

Ecology of Australian Euphorbiaceae

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Species of Euphorbiaceae can be located in most terrestrial habitat types in subtropical and tropical Australia. Their occurrence in alpine and marine ecosystems is virtually nil and there is a much reduced presence in temperate habitats, apart from some exotic, weedy species. The following discussion is based on many generalizations and suppositions as the majority of species are little studied from an autecological or any other point of view.

Australian Euphorbiaceae comprise a diverse array of life-forms, *viz.* annual or perennial herbs, subshrubs, shrubs or trees, rarely twiners or lianes. Rootstocks are largely unknown, but are generally fibrous; subterranean tubers or caudices are not known. Stems vary from herbaceous to woody. Leaves may be mesophytic and well developed to xerophytic and greatly reduced, although true sclerophylly is absent. Indumentum is highly variable ranging from simple trichomes to lepidote scales and stinging hairs. Most perennial species are evergreen, although seasonal deciduousness is prevalent in many of the species from the 'Wet-Dry' tropics (e.g. species of *Antidesma*, *Croton*, *Flueggea*, *Margaritaria*), or there is a fleeting leaf drop and renewal associated with rain events (Forster 1997). True succulence, which is so prevalent in the family in Africa and Arabia, is nearly totally absent in the Australian taxa. Notable exceptions are the endemic *Euphorbia sarcostemmoides*, a stem succulent with scale leaves that occurs in a series of ancient and highly disjunct duricrust landforms in the arid zone (Forster 1987), the non-endemic *E. plumerioides* with succulent stems and annual mesophytic leaves that occurs in rocky coastal or subcoastal habitats (Forster 1991, 1994) and the fleshy short-lived perennials *E. boophthona*, *E. parvicaruncula*, *E. planiticola*, *E. stevenii* and *E. tannensis* (Hassall 1977; Forster 1992).

Landscape Ecology

Rainforest Species

Euphorbiaceae species (e.g. *Drypetes deplanchei*) may be common and dominant in some rainforest types in Australia, especially the drier communities (Webb *et al.* 1984; Williams *et al.* 1984; Forster *et al.* 1991; Russell-Smith *et al.* 1993, 1998; Fensham 1995, 1996; Smith *et al.* 2005). Their presence in rainforests is ancient, probably dating to the early Paleocene (61.0 Ma) (Davis *et al.* 2005). Broadly speaking, most of the rainforest species are shrubs or trees (with a handful of twiners and lianes) and are either short-lived pioneers (e.g. *Aleurites*, *Breynia*, *Claoxylon*, *Glochidion*, *Homolanthus*, *Macaranga*, *Mallotus*) colonizing gaps and other areas of disturbance (Webb *et al.* 1972; Slik *et al.* 2003), or in comparison long lived inhabitants (e.g. *Austrobuxus*, *Choriceras*, *Croton*, *Dissiliaria*, *Whyanbeelia*) of mature phase forests. Epiphytic species do not occur in Australia nor are found elsewhere (Benzing 1990). Many of the pioneer species are prevalent on the rainforest margin or as isolated examples of dispersal in other habitats (cf. Toh *et al.* 1999) and although they are quick to colonise disturbed areas, there is limited ability to regrow after further disturbance, e.g. clearing or fire (Benson & McDougall 1995; Marrinan *et al.* 2005). In comparison many of the 'mature phase' species are capable of suckering from rootstocks after gross disturbance (Webb *et al.* 1972; Russell-Smith 1996; Adam & Williams 2001; Forster, pers.obs.).

Although many species are prevalent in the understorey and midstorey (e.g. species of *Actephila*, *Bridelia*, *Cleistanthus*, *Codiaeum*, *Croton*, *Dimorphocalyx*, *Fontainea*), others form large canopy trees (e.g. *Austrobuxus*, *Bischofia*, *Dissiliaria*, *Rockinghamia*, *Whyanbeelia*). The distribution of particular species is often clumped (e.g. *Actephila*, *Baloghia*, *Cleistanthus*, *Dissiliaria*, *Sankowskya*, *Whyanbeelia*) indicating dispersal-limited distribution (Jayasuriya & Pemadasa 1983; Primack & Miao 1992; Fensham 1995, 1996; Russell-Smith 1996; Forster 2005, unpubl. obs.). Undoubtedly the most common and widespread species is *Drypetes deplanchei* followed by *Croton insularis* (Forster 1996, 2003).

Heathland/Shrubland/Woodland/Open Forest Species

The majority of the high diversity of herbaceous *Euphorbia*, *Phyllanthus* and *Synostemon* species are found in eucalypt or acacia dominated communities where fire and droughts are of irregular occurrence (Hassall 1982; Hunter 2005). A suite of shrubs or small trees (e.g. *Adriana*, *Bridelia*, *Croton*, *Excoecaria*, *Flueggea*) may be locally abundant. Changing management regimes (fire, grazing) may favour certain Euphorbiaceae (*Excoecaria parvifolia*) to colonise via seed dispersal, areas previously dominated by grassland (Sharp & Whittaker 2003); others (e.g. *Breynia* spp., *Drypetes deplanchei*, *Macaranga subdentata*) are able to resprout from rootstocks (Benson & McDougall 1995; Russell-Smith 1996; Russell-Smith *et al.* 1998; Marrinan *et al.* 2005). Some geophytic species (*Phyllanthus*, *Synostemon*) may

be prevalent early in the monsoonal season or after fire (Russell-Smith *et al.* 2002).

