

# 1 Categorising rainforest plants

## THE DAWNING OF VASCULAR PLANTS, AND THOSE THAT ARE DEAD

*‘The colonisation and radiation of multicellular plants on land that started over 470 million years ago was one of the defining events in the history of this planet.’*

*(Pires and Dolan 2012)*

Originating from aquatic forebears, vascular plants (plants with woody conducting tissue) came to occupy primordial land habitats and are now the dominant plant forms on the Earth’s landmasses (Rensing 2018). Vascular plants probably originated from multicellular green algae (e.g. Charophyceae [see Nishiyama 2007]) during the Silurian period ~440 million years ago (mya) (Taylor *et al.* 2009), with perhaps the most rapid evolution unfolding during the broader Silurian-Devonian time interval (Niklas and Crepet 2020). Developments that defined the successful invasion of land by vascular plants included the possession of spores that were protected from drying out, the protection of the plant body from the extremes of evaporation, and the evolution of the phloem and xylem which allowed the efficient conduction of water and nutrients (Brodribb *et al.* 2010; Raven *et al.* 1992); with laminate (leaf-like) sporophylls and bracts occurring independently in several distantly related Early Devonian plant lineages (Hao and Xue 2013). Ultimately several lineages developed seeds, an outstanding feature which provided a major

element in the dominance of terrestrial vascular plants. The seed protects and nourishes (via the seed-coat or testa, and the nutritive endosperm and perisperm) the embryonic plant in uncertain and sometimes harsh environments, allowing a period of dormancy during conditions not ideal for germination and subsequent growth.

Today more than a quarter of a million species of vascular plants are recognised, divided into four extinct and about eight living groups (authors differ on the number and placement of taxa). The extinct divisions are represented by the Rhyniophyta (e.g. *Rhynia* [Taylor *et al.* 2009]), which are known first from Silurian fossils, and the Zosterophyllophyta (*Zosterophyllum* [Taylor *et al.* 2009]), which date at least from the Late Silurian and are considered by some palaeobotanists to be the ancestors of the living club mosses (Lycophyta [= Lycopsidea]) (e.g. see Crane 1989). Zosterophyllophyta were diverse by the Late Silurian, and by the Early Devonian are known from Gondwana (Taylor *et al.* 2009). A third early group of now extinct vascular plants is the Trimerophytophyta (*Psilophyton* [Taylor *et al.* 2009]), first recorded from the Lower-Middle Devonian ~360 mya.

Rhyniophyta have traditionally been considered the most ancient and simplest group of vascular plants but more recent information indicates that some taxa are not true Rhyniophyta at all but share characteristics of bryophytes (plants lacking vascular tissue; i.e. liverworts, hornworts, mosses [see Bell *et al.* 2020]) and vascular plants (Taylor *et al.* 2009). The Rhyniophyta were

dichotomously (in successive dual divisions) branched plants, believed to have inhabited mudflats and marshes. Rhyniophytans were seedless and their bodies did not possess distinguishable roots or leaves. Known Zosterophyllophyta species were also dichotomously branched, and may have been aquatic with the lower branches possibly anchored in mud. This conjecture is based on the restriction of stomata (structures in the leaf surface allowing gaseous exchange during respiration and photosynthesis, and the transpiration of water) to the uppermost branches. The lateral and downward growth of some branches may have provided support within the substrate, consequently allowing further outward growth of the parent. Trimerophytophyta may have been derived from the Rhyniophyta (Taylor *et al.* 2009) and are possibly the progenitors of the ferns, progymnosperms and horsetails (Sphenopsida). However, the Trimerophytophyta possess a more complex branching pattern and a more massive vascular strand than the Rhyniophyta, which likely permitted the development of a relatively large-sized plant. These three groups of early vascular plants produced only a single kind of spore in their sporangia and so their reproductive systems were like those of nearly all the present-day ferns, in addition to the less-known living groups Psilopsida, Sphenopsida and several of the Lycophyta.

