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Biology of Invasive Plants

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Biology of Invasive Plants 2. *Lycium ferocissimum* Miers

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Scientific Classification

Domain: Eukaryota

Kingdom: Plantae

Phylum: Spermatophyta

Subphylum: Angiospermae

Class: Dicotyledonae

Order: Solanales

Family: Solanaceae

Subfamily: Solanoideae

Tribe: Lycieae

Genus: *Lycium*

Species: *ferocissimum* Miers (Miers 1854)

Synonyms: *Lycium campanulatum* E.Mey. ex C.H.Wright and *Lycium macrocalyx* Domin., *Lycium afrum* L. (misapplied), *Lycium europaeum* L. (misapplied), and *Lycium horridum* Thunb. (misapplied)

EPPO Code: LYUFE

Names and Taxonomy

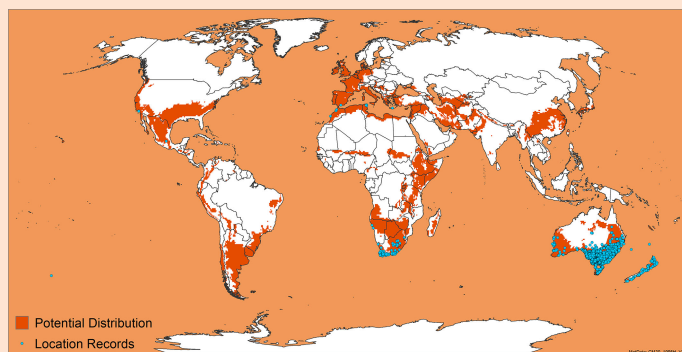
The name of the genus *Lycium* originates from the Greek name *lykion* for a thorny shrub, derived from *Lycia*, the name of an ancient country in Asia Minor where a similar spiny shrub was found. The specific epithet *ferocissimum* comes from the Latin *ferox*, meaning “bold” or “fearless,” referring to the very spiny nature of the shrub (Green 1994; Parsons and Cuthbertson 2001).

Common names for *Lycium ferocissimum* are African boxthorn, boxthorn, snake-berry (*slangbessie* in Afrikaans). “Boxthorn” is believed to be derived from the Dutch *boksdorn*, the name Dutch settlers to South Africa gave the plant (Parsons and Cuthbertson 2001).

Lycium ferocissimum belongs to the genus *Lycium*, tribe Lycieae, within the subfamily Solanoideae of the family Solanaceae (Levin et al. 2011; Särkinen et al. 2013; Stevens 2019). Members of *Lycium* tend to be woody shrubs with short lateral branches, usually ending in a spine, and are deciduous or evergreen (Webb et al. 1988). *Lycium* species typically inhabit arid to semiarid environments (Adamson 1938; Levin et al. 2007). The genus includes approximately 90 species, widely distributed, with centers of diversity in southern South America, southwestern North America, and southern Africa (Levin et al. 2011; Stevens 2019). It is considered likely that *Lycium* arose in the Americas (probably South America) and then dispersed to Africa, Eurasia, and elsewhere, including a single species (*Lycium australe* F. Muell.) to Australia (Fukuda et al. 2001; Levin et al. 2007). The taxonomy and phylogeny of *Lycium* is highly complex, with evidence of hybridization and many undescribed species within numerous species complexes now emerging in South African populations (Levin et al. 2007; McCulloch et al. 2020; Venter 2000). Despite this, recent genetic analyses found no evidence of hybridization with any other *Lycium* species in Australia (McCulloch et al. 2020). The fleshy, bird-dispersed fruits of *Lycium* species most likely contributed to the cosmopolitan distribution of the genus (Fukuda et al. 2001; Levin et al. 2011). *Lycium ferocissimum* is a species native to southern Africa and part of the “Old World” clade within *Lycium* (Levin et al. 2007). Close relatives of *L. ferocissimum* in this clade, especially the Eurasian goji berry species *Lycium barbarum* L. and *Lycium chinense* Mill., are also recognized as invasive plants (Randall 2017).

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***Lycium ferocissimum* at a glance . . .****Impacts**

- Forms spiny, impenetrable thickets
- Competes with native vegetation
- Provides shelter for pest organisms such as rabbits and rats

**Dispersal**

- Primarily seed dispersed by many types of wildlife, predominantly birds

**Management**

- Can regenerate from rootstock, stems, and seed, so needs an integrated management program applied over many years
- Biological control methods under investigation in Australia

**Biosecurity**

- Historically deliberately imported as seeds for hedging
- Spread by birds and other animals to islands and at invasion fronts
- Potential for expansion into Mediterranean climates, especially Europe and North and South America

**Description**

Lycium ferocissimum is a densely branched perennial shrub that can grow up to 5-m high (but more often 2 to 3 m) and up to 5-m across (though most commonly up to 3 m) (McCulloch et al. 2020; Parsons and Cuthbertson 2001) (Figure 1A). However, in wind-prone situations such as coastal sites, its habit is often quite different. There it is wind-pruned, very dense, and often relatively short, with its shape determined by the predominant wind direction (Noble and Rose 2013; Taylor and Tennyson 1999) (Figure 1B).

Stems are silver-gray when young, turning light brown to gray as they mature, and becoming fissured with age. The main stems grow large spines (to 15 cm), with smaller spines on branches. Leaves of *L. ferocissimum* (to 40-mm long and 20-mm wide) have very short petioles; are slightly fleshy, simple and entire, ovate, obovate to elliptic in shape, and glabrous; and cluster at nodes (Figure 2). Inflorescences are solitary or in pairs and form in the leaf axil (Figure 2). They are 8 to 12 mm in diameter and 10- to 12-mm long. Petals are white to lilac with purple markings toward the inside (Figure 2). The pedicel is 5 to 16 mm, there is a calyx with five unequal sepals, there are five petals, and there are 5 to 6 exerted stamens. Flowers (Figure 2) are present most of the year but are most prolific during summer. The fruit is a smooth round berry, initially green, but ripening to orange-red, up to 12 mm in diameter and with a prominent calyx, and typically containing between 20 and 70 dull yellow seeds (Blood 2001; Green 1994; McCulloch et al. 2020; Muyt 2001; Parsons and Cuthbertson 2001; Purdie et al. 1982) (Figure 2B).

Economic Importance and Environmental Impacts**Detrimental**

Lycium ferocissimum is an invasive weed of environmental and agricultural ecosystems. It is considered a Weed of National Significance in Australia (Australian Weeds Committee 2013), and both environmental and agricultural stakeholders consider it to be difficult and costly to control (Cousens et al. 2013; Ireland et al. 2019b) (Table 1). By forming impenetrable spiny thickets, the plant impedes the habitat needs of wildlife and movement of livestock, outcompetes native vegetation, and can harbor nonnative pest species such as rabbits (*Oryctolagus cuniculus* L.), rats, and fruit flies (Noble and Adair 2014; Noble et al. 2014; Noble and Rose 2013).

In Australia, displacement of native vegetation and the encouragement of establishment and persistence of other invasive pest species such as rabbits and rats have been identified as the main environmental impacts, while damage to machinery and prevention of stock access to water have been identified as the main agricultural impacts (Ireland et al. 2019b).

In an environmental context, *L. ferocissimum* is known to displace native vegetation and degrade faunal habitat, directly impact native fauna (e.g., by ensnaring birds), and likely facilitates the degradation of cultural heritage sites (Noble and Adair 2014; Noble et al. 2014; Noble and Rose 2013). *Lycium ferocissimum* adversely impacts a significant range of vegetation species and communities.

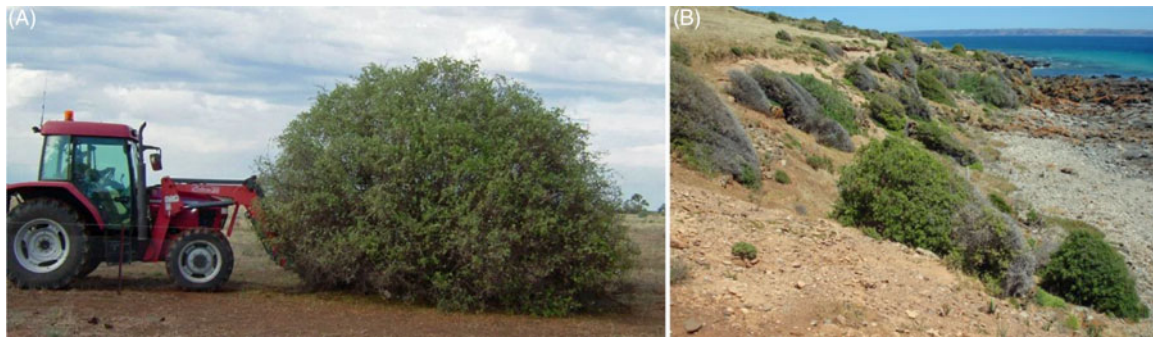


Figure 1. Growth form of *Lycium ferocissimum* (A) in pastures and (B) on the South Australian coastline, where the species is wind-pruned by prevailing winds. (Photo credits: (A) New South Wales National Parks and Wildlife Service; (B) Matt Rose, Natural State.)