Fire plays a pivotal role in the ecology of some euphorbs and many herbaceous species are stimulated to germinate with a post-fire peak in individual numbers (e.g. *Euphorbia tannensis*, *Poranthera microphylla*, *Monotaxis macrophylla*) (Specht *et al.* 1958; Purdie & Slater 1976; Purdie 1977; Warcup 1980; Russell-Smith *et al.* 2002; Hill & French 2003; Forster, unpubl. obs.). Many of these species are able to persist in the soil seed bank for many years, only appearing after major disturbance. Fires also kill many adult plants of woody euphorbs such as *Bertya* and *Ricinocarpos* species with the populations recruiting via the soil seed bank or resprouting from root-stocks (Benson & McDougall 1995). Some species such as *Bertya ernestiana* are endangered due to too frequent burning of the habitat.

Mangrove Species

Two species of Euphorbiaceae, namely *Excoecaria agallocha* and *E. ovalis* occur in this community type and may be locally abundant. They usually occur towards the back of the mangrove ecosystem and have no special root adaptations to deal with the inundated environment (Tomlinson 1986).

Reproductive Ecology

Pollination

Little has been recorded about the pollinators or pollination systems of Euphorbiaceae in Australia and much has to be inferred from studies of related or morphologically similar taxa from elsewhere. All Euphorbiaceae have unisexual flowers, many species are monocious (especially in Australian rainforests, *cf.* Gross 2005), lesser numbers dioecious. Some species are probably functionally androdioecious or andromonoecious, i.e. bearing both hermaphrodite and staminate flowers (or cyathia in the case of Euphorbioideae) (Charlesworth 1984; Thomson *et al.* 1989; Kiflawi 2000; Narbona *et al.* 2002; Narbona *et al.* 2005b), perhaps forming a transitional state between dioecy and monoecy and promoting outcrossing. Some of these species may initially appear to be dioecious; however, they are actually gender diphasic, i.e. the plants 'change sex' (Lloyd 1982; Korpelainen 1998; Richardson & Clay 2001), with many of the 'male' plants later having both male and female flowers.

Casual observations of the flowers of many monoecious euphorbs indicate that the female flowers towards the base of the inflorescence open first, followed by the males towards the top. The ratio between male and female may be related to the age of the plant (Shaanker & Ganeshiah 1984); however, there is often a preponderance of male flowers (Solomon Raju & Ezradanam 2002), especially if the plants have been subjected to drought (Forster 2003). This pattern of non-synchronous floral development (or temporal dioecy) seems to be widespread in monoecious Euphorbiaceae and tends to favour outcrossing (Bawa *et al.* 1982; Freitas *et al.* 2001). In many instances, however, there are both male and female flowers open at the same time in the one inflorescence, and certainly on the one individual.

Many species of Euphorbiaceae are pollinated by small invertebrates, others are anemophilous and some of the herbaceous species are self-compatible. Bats, primates and marsupials have been documented as the pollinators of *Mabea* spp. in South America (Torres de Assumpção 1981; Steiner 1983; Vieira *et al.* 1991; Vieira & de Carvalho-Okano 1996); however, there are no published observations of vertebrate pollination of Australian Euphorbiaceae. The flowers of many Euphorbiaceae seem to be most suitable for bee or wasp (Hymenoptera) pollination (Endress 1994), e.g. *Antidesma* spp., *Bridelia* spp., *Drypetes deplanchei*, *Excoecaria agallocha* (Tomlinson 1986; Williams & Adam 1997; Hansman 2001). Other insects such as various Coleoptera and Lepidoptera have been recorded as pollinators of the Argentinian *Croton sarcopetalus* (Freitas *et al.* 2000), and it is not unreasonable to predict that such broad guilds of insects would also visit the flowers of Australian species, especially those with flowers suited for generalist pollinators (Hansman 2001). The presence of foetid smelling flowers in species such as *Actephila foetida* and *A. traceyi* may indicate that flies are the primary pollinators and this group of insects are sometimes the only pollinators in dioecious species (Bawa 1980; Charlesworth 1993; Renner & Feil 1993). Complex pollination mutualisms exist between some insects and Euphorbiaceae species with minute thrips pollinating flowers of *Macaranga* (Moog *et al.* 2002) in Malesia and moths pollinating flowers of *Breynia*, *Glochidion* and *Phyllanthus* in New Caledonia (Kato *et al.* 2003; Kawakita & Kato 2004; Kawakita *et al.* 2004). Similar pollination systems are likely for related or morphologically comparable Australian species. Although the possibility of wind pollination for some of the rainforest species with light, unsculptured pollen (Lock & Hall 1982; Williams & Adam 1999; Hansman 2001) cannot be discounted without experimentation, it is perhaps less likely due to the occurrence of many euphorbs in rainforest understorey where wind speed is greatly reduced (Turner 2001). *Mercurialis annua*, a weed of open situations is considered anemophilous (Lisci *et al.* 1994) and

possesses light, unsculptured pollen. This may well be the case for many of the small herbaceous species of *Euphorbia* and *Phyllanthus*, although it is perhaps more likely that they are mainly self-pollinating with incidental insect pollination by unspecialised visitors (Ehrenfeld 1976). Some rainforest margin species such as *Croton* spp., *Macaranga* spp. and *Mallotus* spp. could also be wind pollinated. Observations of flowering *Beryta ingramii* and *B. rosmarinifolia* indicated no or only incidental insect visitation, inferring that wind pollination was the norm (Scott & Gross 2004).