The fourth group of extinct ancient vascular plants, the progymnosperms, stands aside from the Rhyniophyta, Trimerophytophyta and Zosterophyllophyta. The progymnosperms (e.g. *Archaeopteris* and *Triloboxylon* [Taylor *et al.* 2009]) are considered precursors to true gymnosperms, being intermediate in aspects of their development between gymnosperms and the Trimerophytophyta – they reproduced by spores but possessed a more complex branching and vascular system. Known from the Palaeozoic era, some, such as *Archaeopteris*, resembled tall leafy branched conifers. *Archaeopteris* is widespread in the fossil record, particularly the Northern Hemisphere, and is also known from Australia. During the Carboniferous period, ~300 mya, the ‘seed ferns’ (e.g. Medullosales, Glossopteridales, Caytoniales, Corystospermales), appeared in the Australian fossil record. Related to the progymnosperms, seed ferns (which are neither a natural nor monophyletic group [Taylor *et al.* 2009]), became extinct by the end of the Cretaceous. However, amongst their various members is the genus *Caytonia*, which was originally considered as representing a new group of angiosperms, possessing features showing possible affinity with an angiosperm carpel.

## LIVING VASCULAR PLANTS

All living vascular land plants are now grouped within the Equisitopsida (see Angiosperm Phylogeny Group III 2009). Species that occur today within the divisions of the plant world can be grouped into those that are seedless and those that produce seeds of various kinds (Kramer *et al.* 2013; Kubitzki 2013). Among the former the most numerous are the Filicopsida (true ferns) and the more poorly represented are Psilopsida (fork ferns), Lycophyta (club mosses, quillworts) and Sphenopsida (horsetails) (Niklas and Crepet 2020; Taylor *et al.* 2009). Only the Sphenopsida do not naturally occur in Australia (although they were present millions of years ago). However, one sphenopsid species (*Equisetum arvense*) is locally naturalised (Harden 1990) and is regarded as a potential major weed. All four classes lack flowers and reproduce by the production of spores.

In Australia the Psilopsida consist of two genera, *Psilotum* and *Tmesipteris*, encountered in rainforest as epiphytes, particularly on the trunks of tree ferns (Harden 1990). *Psilotum* is sometimes referred to as a ‘living fossil’ as it resembles some of the first terrestrial plants, such as the extinct *Cooksonia* (however, *Cooksonia* may represent a separate lineage because the connective tissues are different from vascular plants [Niklas and Crepet 2020; Taylor *et al.* 2009]). Some modern Psilopsida are also terrestrial in habit, though all are small in size. *Psilotum nudum* can be found growing on shaded rock overhangs in rainforest, and is even recorded from rock outcrops adjacent to Sydney Harbour. Psilopsida do not possess true roots, rather being differentiated into a creeping rhizome and stems with reduced leaves that resemble scales (as in *Psilotum*) or more conspicuous leaves (*Tmesipteris*). But even in *Tmesipteris* the ‘leaves’ are not true leaves, but outgrowths of the stem epidermis. In the Lycophyta the herbaceous plants comprise true roots, with leaves arranged spirally about the aerial stems or arising in a grass-like manner. The class includes terrestrial and epiphytic species found in rainforest as well as other types of plant communities. Lycophyta fossils are known from the Late Silurian (Taylor *et al.* 2009), and during the Carboniferous the Lycophyta included tree-like species (lepidodendrids) that reached 25 m in height and dominated much of the part of the Carboniferous that is popularly called the ‘Age of Coal’ (predominantly Northern Hemisphere, as the Australian coal basins are younger). Among the fossil forms recorded from Australia is the enigmatic Upper Silurian-Lower Devonian genus *Baragwanathia*

## 4 Introduction to breeding systems

### INFLUENCE OF BREEDING SYSTEMS

Many tropical and subtropical trees and shrubs are characterised by wide geographical and altitudinal distributions, but at individual sites species often have low population densities. Due to the fragmentation and spatial reduction of rainforests, especially lowland tropical and subtropical rainforests, the local populations of many species are now very small, in some cases reduced to single individuals per stand (Fox *et al.* 1997; Hobbs and Yates 2003; Neal *et al.* 2010).

Knowledge of the reproductive biology/breeding system of species is an important prerequisite to understanding their resilience to environmental change (extinction risk), and changes in population density and pollinators (Gauli *et al.* 2013; Sjöström and Gross 2006). This is a scenario not restricted to rainforest plants, and although mating systems of plants may vary depending on their pollination biology and life history, as plant populations of any vegetation community get smaller there is likely a progressive trend towards increased inbreeding, smaller effective sizes of pollen pools, and greater variation in out-crossing. Whether a species has the ability to self-fertilise and whether there is plasticity in requirements for pollinators (i.e. numerous alternative species can fulfil the role) are particularly important to a species' ability to successfully colonise new sites, to survive in highly disturbed remnants, and is highly relevant to the management and preservation of remnant rainforest stands.

