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Seed dormancy and germination in Myrtaceae: a palaeohistory, tribe, life cycle and geographical distribution perspective

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Review Paper

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Abstract

The Myrtaceae is the ninth largest angiosperm family with *c.* 6000 species, and it diverged from its closest relative the Vochysiaceae *c.* 100 Ma in southern Gondwana before the final separation of South America and Australia from Antarctica. The family has trees and shrubs and a few viny epiphytes but no herbs and mainly occurs in the tropics and in temperate regions with a Mediterranean climate. Numerous fleshy-fruited species and dry-fruited species have evolved in moist and seasonally dry (fire-prone) regions, respectively. Five kinds of fully developed embryos are found in Myrtaceae seeds, and at maturity seeds are either nondormant (ND) or have physiological dormancy, regardless of embryo morphology, kind of fruit produced, life form, habitat/vegetation region or tribe. Dormant seeds of fleshy-fruited species in wet habitats become ND and germinate at high temperatures. Dormant seeds of dry-fruited species in seasonally dry habitats become ND during the hot, dry season and germinate with the onset of the wet season; seeds germinate only at high temperatures or over a range of low to high temperatures, depending on the species. Seeds of fleshy-fruited species are animal-dispersed, and some Myrteae and Syzygieae are desiccation-sensitive and/or exhibit totipotency. Relatively few species form a persistent soil seed bank, but many dry-fruited species in fire-prone habitats form an aerial seed bank (serotiny). Heat and smoke from fires have a negative, neutral or positive effect on germination, depending on the species. Challenges for maintaining the high species richness of Myrtaceae include habitat destruction/fragmentation, pathogenic fungi and climate change, especially patterns of precipitation.

Introduction

The purpose of this review is to further explore the relationship between kinds of seed dormancy/germination, embryo morphology, life form, geographical distribution, habitats (vegetation regions on Earth) and phylogeny in angiosperm plant families. In particular, what do highly speciose, widely distributed families have in common, and how do they differ from families with a low number of species and a narrow geographical distribution? If a speciose family is widely distributed geographically, how diverse is it with regard to kinds of seed dormancy, life form and vegetation in regions in which it grows? These questions can be answered only after we have documented the kinds of seed dormancy in plant families that differ in number of species, habitats and geographical range. As a contribution to the broad objective of understanding the diversity of seed dormancy/germination in angiosperm plant families, we have reviewed available information on the Myrtaceae.

The Myrtaceae is highly speciose and is widely distributed in the Southern Hemisphere, and we have addressed nine specific questions. (1) What kinds of embryos do seeds of Myrtaceae have, and how are they distributed in the tribes of this family? (2) What kinds of seed dormancy, including nondormancy, are found in the Myrtaceae, and what is their occurrence in the tribes and life forms of this family? (3) What is the seed dormancy profile for Myrtaceae in the various vegetation regions where species of the family grow? (4) What environmental conditions are required for dormancy-break and germination of seeds? (5) How many tribes and species of Myrtaceae have desiccation-sensitive seeds? (6) In the totipotent (i.e. plantlet production from seed fragments) species of Myrtaceae, how many plantlets can be produced from a single seed? (7) How is the germination of Myrtaceae seeds affected by the heat and smoke of fires? (8) What is the relative importance of soil and aerial seed banks for Myrtaceae? (9) What are the major challenges involved in maintaining the high species richness of Myrtaceae in the future? However, before considering these questions, information will be provided on the general characteristics, palaeohistory and reproductive biology of Myrtaceae.

General characteristics of Myrtaceae

de Candolle (1828) divided the Myrtaceae into three tribes: Myrteae (with fleshy berries), Leptospermeae (dry dehiscent loculicidal capsules) and Chamelaucieae (dry indehiscent capsules). The genera *Heteropyxis* and *Psiloxylon* have been placed in the Heteropyxidaceae and Psiloxylaceae, respectively (e.g. Johnson and Briggs, 1984). However, Scott (1980) concluded that *Psiloxylon* belonged to the Myrtaceae, and Tobe and Raven (1987, 1990) found embryological evidence that *Heteropyxis* and *Psiloxylon* shared a single ancestor and suggested that the two genera should be included in the Myrtaceae, or close to it. Based on a *mat*K phylogeny that included 66 genera from all alliances and suballiances of core Myrtaceae, *Heteropyxis natalensis* and *Psiloxylon mauritianium*, Wilson et al. (2005) concluded that there are two subfamilies of Myrtaceae: Psiloxyloideae with tribes Heteropyxideae and Psiloxyleae and Myrtoideae with 15 tribes. Three additional tribes have been distinguished for the Myrtoideae, making a total of 18 in this subfamily (Wilson et al., 2022): Backhousieae, Chamelaucieae, Cloezieae, Eucalypteae, Kanieae, Leptospermeae, Lindsayomyrteae, Lophostemoneae, Melaleuceae, Metrosidereae, Myrteae, Osbornieae, Syncarpieae, Syzygieae, Tristanieae, Tristaniopsideae, Xanthomyrteae and Xanthostemoneae.

The Myrtaceae has 126 accepted genera and *c.* 6000 species (POWO; Landrum, 2021) and is the ninth-largest family of angiosperms (Govaerts et al., 2008). Fourteen tribes with 70 genera and *c.* 1700 species occur in Australia (Thornhill et al., 2015; Hardstaff et al., 2022). In contrast, species richness in the Neotropics is due mostly to the tribe Myrteae with 51 genera and *c.* 2500 species (Wilson et al., 2005; Lucas et al., 2007; Vasconcelos et al., 2017). At least 15 genera (*Archirhodomyrtus*, *Austromyrtus*, *Decaspermum*, *Gossia*, *Lenwebbia*, *Lithomyrtus*, *Lophomyrtus*, *Myrtella*, *Myrtuastrum*, *Neomyrtus*, *Octamyrtus*, *Pilidiostigma*, *Rhodamnia*, *Rhodomyrtus* and *Uromyrtus*) and *c.* 450 species of Myrteae occur outside the Neotropics, including Southeast Asia, northeastern Australia and Pacific Islands (Wilson, 2010). Outside the Neotropics, *Eugenia* is found in Africa, Madagascar and Mauritius (Snow, 2000; van der Merwe et al., 2005).

Various species of this family are used as ornamentals, medicines or food by humans (Hardstaff et al., 2022). Species in about 20 genera of Myrtaceae have been introduced into parts of the world beyond their natural range and are considered to be invasive (Mbobo et al., 2022). Both dry- (e.g. *Eucalyptus*) and fleshy- (e.g. *Psidium*) fruited species can be invasive, and fleshy-fruited species are more likely to be invasive on islands than dry-fruited species (Mbobo et al., 2022).

With the exception of *Myrtus* in northern Africa and the Mediterranean region of southern Europe (Wilson, 2010), the Myrtaceae is mostly a tropical family with high species richness in South America and Australia; it also occurs in Africa, Southeast Asia, India and on various Pacific Islands (Wilson, 2010; Thornhill et al., 2015). The family consists of trees, shrubs and a few subshrubs and strangling (viny) epiphytes (e.g. some species of *Metrosideros*). The monotypic shrub/small tree *Osbornia octodonta* is a mangrove, but it does not have pneumatophores. The leaves and stems of Myrtaceae have secretory cavities and lysigenous glands that produce ethereal oils, making plants (e.g. *Eucalyptus*) aromatic (Wilson, 2010).

Flowers of Myrtaceae are actinomorphic and (0-) 4 or 5 (-7)-merous with numerous (10–270) stamens that may be in fascicles opposite the petals. Flowers of *Eucalyptus* and *Corymbia* have an operculum (bud cover) that opens at anthesis and then falls from the flower (Mabberley, 2017). In some species, the stamen display attracts pollinators that collect pollen, but in other species, the thick and sweet petals are the attraction for pollinators. Flowers have a hypanthium, and the ovary may be superior, inferior or half-interior. There is one pistil, and the ovary is 1-6[-18] locular and carpellate. Placentation is axile, basal or parietal with 2–300(-500) ovules in the ovary (Wilson, 2010; Vasconcelos et al., 2019; Landrum, 2021).

Wilson (2010) described six general kinds of fruits/dispersal units for the Myrtaceae: (1) three-loculed soft fruit or berry developed from a superior ovary, *Psiloxylon*; (2) fruit with an inferior ovary and fleshy hypanthium, usually called a ‘berry’, Syzygieae; (3) drupe-like fruits with a thin fleshy covering over a mass of seeds with bony seed coats, *Myrtella* and *Lithomyrtus*; (4) indehiscent, leathery fruit, *Osbornia*; (5) dry, indehiscent fruits (‘nut-like’), *Chamelaucium*, *Corynanthera* and *Thryptomene* and (6) dry, dehiscent capsule, Leptospermeae and Melaleuceae. Seeds of Myrtaceae have little or no endosperm. The embryo in mature seeds is starchy or oily, fully developed (does not grow inside the seed prior to initiation of germination) and may be straight, coiled or folded (Zomlefer, 1994; Snow, 2000; Simpson, 2006; Wilson, 2010; Retamales et al., 2014; Ribeiro et al., 2021; Neto et al., 2022). The seed coat may be membranous, bony or somewhat leathery, depending on the tribe/genus (Corner, 1976; Landrum and Sharp, 1989; Retamales et al., 2014; Ribeiro et al., 2021; Sbais et al., 2022), but it does not have a palisade layer of Malpighian cells, i.e. specialized macrosclereids with a light line that are found in water-impermeable seeds (Corner, 1976; Werker, 1997). Seeds are 0.5–20 mm in length, depending on the species (Kirkbride et al., 2006).

Palaeohistory of Myrtaceae

Berger et al. (2016) reported that the Myrtales diverged from the Geraniales *c.* 124 Ma with a crown age of *c.* 116 Ma and that the Myrtales originated in West Gondwana (i.e. South America and Africa). However, Zhang et al. (2021) concluded that the Myrtales differentiated from the Geraniales *c.* 111.5 Ma with a crown age of *c.* 104.9 Ma. Laurasia had separated from Gondwana at 116–104.9 Ma, and the southern and central parts of South America and Africa separated between 135 to 105 and 119 to 105 Ma, respectively (McLoughlin, 2001). Based on data from studies on molecular phylogeny, the divergence of the Myrtaceae has been placed at 85 (Thornhill et al., 2015; Berger et al., 2016) to 80 Ma (Sytsma et al., 2004), which was before the final separation of South America from Antarctica and the separation of Australia from Antarctica *c.* 30 Ma with opening of the Drake Passage and Tasman Straight, respectively (Scotese and Golonka, 1992; Lawver and Gahagan, 2003; Scotese, 2021). However, Gonçalves et al. (2020) used data for 78 plastid protein-coding genes from 125 species representing 8 myrtalean families, including 8 genera and 51 species of Vochysiaceae, and fossils from 4 myrtalean families and estimated the crown age of Myrtales as 125.5 Ma. These authors placed the divergence of Myrtaceae from its closest relative the Vochysiaceae at *c.* 100 Ma with a stem age of 115 Ma. Based on these dates, the Myrtaceae diverged before the beginning of the separation of West Gondwana and South America.

Hill and Scriven (1995) and McLoughlin (2001) concluded that the disturbance caused by continental rifting may have provided new environmental conditions that promoted the diversification and dispersal of angiosperms, including the Myrtaceae. Jordan et al. (2016) thought that continental movements probably do not explain the increase in a number of terrestrial species but that changes in climates due to the movements of continents may have promoted increased speciation.

Thornhill et al. (2015) reported that Myrtaceae had a Gondwanan origin and that at least 6 of the 22 sister groups of this family included in their study may be a product of vicariance. Three of the 22 sister groups had evidence of overland dispersal events, while the other 13 had undergone transoceanic long-distance dispersal. Some researchers, e.g. Sytsma et al. (2004), have suggested that the origin of extant Myrtaceae was in Australasia since tribes such as Chamelaucieae, Eucalypteae, Leptospermeae, Lindsayomyrteae, Lophostemoneae, Melaleuceae and Xanthostemoneae are not found in South America or Africa. Thornhill et al. (2015) suggested that radiation of subfamily Myrtoideae occurred in the part of Gondwana that eventually became Australia. Berger et al. (2016) found a significant increase in diversification rates in Myrtaceae at *c.* 75 Ma, and speciation was 0.32 species Ma^{-1} and extinction 0.15 species Ma^{-1}. These authors determined that extensive radiation of Myrtaceae occurred in Australia from the Eocene into the Miocene, as the cooling and drying of the climate increased.

The crown age of subfamily Myrtoideae is *c.* 75 (Biffin et al., 2010) to 71.5 Ma (Thornhill et al., 2015), and it is *c.* 39.7 Ma for subfamily Psiloxyloideae (Thornhill et al., 2015). The divergence of *Heteropyxis* and *Psiloxylon* was *c.* 18 Ma (Berger et al., 2016). The crown age of the tribe Myrteae is 50.7 Ma (Thornhill et al., 2015), and its likely ancestral area is eastern Gondwana (Australia, New Caledonia, New Guinea and New Zealand) (Vasconcelos et al., 2017; Estrella et al., 2019). The divergence of Australasian and South American Myrteae was 43.9 Ma, after which much radiation occurred in both regions (Thornhill et al., 2015). Dispersal events between Australia and South America were possible in the Tertiary via Antarctica (Sytsma et al., 2004).

Fossilized parts of Myrtaceae plants of various ages have been found: flowers, Early Eocene, Argentina (Zamaloa et al., 2020); flowers and fruits, Eocene, Australia (Basinger et al., 2007); fruits and seeds, Eocene, British Columbia (Canada) and Palaeocene, North Dakota (USA) (Pigg et al., 1993; Manchester, 1999); leaves, Early Miocene, Australia (Tarran et al., 2018); leaves, Middle Eocene, Argentina (Panti, 2016); pollen, Cretaceous–Eocene, Sarawak (Malaysia) (Muller, 1968); pollen, Palaeogene–Neogene, Australia (Thornhill and Macphail, 2012); wood, Late Cretaceous–Early Tertiary, Antarctica (Poole et al., 2003) and wood, Late Cretaceous, India (Shukla et al., 2012). Fossils can be helpful in dating a phylogeny, but in the case of Myrteae differences in crown mode have resulted, depending on the kind of fossils considered. For example, Vasconcelos et al. (2017) using macrofossils and fossil pollen of Myrteae obtained a crown node for Myrteae of 65.55 Ma (Cretaceous–Palaeocene boundary) and 40.76 Ma (mid-late Eocene), respectively.

Radiation of Myrtaceae resulted in tribes with dry (capsular) fruits and those with fleshy fruits (Thornhill et al., 2015). Sytsma et al. (2004) found that fleshy, indehiscent fruits have originated at least three times in the Myrtaceae: Myrtoid group (Myrteae), *Acmena* group (Syzygieae) and *Osbornia* (Osbornieae). Compared with other lineages of Myrtaceae, tribes Syzygieae and Myrteae have had high rates of diversification, and the increased rate is associated with a shift from dry to fleshy fruits, which occurred independently in both tribes (Biffin et al., 2010). Nine of the 13 long-distance dispersal events proposed by Thornhill et al. (2015) involved taxa with fleshy fruits that could be dispersed by birds or bats. The presence of *Myrtus* in the Mediterranean Region perhaps is due to a long-distance dispersal event from East Gondwana to the Mediterranean via northern Africa during the Eocene (Thornhill et al., 2015).