The major reward for pollinator attention is probably both pollen and nectar, and the small male flowers of many Euphorbiaceae perfectly fit what Endress (1994) termed as ‘bowl’ flowers that are mainly visited by diverse insects with short proboscises. Small ants are also common visitors to such flowers, and although they probably mainly act as pollen and nectar robbers, it is possible that they are more than incidental in pollination efficiency. Interestingly enough, for the herbaceous *Croton suberosus* H. B. & K. from Mexico, it has been found that floral nectar seems mainly to attract ants that act as herbivore predators, rather than as pollinators (Dominguez *et al.* 1989). In certain species of *Dalechampia*, the floral visitors (bees) gather resins that they use in nest construction (Armbruster 1984).

Many euphorbs when cultivated in areas well removed from their natural habitats still produce fruit with fertile seed and this has been dubiously interpreted as indicating that generalist pollination by opportunistic insects is occurring (Tucker & Simmons 2004). The possibility of apomixis or agamospermy (i.e. “the development of seeds without preceding fertilization”), as found for *Alchornea ilicifolia* (Smith 1841; Baillon 1866; Endress 1994; Bicknell & Koltunow 2004) is more likely, but needs to be experimentally confirmed for other species. Agamospermous reproduction may also explain the apparent morphological uniformity of plants within any given population of some euphorbs (e.g. *Actephila*, Forster 2005) resulting from long-term recruitment of genetically similar individuals.

Dispersal

Australian Euphorbiaceae produce two main types of fruit: explosively dehiscent ballistochores and fleshy, indehiscent drupes. In the former the fruits are hard-walled capsules (schizocarps) (*Acalypha*, *Austrobuxus*, *Beryta*, *Beyeria*, *Choriceras*, *Croton*, *Dissiliaria*, *Euphorbia*, *Jatropha*, *Euphorbia*, *Macaranga*, *Mallotus*, *Microstachys*, *Phyllanthus*, *Ricinocarpos*, *Rockinghamia*, *Sankowskya*, *Shonia*, *Tragia*, *Wetria*, *Whyanbeelia*), usually splitting into three equal cocci (mericarps), each containing a single seed, as well as a residual central columella. The seeds in some species with this fruit type may be explosively and loudly flung for several metres, usually less than 10 (Narbona *et al.* 2005), thus being considered as short-distance dispersal (< 100 m) (Cain *et al.* 2000). Within the Euphorbiaceae *s.l.*, few ballistic dispersal distances are known (**Table 1**) and while incredible distances of 45 m for *Hura crepitans* were observed by Swaine & Beer (1977), it is unlikely that most species are ballistically dispersed much more than 10 m (Gómez & Espalader 1998b; Narbona *et al.* 2005); however, this is also dependent on the height of the plant and the amount of surrounding vegetation. Some authors have proposed that rain triggers this explosive separation (Griz & Machado 2001); however, it is unclear whether this is the case for Australian species and in many instances the seed is dispersed with increasing dryness of the habitat as found for *Euphorbia balsamifera* in the Canary Islands (Berg 1990) and *Hura crepitans* in West Africa (Swaine & Beer 1977). In some species the dehiscence is weakly produced and the capsule cocci often remain loosely attached to the columella (e.g. *Dissiliaria*) resulting in ‘drop and roll’ dispersal (Forster 1997). Seeds of many species with this fruit type have fleshy caruncles attached, thus making them attractive to birds and insects (especially ants). The species with indehiscent fruit are either ‘soft-fleshy’ (*Antidesma*, *Flueggea*) or ‘hard-fleshy’ (*Drypetes*) and usually coloured (dull to shiny, pink, red, yellow or white).

Dispersal in Euphorbiaceae with dry dehiscent fruits is labeled as autochorous (i.e. ballistic dispersal), often followed by diplochory in association with myrmecochory (Berg 1975a; Hughes & Westoby 1992; Esser 2003; Bebawi & Campbell 2004; Scott & Gross 2004). One introduced species (*Euphorbia paralias*) has seeds that are dispersed by ocean currents once they are liberated from the capsule (Heyligers 2002). Ants seek out elaiosomes (structures attractive to ants as food items; in the case of Euphorbiaceae these are fleshy caruncles formed from an integumentary protuberance) that are usually firm in texture and pale coloured with a role in water exchange between the seed and surrounding environment (Berg 1975a; Bianchini & Pacini 1996; Rodgers 1998) and may disperse or aggregate the attached seeds into niches more conducive to germination and establishment, especially after fire (Hughes & Westoby 1992). Certain ants may predate the entire seed, rather than just the caruncle (Espalader & Gómez 1996; Scott & Gross 2004). Removal of the caruncle also may result in more rapid germination due to the removal of inhibitory chemicals that induce dormancy (Lagôa & Pereira 1987; Pacini 1990; Pujol *et al.* 2002). As noted by Berg (1975a), the presence of elaiosomes (as a caruncle) is almost

universal in genera of Euphorbiaceae that are endemic to Australia; less so for genera with wider distributions. This prevalence may be an indication of the high diversity and significance of ants in Australian vegetation. Avian zoochory of the ripe, yet unexploded whole fruit, or of autochorously dispersed seeds of many Euphorbiaceae is also likely (e.g. *Glochidion ferdinandi*, *Mallotus philippensis*) given the dispersal and subsequent recruitment of seedlings under isolated trees away from the parent trees (Toh *et al.* 1999).