Rainforest plants that cannot reproduce vegetatively, and obligate out-crossers that are incapable of producing seed by selfing, are unable to establish colonies from single recruits. Where such populations are reduced to single individuals and are isolated from external pollen sources, the species are functionally extinct within individual remnants.

The requirement for a pollination vector is dependent upon the particular breeding system of a plant species. Essentially, there are three main categories of breeding systems in plants (though overall angiosperm pollination strategies comprise a continuum). These are represented by obligate out-crossing species (dioecious and self-incompatible hermaphroditic species), facultative out-crossers (monoecious, gynodioecious, protandrous and protogynous species) including some self-compatible hermaphrodites, and facultative inbreeders (self-compatible and apomictic plants) (Gross 2005; House 1985). In the third group are some apomicts (discussed below), in which inbreeding is obligatory. Self-pollinating plants are less reliant on pollinators, however, pollinators may remain heavily dependent on the plant for pollen and/or nectar (Spigler and Kalisz 2017).

Approximately 50% of flowering plants show some level of self-incompatibility (Gibbs 2014), with obligate out-crossing, due to self-incompatibility, being reported from more than 100 angiosperm families and estimated to occur in ~39% of species (Igic *et al.* 2008). However,

self-incompatibility frequently has been lost during the evolution of flowering plants; and there is no evidence that once this has been lost it has been regained (Igic *et al.* 2008). For individuals of obligate out-crossing species within plant populations that are widely separated from one another, inadequate receipt of pollen and commensurate limitation of female success (fruit- and seed-set) may be common. Studies in various foreign rainforests have indicated that out-crossing generally predominates (e.g. Murawski *et al.* 1994); in Brazilian tropical dry forest 83% of all growth forms were hermaphrodites but obligate self-incompatibility occurred in more than 60% of the 147 species studied (Machado *et al.* 2006). However, the spatial isolation of trees may influence the degree of out-breeding and fecundity (lower levels of fertilisation and less seeds produced) (House 1985, 1992). This is the situation for Australian subtropical rainforests, but many bisexual species retain some capacity for self-pollination (Table 4.1). This ability may be important for the survival of biodiversity in the face of continuing disturbance to rainforest, and may explain rainforest and species survival during periods of naturally rapid environmental change. Historically, however, the level of self-incompatibility and requirement for out-crossing in tropical rainforest trees has been a contentious topic. Fedorov, discussing in 1966 the structure of tropical rainforest and speciation in the humid tropics, suggested that out-crossing was rare (due to the spatial isolation of species in complex tropical rainforests) and that self-compatibility was general among rainforest trees. Corner, in 1954, argued that selfing is the tendency of all trees even though it will tend to reduce heterozygosity in populations. Ashton (1969) partly summarised Fedorov's case, taking into account the low densities of rainforest species, as 'given the lack of marked seasonality which leads to irregularity and lack of coincidence in flowering' and assuming that pollen dispersal in temperate and tropical regions was equally efficient, 'then the effective populations in tropical tree species must contain on average fewer individuals than their temperate counterparts, and indeed, self-fertilisation must be the rule'. He later argued that, if Fedorov (1966) and Corner (1954) were correct, dioecism and other breeding systems promoting out-crossing would be eliminated. However, Ashton (1969) showed that contrary to this prediction and based upon his own field investigations, that a significant proportion (26%) of tree species in a Sarawak mixed dipterocarp forest study site were dioecious, and thus obligate out-crossers. He argued on the basis of plant sexual

systems, as indicated by floral morphology, but had no data on the potential for self-compatibility in non-dioecious species.

The majority of woody tropical rainforest plant species which have been studied have adaptations for out-crossing (Sands and House 1990), although the rate of out-crossing in populations and fecundity levels in individuals may depend upon the density of trees in flower (House 1992, 1993). A reduction in population density and fecundity levels due to habitat fragmentation and consequent increased distances between obligate out-crossed rainforest plants may threaten the long-term viability of local populations. Thus an ability to self-fertilise reduces vulnerability to extinction. Out-crossing is often obligatory (e.g. in dioecious species such as the Australian *Neolitsea dealbata* [Lauraceae]) and self-incompatibility in tropical trees, especially pioneer species, has been reported as widespread throughout the world's rainforests (Dayanandan *et al.* 1990; Perry and Starrett 1980). However, because of the occurrence in rainforests of populations and individuals with intermediate levels of self-incompatibility categorisation of the expression of self-incompatibility of a species may prove complex.