Two large genera of Myrtaceae with dry (capsular) fruits are *Eucalyptus* (tribe Eucalypteae) and *Metrosideros* (tribe Metrosidereae). The Australasian eucalypt group includes *Allosyncarpia*, *Angophora*, *Arillastrum*, *Corymbia*, *Eucalyptus*, *Eucalyptopsis* and *Stockwellia* (Ladiges et al., 2003), with *Eucalyptus* being the largest with 712 species (POWO, 2024). Some species diversification of the *Eucalyptus* group is related to the cooling and drying of Australia and increased fire frequency (Ladiges et al., 2003). Crisp et al. (2011) reported that the sclerophyllous woodlands and savannas in Australia are dominated by species of *Eucalyptus*, many of which can resprout after fire. Using trait mapping on a dated phylogeny of Myrtaceae, these authors found that epicormic resprouting (from buds on the stem) in Myrtaceae was correlated with the development of fire-prone *Eucalyptus*-dominated habitats beginning 60–62 Ma.

Metrosideros with *c.* 60 species has high richness in Australia, New Caledonia and New Guinea, and it occurs on various Pacific islands such as Bonin, Fiji, Hawaii, Marquesas, New Zealand and Samoa (Wilson, 1996; Mabberley, 2017; Wright et al., 2021). *Metrosideros angustifolia* is the only species of Myrtaceae with capsular fruits in Africa (Sytsma et al., 2004; Mabberley, 2017), and *M. stipularis* is the only one in the New World (Sytsma et al., 2004). Seeds of *Metrosideros* are wind dispersed and can be lifted by wind speeds of 5–18 $\mathrm{km\,h}^{-1}$ (Wright et al., 2000). Thus, long-distance dispersal by wind may help account for the occurrence of this genus on widely separated Pacific islands.

Except for *M. stipularis* with dry fruits in Chile and Argentina, all Myrtaceae in the Neotropics belong to the tribe Myrteae and have fleshy fruits (Lucas et al., 2005, 2011; Wilson et al., 2005; Neto et al., 2022). Species diversification in Myrteae accelerated in the Neotropics compared with that of Myrteae in the Old World (Vasconcelos et al., 2017). The development of new embryo traits [e.g. large storage cotyledons or large leaf-like folded cotyledons) (Landrum, 1986; Landrum and Stevenson, 1986), polyploidy (Costa et al., 2017) and bony seed coats as in *Psidium* (Landrum and Stevenson, 1986)] have been suggested as new adaptive advantages associated with the increased rates of speciation of fleshy-fruited species.

Eugenia (Myrteae) with 1218 species (POWO) is the largest genus of Myrtaceae in the Neotropics (Mazine et al., 2018). After the ancestors of *Eugenia* migrated to southern South America, there was species diversification and dispersal to northern South America and the Caribbean region. The highest numbers of *Eugenia* species in South America are in the Atlantic Forest, Amazon Forest and Cerrado (Brazilian savanna) with 250, 91 and 74 species, respectively (Bünger et al., 2016). For *E. uniflora*, there are two evolutionary lineages in the Atlantic Forest, one in the north and another in the south (Turchetto-Zolet et al., 2016). *Eugenia* was dispersed from South America to Southeast Asia and Africa (van der Merwe et al., 2005; Lucas et al., 2007; Mazine et al., 2018). Two clades of *Eugenia* occur in southern Africa: one related to New World *Eugenia* and one related to Old World *Eugenia* (van der Merwe et al., 2005).

Using chloroplast and nuclear DNA sequences of the genus *Myrceugenia* (Myrteae), Murillo-A et al. (2016) determined that four lineages of the genus had diverged in South America by the early Miocene: three in Chile and one in southeastern Brazil. One Chilean lineage dispersed northward, and species became part of the subtropical montane flora; part of this lineage subsequently migrated southward. The other two Chilean lineages migrated south, and species became part of the cool-temperate rainy forest flora. The lineage in southeast Brazil diversified, with species now growing in the Paraná (*Araucaria angustifolia*) forest, tropical semi-deciduous forests, pampas and Cerrado.

Myrcia (Myrteae) is a large genus with *c.* 800 species, and it is divided into nine sections (Lima et al., 2021). Santos et al. (2017) concluded that *Myrcia* originated in the Montane Atlantic Forest of eastern Brazil in the late Eocene to early Miocene, after which some lineages diversified in the region. Other lineages migrated northward to the Amazon, Guyana and Caribbean regions, where diversification occurred. Also, lineages of *Myrcia* dispersed from the Atlantic Forest to regions with Cerrado, Yungas (subtropical cloud forest) and savanna vegetation, which was followed by diversification of new species (Amorim et al., 2019). In fact, *Myrcia* section *Aguava* seems to have originated in the Cerrado in the mid-Miocene (Lima et al., 2021).

Syzygium (Syzygieae) with 1231 species (POWO) is an Old World tropical/subtropical genus of trees or rarely shrubs, many of which are cultivated for their edible fleshy fruits (Uddin et al., 2022). Using data from molecular phylogenetic studies of *Syzygium*, Low et al. (2022) determined that the genus originated in Sahul, which was a land mass consisting of Australia, New Guinea and the Aru Islands that was connected due to low seas levels during the Last Glacial Maximum, e.g. *c.* 23,000–19,000 years ago (Clark and Mix, 2002). Migration of *Syzygium* from Sahul to the Sunda Islands (Brunei, East Timor, Indonesia, Malaysia and Singapore) has occurred at least 12 times, and each dispersal event was followed by species diversification. Dispersal and diversification have resulted in various species of *Syzygium* growing in the Northern Pacific, India and Africa (Low et al., 2022). These authors note that dispersal to a new region often has resulted in rapid speciation.

Background information on reproductive biology

Apomixis, polyploidy and polyembryony

The basic haploid chromosome number for the Myrtaceae is $n = 11$, and '… the vast majority of species are diploid with $2n = 22$ …', e.g. *Eucalyptus* spp. (Grattapaglia et al., 2012). However, there are triploid and tetraploid species of Myrtaceae (Costa and Forni-Martins, 2007). Polyploidy is frequent in fleshy-fruited genera such as *Eugenia*, *Myrcia*, *Psidium* (Costa and Forni-Martins, 2007; Neto et al., 2022) and *Syzygium* (Ouadi et al., 2023). Neto et al. (2022) concluded that hybridization and allopolyploidy have contributed to speciation in the Myrteae. Further, Silveira et al. (2016) found that polyploid individuals of *Eugenia* species grew in habitats with more adverse environmental conditions than diploid individuals.

Apomixis (agamospermy) has been reported for several species of Myrtaceae, and in *Syzygium cumini*, *S. jambos* and *S. paniculatum* asexual embryos are derived from the ovules, either the integuments or nucellus (Souza-Pérez and Speroni, 2017), i.e. adventitious embryony or sporophytic apomixis (van der Pijl, 1934; Gustafsson, 1947). In *S. jambos*, up to 13 embryos have been found in a seed (van der Pijl, 1934), and, in *S. cumini*, the number of embryos in a seed ranges from 1 to 7 (Rekha et al., 2020). In *Psidium cattleianum*, however, the asexual embryos are of diplosporic origin, i.e. the megaspore mother cell forms an embryo sac (Souza-Pérez and Speroni, 2017).

In some cases, both asexual (adventitious embryony) and sexual embryos are formed in the same seed (i.e. polyembryony of Ganeshaiah et al. (1991)), and they are in close proximity to each other (Koltunow, 1993). In seeds of *Syzygium paniculatum* (a rare polyploid rainforest tree in Australia) with two embryos, the sexual embryo is larger than the asexual one (Thurlby et al., 2012). However, if seeds of *S. paniculatum* have more than two embryos, the sexual embryo is not the largest one. The largest embryo in a seed (be it sexual or asexual) produces the largest seedling. Ganeshaiah et al. (1991) concluded that '… polyembryony is a maternal counter strategy to compensate for the loss in her fitness due to brood reduction caused by sibling rivalry'.

Flowering of fleshy-fruited species

The flowering season often begins with the onset of the rainy season, e.g. in Australia (Shapcott, 1998), Brazil (Torezan-Silingardi and Oliveira, 2004; Staggemeier et al., 2010; Vogado et al., 2016) and Venezuela (Zapata and Arroyo, 1978). *Rhodomyrtus tomentosa* grows in a subtropical monsoon climate in China and flowers in spring, which is at or near the beginning of the summer wet season (Wei et al., 2009). On Chiloé Island (Chile), the flowering of 13 species of Myrtaceae mostly occurred in summer, at which time the mean maximum temperature was 17.6°C (Smith-Ramírez et al., 1998). *Syzygium alternifolium* grows in tropical deciduous forests in India and flowers in the dry season (late winter and early spring) when temperatures are relatively low (Raju et al., 2014). Many species of *Eugenia* in South Africa flower in spring, but a few species flower in early summer; *E. verdoorniae* flowers in winter (Van Wyk and Lowrey, 1988). Drought can delay flowering causing some *Eugenia* species not to flower for one or more seasons. In the case of the rhizomatous *E. albanensis*, grassland fires promoted flowering (Van Wyk and Lowrey, 1988).

In the Atlantic Forest of eastern Brazil, 24 of 34 (70%) species of Myrtaceae flowered during the wet season; however, fruits were available for animals all year. At least one species of Myrtaceae had ripe fruits each month of the year, but, in some months, six or more species had ripe fruits (Staggemeier et al., 2010). Although most of the 13 taxa of Myrtaceae studied on Chiloé Island (Chile) flowered in summer, the duration of flowering varied from 2 to 5 months with a mean flowering time of 3.0 months (Smith-Ramírez et al., 1998). Further, one or more taxa had ripe fruits in each month of the year. In the sandy coastal plain in southeastern Brazil, at least one species of Myrtaceae also had ripe fruit at all times of the year (Oliveira et al., 2022).

Mass flowering occurs in various species of fleshy-fruited Myrtaceae, e.g. *Eugenia* spp. (Silva and Pinheiro, 2009), *Syzygium alternifolium* (Raju et al., 2014), *S. nervosum* (Shapcott, 1998) and *S. tierneyanum* (Hopper, 1980). Proença and Gibbs (1994) found four flowering strategies among eight sympatric species of Myrtaceae in central Brazil: *big bang*, synchronized mass flowering that is completed in about 1 week; *pulsed-bang*, synchronized flowering for about 1 week but with intervals of up to several days when no flowers open; *cornucopia*, many flowers produced per plant over a period of about 1 month and *steady state*, plants produce only a few flowers each day for about 1 month. Torezan-Silingardi and Oliveira (2004) found that plants of *Myrcia rostrata* flowered in pulses over a period of 13 weeks with many or a few flowers opening each day. Since flowering in the *M. rostrata* population was not well synchronized, this seems to be a modified steady-state pattern of flowering. Plants of *M. tomentosa* had a pulsed-bang flowering strategy with three synchronized flowering events each year.

Flowering of dry-fruited species

In Australia, most capsular-fruited species of Myrtaceae flower in spring, e.g. *Eucalyptus* (Birtchnell and Gibson, 2006), *Leptospermum* and *Melaleuca* (Beardsell et al., 1993), presumably in response to increased day length and/or temperature (Beardsell et al., 1993). However, the flowering of *Chamelaucium uncinatum* is promoted by short days and temperatures of 20–25°C resulting in flowering during winter (Dawson and King, 1993). In Victoria (Australia), the commencement of flowering for 28 species of *Eucalyptus* ranged from late winter to mid-autumn (Birtchnell and Gibson, 2006). The duration of the flowering period of these 28 species ranged between 1 and 8 months; thus, pollinators (e.g. bees) had a continuous supply of *Eucalyptus* flowers to visit throughout the year. The flowering frequencies of the 28 species were 1–7 years, but most species flowered every 2–4 years. Even in off-years for flowering of a species, a few individuals produced flowers.

Franklin et al. (2016) investigated the mass flowering of *Eucalyptus mediocris* in dry sclerophyll forests in northern Queensland (Australia). Trees flowered from late autumn to late summer, and most (75%) of them flowered heavily. Mass synchronized flowering occurred about once each decade, i.e. flowering occurred at irregular intervals with high seed production following each flowering event (masting). In contrast to *E. mediocris*, *Metrosideros excelsa* flowered profusely for about 2 weeks in summer (Schmidt-Adam et al., 1999, 2000), which was a big bang flowering strategy.

Pollinators of fleshy-fruited species

Flowers of fleshy-fruited species are pollinated by a diversity of organisms, and the reward for visitors may be nectar and/or pollen. If nectar is the reward, anthers and/or pollen grains smell sweet, e.g. *Eugenia* (VanWyk and Lowrey, 1988). *Eugenia* flowers are pollinated by insects, in particular bees (Hymenoptera) including the honeybee *Apis mellifera* (Zapata and Arroyo, 1978; Van Wyk and Lowrey, 1988; Silva and Pinheiro, 2009). Coleoptera and Diptera also visit the flowers of *Eugenia* (Silva and Pinheiro, 2009). In central Brazil, flowers of *Blepharocalyx salicifolia*, *Campomanesia pubescens*, *C. velutina*, *Eugenia dysenterica*, *Myrcia linearifolia*, *M. rhodosepala* (Proença and Gibbs, 1994), *M. rostrata*, *M. tomentosa* (Torezan-Silingardi and Oliveira, 2004), *Psidium firum* and *Siphoneugena densiflora* (Proença and Gibbs, 1994) have a sweet odour but no nectar, and pollen is the reward for flower visitors, which are various species of bees.

Fleshy-fruited species such as *Eugenia speciosa*, *Gomidesia schaueriana*, *Myrcia multiflora*, *M. racemosa*, *M. splendens* and *Psidium cattleianum* growing in the coastal plain forest of São Paulo state in Brazil begin to flower during the onset of the rainy season in spring (September–October) (Fidalgo and Kleinert, 2009). Flowers mainly were visited by bees, which either touched the anthers or buzzed (sonicated) them to collect pollen. The breeding system for *E. speciosa*, *G. schaueriana*, *M. racemosa* and *M. splendens* was xenogamy (required cross-pollination) and that of *M. multiflora* and *P. cattleianum* facultative xenogamy, i.e. adapted for cross-pollination by insects but if pollinators are not present selfing occurs.

Twelve of 16 species of insects (Apidae) that visited flowers of *Rhodomyrtus tomentosa* growing in southeastern China had pollen grains on their bodies, which became attached to the stigma when bees were allowed to visit virgin flowers (Wei et al., 2009). Pollen is the reward for insects visiting the flowers of *R. tomentosa*. The bees *Amegilla florea* and *Xylocopa nasalis* were the primary visitors/pollinators, and females were observed collecting pollen into the pollen basket on their hind legs.

