

Weird and wonderful plants of South Australia

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Abstract: Far from being just a saltbush-strewn desert, the South Australian flora contains a wide variety of plants with unusual biologies and evolutionary histories. Ranging from bizarre tiny waterlily relatives that mimic grasses so well, it took DNA to sort them out; hybrid tobaccos that evolve by dropping chromosomes; diverse carnivorous and parasitic plants; to opportunistic desert dwelling lilies that can wait over a decade before carpeting the ground with masses of blooms after rain then disappearing in a few weeks. If you know where to look and when, the South Australian flora is anything but boring or uniform. However, if the DEWNR policy of "No Species Loss" is to be successful, it needs to be underpinned by one of "No Species Omitted" so that all species have a chance of being conserved.

Keywords: Flora, South Australia, effective conservation, biodiversity, species recognition

Introduction

South Australia is home to over 5,000 taxa of vascular plants in c. 166 plant families. There are 3,469 currently accepted names for native flowering plants (Kellermann & Lang, NRM Science Conference 2016 presentation), making it comparable to the floral diversity of the British Isles (4,800 spp.; Stace 2010) and 1.5 times the native flora of New Zealand (2,414 native spp.; de Lange & Rolfe 2010).

Despite the common perception that much of the vegetation of South Australia is desert-like saltbush or mallee, there is actually a wide range of ecosystems and vegetation types represented, with 16 of the 89 nationally defined IBRA bioregions and 72 of the 419 subregions present in South Australia (Australian Government Department of the Environment 2012). These also include locally biodiverse areas, such as Kangaroo Island, the Finders Ranges, the far southeast of the State and the Adelaide region (Specht 1972; Specht & Specht 1999; Wallace 1986). The Adelaide Bioregion in particular shows high floristic diversity and heterogeneity (Lange 1976; Martin & Specht 2005) and the area of greater Adelaide at the time of settlement had over 800 indigenous plant species in 21 distinct plant associations, though many of these are now threatened or extinct locally (Kraehenbuehl 1996, 2005; DEW 2013).

The long-term ecological effects on the evolution of the vegetation from rainforest to desert during the Cenozoic (Hill 1994, 2004; Hill *et al.* 2018) mean that there are many specialisations seen in the South Australian flora, which enable the plants to survive and evolve in unexpected ways. This also means that many of the plants have specific habitat or environmental requirements, making them potentially susceptible to climate change and impacts from anthropogenic interactions. Accordingly, if the flora of South Australia is to be conserved effectively, its biology and ecosystems need to be understood in order to ensure their longterm survival.

Is South Australia really 'saltbush central'?

Amongst the major plant families of the State, Chenopodiaceae (saltbushes) are a prominent element with 19 genera and 223 spp. (Wilson & Chinnock 2013) and a primary fodder source for sheep (often marketed as 'saltbush lamb'). Although recent classifications nest the family within an expanded Amaranthaceae (Angiosperm Phylogeny Group 2009, 2016), Australian flora treatments and many recent studies continue to recognise the family as distinct (Shepherd 2008). Chenopod-dominated ecosystems in Australia are predominantly located in the arid zone of southern Australia, often on saline/alkaline soils (calcarosols) or in association with coastal salt marshes and inland saline lakes and waterways (Specht & Specht 1999, 2005; Saintilan 2009). They form low shrublands in places like the Nullarbor Plain, the Lake Eyre Basin and Murray Basin (Specht 1972), but also occur as significant understorey components of mulga, mallee and other dry woodlands (Fig. 1A), as well as comprising the dominant vegetation in many waterlogged, hypersaline environments (Fig. 1B).