Low or variable levels of self-compatibility may occur in otherwise out-crossing species (e.g. Appanah 1982; Crome and Irvine 1986) and this may result in successful pollinations where cross-pollination is unpredictable or pollinators are absent. Self-compatibility may result in reduced offspring vigour but, where species are vulnerable to or undergo frequent colonisation and extinction cycles, as do many short-lived rainforest pioneers (e.g. *Commersonia fraseri* – Malvaceae/Sterculiaceae [Plate 44]), levels of self-compatibility in an otherwise predominantly self-incompatible breeding system would be advantageous for long-term species survivorship. Among cosexual species (those with bisexual or monoecious breeding systems; such as the ephemeral monoecious vine *Diplocyclos palmatus* (Cucurbitaceae [Plate 23]) out-crossing may be obligatory because of self-incompatibility. However, if self-pollination can occur there is the possibility of seed-set in the absence of pollination vectors, or where the plant population size is so small as not to attract pollinators. Environmental conditions can affect the degree of self-compatibility, for example, many tree species in Neotropical montane forests are self-compatible (Bawa 1990). The frequently cold and wet montane climates, which limit pollinator activity, may explain this preponderance of self-compatibility.

There have been few studies of pollination systems in Australian rainforest species but, as a broad generalisation based on floral morphology and patterns of anthesis, it appears that many species are either facultative or obligate out-crossers (see Tables 4.1, 4.2). Some of these species are dioecious (*Rhodosphaera rhodanthema* [Anacardiaceae] (Plate 95), *Drypetes deplanchei* [Putranjivaceae/Euphorbiaceae] and *Citronella moorei* [Icacinaceae/Cardiopteridaceae]) but descriptions of floral structure in ‘Floras’ and botanical handbooks may be inaccurate and convey misleading impressions of possible breeding systems. For example, *Wilkiea huegeliana* (Monimiaceae) (Plate 48), though reported to be dioecious, is frequently found to be monoecious and *Euroschinus falcatus* (Anacardiaceae) (Plate 7) is reported

as polygamous but is frequently dioecious, at least in those New South Wales populations that have been studied (G. Williams 1995; Williams *et al.* 2001).

A high proportion (>50%) of trees in Australian tropical and subtropical rainforests are hermaphrodites but their capacity to self-pollinate (and the degree of self-compatibility) is largely unstudied. In the Australian tropical rainforest herb *Hornstedtia scottiana* (Zingiberaceae) self-pollination is effected (almost 100% of the time) by the rapid elongation of the corolla tube should flowers not be otherwise pollinated by their bird (Melphagidae) pollinators (Ippolito and Armstrong 1993). This delayed self-pollination strategy is characteristic of self-compatible species which initially offer opportunity for out-crossing (Willmer 2011). However, data on the