Table 1. Ballistic seed dispersal in some Euphorbiaceae *s.l.*

Plant	Mean seed Weight (mg)	Mean distance of ballistic seed dispersal	Maximum ballistic distance	Reference
<i>Cnidoscolus stimulosus</i>	54.5 ± 4.2	0.62 ± 0.35 m	1.15 m	Stamp & Lucas 1990
<i>Croton capitatus</i>	12.8 ± 1.5	n/a	c. 4–5 m	Garrison <i>et al.</i> 2000
<i>Croton priscus</i>	n/a	3.4 m	12 m	Passos & Ferreira 1996
<i>Dalechampia</i> spp.	n/a	1–6 m	n/a	Armbruster 1982
<i>Euphorbia balsamifera</i>	16.8	n/a	20 m	Berg 1990
<i>Euphorbia boetica</i>	5.0 ± 0.04	1.75 m	8 m	Narbona <i>et al.</i> 2005
<i>Euphorbia characias</i>	n/a	1.34 ± 0.09 m	9.4 m	Gómez & Espadaler 1998
<i>Euphorbia nicaeensis</i>	5.8 ± 0.05	1.48 m	5 m	Narbona <i>et al.</i> 2005
<i>Euphorbia paralias</i>	n/a	c. 2 m	n/a	Heyligers 2002
<i>Hura crepitans</i>	100.2	n/a	45 m	Swaine & Beer 1977
<i>Jatropha gossypifolia</i>	n/a	2.8 m	7.2 m	Bebawi & Campbell 2002
<i>Stillingia sylvatica</i>	40.2 ± 10.8	1.08 ± 0.83 m	3.00 m	Stamp & Lucas 1990

In those Euphorbiaceae where the fruit is indehiscent, dispersal is generally zoochorous (Esser 2003), with birds or mammals attracted to the fruit for the external pulp, the fleshy caruncles attached to the seeds or perhaps in some instances the seed itself. Large fruit that lack coloured, fleshy external pulp or conspicuous elaiosomes (e.g. *Aleurites*, *Omphalea*) are dispersed by mammals that gather the fallen fruit from the ground (Dennis 2002, 2003); however, the possibility that such fruit are more suited for dispersal by a now extinct megafauna as has been found for *Trewia nodiflora* and *Rhinoceras unicornis* in Nepal (Dinerstein & Wemmer 1988) cannot be discounted. Both *Aleurites* and *Omphalea* are also dispersed by water and comprise part of the ‘drift’ seed flora of the south-west Pacific (Smith 1992; Fortune-Hopkins 2000). Dispersal syndromes in Australian Euphorbiaceae are summarized in **Table 2**.

Table 2. Dispersal syndromes in Australian Euphorbiaceae (mainly taken from Esser 2003, but with corroboration for Australian or naturalised taxa).

Genus	Dispersal Syndrome	References
<i>Acalypha</i>	autochorous/diplochorous	Berg 1975a; Esser 2003
<i>Actephila</i>	autochorous/diplochorous	Esser 2003; Forster 2005
<i>Alchornea</i>	autochorous/diplochorous	Esser 2003
<i>Adriana</i>	autochorous/diplochorous	Berg 1975a
<i>Aleurites</i>	zoochorous; hydrochorous	Smith 1992; Fortune-Hopkins 2000; Esser 2003; Cooper & Cooper 2004
<i>Amperea</i>	autochorous/diplochorous	Berg 1975a
<i>Antidesma</i>	zoochorous	Esser 2003
<i>Austrobuxus</i>	autochorous/diplochorous	Esser 2003
<i>Baloghia</i>	autochorous/diplochorous	Robinet <i>et al.</i> 2003
<i>Bertya</i>	variable, primarily autochorous/diplochorous often subsequently zoochorous	Berg 1975a; Kentish & Westbrooke 1993; Scott & Gross 2004
<i>Beyeria</i>	variable, primarily autochorous/diplochorous often subsequently zoochorous	Berg 1975a; Kentish & Westbrooke 1993
<i>Bischofia</i>	zoochorous	Abe <i>et al.</i> 2002; Esser 2003; Yamashita <i>et al.</i> 2003; McConkey <i>et al.</i> 2004
<i>Breynia</i>	zoochorous	Crome 1975; Esser 2003
<i>Bridelia</i>	zoochorous	Esser 2003
<i>Calycopeplus</i>	autochorous/diplochorous	Berg 1975a
<i>Choriceras</i>	autochorous/diplochorous	Esser 2003
<i>Chrozophora</i>	zoochorous	Esser 2003
<i>Claoxylon</i>	zoochorous	Esser 2003
<i>Cleidion</i>	autochorous/diplochorous	Esser 2003