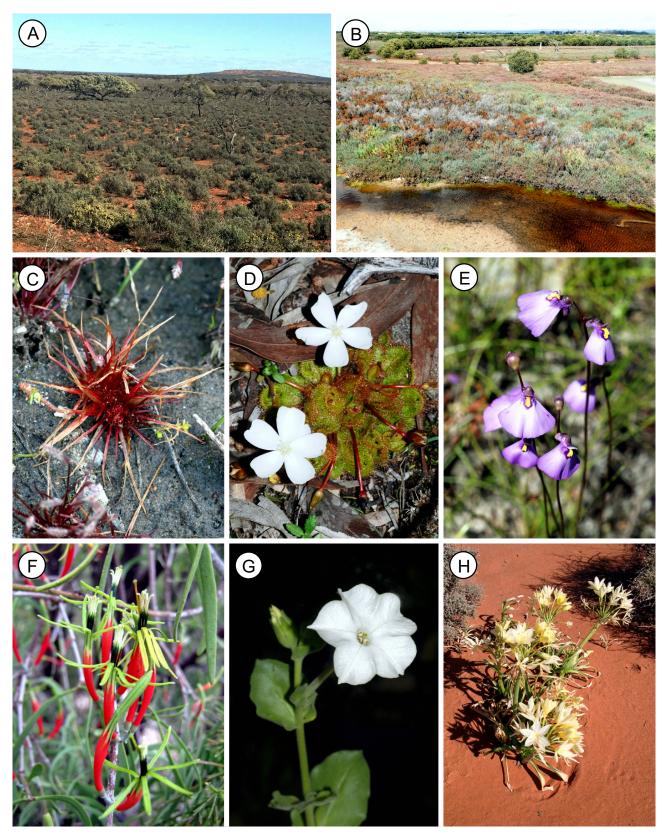


Fig. 1. Example vegetation and unusual floral types described in this paper. **A** Semi-arid chenopod-dominated shrubland with scattered Myall woodland near Iron Knob; **B** Hypersaline tidal chenopod saltmarsh, Torrens island; **C** Tiny grasslike waterlily relative *Trithuria submersa* (Hydatellaceae) at Muddy Flat Nature Reserve; **D** Dryland tuberous carnivorous sundew (*Drosera whittakeri*) at Anstey Hill Recreation Park; **E** Wetland-growing carnivorous bladderwort in the *Utricularia dichotoma* species complex at Muddy Flat; **F** Parasitic harlequin mistletoe (*Lysiana exocarpi*) at Anstey Hill Recreation Park; **G** Rare, short-lived perennial night-flowering desert tobacco *Nicotiana burbidgiae*, Witjira National Park; **H** Desert lily (*Crinum luteolum–C. flaccidum* species complex) two weeks after heavy autumn rain near Woomera. Photos: J.G. Conran.

However, most of these habitats have apparently only been widespread in Australia since the Oligocene, expanding throughout the Miocene and again in the Pliocene (Hill 1994, 2004; Hill et al. 2018; Byrne et al. 2011). The development of these ecosystems through long-term climate change has probably helped to drive evolution within both Chenopodiaceae and the wider Amaranthaceae (Kadereit et al. 2003), especially the genus Ptilotus (Hammer et al. 2015; Palmer et al. 2014), as well as within other high-diversity arid zone families and genera such as *Eremophila* (Scrophulariaceae [-Myoporaceae]; Chinnock 2007) and Goodeniaceae (Jabaily et al. 2014). This is in part related to biome conservatism in the region, where it was hypothesised that the arid zone Australian flora was derived from a more widespread and diverse sclerophyllous vegetation (Crisp & Cook 2013), including apparently fairly recent more mesic elements in areas which are now much drier (Sniderman et al. 2016).

Nevertheless, chenopods are not the only plants in the flora and given the breadth of ecosystems and taxa present in the State, there is a wide range of plants which might be regarded as weird and wonderful. Accordingly, the plants chosen here are a selection of taxa with particular characteristics which both make them of broader interest to the public, as well as in most cases having conservation and/or ethnobotanical relevance.

Primitive angiosperms

Hydatellaceae are a semi-aquatic family of tiny, grasslike plants (Fig. 1C) represented by the sole genus Trithuria with highly modified/reduced flowers largely confined to Australia and New Zealand, with a single species in South Australia (Conran 2011). However, molecular studies showed that they are not strange monocots, but rather Basal Angiosperms related to waterlilies in the Nymphaeales (Rudall et al. 2007; Saarela et al. 2007). They usually grow in temporarily inundated areas as short-lived aquatics (Iles et al. 2014), although the New Zealand submerged aquatic species can live for several years (Pledge 1974). The single South Australian member (T. submersa Hook.f.) belongs to a group of three closely related species (Sokoloff et al. 2008) and two well-separated lineages divided by the Nullarbor plain, possibly representing cryptic species (Iles et al. 2014; Marques et al. 2016) and requiring further study.