**Table 4.1.** Self-compatibility in Australian lowland subtropical rainforest species (after Adam and Williams 2001).

Family/species	%	Family/species	%
<b>Anacardiaceae</b>		<b>Monimiaceae/ Atherospermataceae</b>	
<i>Euroschinus falcatus</i>	0.6 (20.1)	<i>Daphnandra micrantha</i>	2.1 (7.1)
<b>Celastraceae</b>		<b>Myrsinaceae/ Primulaceae</b>	
<i>Denhamia celastroides</i>	0 (7.2)	<i>Myrsine howittiana</i>	0 (0)a
<b>Ebenaceae</b>		<b>Myrtaceae</b>	
<i>Diospyros australis</i>	2 (24.6)	<i>Archirhodomyrtus beckleri</i>	0 (31.3)
<b>Elaeocarpaceae</b>		<i>Rhodomyrtus psidioides</i>	0 (2.2)
<i>Elaeocarpus reticulatus</i>	36.9 (16.1)	<i>Syzygium floribundum</i>	0.8 (20.1)
<b>Ericaceae/Epacridaceae</b>		<i>Syzygium smithii</i>	3.6 (4)
<i>Trochocarpa laurina</i>	0 (9.1)	<i>Tristaniaopsis laurina</i>	0 (19.1)
<b>Escalloniaceae/Rousseaceae</b>		<b>Pittosporaceae</b>	
<i>Abrophyllum ornans</i>	16.1–29.4 (93.9)	<i>Hymenosporum flavum</i>	0 (2.1)
<i>Cuttsia viburnea</i>	0.8 (2.9)	<b>Rhamnaceae</b>	
<b>Eupomatiaceae</b>		<i>Alphitonia excelsa</i>	0 (5.4)
<i>Eupomatia laurina</i>	9.7 (59.1)	<b>Rutaceae</b>	
<b>Flacourtiaceae/Salicaceae</b>		<i>Acradenia euodiiformis</i>	10.3 (4)
<i>Scolopia braunii</i>	17.8 (28)	<i>Acronychia imperforata</i>	0 (0)b
<b>Lamiaceae/Verbenaceae</b>		<i>Geijera salicifolia</i>	0 (8.9)
<i>Clerodendrum tomentosum</i>	0.5 (1.2)	<b>Sapindaceae</b>	
<b>Lauraceae</b>		<i>Alectryon coriaceus</i>	0 (0–7.8)
<i>Cryptocarya glaucescens</i>	18.1 (24.7)	<i>Cupaniopsis anacardioides</i>	9.2 (19.8)
<i>Cryptocarya rigida</i>	0 (3.8)	<i>Guioa semiglauca</i>	0.8 (8.9)
<b>Malvaceae</b>		<i>Mischocarpus pyriformis</i>	0 (9.7)
<i>Hibiscus splendens</i>	9.1 (29)	<b>Winteraceae</b>	
		<i>Tasmannia insipida</i>	58.7 (97.7)

Unenclosed (%) values represent percentage of developing fruit from inflorescences at conclusion of flowering in which pollinators were excluded; values in parentheses represent percentage of developing fruit from open pollinated flowers to which pollinators were given unobstructed access. All values are indicative only. Lower or zero values for some open pollination results illustrate the uncertainty of the pollination environment.

a: Species represented by only one tree in population, suggesting it is an obligate outcrosser.

b: No plants in population set seed in year of study.



flowers and some that are functionally male) and others are hermaphroditic (Worboys and Jackes 2005). In *Daphnandra micrantha* (Plate 47) anther dehiscence may occur more than two days after initial opening of the flower so that a relatively long period of time can elapse, allowing the stigma to receive foreign pollen (G. Williams 1995). Some species appear to be only slightly protogynous, such as *Cuttsia viburnea* (Plate 31) and *Acradenia euodiiformis* (Plate 80). The effectiveness of the protogynous function is increased where the stigma is exerted beyond the perianth before the numerous anthers have been exposed (as in *Scolopia braunii*), these being held for a time by the unopened corolla. But by whichever method protogyny is expressed, in general it is a surer guard than protandry against the possibility of self-pollination or contamination by a plant's own incompatible pollen. And

though, in the absence of a better choice, self-pollination in self-compatible species is not necessarily a bad thing, out-crossing is the preferred strategy because it results in the heterozygous blending of genetic attributes from different parent plants.

Comparative studies undertaken at the species level indicate protandrous flowering plants tend to be pollinated by bees or flies, but in protogynous species there is a tendency to wind or beetle pollination. This has been taken to suggest that a functional role for pollinators exists as a driving mechanism in the evolution of dichogamy. The mode of pollination (i.e. biotic or abiotic) may not affect transitions between protandrous or protogynous states, rather rates of transition between animal-mediated and abiotic pollination may depend on whether a species is protandrous or protogynous (Sargent and Otto 2004).

### Multiple threats from invasive species – a diversity of enemies

Invasive species, both plant and animal, can pose long-term threats to native plant–pollinator mutualisms, plant breeding systems, and the recruitment and survival of individual native plants species within rainforest stands (Arroyo-Correa *et al.* 2019). Invasion is facilitated where alien plants and animals are able to act in liaison (e.g. as in Gross *et al.* 2017), with the facultative interaction between non-indigenous species gaining recognition as a major driver of plant invasion success (Simpson *et al.* 2005).