Figure 2. *Lycium ferocissimum* flowers (A and B) and fruit (B). (Photo credit: Evans Mauda.)

It is considered a threat to biodiversity in at least two rangeland biodiversity hot spots in Australia (Martin et al. 2006) and is invasive in a number of global biodiversity hot spots, including southwest Australia, the Mediterranean Basin, and New Zealand (GBIF 2020; Mittermeier et al. 2011). In some coastal areas of Australia and New Zealand, *L. ferocissimum* has become the only woody plant present, changing the vegetation structure in some small island and coastal dune environments (Lavers 2014; Timmins and Mackenzie 1995; Webb et al. 1988; Ziegler and Hopkins 2011). In salt marshes where *L. ferocissimum* has become established in Australia, bird species assemblages and behavior appear altered by the presence of the weed (Carlos et al. 2017). This reduces habitat suitability for some native species and makes these areas more hospitable for pest animals such as starlings (*Sturnus vulgaris* L.) or more aggressive raptor birds, which may make use of the increased roosting sites afforded by *L. ferocissimum* to prey on other native and exotic fauna.

Lycium ferocissimum can significantly alter and interfere with native fauna habitats. Several native Australian animals have been recorded as being adversely impacted by the presence of *L. ferocissimum*. The fine, dense root mass of *L. ferocissimum* has been observed to impede the burrowing efforts of short-tailed shearwaters (*Ardenna tenuirostris* Temminck) (Lawley et al. 2005). Thorns of *L. ferocissimum* can ensnare, injure, and kill coastal native birds, including the short-tailed shearwater, New Zealand fairy prions (*Pachyptilla turtur* Kuhl), and white-faced storm petrels (*Pelagodroma marina* Latham) (Lohr and Keighery 2016; Noble

and Rose 2013; Phillips 2014; Taylor 1968; Ziegler and Hopkins 2011). On islands off South and Western Australia, *L. ferocissimum* disrupts seal (*Arctocephalus* spp.) and sea lion (*Neophoca cinerea* Péron) breeding, by displacing the native shrub *Nitraria billardieri* DC., which is used by seals for sheltering pups (Hussey et al. 2007; Western Australian Herbarium 1998–). *Lycium ferocissimum* does not provide the equivalent quality of nursery habitat, leaving pups more vulnerable to predation (Humphries et al. 1994).

Cultural heritage site degradation may be facilitated by the presence of *L. ferocissimum*. Coastal areas in Australia, where *L. ferocissimum* is known to occur (Cousens et al. 2013; Erkelenz 1994; Lohr and Keighery 2016), are also likely locations for indigenous heritage such as middens, artifacts, and other evidence of occupation (Cann et al. 1991; Veth et al. 2017). These sites may be degraded through increased rabbit and fox (*Vulpes vulpes* L.) burrowing associated with *L. ferocissimum*, which may cause direct or indirect damage to artifacts and historical sites (Noble and Adair 2014; Noble et al. 2014; Noble and Rose 2013).

In an agricultural context, *L. ferocissimum* has been associated with reducing access to pasture and water in grazing systems (Brown 1969; Lee 1978), harboring pest animals such as rabbits, foxes, and pest birds, and puncturing tires and injuring livestock and people with its thorns (Hoskin 2006; Noble and Adair 2014). It also hosts key insect pests and diseases of concern to agriculture, including the Queensland fruit fly *Bactrocera tryoni* Froggatt (Plant Health Australia 2017) and tomato-potato psyllid *Bactericera cockerelli* Sulc (Vereijssen et al. 2018). *Bactericera cockerelli* is a North

Table 1. Major impacts of *Lycium ferocissimum* in Australia, as perceived by stakeholders (Ireland et al. 2019b).

Impact area	Impact type
Agricultural and environmental Agricultural	Difficult to control
	Expensive to control
	Reduces stock access to pasture and water
	Injurious to machinery (i.e., tire punctures)
	Injurious to stock (i.e., physical injury, toxicity)
Environmental	Acts as a reservoir for plant pests (i.e., aphids, fruit fly)
	Interferes with crop growth/reduces crop yield
	Displaces native vegetation
	Encourages other invasive species (i.e., rabbits, foxes, starlings) to establish and persist
	Threatens biodiversity
	Degrades fauna habitat

American psyllid species that, in its place of origin, overwinters on several native and nonnative *Lycium* species (Cooper et al. 2019; Thinakaran et al. 2017). It is a major pest of solanaceous crops, as it is the vector of the plant bacterium *Candidatus Liberibacter solanacearum* Jagoueix et al. (CLso), the causal agent of zebra chip disease in potatoes (*Solanum tuberosum* L.) (Liefing et al. 2009; Munyaneza 2012). Populations of *B. cockerelli* may build up or survive on overwintering hosts such as *L. ferocissimum* and then colonize commercial crops in spring (Vereijssen et al. 2018), so the presence of *L. ferocissimum* in agricultural areas is likely to be of significant concern when managing populations of the psyllid.

Beneficial

Lycium ferocissimum may also provide significant social amenity and refuge benefits to native flora and fauna, particularly where native habitat has been removed or degraded. It was considered a valued hedge and windbreak in southern Africa (Venter 2000), Australia (Herbiguide 2015; Parsons and Cuthbertson 2001), and New Zealand (Lambert 2015) during the 1800s and early 1900s. It is also known to provide refuge for more palatable plant species in heavily grazed situations where those species might otherwise be lost (Rutherford et al. 2014). For example, on the Eyre Peninsula in South Australia, *L. ferocissimum* may protect threatened west-coast mint bush (*Prostanthera calycina* F.Muell. ex Benth.) juveniles from grazing (Pobke 2007). In Africa, *L. ferocissimum* is recognized for playing a similar role as a component of native vegetation (Todd 2000). Within its native range in South Africa, *L. ferocissimum* is recognized for its potential in restoring degraded landscapes. Its hardiness, thorns, and limited palatability mean it has the capacity to withstand herbivore-driven degradation (Rutherford et al. 2014). There, it is considered also to have potential as a keystone restoration species, due to its regular and large crops of fruits, which are attractive to birds that might then disperse other native plant species (van der Vyver et al. 2012).

In regard to fauna, *L. ferocissimum* is considered to confer significant benefits to a range of vulnerable Australian species, though these interactions are complex. For example, the critically endangered orange-bellied parrot’s (*Neophema chrysogaster* Latham) habitat in coastal Victoria and South Australia now includes *L. ferocissimum* thickets. However, where the parrot’s habitat is intact, *L. ferocissimum* and other invasive species are a threat to the parrot’s foraging habitat (Orange-bellied Parrot Recovery Team 2006). In some coastal locations, little penguins (*Eudyptula minor* J.R. Forster) and yellow-eyed

penguins (*Megadyptes antipodes* Hombron & Jacquinot) may utilize the shelter of thorny *L. ferocissimum* shrubs for nesting and protection from predators (Lalas et al. 1999; Noble and Rose 2013). Positive correlations have been documented between wombat (*Vombatus ursinus* Shaw) burrows and *L. ferocissimum* in Australia (Roger et al. 2007; Taylor 1993). However, this beneficial role of *L. ferocissimum* for wombats is likely related to the species replacing the structural role played by native shrubs, which may have been displaced by *L. ferocissimum* or other edaphic or anthropogenic causes. The nationally endangered southern brown bandicoot (*Isodon obesulus* Shaw) and nationally vulnerable eastern barred bandicoot (*Perameles gunnii* Gray) in Australia are both known to consume *L. ferocissimum* fruit (Heinsohn 1964; Moloney 1982; Quin 1985). These species may also gain predator shelter benefits from *L. ferocissimum*, particularly where native alternatives are not available. The nationally vulnerable Australian native greater stick-nest rat (*Leporillus conditor* Sturt) is reported to use *L. ferocissimum* on islands off South Australia for shelter from its primary predator, barn owls (*Tyto delicatula* Gould). The rats have been observed feeding on *L. ferocissimum* foliage, and when the rodent numbers are exceptionally high, consumption of bark has also been evident. The greater stick-nest rat has also been observed using *L. ferocissimum* segments as building material to construct its stick nests (J van Weenen, South Australian Government, personal communication, 2013). On islands in the Bass Strait of Australia, Tasmanian pademelons (*Thylogale billardierii* Desmarest) have been recorded as being common in *L. ferocissimum* bushes, having climbed to various heights up to 3 m (Figure 3). Pademelons were found to have established routes up through the bushes, allowing them access to browse leaves and fruit (Driessen 2011). *Lycium ferocissimum* has also been recorded as providing some cover for Tasmanian devils in Australia (*Sarcophilus harrisii* Boitard) (Guiler 1970). While a range of both common and endangered native birds and mammals make use of *L. ferocissimum* for supplemental habitat and food in its invaded range (Carlos et al. 2017; Noble and Rose 2013; Zann 1994), these relationships are complex, and the overall nature of the impact of *L. ferocissimum* presence on biodiversity in these regions is unclear.

Geographic Distribution

Lycium ferocissimum is native to South Africa, with a nonnative global distribution that is spatially limited, but intensive where it occurs, particularly in Australia and New Zealand. The plant is naturalized and invasive in parts of Europe and has limited naturalized presence in the United States. (Figure 4A).