Carnivorous plants

The soils in Australia are some of the most nutrient deprived in the world. This has led to the evolution and radiation of plant carnivory (catching, killing and digesting insects) as a means of obtaining otherwise scarce essential nutrients. Although carnivorous plants in many other parts of the world tend to be swamp- or rainforest-associated, a significant number in Australia are dryland species, usually found in sclerophyllous heathlands and open forests (Lowrie 2014). However, as the vast majority of species are salt-sensitive, they are virtually absent from chenopod-dominated systems, to the point that the presence of *Drosera* spp. is considered to be a defining feature of heathlands and related vegetation in Australia (Specht & Specht 1999). In South Australia this means that they mainly occupy areas that have not been subject to recent marine incursion or the effects of dryland salinity. They are also very sensitive to soil nutrient poisoning and changes in water table regimes, making them useful early warning "canaries" of land degradation.

Droseraceae. Australia is the centre of diversity for the sundew family Droseraceae, but although the highest diversity is in south-west Western Australia, there are still c. 14 Drosera species in South Australia, where they occur in a range of habitats from swamps to dry heathland and open forest environments (Conran & Marchant 2011). Many of the South Australian species have tubers to allow aestivation over summer (Conran 2008), especially members of the locally diverse D. whittakeri Planch. (Fig. 1D) and D. peltata Thunb. species complexes (Lowrie & Conran 2008; Gibson et al. 2014). A red naphthoquinone dye derived from tubers of some of these species (especially Drosera whittakeri) was used for colouring string and decorating shields by the Kaurna people of the Adelaide region (Clarke 2013). This dye also shows antiseptic properties, but although related Drosera species are used in other countries, it is unclear whether the local ones were used by indigenous Australians. Some species may have been used by early settlers as a herbal remedy for respiratory disorders in place of the European D. rotundifolia L. (Williams 2010).

One carnivorous South Australian biogeographic oddity is Drosera stricticaulis (Diels) O.H.Sarg. Although previously regarded as a Western Australian endemic from heathlands east of Perth, it also occurs in South Australia on the lower Eyre Peninsula and on the top of Dutchmans Stern in the southern Flinders Ranges, c. 2000 km east of its Western Australian range. The South Australian localities are mainly erosional or plains landforms above 200 m altitude with infertile, Eocene-derived brown to red duplex or red loam soils over Cambrian or older rocks. This suggests that the species is a relictual vicariant in areas that are climatically similar (moderate winter rainfall, hot dry summers) on soils that have not been subject to past extensive marine incursion or inundation events leading to salinity (Conran & Lowrie 2007).

Lentibulariaceae. The bladderwort family is represented in Australia by the genus *Utricularia* (Fig. 1E), of which there are at least eight species present in South Australia, growing in damp low-nutrient soil or clean freshwater (Taylor 1986, 1989). These plants get their names from the small bladder-like traps with hinged doors growing along their stems or roots. The bladder of the trap is pumped empty of water and then trigger hairs near a hinged opening cause the trap to spring in response to the presence of prey which are then vacuumed inside and digested.

Stylidiaceae. The triggerplant family Stylidiaceae is represented by 2 genera (Stylidium and Levenhookia) and 14 species in South Australia. Some of these species are shared with Western Australia or the eastern states, but S. tepperianum (F.Muell.) Mildbr. is endemic to Kangaroo Island (Toelken 1986; Lowrie & Conran 2011). Although perhaps best known for their pollination biology, where a hinged and spring-loaded style forms a pollen presenter that springs up and clubs the pollinator to transfer pollen (Bourke 2009; Yeo 2012), the family was recently found to be apparently carnivorous (Darnowski et al. 2006; Darnowski 2017), trapping insects with mucilage-secreting glandular hairs held on their inflorescences and some floral parts that produce digestive enzymes (proteases). However, protocarnivory in Stylidium was challenged recently by Nge & Lammers (2018), based on $\delta 15N$ signatures that suggest their nitrogen is derived mainly from nonanimal sources.

There is considerable variation within several of the species, especially those that are widespread across southern Australia (Toelken 1986) and there are known chromosome races within the south-east Australian *S. graminifolium* complex (Jackson & Wiltshire 2001; Raulings & Ladiges 2001). The taxonomy of some of these variants requires further study to determine if there are regionally distinct and ecologically threatened taxa in need of better conservation.