Observations of invasive flower-frequenting animals in Australian rainforests are generally restricted to the honey bee *Apis mellifera*. This 'super-generalist' pollinator will enter both disturbed and undisturbed rainforest stands to forage, and can take residence in tree hollows. *Apis mellifera* has been recorded from numerous mass-flowering trees and shrubs, but its impact on the reproductive ecology of rainforest plants in Australia is little studied. Although it competes with native anthophilous species for floral resources (e.g. Gilpin 2017; Williams and Adam 1997), with Hermansen *et al.* (2014b) suggesting it may have displaced native pollinators of the mangrove *Avicennia marina*, its impact to the detriment of native plant sexual reproduction in Australian rainforests has not been clearly demonstrated. However, *Apis mellifera* is known to forage at a wide taxonomic range of highly invasive plants in Australian rainforests, such as *Asparagus* spp. (Asparagaceae) and *Chrysanthemoides monilifera* (Asteraceae), in littoral rainforest, *Ligustrum sinense* (Oleaceae) in riparian rainforest, *Anredera cordifolia* (Basellaceae) in lowland floodplain rainforest, and *Lantana camara* (Verbenaceae) extensively in eastern mainland Australia, with consequent *Apis mellifera*-induced pollination promoting high levels of seed production and further weed infestation.

However, five additional exotic bees, *Bombus terrestris*, *Apis cerana*, *Megachile rotundata*, *Afranthidium repititum* and *Seladonia hotoni* are resident in Australia (T. Houston 2018). The large European bumblebee *Bombus terrestris* (Apidae) was introduced to Tasmania in 1992 where it is now widely established, spreading to numerous vegetation formations from sea level to elevations above 1400m. It is a generalist feeder (Moore and Gross 2012) that forages at both native and exotic plants, and has been recorded competing with, and displacing, native megachilid bees (McQuillan and Hingston 1999). *Bombus terrestris* has the potential to spread widely throughout temperate mainland Australia, with the likelihood of impacting on native plants not previously known to be visited by exotic bees (Kingston and McQuillan 1998). The foraging activities of *Apis mellifera* and *Bombus terrestris* threaten the declining swift parrot *Lathamus discolor* (Hingston and Wotherspoon 2017), which feeds largely on nectar and pollen of eucalypts. Hingston and Wotherspoon found that *Bombus terrestris* and *Apis mellifera* compete with swift parrots for the nectar of flowering *Eucalyptus globulus*, the two bees consuming most of the available nectar in their exposed study blossoms. *Apis mellifera* was the most common species, but

*Bombus terrestris* had greater *per capita* rates of consumption. The introduced bee, *Apis cerana*, was recorded from Cairns, North Queensland, in 2007. Attempts to eradicate *Apis cerana* in Australia have failed. Widely distributed in Asia and the south-west Pacific, the species is resilient to different environmental conditions (Koetz 2013), and given its ability to forage during cool months at high latitudes in the Northern Hemisphere (Kato 2000) *Apis cerana* may be able to invade regions and ecosystems far beyond its currently known Australian distribution. *Megachile rotundata* is a native to Europe and was introduced in attempts to establish it as a pollinator of lucerne crops. It appears restricted to areas where lucerne is farmed. *Afranthidium repitum* is a native of South Africa and is established in Queensland, New South Wales and one record from South Australia. *Seladonia hotoni*, a native of southern Africa, was first detected in the Upper Hunter Valley region of New South Wales in 2004. It visits flowers of introduced plants, including the noxious weed *Galenia pubescens* (T. Houston 2018).

Though currently unexplored, exotic ants may also pose a threat to the reproductive ecology of Australian rainforest plants, this through their interference with pollinators (as has befallen the threatened Mauritian gecko-pollinated plant *Roussea cephediana* (Roussaceae) (Hansen and Müller 2009). A precautionary case is the Yellow crazy ant *Anoplolepis gracilipes* (Lowe *et al.* 2000), potentially capable of inhabiting Australian ecosystems from northern Western Australia, south to parts of inland and coastal New South Wales. Loss of biodiversity and ecosystem integrity followed its invasion of Christmas Island, Indian Ocean, resulting in listing there as a 'key threatening process' under the *Environmental Protection and Biodiversity Conservation Act, 1999*. A second potentially threatening species is *Wasmannia auropunctata*, commonly called the Electric or Little fire ant. This has a limited known occurrence in northern Queensland, but has displaced other ants, or caused a decline in invertebrate populations, wherever it has been introduced.