<i>Cleistanthus</i>	autochorous/diplochorous	Esser 2003
<i>Codiaeum</i>	autochorous/diplochorous	Esser 2003
<i>Croton</i>	autochorous/diplochorous	Berg 1975a; Esser 2003; Forster 2003
<i>Dimorphocalyx</i>	autochorous/diplochorous	Esser 2003
<i>Dissiliaria</i>	autochorous/diplochorous	Forster 1997
<i>Drypetes</i>	zoochorous	Esser 2003; McConkey <i>et al.</i> 2004
<i>Endospermum</i>	zoochorous	Esser 2003
<i>Euphorbia</i>	autochorous/diplochorous	Berg 1975a; Esser 2003
<i>Excoecaria</i>	variable: autochorous/diplochorous or zoochorous	Esser 2003; McConkey <i>et al.</i> 2004
<i>Flueggea</i>	zoochorous	Russell-Smith & Lee 1992; Esser 2003
<i>Fontainea</i>	zoochorous	Dennis 2002, 2003; Esser 2003
<i>Glochidion</i>	zoochorous	Crome 1975; Esser 2003
<i>Hevea</i>	autochorous/diplochorous	
<i>Homolanthus</i>	zoochorous	Crome 1975; Esser 2003
<i>Hylandia</i>	zoochorous	Cooper & Cooper 2004
<i>Jatropha</i>	autochorous/diplochorous	Esser 2003; Bebawi & Campbell 2004
<i>Macaranga</i>	variable; mainly zoochorous in Australia, but with some species autochorous/diplochorous	Esser 2003
<i>Mallotus</i>	variable; mainly zoochorous in Australia, but with some species autochorous/diplochorous	Esser 2003
<i>Manihot</i>	autochorous/diplochorous	
<i>Margaritaria</i>	zoochorous	Esser 2003
<i>Mercurialis</i>	autochorous/diplochorous	Lisci & Pacini 1997
<i>Micrantheum</i>	autochorous/diplochorous	Berg 1975a,b
<i>Micrococca</i>	zoochorous	Esser 2003
<i>Microstachys</i>	autochorous/diplochorous	Berg 1975a; Esser 2003
<i>Monotaxis</i>	autochorous/diplochorous	Berg 1975a
<i>Neoroepera</i>	autochorous/diplochorous	
<i>Notoleptopus</i>	autochorous/diplochorous	Esser 2003
<i>Omphalea</i>	variable; probably zoochorous in Australia; also hydrochorous	Fortune-Hopkins 2000; Dennis 2003; Esser 2003
<i>Pedilanthus</i>	autochorous/diplochorous	
<i>Petalostigma</i>	zoochorous followed by autochorous/diplochorous	Clifford & Monteith 1989
<i>Phyllanthus</i>	variable	Esser 2003
<i>Pimelodendron</i>	zoochorous	Esser 2003
<i>Poranthera</i>	autochorous/diplochorous	Rodgers 1998
<i>Pseudanthus</i>	autochorous/diplochorous	Berg 1975a
<i>Ricinocarpos</i>	autochorous/diplochorous	Berg 1975a
<i>Ricinus</i>	autochorous/diplochorous	Bianchi & Pacini 1996
<i>Synostemon</i>	variable: autochorous/diplochorous or zoochorous	Esser 2003
<i>Shonia</i>	autochorous/diplochorous	
<i>Stachystemon</i>	autochorous/diplochorous	Berg 1975a
<i>Suregada</i>	zoochorous	Esser 2003
<i>Synadenium</i>	autochorous/diplochorous	
<i>Tragia</i>	autochorous/diplochorous	Esser 2003
<i>Triadica</i>	zoochorous	Renne <i>et al.</i> 2002
<i>Trigonostemon</i>	autochorous/diplochorous	Esser 2003
<i>Vernicia</i>	autochorous/diplochorous	Esser 2003
<i>Wetria</i>	autochorous/diplochorous; possibly zoochorous	Esser 2003
<i>Whyanbeelia</i>	unknown; probably autochorous/diplochorous	

Mutualisms, Host Dependencies and Opportunistic exploitation

Dependent obligate pollination mutualisms between moths or thrips and a number of euphorbs in the subfamily Phyllanthoideae have been documented for species of *Breynia*, *Glochidion*, *Macaranga* and *Phyllanthus* outside of Australia (Moog *et al.* 2002; Kato *et al.* 2003; Kawakita & Kato 2004; Kawakita *et al.* 2004). In these mutualisms pollination is mediated by the insect species that also undertakes other parts of its lifecycle in close association with the plant.

Various Lepidoptera (butterflies and moths) utilise a range of Euphorbiaceous plants as hosts for larval development (**Table 3**). While some species (e.g. *Achaea janata*; *Syntherata janetta*) are polyphagous, feeding on a wide range of species, others are highly specific (e.g. *Alcides zodiaca*) and totally dependent on the host plants to complete their lifecycle. Specific chemicals (alkaloids with potential insecticidal properties) in some of the hosts (e.g. *Endospermum*, *Omphalea*) are accumulated in

Table 3. Lepidopteran host dependencies on Australian Euphorbiaceae.