Syzygium species have both pollen and nectar as rewards for pollinators, and flowers are visited by many insects. For example, in the southern Eastern Ghats of India, flowers of *S. alternifolium* were visited by 32 species of insects, including bees, beetles, butterflies, flies, hawkmoths and wasps, and by the African fat-tailed gecko (*Hemitheconyx caudicinctus*). All flower visitors collected nectar, while the bee *Trigona iridipennis* collected both nectar and pollen (Raju et al., 2014). In Zambia, Hymenoptera, Diptera, Coleoptera and Lepidoptera visited flowers of *S. guineense*, and nectar-collecting was the most common behaviour observed (Coppinger and Stanley, 2023). *Apis mellifera* was the most frequent flower visitor followed by *Braunsapis* bees, wasps and Diptera. Among the various invertebrate visitors to flowers of *S. cormiflorum* in the Australian rainforest, only the bodies of moths, ants, cockroaches, mites and a Staphylinid beetle had pollen on them (Crome and Irvine, 1986). In addition, four species of honeyeater birds (Meliphagidae) and two species of small blossom bats (Pteropodidae) were daily visitors of *S. cormiflorum* flowers; bats visited after dusk and before dawn. Flowers of *S. tierneyanum*, a species of northern Australian rainforests, were visited by 45 species of animals: bats, birds, bees (*Apis mellifera*), butterflies, hawkmoths and four other kinds of moths and honeyeaters (Hopper, 1980). Hawkmoths and honeyeaters were the most frequent native pollinators, and nectar was the reward for flower visitors. In the bird-pollinated flowers of *Acca sellowiana* and *Myrrhinium atropurpureum*, the reward is fleshy, sweet petals (Gressler et al., 2006).

Pollination of dry-fruited species

Pollinators include insects such as ants, bees, beetles, butterflies, flies, moths and wasps and vertebrates such as bats, birds and small marsupials (Beardsell et al., 1993; Carthew and Goldingay, 1997; Yates et al., 2005; Sharanya et al., 2014; Groom and Lamont, 2015; Chauhan et al., 2017). For Australian genera such as *Callistemon, Eucalyptus* and *Melaleuca*, bees, especially those in the family Colletidae, are important pollinators, and they collect both pollen and nectar (Beardsell et al., 1993). However, the honeybee (*Apis mellifera*) is sometimes the most common pollinator (Yates et al., 2005).

Bird pollinators include various species of honeyeaters, lorikeets (Ford et al., 1979), honeycreepers (Carpenter, 1976), sunbirds, parrots and oriental white-eyed sparrows (Chauhan et al., 2017). Phillips et al. (2010) concluded that bird pollination results in the movement of pollen for relatively long distances and could help reduce inbreeding compared with insect pollination. However, there was no significant difference in the fruit set of honeyeater-pollinated flowers of *Calothamnus quadrifus* growing in large *versus* small fragments of Kwongan Sand Plain (Mediterranean) shrubland in south-west Australia (Yates et al., 2007). Also, seed germination, seedling development and seedling mortality did not increase significantly with increased fragment size; mean seed germination across all population sizes ranged between 78 and 100%. However, the authors concluded that bird movement of pollen between population fragments would not prevent inbreeding depression from occurring in small fragments. Bats are also long-distance pollinators, and they can deposit large amounts of pollen with a variety of genotypes on flower stigmas (Fleming et al., 2009).

Breeding systems

Self-compatibility *versus* self-incompatibility is one of the first considerations in understanding the breeding system of a species, and many hand cross- and hand self-pollination experiments have been done with Myrtaceae. Much variation in self-compatibility and self-incompatibility is found in the Myrtaceae. Some species of *Eugenia* are self-compatible, but others are self-incompatible (Proença and Gibbs, 1994; Silva and Pinheiro, 2009). *Blepharocalyx salicifolius*, *Campomanesia velutina* and *Siphoneugenia densiflora* are strictly self-incompatible; *Myrcia linearifolia* and *C. pubescens* mostly self-incompatible but with low selfing; and *Eucalyptus argutifolia* (Kennington and James, 1997), *Eugenia dysenterica*, *M. rhodosepala*, *Psidium firmum*, *Syzygium guineense* (Coppinger and Stanley, 2023) and *S. nervosum* (Shapcott, 1998) self-compatible (Proença and Gibbs, 1994). *Kunzea pomifera* is mostly self-compatible, and one barrier to self-fertilization is that pollen tubes do not grow into the ovules (Page et al., 2010). Not only is *E. argutifolia* self-compatible, but Kennington and James (1997) concluded that geitonogamous pollination (i.e. pollen from other flowers on the same plant) was probably more common than outcrossing. High seed abortion in the late stages of development prevents the occurrence of high homozygosity in the population.

Some trees of *Metrosideros excelsa* are self-compatible and others self-incompatible (Schmidt-Adam et al., 1999). Seed germination was 98.4% for fertile seeds of *M. excelsa* from all pollination treatments; thus, no inbreeding depression was detected. In Hawaii (USA), flowers on red-flowered trees of *M. collina* are partly self-incompatible, but those on yellow-flowered trees are totally self-compatible (Carpenter, 1976). In New Zealand, the endangered *M. bartletti* is self-incompatible and cross-pollination is required for seed set (van der Walt et al., 2022).

Fruit set and seed formation in *Myrcianthus coquimbensis* did not differ significantly between outcrossed and selfed flowers (García-Guzmán et al., 2020). The germination of seeds from outcrossed, selfed and control flowers of *Myrtus communis* was 79, 52 and 45%, respectively, i.e. no inbreeding depression (González-Varo and Traveset, 2010). These authors found that outcrossing enhanced the number of seeds per fruit, seed germination and seedling growth, but it did not enhance fruit set. Furthermore, the authors acknowledged that their sample size of 10 mother plants is very modest with low statistical power, and one of the main conclusions is that pollen limitation may be genotype-dependent. However, the mass of seeds from selfed flowers *of M. communis* was significantly higher than that of seeds from outcrossed flowers, suggesting a trade-off between seed number and mean seed mass within a fruit.

Fruit set for flowers of *Campomanesia pubescens* that were bagged, hand self-pollinated, cross-pollinated or nonbagged (natural pollination) was 0, 40.3, 65.7 and 17.8%, respectively, and germination was 0, 78.5, 100.0 and 87.7%, respectively (Rodrigues et al., 2017). Seeds from hand cross-pollinated flowers had faster germination and seedling growth than those from hand self-pollinated flowers. Fruit set for flowers of *Eugenia uniflora* that were bagged, hand self-pollinated, and cross-pollinated or nonbagged/natural pollination was *c.* 15.5, 11.1, 34.4 and 52.0%, respectively, and germination was 93.6, 98.5, 94.6 and 91.6%, respectively (Fidalgo et al., 2019). That is, there was no inbreeding depression for seed germination. The average germination per gram of seeds (plus chaff) was 280 and 327 for seeds from self- and cross-pollinated flowers of *Eucalyptus regnans*, respectively (Eldridge and Griffin, 1983). Compared with outcrossing, self-pollination significantly decreased the seed set of *E. globulus* subsp. *globulus*, but there was no effect on seed germination percentage or rate (Hardner and Potts, 1995).

Self-pollinated flowers of *Syzygium rubicundum* had *c.* 2.1% fruit set, and as the crossing distance increased to 1–2 km fruit set increased to *c.* 9.5% (Stacy, 2001). However, an increase in crossing distance up to 12 km decreased fruit set to *c.* 3%. Regardless of crossing distance, seed germination percentages were not significantly affected, while cumulative fitness was similar to fruit set. A pollen donor from a close-neighbor tree resulted in biparental inbreeding depression, but that from trees in separate/distant forests resulted in outbreeding depression.

Some species in various genera of Myrtaceae have male and hermaphroditic flowers on the same plant (andromonoecy), including *Beaufortia*, *Conothamnus*, *Eucalyptus*, *Leptospermum*, *Melaleuca*, *Phymatocarpus* and *Regelia* (Carr et al., 1971; Primack and Lloyd, 1980; Beardsell et al., 1993). Other breeding systems reported for species of Myrtaceae include dioecy and gynodioecy. Dioecious species have male and female flowers on different individual plants, e.g. *Myrcia almasensis* (Nic Lughadha, 1994), and the most common pollinators are small bees (Bawa, 1980). Dioecy is rare among angiosperms, but it has been reported in the Myrtaceae (Landrum, 1986; Nic Lughadha, 1994; Renner, 2014; Käfer et al., 2017), e.g. *Pimenta guatemalensis* (Landrum, 1986). Cryptic dioecy also occurs in the Myrtaceae (Chapman, 1964; Van Wyk and Lowrey, 1988; Nic Lughadha and Proença, 1996). For example, populations of about 15 species of *Eugenia* native to South Africa consist of plants that are either male or have hermaphroditic flowers (androdioecious), but these plants are functionally dioecious (Van Wyk and Lowrey, 1988). Fruits are formed only when hermaphroditic flowers are pollinated with pollen from male flowers because pollen from hermaphroditic flowers is not viable.

Gynodioecious species have only female (male sterile) flowers on some plants and hermaphroditic flowers on other plants in the same population. The ratio of female and hermaphroditic flowers can vary greatly within and among populations. Gynodioecy occurs in only about 2% of the angiosperm genera, but it is taxonomically widespread and occurs in eumagnoliids, monocots and eudicots (Dufay et al., 2014; Baskin and Baskin, 2020). The Myrtaceae is 1 of 81 families with this kind of breeding system (Dufay et al., 2014). However, the only example of a gynodioecious Myrtaceae that we have found in the literature is *Eucalyptus leucoxylon* subsp. *leucoxylon* (Ellis and Sedgley, 1993). In this taxon, some trees in the population have female flowers and others have hermaphroditic flowers. Anthers in the hermaphroditic flowers dehisced before the flowers opened resulting in *c.* 93% of the pollen being deposited on the stigma; the other 7% of the pollen was available for cross-pollination. Female flowers were cross-pollinated. However, there was no difference in seed set from cross-pollination for the two flower morphs.

Seed dispersal

Fleshy fruits of Myrtaceae are eaten by various animals, including birds, bats, carnivorous mammals, lemurs, monkeys, rodents, marsupials and ungulates (Dew and Wright, 1998; Pizo, 2002, 2003; Côrtes et al., 2009; Sinu et al., 2012; Tang et al., 2012; Lessa et al., 2013; Chaves et al., 2018). Seed dispersal of Myrtaceae in the Atlantic Forest of Brazil included birds (dispersing 14 Myrtaceae genera), bats (2), carnivorous mammals (6), monkeys (9), rodents (1), marsupials (2) and ungulates (2) (Pizo, 2002). Nine of the 14 genera had only one to two seed disperser(s), while *Campomanesia*, *Eugenia*, *Myrcia*, *Myrciaria* and *Psidium* had 4, 5, 3, 3 and 6 dispersers, respectively.

Many species of birds eat fleshy fruits of Myrtaceae and then disperse the seeds (Pizo, 2002, 2003; Bollen et al., 2004; Côrtes et al., 2009; Sinu et al., 2012; Hicks and Elliott, 2020). Birds differ in their fruit-eating behaviour: (1) swallow the whole fruit, (2) roll the fruit around in the mouth and spit out the seeds and (3) eat some of the fruit while leaving the seed attached to the parent plant (Sinu et al., 2012). Only birds that swallow the fruit and defecate or regurgitate the seeds at sites away from the parent plant are effective seed dispersers. For example, in the Atlantic Forest of Brazil, 17 species of birds visited fruits of *Eugenia umbelliflora*, but only *Turdua amaurochalinus* and *T. rufiventris* had the highest probability (0.28 and 0.24, respectively) of dispersing seeds (Côrtes et al., 2009). The crab-eating fox (*Cerdocyon thous*) is a secondary disperser of *E. umbelliflora* seeds initially dispersed by birds and then dropped to the soil surface (Cazetta and Galetti, 2009). Germination percentage was not increased by gut passage through the fox, but germination speed was increased significantly.

In the Atlantic Forest of Brazil, bats eat the fruits of *Eugenia stictosepala*, *Psidium catleianum* and *P. guajava* and disperse the seeds (Pizo, 2002). The bat species *Cynopterus sphinx* and *Rousettus leschenault* removed fruits from *Syzygium oblatum* trees growing in Yunnan Province, China, and carried them for up to 73 m away from the parent trees (Tang et al., 2012). Seedling survival of *S. oblatum* under parent trees, in forest gap and under feeding-roost trees was 78.3, 91.7 and 86.7%, respectively. The carnivorous mammals coatis and canids and the ungulates tapirs and deer in the Atlantic Forest eat fruits of Myrtaceae that have fallen on the ground (Pizo, 2002). The rodents agoutis (*Dasyprocta*) and spiny rats (Echimyidae) also collect fleshy fruits of Myrtaceae from the soil surface, and they may cache some of them in soil/litter up to 6.1 m away from the fruiting trees (Pizo, 2002).

Monkeys eat fleshy fruits of various species of Myrtaceae. Brown howler monkeys are legitimate seed dispersers of Myrtaceae and other plant families with fleshy fruits that grow in their habitat (Chaves et al., 2018). Monkeys swallow the fruits and later defecate seeds in new locations away from the parent trees. Monkeys defecate seeds in groups, while birds may drop individual seeds (Pizo, 2003). A comparison of seedling survival for clumped *versus* individual seeds in the seed-deposition site revealed that the isolated seeds of *Gomidesia anacardiifolia* and *Marlierea obscura* (i.e. bird-dispersed seeds) had higher survival than clumped seeds. Marsupials in particular didelphids eat fleshy fruits of angiosperms, including those of Myrtaceae (Lessa et al., 2013). After gut passage, seeds of *Myrcia* sp. germinated to higher percentages than control seeds, while those of *Psidium* sp. germinated to a lower percentage than control seeds (Lessa et al., 2013).

The fleshy fruits of *Myrtus communis* in the Mediterranean shrublands of southern Europe are dispersed by birds (Herrera, 1995; Traveset et al., 2001) and the carnivorous mammals red fox and pine marten (Aronne and Russo, 1997; Traveset et al., 2001). Also, seeds of *M. communis* have an elaiosome (fleshy body on seed that is rich in lipids and proteins) and are dispersed by ants (Aronne and Wilcock, 1994).

After dry fruits of Myrtaceae, e.g. *Calothamnus*, *Corymbia*, *Eucalyptus* and *Melaleuca*, open and release seeds and indehiscent fruits, e.g. *Calytrix*, *Darwinia* and *Micromyrtus*, fall from the parent plant, both gravity and wind facilitate dispersal. Fruits of *Calytrix* retain the calyx, which promotes dispersal by wind (Groom and Lamont, 2015). Seeds of *Metrosideros polymorpha* are dispersed by wind and can reach seed densities of 363, 137, 37, 25 and 20 m^{-2} at distances of 25, 50, 100, 150 and 250 m, respectively, beyond the edge of the forest (Drake, 1992).