Parasitic plants

A parasitic plant is an angiosperm that attaches itself to another plant using a modified root (haustorium), morphologically and physiologically linking it to its host to obtain water, nutrients and/or photosynthates (Kuijt 1969; Kuijt & Hansen 2015). There are c. 4,100 species of parasitic plants in 19 families scattered across the angiosperm evolutionary tree (Nickrent & Musselman 2004). Parasitic plants can be divided morphologically into root and aerial parasites, as well as physiologically into hemiparasites (partly photosynthetic) and holoparasites (nonphotosynthetic and fully dependent on the host). In South Australia there are nine genera of root parasites (20 spp., including two holoparasites) and six genera (21 spp.) of aerial parasites. These are members of seven different families: Santalaceae (5 genera/16 species), Loranthaceae (4/17), Orobanchaceae (2/3), Lauraceae (1/5), Olacaceae (1/1) and Convolvulaceae (1/2). In addition, worldwide about 400 angiosperms and one gymnosperm are mycoheterotrophs, where they parasitise fungi, often also allowing them to exploit resources from other plants via mycorrhizal connections with the fungus. This group also occurs in South Australia, the most common examples being certain

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orchids, such as the hyacinth orchid (*Dipodium*) and potato orchid (*Gastrodium*).

Mistletoes. The best known of the aerial hemiparasites are the mistletoes, represented in South Australia by the families Santalaceae (1/1) and Loranthaceae (4/17) (Lang & Barlow 2013). Some of these plants have evolved to look like their host (some resemble Eucalyptus, others Casuarina), with some highly hostspecific (Downey 1998), whereas others such as the Ĥarlequin mistletoe, Lysiana exocarpi (Behr) Tiegh. (Fig. 1F), attack a wide range of native and introduced hosts. Parasites have the ability to undergo regular mass flowering and fruiting because the resources used are stolen from their host and they often show poor water control relative to their host. They produce berries with sticky seeds that are ingested by birds and defecated or wiped onto host branches, with the primary root an haustorium, grafting the seedling to host.

Ecologically, mistletoes tend to be seen as pests of native trees, but in reality they are a critical part of the landscape, providing food over summer for nectar- and fruit-eating birds (Reid 1990), as well as nesting sites (Cooney & Watson 2008). They are also the sole larval food plants for several endangered lycaenid butterflies (Symon 1980).

Mistletoes have been used medicinally for a long time, including in traditional Australian medicine (Williams 2013). Antibacterial activity has been documented in *Amyema quandang* (Lindl.) Tiegh. (Palombo & Semple 2001) and other species apparently show some activity against *Candida albicans* and are the subject of active research by the Australian Bioactive Compounds Centre (ABCC: https://www.adelaide.edu.au/environment/ abcc/).

Santalaceae. The sandalwood and quandong family Santalaceae is a group of hemiparasitic root parasites closely related to Viscaceae. There are five genera and 15 species in South Australia (Lepschi & Barlow 2012) and although they are all photosynthetic, many species are leafless or with reduced or yellowish foliage (e.g. *Exocarpos, Choretrum*). Development of a succulent fleshy fruit or pedicel as a reward in most species means that they are animal-dispersed (Kuijt & Hansen 2015). Emu-dispersed species usually have large, gizzard-proof seeds (Calviño-Cancela *et al.* 2006) and often show mass fruiting due to reduced restrictions on resource availability (Davies & Kenny 2013).

Quandong, *Santalum acuminatum* (R.Br.) A.DC., fruits are grown commercially as bush food and the fleshy fruits of *Exocarpos* species (native cherries) are also edible, particularly those of *E. cupressiformis* Labill. Several members of the family are also used medicinally (Williams 2010), as a result many *Santalum* species (sandalwoods) are under threat due to wood harvesting for essential oils (Teixeira da Silva *et al.* 2018). Some Australian sandalwood species are further threatened by the rarity or extinction of key seed dispersers, such as *S. spicatum* (R.Br.) A.DC., which appears to have been dispersed largely by endangered or now locally extinct bettongs (*Bettongia* spp.) (Murphy *et al.* 2005; Chapman 2015).