In the plant’s native range of South Africa, it is widespread and native to the Eastern and Western Cape provinces (Venter 2000). Further afield from its native range within South Africa there are distribution records for populations in the Free State, Kwazulu-Natal, Mpumalanga, and Northern Cape provinces of South Africa, and northern Lesotho, most likely occurring due to the species being planted as a hedge (GBIF 2020; Venter 2000; Welman 1993; Welman 2003) (Figure 4B). While *L. ferocissimum* has been recorded as occurring in Namibia (GBIF 2018), the veracity of these records is questionable, especially given the age of the records (1963 and 1976) and the complexities of *L. ferocissimum* and *Lycium* spp. identification and taxonomy (Levin et al. 2007; McCulloch et al. 2020; Venter 2000).

Lycium ferocissimum is recorded as being present in a number of northern African and European nations within the Mediterranean Basin. It is recorded as introduced to Tunisia (Monastir, Nabeul, and Siliana governorates) (GBIF 2020;



Figure 3. Tasmanian pademelons on Inner (West) Sister Island climb to 3 m to feed on *Lycium ferocissimum* leaves and fruit. (Photo credit: Michael Driessen.)

Venter 2000) and introduced and naturalized in coastal Morocco (Gharb-Chrarda-Béni Hssen, Marrakech-Tensift-Al Haouz, and Rabat-Salé-Zemmour-Zaer regions) (GBIF 2020; Lambinon and Lewalle 1986; Venter 2000), coastal southwestern Spain (Málaga Province, plus a single introduced site in the city of Guadalajara in central Spain) (GBIF 2020; Perez Latorre et al. 2006), and Cyprus (recorded from shores of Lake Akrotiri in the south, to abandoned mine sites in the northeast) (Cetinkaya and Sozen 2011; Gallego 2012; Hand 2000; İlseven and Baştaş 2018; Meikle 1985; Perez Latorre et al. 2006; Peyton and Mountford 2015; Venter 2000). The most recent European records of the species, in the southern provinces of Cagliari and Medio Campidano on the island of Sardinia, Italy (Lazzeri et al. 2013), and in the coastal area of Aude in France (EPPO 2020; Fried 2020), are considered to be invasive and naturalized in nature, respectively. Two unverified records of *L. ferocissimum* were also made on the Greek island of Crete in 2017 and 2018 (GBIF 2020).

In the United States, *L. ferocissimum* has been recorded as naturalized, but rare, in California (Calflora 2013; DiTomaso and Healy 2007; GBIF 2020; USDA-NRCS 2019).

Many unverified iNaturalist records of *L. ferocissimum* have also been made, most notably in the Philippines and Mexico (GBIF 2021). These are both single, unverified iNaturalist records in the City of Davao on the island of Mindanao in the Philippines and on the northern outskirts of Mexico City in Mexico. EPPO (2020) also lists Indonesia and Bolivia as countries with distributions of *L. ferocissimum*, but it is unclear where these records are derived from. Similar to the records of *L. ferocissimum* in Namibia,

given the complexities of *L. ferocissimum* and *Lycium* species identification and taxonomy (Levin et al. 2007; McCulloch et al. 2020; Venter 2000), the veracity of all of the distribution records noted should be considered questionable and not necessarily representative of the true range of this species.

It is only widespread and troublesome on a national scale in Australia and New Zealand (Parsons and Cuthbertson 2001) (Figure 4C). In New Zealand, it is present on both the North and South Islands, where it is largely restricted to coastal areas; here it persists in large agroecosystem distributions as established hedges, with spread also recorded into forest and scrub reserves (Breitwieser et al. 2019; Popay et al. 2010; Timmins and Mackenzie 1995; Timmins and Williams 1991) (Figure 4C). In Australia, *L. ferocissimum* is widespread in coastal to semiarid inland habitats and islands of southern Australia, with records from every jurisdiction (GBIF 2020; Hussey et al. 2007; Noble and Rose 2013; Parsons and Cuthbertson 2001) (Figure 4C). It is found predominantly in the southern part of the Australian continent in coastal and island situations (except Queensland). *Lycium ferocissimum* occurs on islands off the southern half of the Western Australian coastline, along with the islands of the Great Australian Bight and Bass Strait, and on Lord Howe Island and Norfolk Island (Erkelenz 1993; Green 1994; Keighery 2010; Keighery et al. 2002; Lawley et al. 2005; Western Australian Herbarium 1998–; Ziegler and Hopkins 2011). Inland, *L. ferocissimum* is abundant in areas of New South Wales, Victoria, and South Australia, where it is a common weed of semiarid pastures and rangelands and is often found growing along dry streambeds (Parsons and Cuthbertson 2001). It has a lesser, but significant presence in southeast Queensland, southern Western Australia, and Tasmania. *Lycium ferocissimum* currently does not occur in higher-altitude areas of Australia, having no substantial presence in the Victorian, New South Wales, and Tasmanian alpine areas.

Invasion History

Lycium ferocissimum has not been widely distributed throughout the world and is only considered invasive in Australia and New Zealand, where records indicate that from at least as early as 1845 it was deliberately imported for use as a hedge and windbreak (Parsons and Cuthbertson 2001). It was considered naturalized in Australia by the mid-1800s, and New Zealand by the late 1800s, and an invasive plant in Australia by the early 1900s, and in New Zealand by the 1950s (Fuller 1998; Lambert 2015; Parsons and Cuthbertson 2001; Webb et al. 1988). In the mid-2010s it was reported as invasive in southern Sardinia, Italy (Lazzeri et al. 2013), aside small-scale introduced and naturalized populations in the Mediterranean Basin nations of Spain, Morocco, Cyprus, and Tunisia (Gallego 2012; Hand 2000; Meikle 1985; Perez Latorre et al. 2006; Venter 2000). Most recently it was recognized as naturalized in the coastal area of Aude in France in 2019 (Fried 2020), increasing concern for the invasive nature of *L. ferocissimum* in Europe, with an EPPO alert being published in July 2020 (EPPO 2020).

The first reports of *L. ferocissimum* in Australia consist of its listing on the Tasmanian nursery list in 1845. At that time, several names were used (e.g., *Lycium europaeum* L.), but there is little doubt reference was being made to *L. ferocissimum* (Parsons and Cuthbertson 2001). *Lycium ferocissimum* was advocated as an excellent hedgerow and windbreak plant and was deliberately introduced and distributed for this purpose. There remain situations in Australia where it continues to be maintained as a

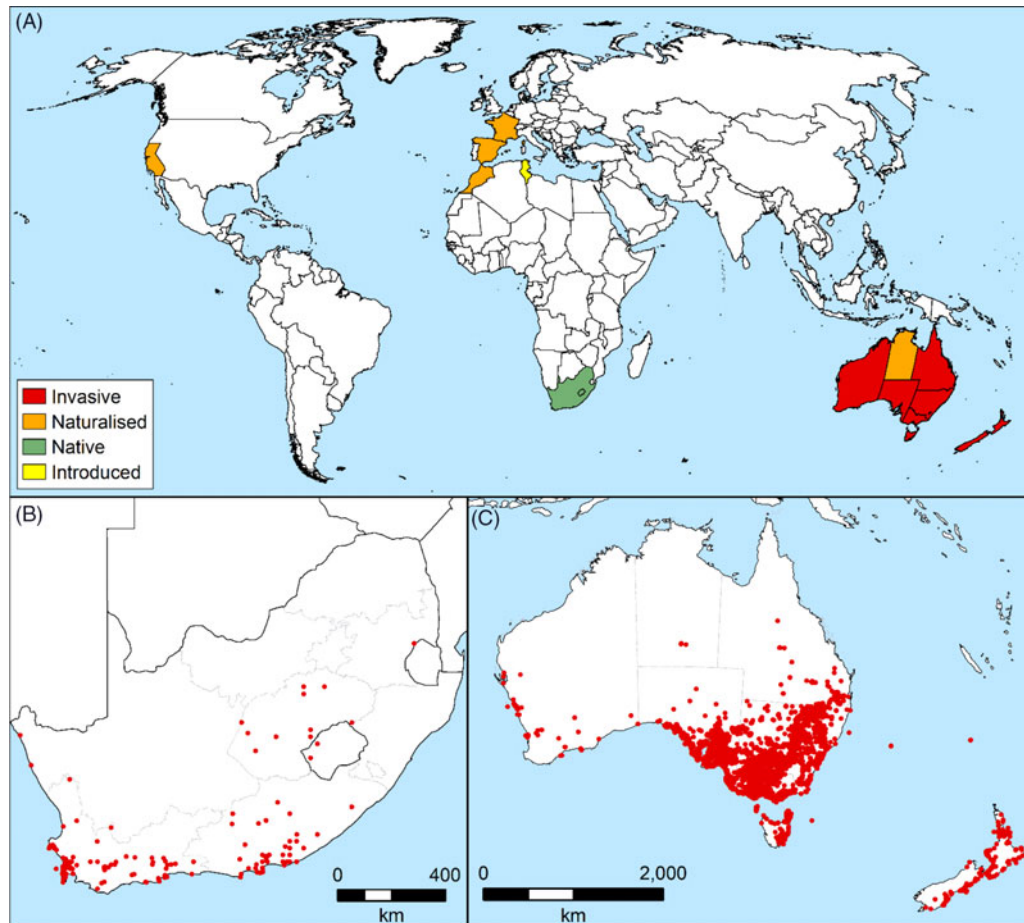


Figure 4. *Lycium ferocissimum* (A) global, (B) native, and (C) Australasian invaded range distributions. Invasion status and distribution inferred from the literature (see text for full details) and records downloaded from GBIF.org (GBIF 2018, 2020) (projected for B and C).