Following the dispersal of seeds/fruits via gravity and wind, ants may take them and thus serve as secondary dispersers (e.g. Andersen and Ashton, 1985; Myerscough, 1998). After the fruits of *Corymbia torelliana* open, *c.* 88% of the seeds are dispersed by gravity, but a few seeds in each fruit are embedded in resin in the open fruits and are not dispersed (Wallace et al., 2008). Stingless bees in the genus *Trigona* collect the resin, and as they do so they collect seeds of *C. torelliana*. Bees carry the seeds and resin to their nests 20–220 m away from the parent trees, after which they discard the seeds from their nests; these seeds germinate to about 95%.

It should be noted that the seeds of Myrtaceae taken by ants, beetles, birds, lemurs, lygaeid bugs, monkeys, rodents and other animals may serve as food for the animals, i.e. seed predation (Ashton and Frankenberg, 1979; Ashton, 1979; Andersen and Ashton, 1985; Wellington and Noble, 1985; Dew and Wright, 1998; Silva and Pinheiro, 2009; Carvalho and Pizo, 2023). For example, no seeds of *Eucalyptus regnans* were found in/on the soil in mature forests of this species, although seed rain/fall was good each year (Ashton, 1979). Seeds were eaten/destroyed by several species of ants including *Chelaner leae*, *Prolasius frunneas*, *P. flavicorns* and *P. pallidus*. After a fire, however, massive seed fall from canopy-stored seeds not only satiated the ants, but there was ‘a temporary interference of ant foraging activity’. In southeastern Australia, the number of viable seeds in the annual seed rain of *Eucalyptus baxteri*, *Leptospermum juniperinum* and *L. myrsinoides* was 13, 480 and 800 seeds $m^{-2}\,yr^{-1}$, respectively, but the number of seeds remaining after predation was 1.3, 48 and 80 $m^{-2}\,yr^{-1}$, respectively (Andersen, 1989).

Kinds of embryos in seeds of Myrtaceae

Martin (1946) listed bent, folded and linear embryos for Myrtaceae, but investing and spatulate embryos also occur in this family (e.g. Dawson, 1970; Landrum and Kawasaki, 1997; Wilson, 2010). Thus, five morphologically distinct kinds of embryos are found in Myrtaceae (Fig. 1). A linear-full embryo (i.e. a fully developed linear embryo) is long, usually curved with small, recurved cotyledons and an enlarged hypocotyl that is greatly swollen in some species (Fig. 1A). A spatulate embryo has spoon-shaped cotyledons attached directly above a straight (easily visible) hypocotyl/radicle (Fig. 1B). A bent embryo has rounded cotyledons and a hypocotyl that curves sharply around the end of the cotyledons (Fig. 1C). A folded embryo has large foliaceous cotyledons that are folded together and an obviously protruding hypocotyl that may be somewhat curved (Fig. 1D). An investing embryo has thick fleshy cotyledons that cover most, or all, of the embryo axis (Fig. 1E). The investing embryo of Myrtaceae has been described as massive but undivided, i.e. undifferentiated (McVaugh, 1956). However, Justo et al. (2007) clearly showed that the investing embryo of *Eugenia pyriformis* was differentiated and had an embryo axis *c.* 1.0 mm in length located between the cotyledons.

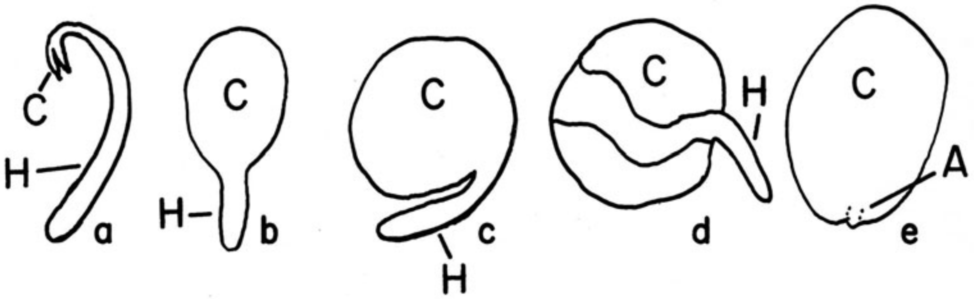

Figure 1. Embryo types of Myrtaceae. (A) Linear-full (myrtoid); (B) spatulate; (C) bent; (D) folded (myrcioid) and (E) investing (eugenioid). A, axis (which is covered by cotyledons); C, cotyledons; H, hypocotyl.

Investing, folded and linear-full embryos in tribe Myrteae have been called eugenioid, myrcioid and myrtoid embryos, respectively (e.g. Landrum and Stevenson, 1986; Lucas et al., 2007; da Silva and Mazine, 2016). However, in this review, we refer to all embryos using the embryo classification system of Martin (1946) as modified by Baskin and Baskin (2007).

In seeds of Myrtaceae with a bent, folded, investing or linear-full embryo, there is a shoot apical meristem between the cotyledons and a root apical meristem at the lower end of the hypocotyl. The hypocotyl is the first structure to emerge from seeds with a bent, folded, investing and linear-full embryo (see spatulate embryo below), after which the primary root and a shoot are produced by the apical meristems (Beltrati, 1978; Landrum and Stevenson, 1986; Aronne and de Micco, 2004; Meza and Bautista, 2007; Rego et al., 2011; Bardales et al., 2014; Cosmo et al., 2017; Freitas et al., 2018). The amount (length) that the hypocotyl extends from seeds before the primary root is visible varies, resulting in some seedlings with a relatively long hypocotyl (between the seed and root) (Aronne and de Micco, 2004) and others with a short hypocotyl (Beltrati, 1978; Nacata and Andrade, 2020). This kind of seed dormancy was placed in *Subclass 4* (Hypocotylar) of Class physiological dormancy (PD) by Baskin and Baskin (2021). The dormancy formula they suggested for seeds is $C^{m'}_{xb}$, where *C* is class physiological dormancy (PD), × level 1 (nondeep), 2 (intermediate) or 3 (deep) of PD, subscript *b* that warm temperatures are required to break PD and superscript *m′* that the root and shoot arise from meristematic tissue on opposite ends of the hypocotyl after the hypocotyl has emerged from the seed. For nondormant (ND) seeds, the formula is $C^{m'}_{\mathrm{nd}}$, where subscript nd means nondormant (Baskin and Baskin, 2021).

Information about the germination morphology of seeds with a spatulate embryo is not clear. Some authors (e.g. Ladiges et al., 1981; Robinson et al., 2008; Baumann and Hewitt, 2023) have said that radicle emergence was the criterion for germination. However, the photographs of *Melaleuca alternifoli*a seeds in various stages of germination show the first stage as having a hypocotyl that is twice as long of the radicle (Pinheiro et al., 2020), causing us to wonder if germination morphology in seeds with a spatulate embryo is like that in the other kinds of Myrtaceae seeds, i.e. the radicle does not grow until the hypocotyl has emerged from the seed.

A literature search was conducted to increase the size of our embryo database for the Myrtaceae. In total, we have information on embryo morphology for 240 species in 123 genera and 20 tribes of Myrtaceae (Supplementary Table S1). Some tribes of Myrtaceae have only one kind of embryo, e.g. Chamelaucieae has only linear-full and Heterophyxideae, Lindsaomyrteae, Lophostemoneae, Psiloxyleae, Syncarpieae and Syzygieae have only investing embryos (Table 1). Xanthomyrteae and Xanthostemoneae have only bent embryos; Tristaniopsideae only folded embryos; and Cloezieae, Leptospermeae, Melaleuceae, Metrosidereae, Osbornieae and Tristanieae only spatulate embryos. Backhousieae (bent, linear-full), Eucalypteae (folded, investing) and Kanieae (linear-full, spatulate) have two kinds of embryos, while the Myrteae have four kinds: bent, folded, investing and linear-full.

According to Martin (1946), bent, folded, investing, linear and spatulate embryos have a central (axile) position inside the seed. Martin's family tree of seed phylogeny shows the linear embryo as being in about the middle of the tree, and the upward progression of embryos on the tree is linear → spatulate → bent → folded → investing. That is, the investing embryo is at the top of Martin's tree. However, when compared to the crown age of the various tribes of Myrtaceae (Thornhill et al., 2015), no clear pattern of phylogenetic relationships between the various kinds of embryos in Myrtaceae is evident. For example, the crown age of Lophostemoneae and Syzygieae with an investing embryo is 41.3 and 29.3 Ma, respectively, while that of Melaleuceae and Metrosidereae with spatulate embryos is 55.5 and 24.9 Ma, respectively. The crown age of Myrteae with bent, folded, investing and linear-full embryos is 50.7. The crown age of Xanthostemoneae and Backhousieae with a bent embryo is 55.6 and that of Backhousieae with bent and linear-full embryos is 18.5 Ma.

Vochysiaceae is the closest relative of Myrtaceae (Gonçalves et al., 2020), and living species of Vochysiaceae have seeds with folded, investing or spatulate embryos (Niembro, 1983; Garwood, 1998; Ferreira et al., 2001; Kirkbride et al., 2006). Thus, it is not surprising to find these three kinds of embryos in various positions on molecular phylogeny trees of Myrtaceae based on either combined plastid or combined nuclear data (Wilson et al., 2022). The presence of two or more kinds of embryos in four tribes of Myrtaceae (Table 1) suggests that there are some possible evolutionary relationships between kinds of embryos in this family that merit research, e.g. what is the origin of the bent and linear-full embryos in the Myrtaceae? Bent and linear-full embryos occur in Backhousieae and linear-full and spatulate embryos in Kanieae; however, the Myrteae have linear-full, bent, folded and investing embryos but no spatulate embryos.

Occurrence of seed dormancy: tribes, life forms and vegetation regions

Since the five kinds of embryos in seeds of Myrtaceae are fully developed (Fig. 1) and seeds are water permeable (e.g.

Table 1. Number of genera with different kinds of embryos in each tribe of Myrtaceae and occurrence of nondormancy (ND) and physiological dormancy (PD) in each tribe

	Kind of embryo						
Tribe	Bent	Folded	Investing	Linear-full	Spatulate	ND	PD
Backhousieae	1			1		+	–
Chamelaucieae				34		+	+
Cloezieae					1	+	–
Eucalypteae		1	4			+	+
Heteropyxideae			1			+	–
Kanieae				5	1	+	–
Leptospermeae					8	+	+
Lindsayomyrteae			1			+	–
Lophostemoneae			3			+	–
Melaleuceae					2	+	+
Metrosidereae					1	+	+
Myrteae	1	3	10	34		+	+
Osbornieae					1	+	–
Psiloxyleae			1			+	–
Syncarpieae			1			+	–
Syzygieae			2			+	+
Tristanieae					2	+	–
Tristaniopsideae		1				+	–
Xanthomyrteae	1					+	–
Xanthostemoneae	3					+	+

Note: +, yes; –, no information.

Pérez-Fernández et al., 2000; Auld and Ooi, 2009; Hue et al., 2013), freshly matured seeds are either ND or have PD. If seeds tested over a range of temperatures and in light and in dark germinate in less than about 4 weeks and show no increase in germination percentages when given a dormancy-breaking treatment, they are ND. On the other hand, if fresh seeds either do not germinate in about 4 weeks or exhibit a widening of range of environmental conditions (e.g. temperature) over which they germinated after receiving a dormancy-breaking treatment, they have PD (Baskin and Baskin, 2014).

To enhance our database for seed dormancy/germination of Myrtaceae in Baskin and Baskin (2014), a literature search was conducted using the name of each tribe of Myrtaceae, seeds, semillas, sementes, germination, germinação and germinación. In total, information on seed dormancy/germination was found for 571 species of Myrtaceae (Supplementary Table S2). Some species in all 20 tribes of Myrtaceae have ND seeds, and species in 8 tribes have seeds with PD (Table 1). For many tribes, however, the absence of PD in the tribe may be due to a lack of detailed germination studies for members of that tribe.

Each of the 571 species was recorded by life form (tree or shrub) in the vegetation region in which it grew (Supplementary Table S2). Then, the proportion of tree and shrub species in each vegetation region with ND seeds or with PD was calculated to create a seed dormancy profile for the Myrtaceae (Table 2). Overall, seeds of 55.6% of the Myrtaceae species had ND seeds, and the other 44.4% had seeds with PD. The highest number of tree species was recorded for tropical rainforest and semi-evergreen rainforest, and that for shrubs was the matorral (sclerophyllous woodlands with winter rain). The relative importance of ND and PD trees and shrubs varied with the vegetation region. In rainforests, the percentage of trees and shrubs with either ND or PD was almost equal (*c.* 50%). In semi-evergreen rainforests and savannas, both trees and shrubs had a higher percentage of ND than PD. In the matorral and broad-leaved evergreen forests, trees had a higher percentage of ND than shrubs, while shrubs had a higher percentage of PD than trees. In hot deserts (trees) and grasslands (shrubs), all species had ND seeds. Tropical montane trees had a higher percentage of PD (68.4) than ND (31.6), but 50% of shrubs had ND seeds and 50% seeds with PD. In dry deciduous forests, trees had 42.9 and 57.1% ND and PD, respectively, but all shrubs had seeds with PD.

Not only did the rainforest and semi-evergreen rainforest have the highest number of species of trees (93 and 104, respectively), but they also had 12 and 9 tribes of Myrtaceae, respectively (Table 3). Shrubs in the rainforest and semi-evergreen rainforest were represented by 3 and 12 tribes of Myrtaceae, respectively. In the other seven vegetation regions, both trees and shrubs were represented by 0–5 tribes. Trees were represented by 0 and 5 tribes in grassland and savanna, respectively, and shrubs by 0 and 5 tribes in hot desert and broad-leaved evergreen forest, respectively.

Table 2. Seed dormancy profile for trees and shrubs of Myrtaceae in different vegetation regions

Vegetation region/life form	Number of species	Nondormancy (%)	Physiological dormancy (%)
Rainforest (RF)			
Trees	93	51.6	48.4
Shrubs	8	50.0	50.0
Semi-evergreen RF			
Trees	104	72.1	27.9
Shrubs	35	88.6	11.4
Tropical montane			
Trees	19	31.6	68.4
Shrubs	4	50.0	50.0
Dry deciduous forest			
Trees	7	42.9	57.1
Shrubs	4	0	100
Savanna			
Trees	37	78.3	21.6
Shrubs	8	75.0	25.0
Hot desert			
Trees	1	100	0
Matorral			
Trees	74	89.2	10.8
Shrubs	148	10.1	90.0
Broad-leaved evergreen			
Trees	6	83.3	16.7
Shrubs	19	31.6	68.4
Grassland			
Shrubs	4	100	0
Total	571	55.6	44.4

Dormancy-break in seeds of Myrtaceae

Since Myrtaceae is mostly a tropical family, it comes as no surprise that the breaking of PD in seeds of many members of this family occurs at warm conditions suitable for germination. Thus, in many studies, seeds have been sown in nurseries or greenhouses without receiving any dormancy-breaking treatments (Supplementary Table S2), and the number of days until seeds germinated was monitored. Methods used in laboratories to break seed dormancy and promote germination include treatment with GA_3 (Cochrane et al., 2002; Scalon et al., 2004; Liang et al., 2013; Saldías and Velozo, 2014; Damiani et al., 2016; Griebeler et al., 2019; Mali et al., 2021; Santos et al., 2022), potassium nitrate (Liang et al., 2013), smoke-infused water (Cochrane et al., 2001), sodium nitrite and potassium cyanide (Bardales et al., 2014). Germination also has been promoted by mechanical scarification (Gentil and Ferreira, 1999; Martinotto et al., 2007; Tafarel et al., 2021) and by removing the seed coat from the embryo (Rizzini, 1970; Gentil and Ferreira, 1999). In a study of the cold hardiness of 15 species of *Eucalyptus* being considered for possible introduction into Ireland, 4 weeks of cold stratification increased germination (compared to fresh seeds) for only one species (Afroze et al., 2021). The positive response of seeds to treatments such as GA_3 and scarification indicates that seeds have nondeep PD.