Orobanchaceae. The eyebrights (Euphrasia) are represented in the State by two hemiparasitic species, one with 6 subspecies (Barker 1982, 1987) whereas the holoparasite broomrape (Orobanche) has three species in South Australia, two weeds (one declared) and a native taxon (O. cernua Loefl. var. australiana (F.Muell. ex Tate) J.M.Black ex Beck), which is listed as 'extremely restricted' with 'very high' taxonomic uniqueness for the Adelaide and Mount Lofty Ranges region (DEH 2008). The precise status of the variety as a separate entity from the widespread weed O. cernua var. cernua is the subject of ongoing research, but genetic differences between these taxa were identified by Park et al. (2007). Because broomrape is a major weed of crops in much of the world, the status of this native taxon is important in order to determine whether control of the former and/ or conservation of the latter should be the main focus of resources (Barker 1986; DEH 2008).

Eyebrights are annual or short-lived perennial hemiparasites, used in herbal medicine in many countries (Grieve 1971), but there do not seem to be reports for use of native species, though this may in part reflect their relative rarity. In South Australia many of the taxa have localised or patchy distributions and some are threatened by habitat loss (Barker 1982, 1987), with *Euphrasia scabra* R.Br. listed by Jessop (1977) as endangered in South Australia.

Lauraceae. *Cassytha* (snotty gobbles) is the only parasitic member of this family of otherwise large rainforest trees. It is the only one to occur naturally in South Australia, where there are five species of this rootless, scrambling haustorial hemiparasite (Weber 1981, 2007). The stems make haustoria whenever they touch any plant (including themselves). Like mistletoes, the berry-like pomes contain sticky seeds and are similarly dispersed by frugivorous birds.

Cassytha has a long tradition of medicinal use in Africa and India and has been shown to contain a range of chemicals potentially active against cancer and trypanosomiasis (Hoet *et al.* 2004). However, although the centre of diversity for the genus is Australia (Weber 2007), few species have been studied for bioactivity and these are a current focus of the ABCC. One species of *Cassytha* is also useful in controlling the spread of invasive leguminous shrubs such as Scotch broom (*Cytisus scoparius*) where the parasite can severely impact host photosynthesis (Prider *et al.* 2009; Shen *et al.* 2010).

Convolvulaceae. *Cuscuta* (Dodder) is a rootless, leafless, twining aerial holoparasite with three native and three introduced declared noxious species in South Australia (Johnson *et al.* 2014). Superficially the plants resemble *Cassytha*, but they are unrelated and

instead members of the Bindweed and Morning Glory family (Convolvulaceae). Aggressive multi-host nonphotosynthetic parasites, there is evidence of differential host plant selection or avoidance, based on chemical recognition (Runyon *et al.* 2006), but in addition to the problem of direct attacks on host plants, the genus is also a vector for cucumber mosaic virus (CMV) (Francki *et al.* 1979). There are three native species in South Australia (Johnson *et al.* 2014) and these are likely to be targeted as collateral damage in control efforts to remove the noxious species and/or to control CMV, so care needs to be taken when eradication programs are underway that they are not eliminated.

Desert-driven specialisations

Plants in the arid zone of Australia mostly fall into three broad categories based on their response to the environment: tolerators, avoiders and ephemerals (Recher et al. 1986); that is: shrubs and trees that withstand harsh conditions; perennials that die down to underground structures like bulbs or tubers, only emerging for a short time in good seasons; and shortlived plants that only grow following rain events, surviving in between as seeds, respectively. The majority of chenopods are tolerators, as is Eremophila (Myoporacae), whereas other prominent families in the region include ephemerals like the Asteraceae (daisies) and Solanaceae (bush tomatoes and native tobaccos) and mixed response families like Amaranthaceae (Ptilotus) and Leguminosae (Acacia and pea flowers), mostly with ephemeral and tolerator species.

Avoiders include diverse 'lilies', particularly members of the Colchicaceae (*Wurmbea*) and Amaryllidaceae (*Crinum*), but these and ecologically similar plants are poorly known [and data deficient] as they often emerge for a few weeks following rain events at specific times of the year and may go decades without appearing or flowering (e.g. Bates 2007; Lykos 2011). This makes cataloguing their diversity and relationships with closely-related or apparently conspecific Western Australian taxa (Hopper & Gioia 2004), let alone understanding their biology for effective conservation, extremely difficult.