hedgerow. Australian *L. ferocissimum* populations likely originated in the Western Cape of South Africa (McCulloch et al. 2020), which is consistent with the most likely historical trade routes and plant production for trade occurring through the port of Cape Town. Occurrence of *L. ferocissimum* at Camden Park, NSW, was recorded by 1850, and by 1857 and 1858, it was recorded at Hobart and Adelaide botanic gardens, respectively (Parsons and Cuthbertson 2001). In Victoria during the late nineteenth century, the planting of *L. ferocissimum* hedges was a requirement of certain leases in the Western District. However, by 1904 the species was declared noxious in certain areas of Victoria (Parsons and Cuthbertson 2001). *Lycium ferocissimum* was first noted as a pest in Queensland in 1917 (Fuller 1998). In 1925, the South Australian Government enacted the Noxious Weeds (African boxthorn) Act of 1925 to identify *L. ferocissimum* as noxious (except where it had been grown as a hedge before the commencement of the Act) (Government of South Australia 2004). Various invasive plant and weed legislations have been imposed in regard to *L. ferocissimum* over the past century in Australia. Currently, *L. ferocissimum* is recognized as a Weed of National Significance (Australian Weeds Committee 2013) and is a declared or controlled weed in all jurisdictions (Agriculture Victoria 2017; Biosecurity SA 2017; Business Queensland 2016; Department of Agriculture, Water and the Environment 2021; Department of Environment and Natural Resources 2018; Department of Primary Industries

Parks Water and the Environment 2019; Department of the Environment Climate Change Energy and Water 2009; NSW DPI 2019), except Western Australia (Department of Primary Industries and Regional Development 2019).

Lycium ferocissimum was introduced to New Zealand in the 1870s as a hedging plant (Hoskin 2006; Wishart 2018). It was offered for sale through the Caledonia Nursery in New Plymouth from at least 1883, and there are records of it being propagated in the nursery industry in the 1920s (Hoskin 2006). It proved particularly popular in the Taranaki region, with some historical hedges still in existence today (Lambert 2015). Boxthorn honey and jam were popular products produced from the species, and the wood was found to burn extremely hot and was used in domestic fires (Hoskin 2006). Similar to the Australian experience, farmers soon found the species to be weedy and problematic to manage, especially before the advent of mechanical hedge trimming (Brown 1979; Hoskin 2006; Lambert 2015). *Lycium ferocissimum* hedges are still widespread in New Zealand, albeit becoming reduced in number (Hoskin 2006). The presence of these hedges in proximity to cropping regions has proved problematic in the management and control of pests such as the tomato-potato psyllid, *B. cockerelli* (Vereijssen et al. 2018). *Lycium ferocissimum* is now classified as a plant pest in New Zealand, with restrictions on further propagation of the species across the country (Lambert 2015).

Elsewhere in the world *L. ferocissimum* may have been introduced in the mid- to late twentieth century, much later than in Australia and New Zealand. *Lycium ferocissimum* was first recorded in the southern Californian county of Los Angeles in 1978, and to this date has not been recorded outside Los Angeles (Calflora 2013; GBIF 2020), indicating the species may not be especially invasive in this environment. In the Mediterranean Basin, *L. ferocissimum* was first recorded as deliberately introduced into a plantation in Cyprus in the early 1900s and naturalized there by 1985 (Meikle 1985), in Tunisia in 1964 (Venter 2000), Morocco by 1986 (Lambinon and Lewalle 1986), and as a hedge in Guadalajara, Spain, by 1986 (Perez Latorre et al. 2006). The species continues to spread naturally via birds in Cyprus (İlseven and Baştaş 2018) and has been considered as a candidate species for abandoned mine site phytostabilization efforts (Cetinkaya and Sozen 2011). The species was well established as a single population in abandoned cropping fields at the mouth of the Vélez River in Malaga, Spain, in the Iberian Peninsula by the time it was first recorded in 2006 (Perez Latorre et al. 2006). These plants most likely formed part of an abandoned hedge on the property, and despite the production of large numbers of fruit and surrounding fertile soils, the species has not been observed to spread (Perez Latorre et al. 2006). *Lycium ferocissimum* was most recently recorded in southern Sardinia for the first time in 2012 (Lazzeri et al. 2013), with at least seven established populations of between two to several hundred plants. While the nature of introduction of these populations is as unclear, Lazzeri et al. (2013) are suitably concerned about continued spread of the species via bird feeding, and research into the biology of *L. ferocissimum* in Sardinia in order to better manage the species is ongoing (Podda et al. 2015).

Dispersal and Establishment

Dispersal of *Lycium ferocissimum* occurs almost always by seed, though the species has been recorded to spread by vegetative means as well. Broken stem and root fragments can remain viable for months before taking root when in contact with moist soil (Muyt 2001). Seeds are dispersed when animals consume fruit and subsequently excrete viable seed. Seed and vegetative material can be dispersed by water, machinery, agricultural products, and soil (Muyt 2001; Noble and Rose 2013; Parsons and Cuthbertson 2001).

The common presence of *Lycium ferocissimum* around the base of trees, fences, and poles in Australia implicates birds as dispersal agents (Parsons and Cuthbertson 2001), and gulls (Laridae) are known to feed on and spread seed in coastal environments (Calvino-Cancela 2011). In Australia alone, at least 21 species of birds, along with four mammal species and two reptile species, have been recorded as consuming *L. ferocissimum* fruit (Noble and Adair 2014) (Table 2). Though many of these records, such as for the southern brown bandicoot (Quin 1985), are limited in extent, the relationship between starlings and *L. ferocissimum* is significant in Australia. The presence of starlings appears to assist the invasive establishment of *L. ferocissimum* (Noble and Adair 2014). Double endochory of *Lycium intricatum* Boiss seed has been recorded in the Canary Islands (Nogales et al. 1998). This occurs where shrikes (*Lanius excubitor* L.) regurgitate pellets containing the remains of lizards (*Galotia atlantica* Peters & Doria) that have fed on *L. intricatum* fruit. The seeds from shrike pellets had higher germination rates than those from both uneaten fruits and lizard droppings. The treatment type and retention times in the guts of

Table 2. Fauna recorded to consume *Lycium ferocissimum* fruit in Australia (Noble and Adair 2014).

Animal type	Species ^a
Bird	Blackbird (<i>Turdus merula</i> L.)
	Buff-banded rail (<i>Gallirallus philippensis</i> L.)
	Cockatiel (<i>Leptolophus hollandicus</i> Kerr)
	Currawong (<i>Strepera fuliginosa</i> Gould)
	Dusky moorhen (<i>Gallinula tenebrosa</i> Gould)
	House sparrow (<i>Passer domesticus</i> L.)
	Kori bustard (<i>Ardeotis kori</i> Burchell)
	Little raven (<i>Corvus mellori</i> Mathews)
	Little wattlebird (<i>Anthochaera chrysoptera</i> Latham)
	Mistletoe bird (<i>Dicaeum hirundinaceum</i> Shaw)
	Mulga parrot (<i>Psephotus varius</i> Clark)
	Pacific gull (<i>Larus pacificus</i> Latham)
	Purple-crowned lorikeet (<i>Glossopsitta porphyrocephala</i> Dietrichsen)
	Red wattlebird (<i>Anthochaera carunculata</i> Shaw)
	Starling (<i>Sturnus vulgaris</i> L.)
	Silver gull (<i>Chroicocephalus novaehollandiae</i> Stephens)
	Silvereye (<i>Zosterops lateralis</i> Latham)
	Singing honeyeater (<i>Lichenostomus virescens</i> Vieillot)
	Spiny-cheeked honeyeater (<i>Acanthagenys rufogularis</i> Gould)
	Stubble quail (<i>Coturnix pectoralis</i> Gould)
	Yellow-faced honeyeater (<i>Lichenostomus chrysops</i> Latham)
Mammal	Eastern barred bandicoot (<i>Perameles gunnii</i> Gray)
	Red fox (<i>Vulpes vulpes</i> L.)
Reptile	Southern brown bandicoot (<i>Isodon obesulus</i> Shaw)
	Tasmanian pademelon (<i>Thylogale billardieri</i> Desmarest)
	Cunningham's skink (<i>Egernia cunninghami</i> Gray)
	Shingleback (<i>Tiliqua rugosa</i> Gray)

^aIntroduced species are listed in bold.

each species are thought to be the factors influencing germination (Nogales et al. 1998). Whether spread of *L. ferocissimum* is likewise influenced by double endochory is unknown.