Seed germination of *Myrtus communis* is promoted by soaking seeds in water, treatment with GA_3 and cold stratification (Benvenuti and Macchia, 2001). Ballesteros et al. (2015) recommended 3 months of cold stratification to break dormancy of *M. communis* seeds. After cold stratification, Benvenuti and Macchia (2001) obtained higher germination percentages at 25–30°C than at 10–20°C. We conclude that seeds of this species also have nondeep PD.

If GA_3 and scarification do not promote germination and if seeds require a long period of time (40–150 d) to germinate (Rizzini, 1970; Smith-Ramírez et al., 1998; Santos et al., 2004; Scalon et al., 2004; Masetto et al., 2009; Simpson, 2011; Saldías and Velozo, 2014), they may have intermediate or deep PD. Unfortunately, no studies have been done to determine if the long-germinating seeds of Myrtaceae have intermediate or deep PD.

There are six types of nondeep PD, and they can be distinguished by the changes in temperature requirement for germination during the dormancy-breaking treatment (Types 1, 2 and 3) or by the temperature range over which seeds will germinate when dormancy is broken (Types 4, 5 and 6) (Baskin and Baskin, 2014; Soltani et al., 2017). In the early stages of dormancy-break, seeds with Types 1, 2 and 3 dormancy germinate at low, high and intermediate temperatures, respectively. As dormancy-break continues, seeds with Types 1 and 2 dormancy exhibit an increase in the maximum temperature for germination and a decrease in the minimum temperature for germination, respectively, while seeds with Type 3 dormancy exhibit an increase in the maximum and a decrease in the minimum temperatures for germination. In the early stages of dormancy-break, seeds with Type 6 dormancy germinate over a range of low to high temperatures. During the continuation of dormancy-break, seeds with Type 6 dormancy do not exhibit an increase in the range of temperatures over which they can germinate, but germination percentages may increase. Seeds with Types 4 and 5 dormancy gain the ability to germinate only at high and low temperatures, respectively.

Seeds of Myrtaceae with PD have been tested at 20, 25 and 30°C (Hossel et al., 2017; Paim et al., 2018; Souza et al., 2018; Leão-Araújo et al., 2019); 25, 30 and 30/20°C (Mugnol et al., 2014) and 20, 25, 30, 35 and 30/20°C (Maeda et al., 1991; Masetto et al., 2009). Among these studies, the ability of seeds to germinate at 20°C varied between the species. Seeds of *Psidium cattleianum* germinated to low percentages at 20°C (Hossel et al., 2017), while those of *Campomanesia adamantium* (Leão-Araújo et al., 2019), *C. guazumifolia* (Souza et al., 2018) *Eugenia pleurantha* (Masetto et al., 2009), *Myrceugenia myrtoides* (Paim et al., 2018) and *Syzygium aromaticum* (Maeda et al., 1991) germinated to high percentages. Seeds of *P. guineense* germinated at 25, 30 and 30/20°C, and after both 20 and 42 d of incubation, the highest percentage was at 30/20°C. After 42 d of incubation, the germination percentage had increased at 30°C (Mugnol et al., 2014).

Some studies have tested seeds with PD at 5, 10 and 15°C. No seeds of *Rhodomyrtus tomentosa* germinated at 5 or 10°C (Liang et al., 2013) or at 10 or 15°C (Hue et al., 2013). There was little or no germination of seeds of *Acca sellowiana*, *Campomanesia xanthocarpa*, *Eugenia involucrata* or *E. pyriformis* at 15°C (Gomes et al., 2016), but seeds of *Psidium guineense* germinated to 35% at this temperature (Santos et al., 2015). Seeds of

Table 3. Tribes of Myrtaceae, vegetation regions (1–9)[a] and life form (tree or shrub)

	Trees									Shrubs								
Tribe	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7	8	9
Backhousieae	x																	
Chamelaucieae											x					x		
Cloezieae											x							
Eucalypteae	x	x	x		x	x	x	x										
Heteropyxideae					x													
Kanieae	x	x																
Leptospermeae	x	x					x				x	x				x	x	
Lindsayomyrteae	x																	
Lophostemoneae	x	x									x							
Melaleuceae	x	x			x		x				x			x		x	x	
Metrosidereae								x			x						x	
Myrteae	x	x	x	x	x			x		x	x	x	x	x		x	x	x
Osbornieae											x							
Psiloxyleae	x																	
Syncarpieae		x																
Syzygieae	x	x	x	x	x			x		x	x		x				x	
Tristanieae												x						
Tristaniopsideae	x									x	x							
Xanthomyrteae											x							
Xanthostemoneae	x	x									x							
total	12	9	3	2	5	1	3	4	0	3	12	3	2	2	0	4	5	1

[a] Vegetation regions: 1, rainforest; 2, semi-evergreen rainforest; 3, tropical montane; 4, tropical dry deciduous; 5, savanna; 6, hot desert; 7, matorral; 8, broad-leaved evergreen and 9, temperate grassland.

Darwinia species and *Melaleuca* species (with PD when freshly matured) germinated at 15°C (Cochrane et al., 2002), but the full range of temperatures for germination of these seeds was not determined.

The general conclusion from studies in which seeds of Myrtaceae were tested over a range of temperatures is that the highest germination percentages were at high temperatures. These results suggest that seeds have Type 4 nondeep PD. However, due to a lack of detailed studies on the temperature requirements for germination during the period of dormancy-break, we cannot rule out the possibility that some species have Type 6 nondeep PD (or other types of nondeep PD) with a temperature range of 20 to about 35°C for germination after PD is broken. Much more research needs to be done on the temperature requirements for germination during the dormancy-breaking period of seeds of Myrtaceae.

In Supplementary Table S2, we have recorded the temperatures (or conditions such as nursery or greenhouse) at(in) which a high percentage of the seeds of each species germinated. For 320 species listed in tropical vegetation regions, only 5 species (1.6%) have 15°C (often along with temperatures >15°C) listed as suitable for high germination; 3 of the species are in the Myrteae and one each in the Eucalypteae and Melaleuceae. For 251 species listed for temperate vegetation regions, 59 species (23.5%) have 15°C listed as a temperature for high germination. All 59 species occur in the matorral, and they belong to the Chamelaucieae, Eucalypteae or Melaleuceae, which are dry-fruited tribes. The ability of seeds of Myrtaceae to germinate at relatively low temperatures, e.g. 15°C, especially in the matorral indicates that germination can be delayed until the onset of the cool, wet season in winter. That is, dormancy-break occurs in summer and seeds germinate when the cool, wet season begins; however, no studies have been done that inform us as to what type of nondeep PD these seeds have.

Seed germination requirements

Many seed germination studies of Myrtaceae species have been conducted in nurseries, shade houses and greenhouses at near natural temperature regimes (Supplementary Table S2). The temperature at which a high germination percentage was obtained is available for 246 species (Supplementary Table S2), and the mean (±SE) of these temperatures is 22.5 ± 0.2°C. Determinations of the light (L)–dark (D) requirements for seed germination have been made for 34 species (Supplementary Table S2): 15 species, L > D; 14, L = D; 3, D > L; and 2 species with mixed results, i.e. one paper reported L = D and another D > L. Germination of *Eucalyptus marginata* seeds was significantly lower in white light than in darkness or in light with peak wavelengths of 430, 450, 490, 520, 570, 640 and 720 nm, as transmitted through

Kodak Wratten photographic coloured filters (Rokich and Bell, 1995). Germination of *E. calophylla* seeds was significantly reduced in white light and at wavelengths of 570 and 640 nm.

Seeds of Myrtaceae differ in their ability to germinate during and after water stress, and not surprisingly the ND, desiccation-sensitive seeds of *Campomanesia pubescens* (Dousseau et al., 2011) and *Eugenia pyriformis* (Andrade and Ferreira, 2000) are dispersed at the onset of the rainy season in the seasonally dry Cerrado of Brazil (Escobar et al., 2021). The ND seeds of *Myrcia guianensis* and *M. splendens*, which also grow in the Cerrado of Brazil, are dispersed at the onset of the rainy season and mid-rainy season, respectively. Thus, seed dispersal in these four species occurs at a time when soil moisture would be adequate for seed germination.

Seeds of *Eugenia brasiliensis*, *E. involucrata*, *E. pyriformis* and *E. uniflora* germinated to 100, 84, 66 and 91% at 0.0 MPa, respectively, but germination of each species decreased with water stress, e.g. 44, 8, 0 and 39% at −1.5 MPa, respectively; and 0, 2, 0 and 0%, respectively, at −2.0 MPa (Inocente and Barbedo, 2019). Seeds of *E. umbelliflora* were dispersed during the dry season in restinga vegetation in Brazil (Braz and de Mattos, 2010). At 0 and −0.37 MPa, seeds of *E. umbelliflora* germinated to 88 and 38%, respectively, and 52 and 54 d, respectively, were required for seeds to reach 50% of final germination. Further, moisture content (MC) of fresh seeds was 45–50%, and after drying at 68% relative humidity for *c.* 17 d, it was 28%, at which point only 30% of them germinated. At −0.1, −0.4 and −0.7 MPa, seeds of *Melaleuca nematophylla* germinated to 58.4, 36.3 and 0.5%, respectively (Merino-Martín et al., 2017). Seeds of *Eucalyptus caesia* subsp. *caesia*, *E. ornata*, and *E. salubris* germinated to 95–100% at −0.1 MPa; to 95, 95 and 70%, respectively, at −0.4 MPa and to 70, 35 and 8%, respectively, at −0.7 MPa (Rajapakshe et al., 2020). However, seeds of *E. salmonophloia* germinated to 50, 4 and 0% at −0.1, −0.4 and −0.7 MPa, respectively. Thus, seeds of the range-restricted *E. caesia* subsp. *caesia* and *E. ornata* were more tolerant of water stress during germination than those of the widely distributed *E. salmonophloia*.

Seeds of *Eucalyptus macrocarpa* and *E. tetragona* from deep sand habitats and those of *E. loxophleba* and *E. wandoo* from lateritic loam habitats germinated to *c.* 100% at a soil moisture potential of −0.1 MPa (Schütz et al., 2002). At −0.5 MPa, seeds of *E. tetragona* germinated to *c.* 95% and those of the other three species to 70–75%. At −1.0 MPa, however, the only germination (*c.* 5%) was for seeds of *E. tetragona*. Seeds of *E. todtiana* incubated on a moist substrate for 24 h at 15°C reached an MC of *c.* 50%. However, when seeds at 50% MC were placed on dry filter paper in an 'air-blown cabinet' at 23° and 55% relative humidity for 48 h MC decreased to *c.* 10% (Pérez-Fernández et al., 2000). Seeds dried for 48 h germinated to 100% and reached 50% germination in *c.* 9 d. Thus, seeds of *E. todtiana* recovered from dehydration and germinated.

Seeds of *Eucalyptus brassiana*, *E. camaldulensis*, *E. grandis*, *E. saligna*, *E. tereticornis* and *E. urophylla* germinated to 8, 39, 9, 4, 46 and 45%, respectively, at a water stress of −0.6 MPa but to only 0, 5, 0, 0, 5 and 9%, respectively, at −0.8 MPa (de Sá-Martins et al., 2019). In a NaCl solution with an osmotic potential of −1.5 MPa, seeds *of E. brassiana*, *E. camaldulensis*, *E. grandis*, *E. saligna*, *E. tereticornis* and *E. urophylla* germinated to 9, 18, 4, 4, 18 and 6%, respectively.

Some species of Myrtaceae grow in habitats that are submerged in water for part, or all, of the year. Seeds of *Leptospermum lanigerum* and *Melaleuca squarrosa* germinated under water, but flooding reduced seedling growth and survival (Zacks et al., 2018). The recalcitrant seeds of *Eugenia stipitata* submerged in 6 cm of water began to germinate after 2 months and after 1 year 87% had germinated (Calvi et al., 2017). Most seeds of *Melaleuca ericifolia* did not germinate while flooded, but even after 3–4 weeks of flooding, seeds germinated to high percentages when transferred to moist germination pads in Petri dishes (Ladiges et al., 1981). Seedlings from the few seeds that germinated under water did not grow past the cotyledon stage while flooded. Fleshy fruits of *Blepharocalyx cruckshanksii* and *Luma apiculata* growing in forested wetlands of south-central Chile floated for 37 and 53 d, respectively (Mora and Smith-Ramírez, 2017). After 90 d in water, seeds of both species germinated (*c.* 80%) inside the fruits, when fruits were removed from water and placed in moist soil. The authors concluded that the fleshy fruits promoted dispersal, but after fruits became lodged on moist soil as water receded seeds inside them could germinate readily.

There is concern that global warming will modify the environment to the extent that dormancy-break, germination and seedling survival will be negatively impacted. In a study of 100 plant species growing in Western Australia that included 37 Myrtaceae species/taxa, *Eucalyptus kruseana*, *E. nigrifunda*, *E. pimpiniana*, *E. jimberlanica* and *Rhodanthe pyrethrum* germinated to higher percentages when incubated at temperatures lower than those in the field during the wet season (Cochrane, 2020). One species germinated to the highest percentages at field temperature during the wet season, while 31 species germinated to higher percentages at temperatures higher than those in the field during the wet season. Thus, based on this small sample of Myrtaceae species, it appears that increased temperatures due to global warming may not significantly impede the regeneration of species of Myrtaceae from seeds. For 26 species of *Eucalyptus* in Western Australia, modelling of seed germination response to temperature revealed that the majority of species will be able to germinate in the future, especially in the cool winter months (Cochrane, 2017).

Although temperatures may be favourable for seed germination of many Myrtaceae species in the future, the question is will there be adequate precipitation for seedling survival? In other words, if precipitation decreases in the driest months will there be enough soil moisture to sustain the seedlings? Some modelling has been done to look at future precipitation patterns, but more is needed. Barrientos-Díaz et al. (2024) predicted that future temperature and rainfall conditions will be favourable for species of Myrteae to live in the Atlantic Forest of Brazil. However, predictions for the future distribution of *Eugenia uniflora* in South America suggest that Argentina and Paraguay will not have suitable habitat for this species, but populations of it may increase on the Brazilian Plateau (Turchetto-Zolet et al., 2016).