In Australia cattle, feral Asian water buffalo (*Bubalus bubalus*) and pigs have been implicated as agents of change to rainforest structure and floristic composition, and as agents of exotic plant infestation (e.g. Gentle and Duggin 1997), to which native pollinators will variously respond. In the Forty Mile Scrub National Park, North Queensland, rooting of soil by pigs has been suggested to cause tree death and subsequent increased light penetration in dry rainforest; this favouring the spread and dense infestation of *Lantana camara* (Fensham *et al.* 1994). *Lantana camara* is widespread in eastern Australia, forming dense infestations in logged and otherwise disturbed mesic forests of northern New South Wales and south-eastern Queensland. It will also invade seemingly little-disturbed rainforest stands, as at Camels Hump Nature Reserve, northern New South Wales; and in such instances lantana can add significantly to the fuel load (and fire potential) in the understorey. However, *Lantana camara* provides a nectar source for numerous native butterflies (e.g. *Graphium agamemnon*, *G. eurypylus*, *G. macfarlanei*, *G. macleayanum*, *G. sarpedon*, *Ornithoptera priamus*, *O. richmondia*, *Pachlioptera polydorus*, *Papilio ulysseus*, *Belenois java* [Plate 114], many Hesperidae) but the ecological implications of their diversion from co-flowering rainforest trees and shrubs is generally unknown.

Native animals can also be functionally invasive. These are species, vertebrate and invertebrate, from adjacent non-rainforest communities that forage on rainforest margins, or owing to the narrow or small patch size of a stand (where no effective 'core' area remains) can penetrate past the rainforest boundary. Where these are species that forage upon floral resources, and in so doing competing with resident faunas, their movements might be such that they perform minimal or no pollination service, yet deplete available sources of pollen and nectar. Flying-foxes can be highly destructive to small rainforest stands (as at Maclean and Wingham Brush Nature Reserve, northern New South Wales) (Plate 142), destroying the canopy, facilitating the invasion of smothering alien plants, and so driving the breakdown of plant reproduction networks. In similar fashion, some native plants can pose a threat to pollination networks, and the floristic composition and structure of stands more generally; for example the rampant vine *Cissus antarctica* (Vitaceae) and the small rainforest tree *Pittosporum undulatum* (Pittosporaceae). *Pittosporum undulatum* has a wide distribution extending from eastern Victoria north to Kaputar National Park, Kroombit Tops and Carnarvon National Park (Harden *et al.* 2006), but is now naturalised beyond this range; and is capable of vigorously invading remnant native bushland and small rainforest stands. *Cissus antarctica* is widespread and can be highly invasive and persistent in mesic forests that have been disturbed by logging, storm damage and fire (Plates 143, 148).

Alien and native plants in rainforests will compete to some degree for pollinators from the same resident pollinator network, and this can cause disruption to native plant–animal interactions. Shade is a major factor that usually limits exotic plant invasion of rainforest, consequently physical disturbance, such as the structural

damage caused by periodic storms, extreme penetrating fire events, logging or natural tree fall can promote invasions by exotic plants that respond to increased light levels on the forest floor (Plate 145). However, alien plants which are able to develop shade tolerance, as Godoy *et al.* (2011) noted for invasive *Prunella vulgaris* in Neotropical temperate evergreen forest, and as *Lantana camara* and various Asparagaceae (Plate 147) exhibit in some eastern Australian forests, pose a potential threat to seemingly undisturbed rainforests. The small, often narrow, size of floodplain and littoral rainforest remnants (subject to high light levels) makes them especially vulnerable to invasion by a large suite of aggressive and persistent exotic plants (e.g. *Asparagus aethiopicus* [Asparagaceae], *Chrysanthemoides monilifera* [Asteraceae], *Gloriosa superba* [Colchicaceae], *Anredera cordifolia* [Basellaceae], *Dolichandra unguis-cati* [Bignoniaceae], *Tradescantia fluminensis* [Commelinaceae]). Vulnerability to invasion, especially by *Chrysanthemoides monilifera*, is exacerbated by fire. Small hinterland rainforests (e.g. narrow lowland riparian stands) are vulnerable to canopy invasion and replacement by profusely seeding *Cinnamomum camphora* (Lauraceae) and *Ligustrum lucidum* (Oleaceae). Their seeds are dispersed by native birds, as are those of the highly invasive *Hedychium gardnerianum* (Zingiberaceae), a large clumping herb native of India and increasingly naturalised in several hinterland mesic forests (and capable of establishing in fully shaded rainforest understoreys). Although it has been argued that *Cinnamomum camphora* should be retained, at least as an interim measure, during rainforest restoration projects (Neilan *et al.* 2006), trees can live for centuries, over which time they can suppress native plant recruits (Kanowski *et al.* 2009).