Invasion Risk and Pathways

Bioclimatic modeling indicates that *L. ferocissimum* has a limited global distribution, relative to the total area of projected climatically favorable regions in which the species may establish and persist (Kriticos et al. 2021) (Figure 5). These climatically favorable regions are dominated by coastal Mediterranean and humid subtropical climates on all continents. Given the opportunity, *L. ferocissimum* could establish in climatically favorable areas of the coastal western and inland southeastern U.S. states, the central highlands of Mexico, central-eastern Argentina, much of Uruguay, parts of southeastern Brazil, some southern coastal regions of Chile, and highlands throughout tropical South America, as well as provinces in southwestern China, including Yunnan (Kriticos et al. 2021) (Figure 5). *Lycium ferocissimum* is not yet widely distributed in climatically suitable invaded regions in Europe and the Mediterranean Basin (Kriticos et al. 2021), and further spread here may be of concern, especially given the relatively recent invasion and proliferation of the species in Sardinia, Italy (Lazzeri et al. 2013), and naturalization in the coastal area of Aude in France (EPPO 2020; Fried 2020).

While *L. ferocissimum* is already present and widely distributed through much of its projected highly suitable habitat range in Australia and New Zealand, one exception appears to be southwestern Western Australia (Kriticos et al. 2021) (Figures 4C and 5). There are several potential explanations for

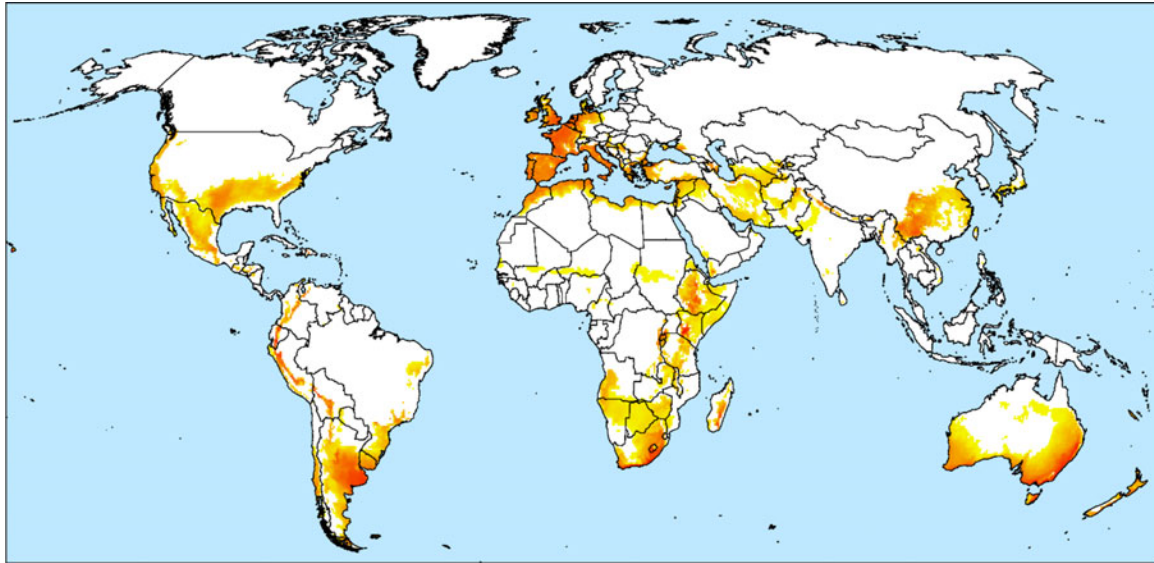


Figure 5. Global projected climatic suitability for *Lycium ferocissimum*. The projection is under the 1981–2010 climate normals, as modeled using CLIMEX by Kriticos et al. (2021). Increased intensity of red color, starting from yellow, indicates higher climatic suitability.

this, including the possibility that *L. ferocissimum* was introduced to Western Australia more recently than elsewhere, or that available distribution data are not as comprehensive as elsewhere, making distribution mapping misleading (Noble and Adair 2014). Another possibility is that the absence thus far of an established population of starlings (*Sturnus vulgaris* L.) and other dispersers in southwestern Western Australia is restricting the distribution of *L. ferocissimum* (Harris and McKenny 1999; Taylor 1968). Nonetheless, indications are that the range of *L. ferocissimum* continues to extend in southern Western Australia (Abbott et al. 2000; Keighery 2010; Keighery et al. 2002). Much of the North Island of New Zealand may also be climatically suitable for *L. ferocissimum* establishment and spread (Kriticos et al. 2021) (Figure 5), although intensive management here may be reducing its spread.

While it has been suggested that the potential distribution of *L. ferocissimum* may be limited to areas where the plant is intentionally planted (CABI 2018), no specific study of the pathways of introduction and establishment of the species has been conducted, and this hypothesis has not been tested. The recent incursion and spread of the species on the island of Sardinia (Lazzeri et al. 2013), as well as continued spread throughout much of Australia outside regions where it was historically planted as a hedge, suggest that given the chance to flower and fruit, the species can become quite invasive and abundant in climatically and edaphically suitable regions of the world. Natural competition and enemies within the native range likely keep the species in check, but it would appear that the species may have the capacity to spread further east and northward and establish more abundant populations in the South African provinces of Kwazulu Natal and Mpumalunga should some of these limitations be removed (Kriticos et al. 2021). Where naturalized populations have been recorded in California, USA, close to the metropolis of Los Angeles (GBIF 2018), there seem to be few areas of suitable habitat for the species to spread into, which may explain its limited distribution in this region. In the Mediterranean Basin, the species may be able to spread farther into areas projected to be climatically suitable along the northern coasts of Morocco, Algeria, and Tunisia, much of Mediterranean Europe, and perhaps as far north as the south of the United Kingdom and into the Netherlands and northwest

Germany. Numerous populations of *L. ferocissimum* in coastal regions of Sardinia in Italy and Aude in France are of concern, as spread of the species may accelerate as fruiting increases and birds feed and disperse the seed to neighboring islands and coastlines. The existence of *L. ferocissimum* on the Greek island of Crete reported in 2017 and 2018 (GBIF 2020) could prove problematic if verified, especially given the projected climatic suitability of this island and coastal mainland Greece (Kriticos et al. 2021).

Habitat

Climate

Lycium ferocissimum occurs across a diverse range of temperate (Group C) and dry (Group B) Köppen-Geiger climate types (Hijmans et al. 2005; Köppen 1936; Kriticos et al. 2012). In South Africa, *L. ferocissimum* predominantly occurs in temperate oceanic (Cfb), cold semiarid (BSk), and warm-summer Mediterranean (Csb) climatic areas, though the recorded species' distribution does extend into areas characterized as hot semiarid (BSh), hot (BWh) and cold (BWk) desert, subtropical highland (Cwb; also in Lesotho), and humid subtropical (Cfa) climates. In Australia, the species predominantly occurs in warm-summer Mediterranean (Csb), as well as cold semiarid (BSk) climatic areas, with some extensions into temperate oceanic (Cfb), hot-summer Mediterranean (Csa), and humid subtropical (Cfa) climates. In New Zealand, the species only occurs in the temperate oceanic (Cfb) climatic zone, which encompasses the whole country. In California, *L. ferocissimum* has been recorded in predominantly cold semiarid (BSk) regions, along with singular sightings in hot (Csa) and warm (Csb) summer climates. Most climatic areas where *L. ferocissimum* occurs in the Mediterranean Basin are hot-summer Mediterranean (Csa) climates, including the southern provinces of Sardinia, where the species is considered invasive.

Plant Community

Lycium ferocissimum is associated with a range of other flora, including coastal fynbos native vegetation in South Africa (Cowling et al. 1995), meadows along riverbeds in Spain (Perez

Latorre et al. 2006), and salt-tolerant shrubs and grasses on Middle Island, off the coast of southern Australia (King et al. 2015). In Cyprus it is often recorded in association with *Eucalyptus* spp. (İlseven and Baştaş 2018; Peyton and Mountford 2015), an observation also made in Australia, which may relate to roosting sites for birds that have fed on *L. ferocissimum* berries. In Australia, *Lycium ferocissimum* is found in a breadth of plant communities from semiarid rangelands through to coastal vegetation and offshore islands (Noble and Rose 2013).

Substrate and Soil Types

In its native range in southern Africa, *L. ferocissimum* is found on sandy soils and dry stony flats (Coates Palgrave et al. 2002; Cowling et al. 1995; Webb et al. 1988). Outside its native range, it has been recorded growing on all soil types, including saline, sandy, volcanic, undisturbed and disturbed, and low- and high-fertility soils (Dodson 1974; Haegi 1976; Lee 1978; Parsons and Cuthbertson 2001; Perez Latorre et al. 2006; Webb et al. 1988). It can occur as a halophyte in the presence of sandy or volcanic soils in Australia, New Zealand, Cyprus, and Italy (Dodson 1974; Haegi 1976; Lazzeri et al. 2013; Peyton and Mountford 2015; Webb et al. 1988). Interestingly, the distribution of *L. ferocissimum* in southern Queensland is centered on the fertile soils of the Darling Downs and on fertile dry scrub soils west of Ipswich, indicating a preference for more arable soils in that state (DAF 2020; Lee 1978). It is often found close to permanent or seasonal water supplies and dry creek beds in arid and semiarid environments (Haegi 1976; Parsons and Cuthbertson 2001), indicating that water availability may be more restricting than soil type for this species. In New Zealand, it is widespread in coastal areas and is notably capable of colonizing unstable dunes (Webb et al. 1988).