Euphorbiaceae species	Lepidopteran species	Reference
<i>Acalypha wilkesiana</i>	<i>Achaea janata</i>	Common 1990
<i>Adriana hookeri</i>	<i>Theclinessthes albocincta</i>	Sibatani & Grund 1978
<i>Adriana quadripartita</i>	<i>Theclinessthes albocincta</i> ; <i>T. hesperia</i>	Sibatani & Grund 1978
<i>Bertya mitchellii</i>	<i>Chloroclystis destructata</i>	Common 1990
<i>Breynia cernua</i>	<i>Eurema hecabe</i>	Manski 1960
<i>Breynia oblongifolia</i>	(1) <i>Eurema hecabe</i> ; (2) <i>Parallelia solomonensis papuana</i> ; <i>Parallelia frontina</i> ; <i>Phyllocnistis diaugella</i>	(1) Waterhouse 1923; (2) Common 1990
<i>Bridelia insulana</i>	<i>Neptis praslini staudingereana</i>	Muller 1998
<i>Bridelia tomentosa</i>	<i>Anthene lycaenoides</i>	Meyer 1996
<i>Drypetes deplanchei</i>	<i>Appias paulina</i>	Smithers 1970
<i>Endospermum myrmecophilum</i>	<i>Alcides zodiaca</i> ; <i>Lyssa patroclus</i>	Monteith & Wood 1987
<i>Euphorbia australis</i>	<i>Achaea janata</i>	Common 1990
<i>Euphorbia coghlanii</i>	<i>Achaea janata</i>	Common 1990
<i>Euphorbia drummondii</i>	<i>Achaea janata</i>	Common 1990
<i>Euphorbia hirta</i>	<i>Achaea janata</i>	Common 1990
<i>Euphorbia litticola</i>	<i>Achaea janata</i>	Common 1990
<i>Euphorbia shakoensis</i>	<i>Achaea janata</i>	Common 1990
<i>Cleistanthus cunninghamii</i>	<i>Echiomima mythica</i>	Common 1990
<i>Codiaeum variegatum</i>	<i>Achaea janata</i>	Common 1990
<i>Croton insularis</i>	<i>Chaetocneme beata</i>	De Baar in Braby 2000
<i>Excoecaria parvifolia</i>	<i>Achaea janata</i>	Common 1990
<i>Glochidion apodogynum</i>	<i>Hypochrysops ignita</i>	Meyer 1996
<i>Glochidion ferdinandi</i>	(1) <i>Arhopala micale</i> ; (2) <i>Candalides helenita</i> ; (3) <i>Aenetus eximius</i> ; <i>Caloptilia xanthopharella</i> ; <i>Caloptilia xanthopharella</i> ; <i>Coscinocera hercules</i> ; <i>Euthrausta holophaea</i> ; <i>Parotis atlitalis</i> ; <i>Stigmella phyllanthina</i> ; <i>Syntherata janetta</i>	(1) Manski 1960; (2) Valentine & Johnson 1988; (3) Common 1990
<i>Glochidion harveyanum</i>	<i>Hypochrysops miskini</i>	Valentine & Johnson 1989
<i>Glochidion lobocarpum</i>	<i>Anisodes turneri</i> ; <i>Hyalobathra filalis</i>	Common 1990
<i>Glochidion philippicum</i>	<i>Philiris nitens</i>	Sands & Fenner 1978
<i>Homolanthus novoguineensis</i>	<i>Coscinocera hercules</i>	Common (1990)
<i>Homolanthus nutans</i>	<i>Caloptilia octopunctata</i>	Common (1990)
<i>Macaranga inamoena</i>	<i>Megisba strongyle nigra</i>	Muller (1998)
<i>Macaranga mallotoides</i>	<i>Philiris nitens nitens</i> , <i>P. sappheira</i>	Ring & Olive (1997); Muller (1998)
<i>Macaranga tanarius</i>	<i>Philiris nitens nitens</i>	Muller (1998)
<i>Mallotus paniculatus</i>	<i>Megisba strongyle</i>	Lambkin & Samson (1989)
<i>Mallotus philippensis</i>	(1) <i>Megisba strongyle</i> ; (2) <i>Addaea subtessellata</i>	(1) Lambkin & Samson (1989); (2) Common (1990)
<i>Mallotus polyadenos</i>	<i>Chaetocneme critomedia</i>	G.A. Wood in Braby (2000)
<i>Notoleptopus decaisnei</i>	<i>Achaea janata</i>	Common (1990)
<i>Omphalea celata</i>	<i>Alcides zodiaca</i>	Forster & Sankowsky (1995)
<i>Omphalea queenslandiae</i>	<i>Alcides zodiaca</i>	Coleman & Monteith (1981)
<i>Petalostigma pubescens</i>	<i>Hypochrysops apelles</i>	Sands (1986)
<i>Petalostigma quadriloculare</i>	<i>Syntherata janetta</i>	Common (1990)
<i>Phyllanthus maderaspatanus</i>	<i>Grammodes ocellata</i>	Common (1990)
<i>Phyllanthus tenellus</i>	<i>Eurema hecabe</i>	Manski (1960)
<i>Ricinus communis</i>	<i>Achaea janata</i> ; <i>Amsacta marginata</i>	Common (1990)

the larval predators and retained to adulthood (Kite *et al.* 1991, 1997; Lees & Smith 1991). In some instances isolated occurrences of a particular host (*viz.* *Omphalea celata*) are accompanied by the disjunct presence of the dependent insect (Forster & Sankowsky 1995). Significant pests (e.g. *Heliothis armigera*) of economic crops such as cotton may use native, naturalized or cultivated Euphorbiaceae (*Acalypha*, *Notoleptopus*, *Ricinus*) as alternative hosts (Zalucki *et al.* 1986).