Tribes and species of Myrtaceae with desiccation-sensitive seeds

Information was found for desiccation sensitivity of 58 species of Myrtaceae, and all of them belonged either to the Myrteae (33 species) or Syzygieae (25 species) (Table 4). According to Wilson (2010), all the genera of Myrteae and Syzygieae represented in Table 4 have fleshy fruits. Seven species of Myrteae have intermediate seed storage behaviour, and the other 26 have recalcitrant seeds. The species of Myrteae with intermediate storage behaviour have seeds with linear-full embryos, and those that

Table 4. Species of Myrtaceae with desiccation-sensitive (recalcitrant [R] or intermediate [I]) seed storage behaviour

Species	Tribe	Embryo	Storage behaviour	References
Archirhodomyrtus beckleri	Myrteae	Linear-full	I	Sommerville et al. (2021)
Blepharocalyx salicifolius	Myrteae	Linear-full	R	Rego et al. (2013) and Pelissari et al. (2018)
Campomanesia adamantium	Myrteae	Linear-full	R	Melchior et al. (2006) and Dresch et al. (2014, 2015)
Campomanesia phaea	Myrteae	Linear-full	R	Maluf and Pisciottano-Ereio (2005)
Campomanesia pubescens	Myrteae	Linear-full	R	Dousseau et al. (2011)
Campomanesia xanthocarpa	Myrteae	Linear-full	R	Vieira et al. (2022)
Eugenia astringens	Myrteae	Investing	R	Delgado and Barbedo (2007, 2012) and Rodrigues et al. (2022)
Eugenia brasiliensis	Myrteae	Investing	R	Hong et al. (1998), Kohama et al. (2006), Delgado and Barbedo (2007, 2012) and Rodrigues et al. (2022)
Eugenia capuli	Myrteae	Investing	R	Subbiah et al. (2019)
Eugenia cerasiflora	Myrteae	Investing	R	Delgado and Barbedo (2007, 2012)
Eugenia dysenterica	Myrteae	Investing	R	Santos et al. (2014)
Eugenia handroana	Myrteae	Investing	R	Subbiah et al. (2019)
Eugenia involucrata	Myrteae	Investing	R	von Bülow et al. (1994), Barbedo et al., (1998), Maluf et al. (2003), Delgado and Barbedo (2007, 2012), Subbiah et al. (2019) and Rodrigues et al. (2022)
Eugenia luschnathiana	Myrteae	Investing	R	Subbiah et al. (2019)
Eugenia pyriformis	Myrteae	Investing	R	Andrade and Ferreira (2000), Delgado and Barbedo (2007, 2012), Mayrinck et al. (2019) and Rodrigues et al. (2022)
Eugenia sonderiana	Myrteae	Investing	R	Pelissari et al. (2018)
Eugenia stipitata	Myrteae	Investing	R	Gentil and Ferreira (1999), Mendes and Mendonça (2012) and Maia et al. (2024)
Eugenia umbellata	Myrteae	Investing	R	Carvalho et al. (2006) and Masetto et al. (2008)
Eugenia uniflora	Myrteae	Investing	R	Delgado and Barbedo (2007, 2012), Mello et al. (2010), Pelissari et al. (2018) and Rodrigues et al. (2022)
Lophomyrtus bullata	Myrteae	Linear-full	I	van der Walt (2022) and van der Walt and Nadarajan (2023)
Lophomyrtus obcordata	Myrteae	Linear-full	I	van der Walt (2022) and van der Walt and Nadarajan (2023)
Myrcia inaequiloba	Myrteae	Folded	R	Carvalho et al. (2006)
Myrcia neoludica	Myrteae	Folded	R	Subbiah et al. (2019)
Myrcia venulosa	Myrteae	Folded	R	José et al. (2007) and Mayrinck et al. (2016)
Myrcianthes coquimbensis	Myrteae	Investing	R	Loayza et al. (2015)
Myrcianthes pungens	Myrteae	Investing	R	Subbiah et al. (2019)
Myrciaria dubia	Myrteae	Investing	R	Subbiah et al. (2019)
Neomyrtus pedunculata	Myrteae	Linear-full	I	van der Walt (2023) and van der Walt and Nadarajan (2023)
Pimenta dioica	Myrteae	Linear-full	R	Subbiah et al. (2019)
Plinia cauliflora	Myrteae	Linear-full	R	Valio and Ferreira (1992) and Subbiah et al. (2019)
Rhodamnia maideniana	Myrteae	Linear-full	I	Sommerville et al. (2021)
Rhodomyrtus psidioides	Myrteae	Linear-full	I	Sommerville et al. (2021)
Syzygium acuminatissimum	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium aqueum	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium aromaticum	Syzygieae	Investing	R	Umarani et al. (2015)
Syzygium australe	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium cordatum	Syzygieae	Investing	R	Hong et al. (1998)
Syzygium cumini	Syzygieae	Investing	R	Umarani et al. (2015)
Syzygium cymosum	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)

(*Continued*)

Table 4. (*Continued.*)

Species	Tribe	Embryo	Storage behaviour	References
Syzygium fullageri	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium grande	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium guineense	Syzygieae	Investing	R	Hong et al. (1998) and Badou et al. (2017)
Syzygium ingens	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium jambos	Syzygieae	Investing	R	Hong et al. (1998) and Subbiah et al. (2019)
Syzygium maire	Syzygieae	Investing	R	Fountain and Outred (1991), Nadarajan et al. (2021) and van der Walt et al. (2022)
Syzygium malaccense	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium moorei	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium multipetalum	Syzygieae	Investing	R	Toublance-Lambault et al. (2019)
Syzygium myrtifolium	Syzygieae	Investing	R	Tsan and Awang (2021)
Syzygium paniculatum	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium phillyreifolium	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium pseudofastigiatum	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium samarangense	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium sandwicense	Syzygieae	Investing	R	Wyse and Dickie (2017) and Subbiah et al. (2019)
Syzygium smithii	Syzygieae	Investing	R	Hamilton et al. (2013)
Syzygium unipunctatum	Syzygieae	Investing	R	Sommerville et al. (2021)
Syzygium wilsonii	Syzygieae	Investing	R	Hamilton et al. (2013)
Uromyrtus australis	Myrteae	Linear-full	I	Sommerville et al. (2021)

are desiccation-sensitive have seeds with investing, folded or linear-full embryos. The 25 species of Syzygieae have desiccation-sensitive seeds, and all have investing embryos.

Among five Brazilian species of *Eugenia* with desiccation-sensitive seeds, the speed of seed drying and the speed of germination help explain differences in geographical range (Rodrigues et al., 2022). For seeds of *E. uniflora*, *E. involucrata*, *E. pyriformis*, *E. brasiliensis* and *E. astringens*, the water content threshold that decreased germination to *c.* 50% was 0.44, 0.33, 0.33, 0.25 and 0.25 g H_2O (g DW)$^{-1}$, respectively, and the species occurred in four, three, two, one and one morphoclimatic domain(s) (based on temperature and precipitation data) in Brazil, respectively. However, under laboratory conditions, seeds of *E. uniflora* had the second highest rate (speed) of germination and the slowest rate of water loss compared with the other species. The authors concluded that rapid germination and slow seed drying help explain why *E. uniflora* has a wider geographical distribution than the other four species.

Plantlet production from seed fragments (totipotency)

One consequence of seed predation is that the predator may not consume the whole seed, especially in the case of large seeds (Vallejo-Marín et al., 2006; Pérez et al., 2008; Loayza et al., 2015). In some species, if fragments of seeds have an intact embryonic axis, there is a possibility that a plantlet will be produced. For example, the large recalcitrant seeds of *Myrcianthes coquimbensis*, a threatened Myrtaceous shrub in the Atacama Desert of Chile, will produce a plantlet if up to 75% of seed mass is removed from either mature or immature seeds (Loayza et al., 2015).

Normal plantlet development occurred when seeds of *Eugenia stipitata* subsp. *sororia* (Anjos and Ferraz, 1999; Calvi et al., 2017), *E. brasiliensis*, *E. involucrata* and *E. uniflora* (Silva et al., 2005) were cut into two parts. Seeds of *E. pyriformis* cut in half longitudinally or transversally and those cut transversally into two parts, i.e. one-fourth of the seed and three-fourths of the seed, produced normal plantlets (Silva et al., 2003). Normal plantlet development occurred for seeds of *E. cerasiflora*, *E. pruinosa* and *E. umbelliflora* cut in half transversally or longitudinally and from three-fourths of a seed (Delgado et al., 2010). When seeds were cut into four equal parts (in a linear fashion), normal plantlets developed from one-fourth (external/end part) of a seed for *E. cerasiflora* and *E. pruinosa* but not for *E. umbelliflora*. Also, normal plantlet development occurred from one-fourth of a seed (internal/central part) for *E. cerasiflora* and *E. umbelliflora* but not for *E. pruinosa*.

In some species, the percentage of plantlet development/germination was higher for pieces of seeds than for intact seeds, e.g. *E. cerasiflora* and *E. pruinosa* (Delgado et al., 2010), but often the percentage for seed fragments and intact seeds did not differ significantly, e.g. *E. umbelliflora* (Delgado et al., 2010) and *E. uniflora* (Silva et al., 2005). However, plantlet formation from *E. pyriformis* seeds cut into 0, 2 and 4 pieces was 97, 73 and 62%, respectively (Costa et al., 2017). The production of normal plantlets from seeds of *E. uniflora* cut into two parts was higher for seeds produced from cross- than from self-pollinated flowers (Fidalgo et al., 2019).

The regeneration of roots and plantlets from fragments of *Eugenia* seeds occurs in seeds taken from both immature and mature fruits (Teixeira and Barbedo, 2012; Amador and Barbedo, 2015; Delgado and Barbedo, 2020). However, there is a reduction in the success of plantlet formation from *E. pyriformis* seed fragments with an overall decrease in seed size, which is related to a number of seeds in fruit (Prataviera et al., 2015). Although seed fragments of *E. pyriformis* (Amador and Barbedo, 2011), *E. brasiliensis*, *E. uniflora* (Amador and Barbedo, 2015) and *E. stipitata* (Calvi et al., 2017) can form a plantlet, only one plantlet is produced if the incision does not completely separate the seed parts. That is, if there is a connection between two seed parts only one of them produces roots and a plantlet.

Normal plantlet development occurred when seeds of *Syzygium myrtifolium* were cut into two parts longitudinally, but when seeds were cut transversally into two parts only one part produced a plantlet (Tsan, 2023). When a seed was cut into four parts longitudinally, at least one of the parts produced a plantlet, with the central and right fractions being the most likely to do so. However, when cut into two longitudinal and two transverse (i.e. four) parts, only the top left and top right parts produced a plantlet.

Effects of fire (heat and smoke) on seed germination

The appearance of Myrtaceae seedlings in the field after a fire (e.g. Mount, 1969; Williams, 2000; Wright, 2018; Wright et al., 2019) has prompted people to conduct experiments on the effects of heat and smoke on seed germination. Heat treatments on seeds of various species have revealed that temperatures simulating those in/at the soil surface during a fire can increase, decrease or have no effect on germination percentages (Table 5). Smoke, in general, either increases or decreases germination percentages of Myrtaceae seeds (Table 6). Seeds of *Baeckea utilis* did not respond to heat in the absence of smoke, but they responded to smoke in the absence of heat (Thomas et al., 2007). For seeds of *Kunzea ambigua* and *K. capitata*, there was an interaction between incubation temperature (15 and 25°C), water stress (0 and −0.9 MPa) and fire cues (heat and smoke) (Thomas et al., 2010). Fire cues increased germination percentages at 15 and 25°C across the range of water stress, i.e. fire cues increased seed tolerance to water stress.

Another aspect of fire in a plant community is that the smoke contains various compounds, including cyanohydrin (glyceronitrile, which in the presence of water releases cyanide), ethylene, karrikins (especially karrikin-1), nitrate and nitric oxide, that are known to promote seed germination (Flematti et al., 2011, 2013; Soós et al., 2019; Cao et al., 2021, 2023; Kępczyański and Kępczyańska, 2023). However, only karrikins and cyanohydrins can persist in the upper layers of the soil after a fire (Flematti et al., 2013). Smoke also contains compounds that are structurally similar to karrikins, i.e. contain a butanolide ring that inhibits germination (Light et al., 2010; Burger et al., 2018). Soós et al. (2019) suggested that after a fire both germination inhibitors and promotors are in the surface layers of soil. However, the promotors cannot be effective in stimulating germination until rain water has removed the inhibitors.

If a fire occurs while seedlings/juveniles are relatively small, they may not be robust/resilient enough to tolerate fire and are killed (e.g. Fordyce et al., 1997; Tozer and Bradstock, 1997; Wardell-Johnson, 2000; Fujita, 2021; Plumanns-Pouton et al., 2023). Thus, regeneration from seeds is not successful if the fire interval is more frequent than the time required for young plants to reach a fire-tolerant size.

Various species of Myrtaceae produce new stems from buds if the aerial portion of the plant is damaged/destroyed, as for example by fire. Epicormic buds (dormant buds located under the bark), arise from meristematic cells (epicormic strands) that are inside the bark, often at the junction of the bark and vascular cambium, e.g. *Eucalyptus* and *Melaleuca* (Burrows, 2002; Clarke et al., 2013). Lignotubers which form at the base of the stem, e.g. in many species of *Eucalyptus*, have many buds that can grow if the stem is killed. The development of a lignotuber begins shortly after seedling emergence, and it increases in size as the plant grows (Fordyce et al., 2000; Nicolle, 2006). Lignotubers were initiated on seedlings of *Eucalyptus cinerea* by the time plants were 6 weeks old (Graham et al., 1998). After 9 months of growth, the size of the lignotubers on *Eucalyptus obliqua* juveniles derived from seeds from 13 provenances in Australia was inversely related to mean annual precipitation in the original habitat (Walters et al., 2005). Interestingly, a molecular marker for lignotuber formation (*Elig*) has been identified in *Eucalyptus* (Bortoloto et al., 2020).

Buds that can replace damaged aerial stems also occur on rhizomes. For example, *Eugenia dysenterica* and *E. pumicifolia*, which grow in the fire-prone Cerrado of Brazil, have a woody rhizome covered with periderm. Silva et al. (2020) found numerous buds (254–517 per plant) on the upper surface of the rhizome of each species.

Global warming is having significant effects on fire regimes, especially in fire-prone habitats (Ooi et al., 2022). There are increases in the severity and frequency of fires, as well as changes in the time of year when fires occur (Ooi et al., 2022). Even if species of Myrtaceae resprout after fire, increased fire intensity and frequency can cause shifts from wet- to dry-plant communities (Furland et al., 2021; Fensham et al., 2024). Further, the pathogenic fungus *Austropuccinia psidii* may retard the regrowth of new stems and leaves following a fire. The impact of *A. psidii* on regrowth of tissues on nine Myrtaceae species following fire in a coastal heathland in New South Wales (Australia) varied between species and ranged between minor leaf damage to dieback and eventual death of the tree (Pegg et al., 2020).