Lycium ferocissimum thrives on sites where soil disturbance has occurred (Cetinkaya and Sozen 2011; Erkelenz 1993; Peyton and Mountford 2015; Rutherford et al. 2014), including low-fertility roadsides, pastures, and within abandoned cropping areas (Lee 1978; Matthews 1982; Perez Latorre et al. 2006). In a South African study, *L. ferocissimum* was the one shrub species that persisted in the face of high-intensity grazing and increases in most soil nutrient levels (Rutherford et al. 2014). Where it infests coastal and island environments containing dense bird colonies, evidence suggests that *L. ferocissimum* may be tolerant of highly nutrient-rich soils (and perhaps soils with high pH) (Gillham 1963).

In relation to soil types, *L. ferocissimum* is predominantly associated with low-fertility sandy soils (xerosols, desert soils with low levels of organic matter; and arenosols, low-fertility sandy soils), and to a lesser extent with clay-based soils, which may lose fertility quickly under cultivation (luvisols), and soils known to limit root growth (leptosols) within its native range of South Africa (FAO 2007; GBIF 2018). By contrast, in Australia, *L. ferocissimum* is associated with largely undifferentiated soils (regosols), infertile acidic soils (podzols), and low-fertility sandy soils (xerosols), and to a lesser extent with soils associated with inland water bodies or proximity to the ocean and clay-based soils, which may lose fertility quickly under cultivation (luvisols). In New Zealand, *L. ferocissimum* is largely associated with tropical “brown soils” (cambisols), which are also associated with rapid losses in fertility and degradation when under cultivation (similar to luvisols), and to a lesser extent with undifferentiated soils (regosols), nutrient-rich volcanic soils (andosols), and clay-based soils (luvisols).

Lycium ferocissimum was also found to most commonly be associated with medium- to coarse-textured soils (FAO 2007;

GBIF 2018). Medium-textured soils were dominant in their associations with *L. ferocissimum* in South Africa and New Zealand, while coarse-textured soils were dominant in this association in Australia. In regard to slope, *L. ferocissimum* was found to most commonly be associated with level to hilly landscapes (slopes ~0% to 30% gradients) in South Africa and Australia, but more commonly with steep slopes (>30% gradient) in New Zealand (FAO 2007; GBIF 2018).

While it is well understood that *L. ferocissimum* can tolerate a wide range of soil types and conditions, the most suitable soils for the species to thrive have not been identified.

Land Use Associations

In relation to land use, *L. ferocissimum* is predominantly associated with shrubs, both in unmanaged systems and with high livestock density, as well as with crops and high livestock density, both globally and in Australia (FAO 2010; GBIF 2018). It is associated to a lesser extent with unmanaged open water, urban land, rainfed crops, forests with agricultural activities or moderate to high livestock densities, and sparsely vegetated areas with moderate or high livestock densities. In New Zealand, *L. ferocissimum* was more commonly associated with urban land, which was also the predominant land use category associated with the species in its native range of South Africa.

Life History

Predominantly a stress tolerator with competitive tendencies (sensu Grime 1977), *L. ferocissimum* can survive and thrive across a range of climatic and edaphic conditions, as discussed earlier. In response to stress (i.e., reduced soil moisture, herbivory, or mechanical damage), plants will shed leaves, presumably to conserve energy reserves, and effectively become dormant until conditions become more conducive to growth. While no field studies of the life cycle of the species have been conducted, seeds can germinate quickly within 1 to 3 wk under optimal conditions, growing into seedlings greater than 10-cm high within the first few months before producing multiple stems and growing into a woody shrub/tree habit over the following years (as observed by the authors, in laboratory and field studies) (Figure 6). Mature plants are typically sprawling, approximately 1 to 3 m in diameter, sprawling at the base, with open to closed canopies (especially when actively hedged). While individual plants are often no taller than 2-m high within the native range, plants can form dense, high (3- to 5-m) thickets, especially in the invaded ranges of southeastern Australia. Leaves, while occasionally larger in seedlings (<6 mo), are generally small and often leathery in the field. Flowering and subsequent fruiting may occur year-round, though they have most commonly been recorded as occurring in summer (Parsons and Cuthbertson 2001). Seed production has been recorded in plants from 2 yr of age (Parsons and Cuthbertson 2001) and may become prolific from the third year (Blood 2001) (Figure 6).

Growth and Development

Root growth in young plants is rapid. Small, fleshy leaves are protected from browsing by woody stems and branches that end in sturdy thorns that are 20- to 150-mm long (Noble and Rose 2013). The rounded thorny *L. ferocissimum* shrubs are resistant to browsing and largely impenetrable to larger fauna. The woody, branched taproot is an important contributor to competitiveness

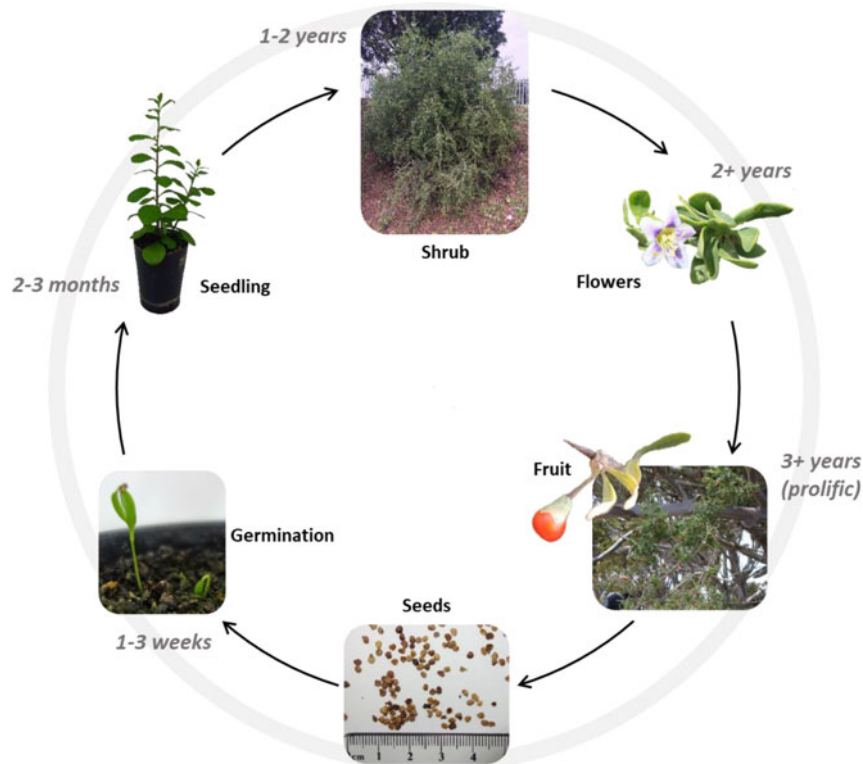


Figure 6. Life cycle of *Lycium ferocissimum*, with putative timeline from seed germination (under optimal conditions) to seed production.

with other species, resprouting vigorously if cut or broken (CRC Weed Management 2007; Muyt 2001; Parsons and Cuthbertson 2001). Damaged plants will reshoot from the base and sucker from roots to regrow and form dense thickets (Muyt 2001; Parsons and Cuthbertson 2001).

Physiology and Phenology

Available information on the physiology of *Lycium ferocissimum* is very limited. In Australia, it is considered tolerant of drought (Muyt 2001) and is found naturalized in semiarid subtropical areas through to areas that experience annual average rainfall of up to 1,200 mm (such as the northern coast of Tasmania). Growth experiments conducted under controlled conditions indicate that the optimal growth temperature range is likely in the range of approximately 15 to 21 °C, with likely slowing of growth at below 10 °C and above 29 °C (Kriticos et al. 2021). While tolerant of salinity (Webb et al. 1988), *L. ferocissimum* is considered to be intolerant of full shade (Muyt 2001; Timmins and Mackenzie 1995). Rutherford et al. (2014) assessed resilience of South Africa's subtropical thicket in the face of herbivore-driven degradation, undertaking monitoring of plant species responses in high and low herbivore browsing situations. *Lycium ferocissimum* was found to recover in the high browsing pressure situations, but not under low browsing pressure. Shade intolerance is considered the factor that may have excluded it from the low browsing pressure (closed thicket) situation (Rutherford et al. 2014).

Lycium ferocissimum is drought deciduous. In South Africa's Western Cape, it occurs in a winter rainfall (Mediterranean) climate, and plants shed their leaves at the start of summer (Cowling et al. 1995). However, where winter rainfall does not

dominate (i.e., rainfall is nonseasonal), such as on the southern coast of South Africa, plants can remain evergreen in similar coastal environments (Cowling et al. 1995). *Lycium ferocissimum* has been recorded as being sometimes winter deciduous in Australia, depending upon location and seasonal conditions (Parsons and Cuthbertson 2001).

Flowering and fruiting occur primarily in summer but can occur at any time of year if sufficient moisture is available (Parsons and Cuthbertson 2001).