Ant-plant mutualisms such as have been documented for *Macaranga* species in south-east Asia and Malesia (Quek *et al.* 2004), have not been discovered in the Australian species. The stems of *Endospermum myrmecophilum* are often filled with colonies of ants (Monteith & Wood 1987). These ants may actively reduce Lepidopteran predation to the plants (Letourneau & Barbosa 1999).

Many Australian Euphorbiaceae (*Adriana*, *Homolanthus*, *Macaranga*, *Mallotus*, *Rockinghamia*) possess extrafloral nectaries that secrete sugary nectars that are utilized by a wide variety of insects, particularly ants (Mackay & Whalen 1991; Blüthgen & Reinfenrath 2003). Ants will often strongly defend these sources of nectar (Mackay & Whalen 1996, 1998); however, while the use is regular it can only be interpreted as opportunistic.

The seeds and fruits of some Australian Euphorbiaceae are recorded as being used as food by both vertebrate and invertebrate animals (Table 4). Large fruit crops of some rainforest species may form significant parts of the diet of birds over short or long periods (Crome 1975), whereas harvesting of the caruncles (elaiosomes) attached to the seeds of other species is important for many ants.

Table 4. Use of Euphorbiaceae diaspores as food by animals in Australia.

Euphorbiaceae species	Diaspore Used/Recorded	Dispersal Agent	Reference
<i>Actephila lindleyi</i>	fruit	birds: Brown Cuckoo-dove	Floyd 1989
<i>Aleurites moluccana</i>	seeds	mammals: Musky Rat-kangaroo; Giant White-tailed Rat	Finkelstein & Grubb 2002; Cooper & Cooper 2004
<i>Aleurites rockinghamensis</i>	seeds	mammals: Giant White-tailed Rat	Finkelstein & Grubb 2002; Cooper & Cooper 2004
<i>Antidesma erostre</i>	fruit	birds: Cassowary; Spotted Cat-bird	Cooper & Cooper 2004
<i>Baloghia inophylla</i>	fruit	birds: King Parrot; Crimson Rosella	Cooper & Cooper 2004
<i>Bertya mitchellii</i>	fruit	birds: Mallee Fowl	Kentish & Westbrooke 1993
<i>Beyeria opaca</i>	fruit	birds: Mallee Fowl	Kentish & Westbrooke 1993
<i>Breynia cernua</i>	fruit	birds: pigeons; doves; Lewin's Honeyeater	Cooper & Cooper 2004
<i>Breynia oblongifolia</i>	fruit	birds: Brown Cuckoo-dove	Cooper & Cooper 2004
<i>Bridelia insulana</i>	fruit	birds: Black Butcherbird; Metallic Starling; Figbird	Cooper & Cooper 2004
<i>Claoxylon australe</i>	seeds	birds: Brown Cuckoo-dove	Innis 1989
<i>Claoxylon hillii</i>	seeds	birds: Eclectus Parrot	Cooper & Cooper 2004
<i>Claoxylon tenerifolium</i>	fruit	birds: Brown Cuckoo-dove	Cooper & Cooper 2004
<i>Cleistanthus cunninghamii</i>	fruit	birds: White-headed Pigeon; King Parrot	Cooper & Cooper 2004
<i>Croton verreauxii</i>	seeds	birds: "parrots"	Barker & Vestjens 1989, 1990
<i>Dissiliaria laxinervis</i>	fruit	birds: Eclectus Parrot	Cooper & Cooper 2004
<i>Drypetes acuminata</i>	fruit	birds: Golden Bowerbird	Cooper & Cooper 2004
<i>Drypetes deplanchei</i>	fruit	birds: Brown Cuckoo Dove; Lewin's Honeyeater; Regent Bowerbird; Satin Bowerbird; Topknot Pigeon; Wompoo Fruit-dove	Innis 1989; Cooper & Cooper 2004
<i>Endospermum medullosum</i>	fruit	birds: unspecified	Snow 1981
<i>Euphorbia dallachyana</i>	"foodplant"	birds: Stubble Quail	Barker & Vestjens 1989, 1990
<i>Flueggea leucopyros</i>	seeds	birds: Pale-headed Rosella	Cooper & Cooper 2004
<i>Flueggea virosa</i> subsp. <i>melanthesoides</i>	fruit flesh	birds: Yellow-spotted Honeyeater; Helmeted Friarbird	Cooper & Cooper 2004
<i>Fontainea picrosperma</i>	fruit	birds: Cassowary mammals: Musky Rat-kangaroo;	Finkelstein & Grubb 2002; Dennis 2002; Cooper &