Microhabitat responses also seem to have contributed to the radiation of native tobacco in Central Australia (*Nicotiana*) (Fig. 1G), where more than 12 native taxa have evolved following dispersal of a polyploid hybrid from South America c. 10 million years ago. The hybrid ancestor was dispersed to Africa and Australia, with subsequent radiation in the central desert through a combination of microniche specialisation and chromosomal alterations (Marks *et al.* 2011; Chase *et al.* 2018). Given the indigenous medicinal use of some species (Symon 2005) and the unexplored potential of several newly discovered taxa (Chase *et al.* 2018), this genus is a current focus of research by the ABCC.

Implications for biodiversity and conservation

Although the current DEWNR policy towards biodiversity in South Australia follows the "No Species Loss Conservation Strategy" (DEH 2007), there are some issues related to this. Firstly, in order to leave none behind there has to be a complete inventory; however, there are taxonomic uncertainties for numerous plant groups in the State, largely due to under-sampling in remote areas at the times when ephemeral or shortlived season-responsive taxa might be present (e.g. the Nullarbor and Great Victoria Desert), but also due to improved species delineation and recognition of cryptic taxa through the application of new technologies. However, for this to happen there is a critical need for more researchers trained in both classical field- and morphology-based techniques, as well as cutting edge molecular systematics to be employed in this task. Otherwise many species are going to become extinct before they can be recognised and conserved.

Tied to this is the need to conserve species by conservation of their ecosystems and that requires both a good understanding of spatial vegetation heterogeneity and the ecology of the different species, their interaction with other species and responses to microhabitat variation (e.g. desert *Nicotiana* species). However, for South Australia much of the data currently available are at too broad a scale to provide clear information to ensure that the (often competing) requirements for all the species being conserved in a given area can be met effectively.

There is also increasing awareness of the critical importance of herbaria, such as the State Herbarium of South Australia (AD), for allowing the mapping of changes to the historical distributions for taxa that are now under threat, data on their phenology, ecology and variability, as well as increasingly, sources of DNA to investigate their historical phylogeography and genetic variability. All of these data are critical if the remaining populations of native plants in the South Australian flora are to be conserved and managed effectively into the future, particularly in the face of climate change and increasing human-induced disturbance. However, before DNA can be utilised effectively to conserve the South Australian flora, herbarium and/ or voucher specimens of suitable quality have to be collected, identified (or verified in the case of historical collections), curated and databased effectively so that the results of any value-added research can be translated back into the field, both for ground truthing and the implementation of any management outcomes. All of these activities require skill sets which are themselves becoming increasingly rare.

For example, co-occurring chenopod species in semiarid rangelands show differential grazing responses (e.g. Heshmatti *et al.* 2002) and this leads to potential conservation issues. In order to maintain biodiversity, stocking rates need to be monitored carefully to maintain a balance between grazing-susceptible more palatable species (decreasers), unpalatable weedy species (increasers) and those species largely unaffected by grazing pressure (tolerators) (Lange 1972), as well as to preserve soil surface structure in grazed systems (e.g. Lunt *et al.* 2007).

Similarly, examination of all the known localities for the single species of Hydatellaceae in South Australia (Trithuria submersa) shows that many of the historical records for this plant in South Australia are no longer located in viable habitats due to salinity or habitat loss. The family is restricted to the margins of shallow, seasonally damp to wet and open freshwater swamps often as highly localised and vulnerable populations, with flowering in late spring tied to the draw-down of the water level. Although plants have been observed to reappear in some of these swamps after more than 10 years of drought and appear unaffected by fire, the plants and their habitats are highly susceptible to salt, nutrient runoff, water table changes or weed incursion and also seem to be reliant in part on regular disturbance to prevent replacement by perennial shrubs (Sokoloff et al. 2011). The same issues apply to many of the small semi-aquatic or helophytic herbs with which they grow, including various Drosera, Utricularia, Euphrasia and Stylidiaceae species (Conran & Lowrie 2006). However, this vulnerability makes them useful species to monitor for signs of environmental degradation in these generally rare and increasingly threatened South Australian ecosystems.

Accordingly, if the weird and wonderful flora of South Australia is to be protected into the future, the laudable objective of "No Species Loss" needs to incorporate the recognition of the need for a policy of "No Species Omitted" to ensure that as many species in the State and the environments in which they grow have been recognised and understood well enough that their conservation and management in the long term can be accomplished. The role of herbaria and the need for more trained systematists with both field and lab-based skills cannot be underestimated if these goals are to be achieved.

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