Reproduction

Floral Biology and Pollination

While no specific studies of natural *L. ferocissimum* pollination have been conducted, species in the genus *Lycium* are predominantly insect pollinated (Galetto et al. 1998; Miller et al. 2008). *Lycium ferocissimum* is strongly self-incompatible. In controlled pollination experiments, 75% of cross-pollinated flowers produced fruit, compared with only 8% producing fruit following self-pollination (Miller et al. 2008).

Seed Production

Lycium ferocissimum is hermaphroditic (Minne et al. 1994). Seed production occurs in plants from 2 yr of age (Parsons and Cuthbertson 2001) but only becomes prolific from the third year (Blood 2001). Each fruit contains up to 70 seeds, with larger fruit containing more seeds (Erkelenz 1993). Large *L. ferocissimum* plants can produce thousands of fleshy fruits annually (Muyt 2001; Parsons and Cuthbertson 2001).

Seed Viability, Germination, and Seedbanks

The very limited information available on *L. ferocissimum* seedbank dynamics suggests that seed is not long-lived in the soil (CRC Weed Management 2007; Herbiguide 2015; Western Australian Herbarium 1998–). This being said, in some areas seeds can germinate year-round (Muyt 2001; Parsons and Cuthbertson 2001), and mass seed germination has been recorded following disturbance of soil containing seeds (Western Australian Herbarium 1998–). Under controlled conditions, seed germination for *L. ferocissimum* appears to be highest at 15 to 20 C with 12- to 14-h photoperiods. A study of Sardinian populations showed that *L. ferocissimum* is capable of germinating within the temperature ranges of 5 to 25 C, with peak germination (~85% to 90%) recorded when seeds were exposed to temperatures in the range of 10 to 20 C with a 12-h photoperiod (Podda et al. 2015). Germination was higher under a 12-h photoperiod across all experiments (though not significant at 5 C) when compared with completely dark treatment regimes (Podda et al. 2015). Podda et al. (2015) also found that *L. ferocissimum* seeds were quite tolerant of saline conditions; germination was recorded even at the highest salt concentration of 500 mM NaCl, though there were some issues of seedling viability following this exposure. Experience growing *L. ferocissimum* at the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Canberra has shown germination to be reliable when seeds are soaked for at least 24 h in a 500-ppm solution of gibberellic acid (Sigma-Aldrich, St Louis, MO, USA), sown directly into moist seed-raising mix (Plugger 111 Seed Raising Mix, Australian Growing Solutions, Tyabb, VIC, Australia) and kept at temperatures of 15 or 21 C with 12- to 14-h photoperiods under LED plant growth lights.

Vegetative Reproduction

Lycium ferocissimum can reproduce vegetatively in the field. As noted earlier, broken stem and root fragments can remain viable for months before taking root when brought in contact with moist soil (Muyt 2001). Propagation from woody or green cuttings has not been successful however (<1% strike rate), despite success with striking cuttings of *L. australe* and *L. chinense* (see Ireland et al. 2019a). *Lycium ferocissimum* recovers readily from fire by resprouting from an extensive and resilient rootstock (Figure 7) and was found to suffer less than 30% mortality in 100% leaf-scorch fire conditions (Choate 1997).

Management Options

Long-term effective control of *L. ferocissimum* requires a combination of treatments over many years due to the capacity of the species to regenerate from rootstock, stems, and seed. *Lycium ferocissimum* seed is dispersed predominantly by birds and other animals, and potential for reinfestation of sites from outside sources should be considered in management planning. Considerations and a planning approach are provided in the *African Boxthorn National Best Practice Manual: Managing African Boxthorn (Lycium ferocissimum) in Australia* (Noble and Rose 2013).

Physical Control Techniques

Physical control of *L. ferocissimum* includes winching, pulling, bulldozing, stick raking, blade plowing, and cultivation (Noble and Rose 2013). These techniques are best used when *L. ferocissimum* plants are not carrying seed (or are carrying minimal seed).



Figure 7. *Lycium ferocissimum* resprouting from rootstock following wildfire, Tasmania. (Photo credit: Karen Ziegler.)



Figure 8. Physical control techniques (A) and machinery (B) for *Lycium ferocissimum*. (A) Winching out an individual *Lycium ferocissimum* plant. (B) *Lycium ferocissimum* puller. (Photo credits: (A) Jon Fallaw; (B) Rob Higgins.)

Otherwise, fresh seed is likely to be deposited into freshly disturbed soil.

Winching and pulling are the lowest-impact physical control techniques for situations where disturbance is a concern, such as where *L. ferocissimum* is growing within native vegetation. Winching involves connecting a chain or cable to the base of large individual plants and using consistent force to remove the plant and as much root matter as possible (Figure 8A). Pulling or plucking involves using hydraulic arms based on a front-end loader,

articulated loader, or excavator to remove individual plants and as much root matter as possible. A hydraulically operated puller has been commercially developed specifically for use on *L. ferocissimum* (Figure 8B). Bulldozing, stick raking, and blade plowing are suitable in less sensitive landscapes (e.g. pasture) and provide a rapid control method for moderate to heavy infestations.

Successful management of *L. ferocissimum* using the techniques noted is dependent on follow-up application of herbicide. This includes the cut-stump technique with immediate application of herbicide for any remaining base/roots after winching and pulling. For all physical control techniques, there is a need to return periodically and carry out foliar spray application and/or machine-based cut stump treatments until there is no regrowth or seedling presence (Noble and Rose 2013).

Chemical Control Techniques

Chemical control of *L. ferocissimum* uses techniques including foliar spraying, cut stump application (including mechanical cut stump), stem injection, stem scrap or frilling (e.g., using chisel cuts), basal bark application, and soil–root zone application.

Foliar spraying of triclopyr–picloram herbicide mixes and of triclopyr, picloram, and aminopyralid are commonly undertaken for management of *L. ferocissimum*. Glyphosate, glyphosate–met-sulfuron-methyl mix, and picloram and 2, 4-D amine-based herbicides can also be foliar sprayed on *L. ferocissimum*. Adjuvants improve herbicide uptake by the plant. Mature *L. ferocissimum* plants demonstrate strong resilience to foliar spraying, with new foliage readily appearing on plants that had seemingly “died off” after spraying. Follow-up applications are usually essential (Noble and Rose 2013).

In situations where vehicular access is impractical or undesirable (such as coastal and island situations), the cut stump technique is often used. Triclopyr–picloram mix (in diesel), triclopyr (mixed with diesel), and picloram are suitable for this technique. Glyphosate (mixed 1:1 with water) has been used successfully with the cut stump technique over many years by Friends of Bass Strait Islands (Ziegler and Hopkins 2011). A significant advantage of the cut stump technique is that it allows for the removal and destruction of *L. ferocissimum* debris. Where dead *L. ferocissimum* debris is left in place, this continues to provide habitat for pest animals such as starlings and rabbits. Also, the thorns continue to present a hazard to people, wildlife (fatally ensnaring birds), and livestock and can potentially puncture car tires.

Picloram-based herbicides can be used for stem-injection application, while glyphosate-based herbicides can be used for frilling or stem-scrape techniques (Noble and Rose 2013). Triclopyr, along with triclopyr–picloram-based herbicides (mixed with diesel) can be applied to *L. ferocissimum* using the basal bark application technique.

Soil–root zone herbicide application is not suitable in environmentally sensitive areas, as there is significant potential for off-target damage. Hexazinone- or tebuthiuron-based herbicide is applied to the soil near the drip line of the target plant.

Natural Enemies/Biological Control

Lycium ferocissimum was first evaluated comprehensively for potential biological control in Australia in 2013 (Adair 2013), and since 2016 CSIRO in Australia has undertaken further research into candidate biological control agents. A variety of generalist plant pests and pathogens have also been recorded on *L. ferocissimum*, both within the native and nonnative ranges.

Native range surveys for candidate agents in South Africa have revealed four promising agents to date: one rust fungus, *Puccinia rapipes* Berndt & E. Uhlmann 2006 (Ireland et al. 2019a), and three leaf-feeding beetles, *Cassida distinguenda* Spaeth (Chrysomelidae), *Cleta eckloni* Mulsant (Coccinellidae), and *Neoplatygaster serietuberculata* Gyllenhal (Curculionidae) (Chari et al. 2020).

The abundance of natural enemies is low in Australia, with herbivory levels on leaves, stems, and fruits of *L. ferocissimum* at <1% (Adair 2013). Fruits are often damaged by birds and either wholly or partially eaten. Fourteen insect and five pathogen associations with *L. ferocissimum* have been recorded in Australia (see Adair 2013). All are generalist species, with many known as pests from commercially utilized crops or ornamental plants, including pests of biosecurity importance such as the Mediterranean and Queensland fruit flies (*Ceratitidis capitata* Wiedemann and *B. tryoni*, respectively). The tomato-potato psyllid, *B. cockerelli*, a serious pest of Solanaceae species, has been found feeding on *L. ferocissimum* in New Zealand and North America and may be a putative host of the destructive bacterium CLso, which is vectored by the psyllid (Liefting et al. 2009; Munyaneza 2012; Vereijssen et al. 2018). *Bactericera cockerelli* is now established in Western Australia (Commonwealth of Australia 2018), and while no associations with *L. ferocissimum* have been reported thus far, it would be likely that the pest would also feed and reproduce on this host in Australia. A new species of psyllid (*Acizzia* sp.) was recorded from *L. ferocissimum* in Australia in 2013 (Adair 2013). This is the first record of a psyllid feeding on Australian *Lycium* and the first record of *Acizzia* from *Lycium*. Three other *Acizzia* species have recently been recorded from other Solanaceae in Australia (Kent and Taylor 2010; Taylor and Kent 2013). *Acizzia* are predominantly associated with *Acacia* (Taylor and Kent 2013). The *Lycium Acizzia* is widespread in the Australian state of Victoria, and densities on *L. ferocissimum* are often high, causing considerable damage by stunting growth and though chlorosis, distortion of foliage, and contraction of internodes. Stem death may also occur. The psyllid may also be widespread in other states and territories, but further surveys are required to determine its full distribution. It is not known at this stage whether Australian populations of the insect are vectors of any *Candidatus* bacteria. The mealy bug *Pseudococcus* sp. commonly shelters and feeds among the compacted growth caused by *Acizzia*, further contributing to stem weakening.