		Giant White-tailed Rat	Cooper 2004
<i>Glochidion benthamianum</i>	fruit	birds: Double-eyed Fig-parrot; Lewin's Honeyeater	Cooper & Cooper 2004
<i>Glochidion ferdinandi</i>	fruit, seeds	birds: Topknot Pigeon; Brown Cuckoo-dove; Australian King Parrot; Figbird; Lewin's Honeyeater; Olive-backed Oriole; White-headed Pigeon	Crome 1975; Barker & Vestjens 1989, 1990; Floyd 1989
<i>Glochidion harveyanum</i>	fruit	birds: many species	Cooper & Cooper 2004
<i>Glochidion hylandii</i>	fruit	birds: Wompoo Fruit-doves	Cooper & Cooper 2004
<i>Glochidion philippicum</i>	fruit	birds: Metallic Starling; Yellow Honeyeater	Cooper & Cooper 2004
<i>Glochidion sumatranum</i>	fruit	birds: Double-eyed Fig-parrot; Victoria's Riflebird; Silvereye; Black Butcherbird; Lewin's Honeyeater	Cooper & Cooper 2004
<i>Homolanthus novoguineensis</i>	seeds	birds: Brown Pigeon; many species	Crome 1975; Cooper & Cooper 2004
<i>Homalanthus nutans</i>	Seeds	birds: Currawong; Brown Cuckoo-dove; Lewin's Honeyeater; Olive-backed Oriole; Silvereye; Satin Bowerbird; Catbird; Brown Pigeon	Buchanan 1989; Floyd 1989; Benson & McDougall 1995; Toh <i>et al.</i> 1999
<i>Hylandia dockrillii</i>	seeds	mammals: Giant White-tailed Rat	Finkelstein & Grubb 2002; Cooper & Cooper 2004
<i>Macaranga inamoena</i>	fruit	birds: King Parrot	Cooper & Cooper 2004
<i>Macaranga mallotoides</i>	fruit	birds: Pied Imperial-pigeon	Cooper & Cooper 2004
<i>Macaranga tanarius</i>	fruit	birds: Eclectus Parrot; Manucode; Figbird; Metallic Starling; Sulphur-crested Cockatoo; Magnificent Riflebird mammals: cuscus	Cooper & Cooper 2004
<i>Mallotus discolor</i>	fruit	birds: many species	Cooper & Cooper 2004
<i>Mallotus mollissimus</i>	fruit	birds: Cassowary; Figbird; Pied Currawong; Silvereye mammals: Giant White-tailed Rate	Cooper & Cooper 2004
<i>Mallotus philippensis</i>	fruit	birds: Figbird; Lewin's Honeyeater	Cooper & Cooper 2004
<i>Micrantheum ericoides</i>	seeds (caruncle)	insects: ants	Rice & Westoby 1981; Westoby <i>et al.</i> 1990; Rodgerson 1998
<i>Omphalea papuana</i>	fruit	birds: Cassowary	Cooper & Cooper 2004
<i>Omphalea queenslandiae</i>	fruit	mammals: Musky Rat-kangaroo	Dennis 2003; Cooper & Cooper 2004
<i>Petalostigma pubescens</i>	fruit seeds	birds: Emu insects: ants	Clifford & Monteith 1989
<i>Poranthera ericifolia</i>	seeds (caruncle)	insects: ants	Rodgerson 1998
<i>Phyllanthus calycinus</i>	seeds (caruncle)	insects: ants	Majer 1982
<i>Rockinghamia angustifolia</i>	fruit	birds: King Parrot	Cooper & Cooper 2004

Weeds

Approximately 10% of the Euphorbiaceae in Australia are naturalized with the genus *Euphorbia* contributing the greatest number of weed species. Most of these are herbaceous annuals or subshrubs, often prevalent in gardens or disturbed areas near habitation (e.g. *Euphorbia cyathophora*, *E. peplus*, *Phyllanthus* spp.). The success of these species can be attributed to several factors, namely pollination by wind or native insects, prolific seed production with dispersal by native insects, continuous reproduction and vegetative growth, high levels of recruitment, strong competitive ability and the ability to utilize a range of habitats (Snell & Burch 1975; Bebawi & Campbell 2004; Suzuki & Teranishi 2005; Suzuki & Ohnishi 2006).

A number of trees (e.g. *Hevea brasiliensis*, *Triadica sebiferum*) are sparingly naturalized in subtropical and tropical parts, the latter regarded as a serious invasive weed in other parts of the world (Barrilleaux & Grace 2000; Renne *et al.* 2002; Rogers & Siemann 2003; Lankau *et al.* 2004). One native

tree species (*Bischofia javanica*) is regarded as a serious weed outside of its natural range (Abe *et al.* 2002; Yamashita *et al.* 2003).

The castor oil plant (*Ricinus communis*) is a widespread and often locally abundant weed of disturbed areas over much of subtropical and tropical Australia, being able to persist in the soil seed bank for many years. The water dispersed *Euphorbia paralias* has seeds that are viable after seven years (Heyligers 2002). One species of *Jatropha* (*J. gossypifolia*) has literally explosively dispersed across the tropical Australian landscape and is the subject of an extensive and concerted, chemical, physical and biological control effort (Csurhes 1999; Bebawi & Campbell 2002a,b,c,d; Smith & Heard 2003; Bebawi & Campbell 2004).

The majority of the naturalized Euphorbiaceae do not currently pose a serious threat to natural ecosystems or agriculture in Australia with only *Croton setigerus*, *Euphorbia heterophylla*, *E. lathyris*, *E. terracina*, *Jatropha curcas*, *J. gossypifolia* and *Ricinus communis* considered as being noxious weeds (Parsons & Cuthbertson 1992). The potential for *Croton glandulosus*, *C. hirtus* and *Triadica sebiferum* to suddenly attain serious weed status cannot be discounted and the spread of these species should be closely monitored.

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