For some species, e.g. *Eucalyptus pauciflora* in the subalpine zone in Victoria, Australia, increased fire frequency has raised serious concerns about the ability of the species to persist in its natural habitat (Coates, 2015). Increased temperatures, decreased precipitation and increased fire frequency are expected to negatively impact the tropical montane species *Melaleuca uxorum* and could result in its extinction as well as the loss of the local specialized flora in the habitat of this species being replaced by widely distributed species (Ford and Hardesty, 2012).

Formation of soil seed banks

In 170 soil seed bank studies, in which soil samples were collected after the seed germination season but before newly matured seeds were dispersed, i.e. samples potentially had at least a short-lived persistent soil seed bank, we found nine papers that contained information for species of Myrtaceae. Seven species in six tribes of Myrtaceae were listed in these nine papers (Table 7). The number of seeds per species in the seed bank ranged from 1 to 32 m^{-2}. However, for *Eucalyptus grandis*, the number of seeds was not given (Gonçalves et al., 2008), and, for *Tristaniopsis* sp., none of the seeds found in the soil samples germinated (Graham and Page, 2018). However, some soil seed bank studies conducted in habitats where species of Myrtaceae were growing did not contain any seeds of Myrtaceae (e.g. Vlahos and Bell, 1986; Yates et al., 1995; Sem and Enright, 1996; Wang, 1997; Hamilton-Brown

Table 5. Effect of dry heat treatments on seed germination of species of Myrtaceae

Species	Change in germination percentage compared with control	Heat treatment (°C)	Heat treatment duration (min)	References
Alutea maisonneuvei	0	100	5	Wright et al. (2019)
Baeckea diosmifolia	+5	100	5	Thomas et al. (2003)
Baeckea imbricata	−20	100	5	Thomas et al. (2003)
Baeckea utilis	−4	100	5	Thomas et al. (2007)
Calothamnus quadrifidus	−10	100	10	Hanley and Lamont (2000)
Darwinia biflora	+40	100	10	Auld and Ooi (2009)
Darwinia biflora	−20	120	10	Auld and Ooi (2009)
Darwinia dimiuta	+45	100	10	Auld and Ooi (2009)
Darwinia dimiuta	+5	120	10	Auld and Ooi (2009)
Darwinia fascicularis	+65	90	10	Auld and Ooi (2009)
Darwinia fascicularis	+10	120	10	Auld and Ooi (2009)
Darwinia glaucophylla	+80	90	10	Auld and Ooi (2009)
Darwinia glaucophylla	+9	120	10	Auld and Ooi (2009)
Darwinia procera	+10	80	10	Auld and Ooi (2009)
Darwinia procera	+45	100	10	Auld and Ooi (2009)
Eucalyptus blakelyi	−4	80	15	Clarke et al. (2000)
Eucalyptus dalrympleana	+5	80	15	Clarke et al. (2000)
Eucalyptus melliodora	−14	80	15	Clarke et al. (2000)
Eucalyptus pauciflora	+4	80	15	Clarke et al. (2000)
Eucalyptus viminalis	+5	80	15	Clarke et al. (2000)
Eucalyptus youmannii	−16	80	15	Clarke et al. (2000)
Kunzea ambigua	+35	50	5	Thomas et al. (2003)
Kunzea capitata	+5	100	5	Thomas et al. (2003)
Leptospermum juniperinum	+7	100	5	Ne'eman et al. (2009)
Leptospermum myrsinoides	+17	100	15	Wills and Read (2002)
Leptospermum polygalifolium	0	80	15	Clarke et al. (2000)
Leptospermum polygalifolium	−16	80	5	Ne'eman et al. (2009)
Leptospermum scoparium[a]	−2	80	60	Battersby et al. (2017b)
Leptospermum squarrosum	+3	100	5	Ne'eman et al. (2009)
Melaleuca acuminata	−10	100	5	Ne'eman et al. (2009)
Melaleuca hypericifolia	−2	100	5	Ne'eman et al. (2009)
Melaleuca squarrosa	−14	100	5	Ne'eman et al. (2009)
Micromyrtus minutiflora	+7[b]	80	30	Bangel et al. (2023)

All studies were conducted in Australia unless otherwise noted.

[a] Study conducted in New Zealand.

[b] Increase in number of seedlings in soil seed bank samples after soil heating.

et al., 2009; Bechara et al., 2020; Neto et al., 2021; Kraaij et al., 2024).

To help determine how long seeds of Myrtaceae live in the soil, seeds of various species have been placed in mesh bags and buried in the field. At intervals over a 1- to 3-year period, some of the buried seeds were exhumed, and the number of viable seeds was determined (Table 8). In general, seeds do not live for long periods of time in the soil. Of the 11 species listed in Table 8, only *Kunzea*

Table 6. Effect of smoke and/or smoke extracts on seed germination of species of Myrtaceae

Species	Change in germination percentage compared with control	References
Agonis linearifolia	+16	Roche et al. (1997a)
Astartea fascicularis	+20	Roche et al. (1997a)
Baeckea camphorosmae	+12	Roche et al. (1997a)
Baeckea diosmifolia	−10	Thomas et al. (2003)
Baeckea imbricata	+6	Thomas et al. (2003)
Baeckea utilis	+20	Thomas et al. (2007)
Calytrix breviseta	+13	Roche et al. (1997a)
Calytrix depressa	+30	Roche et al. (1997a)
Calytrix flavescens	0	Roche et al. (1997a)
Calytrix fraseri	+8	Roche et al. (1997a)
Calytrix tetragona	+13	Roche et al. (1997a)
Darwinia masonii	+69	Elliott et al. (2019)
Eucalyptus marginata	+4	Roche et al. (1997b)
Hypocalymma angustifolium	+26, +2	Dixon et al. (1995) and Norman et al. (2006)
Hypocalymma robustum	+1, 0	Norman et al. (2006)
Kunzea ambigua	+21	Thomas et al. (2003)
Kunzea capitata	+25	Thomas et al. (2003)
Leptospermum juniperinum	−6	Ne’eman et al. (2009)
Leptospermum myrsinoides	+18	Wills and Read (2002)
Leptospermum polygalifolium	−1	Ne’eman et al. (2009)
Leptospermum squarrosum	+1	Ne’eman et al. (2009)
Leptospermum spinescens	+39	Roche et al. (1997a)
Melaleuca acuminata	−5	Ne’eman et al. (2009)
Melaleuca cardiophylla	−3	Commander et al. (2009)
Melaleuca hypericifolia	−21	Ne’eman et al. (2009)
Melaleuca squarrosa	−11	Ne’eman et al. (2009)
Thryptomene baeckeacea	−33, +20[a]	Commander et al. (2009)
Thryptomene saxicola	0	Roche et al. (1997a)
Verticordia aurea	+16	Roche et al. (1997a)
Verticordia chrysantha	+42	Roche et al. (1997a)
Verticordia densiflora	+67, +28	Dixon et al. (1995) and Roche et al. (1997a)
Verticordia eriocephala	+35	Roche et al. (1997a)
Verticordia huegelii	+26	Roche et al. (1997a)
Verticordia nitens	+11	Roche et al. (2002)

[a] Seeds tested at 26/30 and 33/18°C, respectively.

ambigua and *K. capitata* had >50% viable seeds after 2 years (Auld et al., 2000).

Yates et al. (1995) buried seeds of *Eucalyptus salmonophloia* in soil at a depth of 1 cm in 3-cm-diameter areas in Western Australia in summer, autumn, winter and spring. Then, 2, 6 and 12 months after burial in each season, soil cores (from inside the 3-cm-diameter areas) were removed and germination of seeds was monitored. Some seeds buried in summer survived and germinated after 12 months of burial, but few or no seeds buried in autumn, winter or spring survived and germinated after 12 months of burial.

Seeds of 10 species of Myrtaceae were sown in moist soil in a shade house in Western Australia, and seed viability was determined initially

Table 7. Soil seed bank of Myrtaceae

Species	Tribe	Habitat	Number of seeds in samples	References
Baeckea ramosissima	Chamelaucieae	Alpine zone, Australia	3.3–13.3 m^{-2}	Venn and Morgan (2010)
Eucalyptus grandis	Eucalypteae	Dry Pinus plantation, Brazil	Present but no numbers given	Gonçalves et al. (2008)
Eucalyptus obliqua	Eucalypteae	Dry sclerophyll forest, Australia	50 seeds in 20 50 cm^3 samples	Barbour and Lange (1967)
Eucalyptus marginata	Eucalypteae	Jarrah forest, Australia	1 m^{-2}	Ward et al. (1997)
Eucalyptus resinifera	Eucalypteae	Rehabilitated bauxite mine, Australia	1.25 m^{-2}	Grant and Koch (1997)
Kunzea muelleri	Leptospermeae	Alpine zone, Australia	3.3–6.7 m^{-2}	Venn and Morgan (2010)
Metrosideros excelsa	Metrosidereae	Primary succession, New Zealand	1 seedling from 50 0.4 m^2 samples	Clarkson et al. (2002)
Micromyrtus minutiflora	Chamelaucieae	Cumberland Plain, New South Wales, Australia	32 m^{-2}	Bangel et al. (2023)
Syzygium hancei	Syzygieae	Subtropical rainforest, China	1 m^{-2}	Zhu et al. (2006)
Tristaniopsis sp.	Tristaniopsideae	Peat swamp forest, Kalimantan, Indonesia	Seeds found in samples but none germinated	Graham and Page (2018)

and after 1 year: *Agonis linearifolia*, 80 (initially) and 5% (after 1 year) viable seeds; *Astartea fascicularis*, 47 and 14%; *Baeckea camphorosmae*, 52 and 30%; *Calytrix breviseta* var. *breviseta*, 63 and 18%; *C. depressa*, 54 and 20%; *Verticordia aurea*, 60 and 40%; *V. chrysantha*, 63 and 38%; *V. densiflora*, 58 and 23%; *V. eriocephala*, 20 and 11% and *V. huegelii*, 26 and 3% (Roche et al., 1997a).

Seeds of *Baeckea gunniana* and *B. utilis* were buried in the Ginini Flats subalpine bog complex of the Brindabella

Table 8. Longevity of seeds of Myrtaceae placed in mesh bags and buried in soil in the field

Species	Tribe	Initial seed viability (%)	Period of burial (years)	Viable seeds at end of burial (%)	References
Darwinia biflora	Chamelaucieae	85	2	7–22	Auld et al. (2000)
Eucalyptus baxteri	Eucalypteae	50	1	0[a]	Andersen (1989)
Eucalyptus victrix	Eucalypteae	94	0.4	0	Florentine and Fox (2002)
Eugenia duthieana	Myrteae	–[b]	*c.* 0.25	0	Kanzaki et al. (1997)
Kunzea ambigua	Leptospermeae	73	2	60	Auld et al. (2000)
Kunzea capitata	Leptospermeae	92	2	40–70	Auld et al. (2000)
Leptospermum juniperinum	Leptospermeae	18	1	18	Andersen (1989)
Leptospermum myrcinoides	Leptospermeae	16	1	14	Andersen (1989)
Melaleuca quinquenervia	Melaleuceae				
FL (USA) flooded		5.6	1.5	0	Van et al. (2005)
FL (USA) nonflooded		8.8	2.3	5	Van et al. (2005)
Melaleuca quinquenervia *Australia, sandy lake* Shore	Melaleuceae	100	1	36	Baumann and Hewitt (2023)
Psidium cattleianum	Myrteae	86	0.54	0	Uowolo and Denslow (2008)
Verticordia fimbrilepis	Chamelaucieae	15	2.5	10	Yates and Ladd (2005)

[a] All buried seeds had germinated after 1 month; thus, no nongerminated viable seeds were present at the end of the study.
[b] No information.

Mountains (Australian Alps) in southeastern Australia (Guja and Brindley, 2017). After 27 months of burial, the exhumed seeds of both species germinated to *c.* 97%. The germination of *B. utilis* seeds at 25/15 and 20/10°C exhumed after 3, 6, 9, 12, 21 and 27 months revealed that dormancy cycling was occurring with seeds exhumed after 3, 12 and 27 months having the highest germination percentages and those exhumed after 9 and 21 months the lowest percentages.

The application of smoke to field sites has been shown to promote the germination of seeds in the soil. For example, smoke fumigation in *Banksia* woodland in Western Australia significantly increased seed germination of 15 plant taxa, but none of them were Myrtaceae (Dixon et al., 1995). Aerosol smoke and smoke-infused water applied to soil seed bank samples collected in Western Australia promoted seed germination of native grasses, sedges, herbs and woody species, including a few seeds of *Eucalyptus* sp., as well as seeds of weedy herbs in families other than Myrtaceae (Cochrane et al., 2007). In Queensland (Australia), soil seed bank samples from nonburned forest/woodland/shrubland habitats at four sites were subjected to heat and/or smoke treatments (Page, 2009). Following a fire in the four sites, additional soil samples were collected and germination of seeds in them was compared with that of seeds in the treated, nonburned samples. The number of seedlings (m^{-2}) in the heat and smoke-treated samples was higher than that in the control samples with no treatments. However, the number of species and the number of seedlings that emerged from the four sites after the fire were higher than in the nonburned control, except in the burned mixed *Eucalyptus* forest with lower numbers than in the control.

Smoke treatments have been applied in the field in relation to using the soil seed bank from *Eucalyptus*/*Banksia* woodlands in Western Australia as a source of seeds for rehabilitation of surface-mined sites (Roche et al., 1997b). Following smoke treatments of soil in the field, the number of species and the number of seedlings increased significantly, but often the density of Myrtaceae seedlings was low. For example, the density of *Eucalyptus marginata* seedlings increased from 0 to 1.67 m^{-2} after smoke treatments of soil in Western Australia (Roche et al., 1997b). Soil samples collected in a plant community dominated by *Eucalyptus cneorifolia* in South Australia were subjected to heat (80° for 60 min), smoke (from burning barley hay) and heat + smoke treatments in a greenhouse. Compared with the control, all treatments increased the germination of *Thryptomene ericaea*; and heat + smoke increased the germination of *Baeckea crassifolia*, *Calytrix glaberrina* and *E. cneorifolia* (Rawson et al., 2013).

Formation of aerial seed banks

Various species of Myrtaceae growing in fire-prone habits, e.g. in southwestern Australia (Lamont et al., 1991) retain seeds on the mother plant for extended periods of time (Table 9). Prolonged storage of viable seeds in the canopy is called serotiny, and it is more likely to be found in fire-killed, nonsprouting species than in species capable of resprouting after fire (Lamont et al., 1991, 2020). The seed-holding structures in serotinous Myrtaceae are woody capsules (Wellington and Noble, 1985) or infructescences of capsules (Whelan and Brown, 1998; Kim et al., 2009). These capsules can provide some protection of seeds from the heat of fires (Judd and Ashton, 1991; Judd, 1994; Whelan and Brown, 1998; Battersby et al., 2017b).