Periodic cyclones in Tropical Queensland (e.g. Turton 2008) result in extensive foliage and crown loss and widespread tree mortality, which exposes individual stands to alien plant invasion, but the broad ecological consequences (including impacts on pollination services) of invasion following cyclone, storm and fire damage remain poorly understood. In a study of the dynamics of invasive plant recruitment in tropical Queensland rainforest following Cyclone Larry (occurring in 2006), Murphy *et al.* (2008) found that invasive species may comprise a transient component of the regenerating flora in early regenerative stages, but with a persistent aggressive suite of species that can lead to the smothering of tree crowns and the forest floor. These can have long-term effects on the successional trajectory of the rainforest and its future composition and structure (Murphy *et al.* 2008), and though subsequent impacts on pre-existing ecological interactions can be predicted in broad terms, they cannot be foretold in detail.

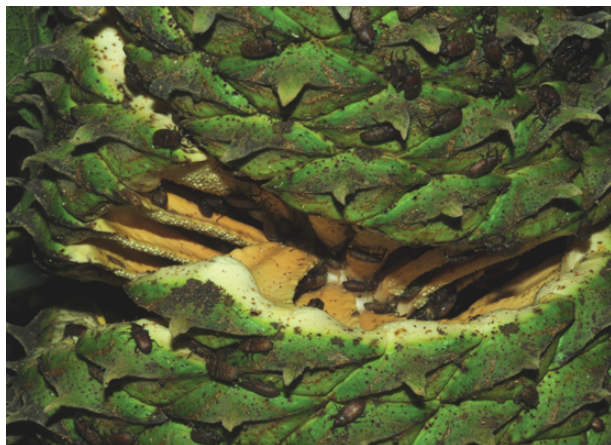
Small rainforest remnants, regrowth forests, and riparian forests have much lower levels of resistance to high energy winds due to patch size and edge effects. Topography can influence storm impacts (Negrón-Juárez *et al.* 2014), such that the nature and degree of damage can be patchy, ranging from severe to localised, but rainforests that are subject to frequent cyclonic events may suffer canopy lowering and changes to species composition; to which surviving native pollinators, and anthophilous animal species more generally, respond. In wet sclerophyll forest logging operations can result in heavy invasion of 'secondary' native vines (e.g. *Cissus antarctica* [Vitaceae]) which suppress regeneration of prior species composition and forest structure (Plates 143, 144). Although this may not result in a gross reduction in floral resources, a reduction in the diversity of flowering species can result in temporal gaps in the seasonal sequence of available nectar and pollen, to which the anthophilous fauna might have otherwise attended.

Invasive pathogens, such as *Phytophthora cinnamoni* (e.g. invasive in the Barrington Tops, northern New South Wales), *Chalara australis* (which threatens *Nothofagus cunninghamii* in southern cool temperate rainforests [Packham *et al.* 2008]), and more recently the widely established Myrtle rust (*Austropuccinia psidii*), also constitute a high level threat to Australian plant species and plant communities; Myrtle rust posing a threat at the landscape scale. Myrtle rust is able to re-infect myrtaceous species in post-fire environments, with infections of coppicing rainforest Myrtaceae causing subsequent flow-on effects to species survival and community dynamics.





**Plate 1.** Emergent *Araucaria cunninghamii* (Araucariaceae)



**Plate 4.** Pollinating *Tranes* weevils on male *Lepidozamia peroffskyana* cone



**Plate 2.** *Macrozamia* sp. (Zamiaceae) in dry rainforest



**Plate 5.** *Dryophila moorei* (Alstroemeriaceae/Luzuriagaceae)



**Plate 3.** Female cone, *Lepidozamia peroffskyana* (Zamiaceae)



**Plate 6.** *Crinum pedunculatum* (Amaryllidaceae/Liliaceae)





Plate 7. *Euroschinus falcatus* (Anacardiaceae)



Plate 10. *Alocasia brisbanensis* (Araceae), showing spathe



Plate 8. *Melodinus australis* (Apocynaceae)



Plate 11. *Archontophoenix cunninghamiana* (Arecaceae) in subtropical rainforest



Plate 9. *Alocasia brisbanensis* (Araceae)



Plate 12. *Calamus caryotoides* (Arecaceae)