convergent evolution in the SWAFR?
5. Do plant clades with more complex pollination also include more rare species?
6. Why do some families have pollination syndrome gradients from pollination by general to specific insects, birds, or wind (Table 4), whereas others do not? Is this due to conflicting needs for more efficient pollination and reducing risks by retaining flexibility?
7. Why have so many very specialised and highly inter-reliant pollination relationships (e.g. oligolectic bees with *Verticordia* flowers) evolved in the SWAFR, despite the apparent risks to both species?
8. Conversely, why are there fewer plants with specific pollination syndromes related to butterflies, moths, flies or beetles in the SWAFR, even though these insects are often present?
9. Why do some very successful species retain both insect and bird pollination in the same flower whereas others become much more specialised?
10. Are pollination transitions to birds effective because larger animals are more consistently available than insects, are more resilient, or have greater mobility after catastrophes?
11. How is pollination complexity linked to ecological factors such as plant growth form, plant productivity, or habitat conditions (e.g. disturbance or fire)?
12. Are some flower types more predisposed to switch syndromes?
13. Why are pollination evolution reversals to less complex syndromes much rarer than transitions to more complex syndromes?
14. What are the likely impacts of ongoing and impending climate changes on very complex and delicately balanced pollination systems?
15. What is the role of pollinators that seem to ignore floral syndromes such as some bees and lorikeets? Are they pollen and nectar thieves or backup pollinators?
16. What happens when relatively specific pollinators such as native bees are in short supply, as we have recently observed in urban areas?
17. Why do the same plant clades that are taxonomically diverse and dominant in ecosystems in the SWAFR also have the most complex traits for nutrition, pollination and fire (Brundrett 2021)?
18. Future research is required to resolve links between species richness and pollination in species complexes including extreme cases where syndromes vary within species.
19. Further research is also needed to untangle the impacts of convergent evolution of flower form due to pollination syndromes on plant taxonomy.

## Conclusions

1. Here we provide the first attempt to consolidate data for floral visitors and morpho-syndromes for the entire vascular plant flora of a floristic region and globally significant biodiversity hotspot. Our approach combined categories defined by the shape, size and colour of flowers with thousands of observations to allocate pollination syndromes for the majority of SWAFR plants. Consistent relationships between floral forms, animal visitor records and plant phylogeny strongly supported the validity of pollination syndromes in our study. These comparisons included floral morphology and colour data from 1843 taxa, as well as >6000 floral visitor records from plant clades with complex pollination syndromes. Our study highlights the benefits of combining data from numerous independent sources and the use of rigorous diagnostic criteria to identify categories of symbiotic interactions.
2. Consistent relationships between flowers and their pollinators have evolved independently across multiple plant lineages and this coevolution is linked to extreme landscape age and other types of trait complexity in plants. The SWAFR includes multiple evolutionary transitions in pollination from insects to birds and insects then to primarily bird-pollinated flowers (Table 4). In some cases, this evolutionary trend continues to include non-flying mammals, especially honey possums, but their significance is likely to be underestimated because they are now uncommon across most of the region (Bradshaw 2014). Similar trends occur in evolution from general insects to highly specific insects or wind pollination. The latter is phylogenetically driven by the importance of families, such as Casuarinaceae, Restionaceae, Cyperaceae in SWAFR, where this is a plesiomorphic trait. There also are multiple origins of wind-pollinated taxa in clades of plants that grow in open windy habitats (e.g. saline areas) or post-fire situations, where pollinators may be scarce. These trends suggest that plants have faced strong selective pressures to increase their floral complexity and energy expenditure on flowering due to intense competition to attract pollinators. One major advantage

- from switching to bird or mammal pollinators is that they are available all year, as opposed to invertebrate pollinators which generally have shorter periods of activity. However, the former requires food availability throughout the year from plant communities with a combined flowering phenology that covers all the seasons.
3. The trend for more specific pollination has led to many evolutionary transitions in the SWAFL (>275, Table S1) and this complexity seems to be unique globally. These include many more than expected transitions to bird, specific insect or wind pollination syndromes, plus very complex flowers with secondary pollen presentation, post pollination colour change, buzz pollination, extremely complex flowers, deception of insects, explosive pollen release, oily pollen, and flowering after fire (Fig. 8). These transitions provide exceptional case studies of convergent evolution of floral forms, especially for bird, mammal, or wind pollination (Figs 2, 14 and 15). These transitions have occurred throughout Australia, but their complexity peaks in the SWAFL. This makes the SWAFL the premier location to study the ongoing evolution of pollination syndromes and their consequences for plant reproductive success. This research would focus on selective forces driving SWAFL floral diversity such as historic biotic, climatic and landscape factors, as well as pollination complexity as a driver of exceptional plant biodiversity.
  4. Pollinator evolution that occurred in parallel with floral trait evolution also requires further investigation. The post-Gondwanan explosion in songbird diversity, including honeyeaters (Meliphagidae), peaked over the past 25 Ma (Oliveros *et al.* 2019). This occurred in parallel with the emergence of many new clades of bird pollinated flowers (Mast *et al.* 2012, 2015; Toon *et al.* 2014; Thornhill *et al.* 2015), with correlated increases in the length of bird bills and flower parts (see Fig. 17g). Impressive co-diversification of key insect groups with flowers has occurred, especially for bees and flies that are highly specialised pollinators. The lack of highly social bees such as *Apis* and *Bombus*, which tend to be able to access a wide range of flower types, may also be a factor in driving the diversity of solitary bee groups and their specialisation on specific flower types.
  5. Floral trait complexity evolution also evolved in parallel with novel traits for plant mineral nutrition and fire recovery, which also peak in southwestern Australia starting in the Paleogene (Crisp *et al.* 2011; Brundrett 2017; He and Lamont 2018) and is also positively correlated with taxonomic diversity in plant families peaking in the Myrtaceae, Proteaceae and Fabaceae (Brundrett 2021).
  6. Pollination complexity also has important human consequences for enjoyment, horticulture and tourism. This is exemplified by the many exceptionally striking bird pollinated flowers, such as kangaroo paws, banksias and bottlebrushes, which stand out in Australian wildflower books and gardens (Fig. 14). This also includes amazingly complex insect-pollinated flowers such as feather flowers, triggerplants, fringe lilies, peas and heaths (Figs 2–10), as well as visually deceptive orchids including the dazzling Queen of Sheba (Fig. 13). The biodiversity and beauty of birds and insects that visit SWAFL flowers are also exceptional.
  7. Links between extreme plant specialisations and rarity require further investigation in the SWAFL to provide essential information for management of threatened species (including pollinating animals) and effective restoration of damaged ecosystems. This knowledge will also help to predict the vulnerability of plants and ecosystems to habitat fragmentation, fire and climate change, which differ for plants and their pollinators.

## Supplementary material

Supplementary material is available [online](#).

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**Data availability.** Additional data is available in ResearchGate ([https://www.researchgate.net/publication/378594577\\_Brundrett\\_et\\_al\\_2024\\_Extra\\_Data\\_Tablesxlsx?](https://www.researchgate.net/publication/378594577_Brundrett_et_al_2024_Extra_Data_Tablesxlsx?)).

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