Table 9. Aerial seed bank (serotiny) in species of Myrtaceae

Species	Time on mother plant	References
Agonis, includes *Taxandria* and *Paragonis*	W	Lamont et al. (2020)
Angophora sp. (*Eucalyptus s.l.*)	W	Lamont et al. (2020)
Beaufortia spp.	W-M	Lamont et al. (2020)
Callistemon spp.	M-S	Lamont et al. (2020)
Callistemon glaucus	2–7 yr	Kim et al. (2009)
Callistemon rigida	3–30 yr	Ewart (1907)
Calothamnus spp.	M	Lamont et al. (2020)
Calothamnus quadrifidus	2–9 yr	Kim et al. (2009)
Conothamnus spp.	W	Lamont et al. (2020)
Eremaea spp.	W-M	Lamont et al. (2020)
Eucalyptus spp.	W-M	Lamont et al. (2020)
Eucalyptus baxteri	>2 yr	Andersen (1989)
Eucalyptus luehmanniana	–	Tozer and Bradstock (1997)
Eucalyptus platypus var. *acutifolius*	5 yr	Hardy (1926)
Kunzea spp.	W or nonserotinous	Lamont et al. (2020)
Kunzea ambigua	–	Judd and Ashton (1991)
Lamarchea spp.	W-M	Lamont et al. (2020)
Leptospermum spp.	W-M	Lamont et al. (2020)
Leptospermum juniperinum	3 yr	Andersen (1989)
Leptospermum scoparium	1 yr	Burrows (1997), Battersby et al. (2017a) and Harris (2002)
Lophostemon spp.	W	Lamont et al. (2020)
Melaleuca spp.	W-S	Lamont et al. (2020)
Melaleuca ericifolia	–	Hamilton-Brown et al. (2009)
Melaleuca parvistaminea	–	Jacobs et al. (2014)
Melaleuca quinquenervia	–	Rayachhetry et al. (1998) and Baumann and Hewitt (2023)
Metrosideros perforata	3 mo	Burrows (1997)
Metrosideros robusta	4 mo	Burrows (1997)
Metrosideros umbellata	6 mo	Burrows (1997)
Phymatocarpus sp.	W-M	Lamont et al. (1991, 2020)
Regelia spp.	W-M	Lamont et al. (2020)
Syncarpia spp.	W	Lamont et al. (2020)
Tristania spp.	–	Lamont et al. (1991, 2020)
Xanthostemon spp.	–	Lamont et al. (2020)

M-S, moderately to strongly serotinous; W, weakly serotinous; W-M, weakly to moderately serotinous; W-S, weakly to strongly serotinous; –, no information; mo, months; yr, years.

Aerial seed banks have advantages for the species, including protection of seeds from granivores on the soil surface such as ants, and the continuous supply of viable seeds although few or no seeds are produced in some years (Lamont and Enright, 2000). When the seeds are dispersed, they can germinate immediately because they are ND (e.g. Kim et al., 2009). However, habitat substrate moisture and temperatures must be favourable for germination at the time of seed dispersal because seeds of serotinous species quickly lose viability on/in the soil (Cowling and Lamont, 1987; Enright and Lamont, 1989), or they may be eaten by predators (Wellington and Noble, 1985).

In some serotinous species, capsules slowly open throughout the year, resulting in a low rate of seed dispersal, e.g. *Eucalyptus luehmanniana* (Tozer and Bradstock, 1997) and *Melaleuca quinquenervia* (Baumann and Hewitt, 2023). In fire-prone habitats in New Zealand, capsules of *Leptospermum scoparium* remain attached to the parent plant and do not open for 1 year or longer, but in other kinds of habitats capsules split and release the seeds within 1 year (Harris, 2002). Mature fruits remain alive on plants of *Callistemon rigida* for 3–4 years or longer, but they die and open when their water supply is stopped (Ewart, 1907). Fruits of *Melaleuca parvistaminea* dried and opened when plants were cut (Jacobs et al., 2014). In *M. ericifolia*, a wetland species, the peak of annual seed dispersal is in April, at which time water levels in the habitat are low (Hamilton-Brown et al., 2009). Fire is an important and reliable seed-releasing factor because it promotes massive capsule opening and seeds are released into sites where fire has removed the standing vegetation (e.g. dos Santos et al., 2015; Hewitt et al., 2015), i.e. fire prepares a good seed bed (Lamont and Enright, 2000). However, if a fire occurs after seed dispersal, it kills seeds on the soil surface (dos Santos et al., 2015).

Future challenges to maintain species richness of Myrtaceae

Invasive species of fungi

The fungus *Austropuccinia psidii* (syn. *Puccinia psidii*) was first identified on guava (*Psidium guajava*) in South America (Winter, 1884), but it now has been found on plants of Myrtaceae growing in many countries, including Australia (Glen et al., 2007; Pegg et al., 2017; Berthon et al., 2018), Mexico (Esperón-Rodríguez et al., 2018), New Caledonia (Giblin, 2013), New Zealand (Campbell et al., 2020; Jo et al., 2022), South Africa (Roux et al., 2013; Paap et al., 2023), Southeast Asia (Fensham et al., 2020; Liu et al., 2024) and the USA in Florida and Hawaii (Marlatt and Kimbrough, 1979; Loope, 2010). Many strains of *A. psidii* have been identified, and research is being conducted to determine which species of Myrtaceae are susceptible to them (Soewarto et al., 2020). Also, germplasm conservation, i.e. seed banking, has been initiated in Australia as a pre-emptive strategy to conserve Myrtaceae species susceptible to damage or death due to attack by *A. psidii* (Dalziell et al., 2024).

Austropuccinia psidii attacks young growing stems and leaves as well as fruits of many species of Myrtaceae, resulting in the death of the infected plant parts. In susceptible species of Myrtaceae, the fungus attacks and kills the regrowth of plants following die-back, prevents seed production and kills seedlings (Fensham et al., 2021). Myrtaceae growing in eastern and southern coastal areas as well as the northern tropical rainforests of Australia are at high risk for fungal infection. Berthon et al. (2018) estimated that under current climate conditions in eastern and northern Australia, 1285 species of Myrtaceae are at risk of being exposed to *A. psidii*. As early as 2007, tests showed that 73 of 83 native species in 16 of 19 genera of Australian Myrtaceae are susceptible to *A. psidii* (Glen et al., 2007), and Fernandez-Winzer et al. (2020) noted that the host range is 370 species of Myrtaceae.

Conditions for germination of spores of *A. psidii* are high humidity (or wetness), light for at least 6 h and warm temperatures (optimum of 25–28°C) (Campbell et al., 2020). Thus, it was hoped that in cool climates, e.g. New Zealand (Campbell et al., 2020), and dry climates, e.g. Western Australia (Berthon et al., 2018), there is a reduced risk of Myrtaceae being infected by *A. psidii*. However, this fungus has been detected in the northern part of Western Australia (Dalziell et al., 2024). Much concern is being expressed about global warming and the increased spread of *A. psidii* in places such as New Zealand (Jo et al., 2022), where climate warming could increase temperature enough to be favourable for the germination of *A. psidii* spores (Campbell et al., 2020). Unfortunately, *A. psidii* now has invaded the North Island of New Zealand, and 24 Myrtaceae species have been infected by it (Toome-Heller et al., 2020).

Due to repeated attacks by *A. psidii* on the regrowth of new stems and leaves, plants may die in 3–4 years, and some Myrtaceae in Australia, e.g. *Archirhodomyrtus beckleri*, *Decaspermum humile*, *Gossia hillii* and *Rhodamnia maideniana*, are in serious decline (Pegg et al., 2017). Species such as *Rhodamnia rubescens* and *Rhodomyrtus psidioides* (Carnegie et al., 2016; Fernandez-Winzer et al., 2020) in Australia, *Eugenia koolauensis* in Hawaii (USA) (Loope, 2010) and *E. gacognei* in New Caledonia (Fensham et al., 2020) are seriously threatened with extinction. Overall, the death of Myrtaceous species due to attack by *A. psidii* is affecting the structure of various plant communities in Australia, including wet sclerophyllous forests, rainforests, wetlands and swamps (Glen et al., 2007; Carnegie et al., 2016; Pegg et al., 2017; Fernandez-Winzer et al., 2020). Other invasive fungi such as *Phytophthora cinnamoni* (Carnegie et al., 2016; Fensham et al., 2020; McDougall and Liew, 2024; McDougall et al., 2024) cause die-back and death of Myrtaceae species. Also, the polyphagous short-hole borer/beetle *Euwallacea fornicatus* and its associated fungus *Fusarium* sp., which can lead to tree death, have been detected in Western Australia, and many Myrtaceae species can serve as hosts (Dalziell et al., 2024).

In the Hawaiian Islands, the vascular wilt fungi *Ceratocystis lukuohia* and the canker pathogen *C. huliohia* have caused the death of many *Metrosideros polymorpha* trees (Camp et al., 2019; Atkinson and Roy, 2023). Not only do the dying trees have a significant impact on forest structure, but this loss of trees has major negative effects on the native birds that depend on the flowers of *M. polymorpha* for food (Camp et al., 2019).

Other challenges and some possible solutions

The ever-increasing effects of human activities on natural ecosystems, in particular the destruction of natural habitats of species of Myrtaceae, are causing many species to become rare and in some cases on the verge of extinction (Breman et al., 2021). In addition to the potential loss of Myrtaceae species and their habitats, the animals in these habitats that use Myrtaceae species as food will be negatively affected, e.g. tropical dry forests in the Andes Mountains (Galván-Cisneros et al., 2023). These authors note that with the loss of animals seed dispersal across the landscape will be decreased, thereby reducing the regeneration of Myrtaceae species from seeds and restricting the distribution of species.

In addition to habitat destruction and loss of seed dispersal, global warming with increased temperatures and modified patterns of precipitation could intensify the negative effects of increased fire intensity and frequency in plant communities dominated by species of Myrtaceae and promote the spread of pathogenic fungi that can kill plants of Myrtaceae. The challenge for the future is to find ways to conserve species of Myrtaceae (and other plant families) that are being threatened with extinction.

Growing plants in botanical gardens (Breman et al., 2021) and storing seeds in seed banks (e.g. Pilatti et al., 2011; Hardstaff et al., 2022) are two conservation options. However, seeds of some Myrtaceae are desiccation-sensitive and can not be stored dry at low temperatures. Thus, cryogenic techniques for storage are being tested/used for pollen, seeds, embryos and shoot tips of Myrtaceae (Kaczmarczyk et al., 2011; Nadarajan et al., 2021). More conservation areas/preserves are needed to protect the habitat and species, e.g. in the Brazilian Cerrado (Oliveira et al., 2019) and the Atlantic Forest of eastern Brazil (Oliveira et al., 2021). Also, methods to propagate critically endangered species, especially from seeds, are needed (e.g. Sarcar et al., 2006; Montalyo et al., 2010; Raju et al., 2014).

One idea for conserving rare species of Myrtaceae, especially in Australia where some species are becoming rare due to fungal attack (Fensham et al., 2021) is to grow plants in regions where the climate is not suitable for the fungi. For example, growing species of Myrtaceae in locations with <900 mm annual precipitation potentially would prevent the plants from being attacked by *A. psidii* (Fensham et al., 2020). However, when growing species of Myrtaceae in new habitats, consideration needs to be given to edaphic factors such as acidity and fertility (Gomes et al., 2020).

Another possibility for conserving species of Myrtaceae threatened by *A. psidii* is to breed/select for resistance to pathogenic fungi (Chock, 2020; Smith et al., 2020; Yong et al., 2021). Further, a spray containing double-stranded RNA from *A. psidii* has shown effectiveness in both preventing and curing infection by *A. psidii* on *Syzygium jambos* trees (Degnan et al., 2023).

Concluding thoughts

In our comparison of the highly speciose, widely distributed plant families, the Asteraceae, Rubiaceae and Myrtaceae, which are the first, fourth and ninth most speciose angiosperm families, respectively (Mabberley, 2017), have been considered. The Asteraceae has trees, shrubs, lianas and herbs, with number of life forms decreasing with distance from the Equator, resulting in only herbs in the tundra (Baskin and Baskin, 2023). Only one kind of embryo (spatulate) is found in cypselae (seeds) of Asteraceae, and seeds may be ND or have PD. The six known types of nondeep PD occur in the Asteraceae, and, depending on habitat/vegetation region, PD is broken by warm summer or cold moist winter conditions. Thus, in Asteraceae, the great species richness is related to seed dormancy-breaking and germination requirements that closely coincide with a wide range of habitats throughout the world, except Antarctica.

The Rubiaceae has trees, shrubs, lianas/climbers and herbs. The highest species richness is in moist tropical forests, but some shrubs and herbs grow in temperate regions and a few herbs in the tundra. The Rubiaceae has five kinds of embryos, and seeds are ND or have morphological, physiological or morphophysiological dormancy. The greatest species richness in Rubiaceae is related to the diversity of seed dormancy, especially among tropical rainforest trees and semi-evergreen rainforest shrubs (Baskin and Baskin, 2024).

The Myrtaceae has only trees, shrubs and a few viny epiphytes but no herbs. The distribution of the family outside the tropics is in regions with a Mediterranean climate, e.g. Australia, South Africa and southern Europe/North Africa, and to a limited extent in temperate vegetation regions such as broad-leaved evergreen forests and grasslands. Five kinds of fully developed embryos are found in seeds of Myrtaceae; however, seeds are either ND or have PD, regardless of tribe, habitat/vegetation region or kind of fruit produced. Great species richness is found in fleshy-fruited Myrtaceae that grow in moist tropical regions. Seeds of fleshy-fruited species are either ND or have PD that is broken during exposure to relatively high temperatures, after which seeds germinate at high temperatures. The only known exception is for seeds of fleshy-fruited *Myrtus communis* that become ND during cold stratification. However, after cold stratification, seeds germinated to high percentages at 25–30°C than at 10–20°C (Benvenuti and Macchia, 2001). Also, seeds of *Baeckea utilis* buried in the subalpine of the Brindabella Mountains (Australian Alps) in southeastern Australia germinated to higher percentages when exhumed in spring (3, 12 and 27 months of burial) than those exhumed in winter or autumn (6, 9 and 21 months of burial) (Guja and Brindley, 2017). These results suggest that cold stratification during winter was breaking seed dormancy.

Great species richness is also found in dry-fruited Myrtaceae species that grow in seasonally dry tropical vegetation regions and in habitats with a Mediterranean climate, e.g. the matorral with hot, dry summer and cool, moist winters. For dry-fruited species, dormancy-break during the hot, dry season is followed by germination when the wet season begins. In tropical vegetation regions, temperatures are high when the wet season begins; thus, both dormancy-break and germination occur at high temperatures. In the matorral, seeds germinate over a range of low to high temperatures that include the temperatures (e.g. *c.* 15°C) of the cool, rainy season. Thus, in the Myrtaceae, we find many fleshy-fruited species in which both seed dormancy-break and germination occur during exposure to warm, wet conditions (e.g. rainforest) and many dry-fruited species in which dormancy-break at warm, dry conditions are followed by germination at either warm, wet (e.g. savannas) or cool-to-warm, wet (e.g. matorral) conditions.

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