Puccinia rapipes (rust fungus)

The rust fungus *P. rapipes* was identified early as a candidate biological control agent (Figure 9), given that it had only been recorded as occurring on *L. ferocissimum* (Berndt and Uhlmann 2006) and that rust fungi have historically performed well as biological control agents (Cullen et al. 1973; Hayes et al. 2013; Morin and Scott 2012; Morris 1997). The fungus infects predominantly young, fleshy leaves, impacting host health and growth through direct loss of photosynthetic tissues where the fungus occurs, and draining host resources to maintain fungal growth. Host-specificity testing in Australia revealed that *P. rapipes* can also infect the Eurasian origin goji berries *L. barbarum*, *L. chinense*, and *L. ruthenicum* (Ireland et al. 2019a). Importantly, *P. rapipes* does not infect the Australian native boxthorn, *L. australe*. These results indicate that *P. rapipes* may be sufficiently host specific to pursue as a biological control agent in an Australian context, should regulators be willing to accept damage



Figure 9. *Puccinia rapipes* pathogen on *Lycium ferocissimum*. (Photographed in South Africa by Alan Wood.)

to the Eurasian goji berries that are grown, albeit to a limited extent, in Australia.

General Outlook

Lycium ferocissimum is a widespread and significant weed in southern Australia and New Zealand that could spread further into suitable coastal Mediterranean and subtropical humid climates around the world. The climatically suitable regions at risk include coastal western and inland southeastern states of the United States, the central highlands of Mexico, central-eastern Argentina, much of Uruguay, parts of southeastern Brazil, some southern coastal regions of Chile, and highlands throughout tropical South America, as well as provinces in southwestern China, including Yunnan (Kriticos et al. 2021). The newest populations in Sardinia are considered the most recently invasive, and further risk of spread in the Mediterranean Basin should not be overlooked. The invasive nature of the shrub may be reliant on it gaining a foothold as a hedge species, though extensive spread may be aided by birds, and so further distribution of the species in the nursery trade should be managed with care. Therefore, research on topics such as seed dispersal, as well as survival and longevity of seed following dispersal, would significantly aid weed management planning. Where the species is established, it may be possible to control and manage spread through carefully targeted removal and chemical control follow-up or potentially via biological control, should candidate agents be deemed safe for release into these environments.

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References

Abbott I, Marchant N, Cranfield R (2000) Long-term change in the floristic composition and vegetation structure of Carnac Island, Western Australia. *J Biogeogr* 27:333–346

- Adair R (2013) Feasibility of Biological Control of African Boxthorn *Lycium ferocissimum*. Unpublished report to Department of Primary Industries, Parks, Water and Environment, Tasmania. 61 p
- Adamson RS (1938) The Vegetation of South Africa. London, UK: British Empire Vegetation Committee. 235 p
- Agriculture Victoria (2017) African Boxthorn. Victoria State Government. <http://agriculture.vic.gov.au/agriculture/pests-diseases-and-weeds/weeds/a-z-of-weeds/african-boxthorn>. Accessed: June 26, 2019
- Australian Weeds Committee (2013) Weeds of National Significance African Boxthorn (*Lycium ferocissimum*) Strategic Plan. Canberra, ACT: Australian Weeds Committee. 30 p
- Berndt R, Uhlmann E (2006) New species, reports, observations and taxonomical changes of southern African rust fungi (Uredinales). *Mycol Progr* 5:154–177
- Biosecurity SA (2017) Plants Prohibited from Sale in South Australia. Government of South Australia–Primary Industries and Regions SA. (PIRSA) https://www.pirsa.gov.au/__data/assets/pdf_file/0003/242715/Plants_banned_from_sale_in_SA_list_-_July_2017.pdf. Accessed: June 26, 2019
- Blood K (2001) Environmental Weeds: A Field Guide for SE Australia. Mt Waverley, VIC: CH Jerram & Associates–Science Publishers. 228 p
- Breitwieser I, Brownsey P, Ford K, Glenn D, Heenan P, Wilton A, eds (2019) New Zealand Plants. *Lycium ferocissimum* Miers. Manaaki Whenua–Landcare Research New Zealand. <http://nzflora.landcareresearch.co.nz/default.aspx?selected=NameDetails&NameId=9CE0B243-C186-4789-AD8C-1FC8288FA5A6&TabNum=4&Dist=1>. Accessed: June 11, 2019
- Brown AL (1969) Sheep production in the pastoral zone. *J Agric SA* 72:272–286
- Brown EA (1979) Vegetation and flora of Ponui Island, Hauraki Gulf, New Zealand. *Tane* 25:5–16
- Business Queensland (2016) African Boxthorn. Restricted Invasive Plants. Queensland Government. <https://www.business.qld.gov.au/industries/farms-fishing-forestry/agriculture/land-management/health-pests-weeds-diseases/weeds-diseases/invasive-plants/restricted/african-boxthorn>. Accessed: June 26, 2019
- [CABI] CAB International (2018) *Lycium ferocissimum* (African boxthorn). In Invasive Species Compendium. Wallingford, UK: CAB International. <https://www.cabi.org/ISC/datasheet/31903>. Accessed: June 17, 2019
- Calflora (2013) Calflora observation hotline. <http://www.calflora.org/entry/observ.html#search=t&ch=t&inat=r&checklist=t&taxon=Lycium+ferocissimum&b=-118.5,34,-118.25,33.75,11>. Accessed: June 11, 2019
- Calvino-Cancela M (2011) Gulls (Laridae) as frugivores and seed dispersers. *Plant Ecol* 212:1149–1157
- Cann JH, De Deckker P, Murray-Wallace CV (1991) Coastal aboriginal shell middens and their palaeoenvironmental significance, Robe Range, South Australia. *Trans. R Soc S Aust* 115:161–175
- Carlos EH, Weston MA, Gibson M (2017) Avian responses to an emergent, wetland weed. *Austral Ecol* 42:277–287
- Cetinkaya G, Sozen N (2011) Plant species potentially useful in the phytostabilization process for the abandoned CMC mining site in Northern Cyprus. *Int J Phytoremediation* 13:681–691
- Chari LD, Mauda EV, Martin GD, Raghu S (2020) Insect herbivores associated with *Lycium ferocissimum* (Solanaceae) in South Africa and their potential as biological control agents in Australia. *Afr Entomol* 28:359–373
- Choate J (1997) Plant Species Response to Fire. Kensington, SA: Department of Environment and Natural Resources, South Australia. 74 p
- Coates Palgrave K, Moll EJ, Drummond RB, Coates Palgrave M (2002) Trees of Southern Africa. 3rd ed. Cape Town, South Africa: Struik Publishers. 1212 p
- Commonwealth of Australia (2018) National Pest and Disease Outbreaks. Current Responses to Outbreaks. Tomato Potato Psyllid. <http://www.outbreak.gov.au/current-responses-to-outbreaks/tomato-potato-psyllid>. Accessed: June 14, 2019
- Cooper WR, Horton DR, Miliczky E, Wohleb CH, Waters TD (2019) The weed link in zebra chip epidemiology: suitability of non-crop Solanaceae and Convolvulaceae to potato psyllid and “*Candidatus Liberibacter solanacearum*.” *Am J Potato Res* 96:262–271
- Cousens R, Kennedy D, Maguire G, Williams K (2013) Just How Bad Are Coastal Weeds? Assessing the Geo-eco-psychosocio-economic Impacts. Canberra, ACT: Rural Industries Research and Development Corporation. Rep. 13/032. 70 p

- Cowling RM, Richardson DM, Paterson-Jones C (1995) Fynbos: South Africa's Unique Floral Kingdom. Vlaeberg, South Africa: Fernwood Press. 151 p
- CRC Weed Management (2007) African Boxthorn (*Lycium ferocissimum*). http://www.aabr.org.au/images/stories/resources/ManagementGuides/WeedGuides/wmg_african_boxthorn.pdf. Accessed: June 17, 2019
- Cullen JM, Kable PF, Catt M (1973) Epidemic spread of a rust imported for biological control. *Nature* 244:463–464
- Department of Agriculture and Fisheries (2020) African boxthorn. *Lycium ferocissimum*. The State of Queensland, Department of Agriculture and Fisheries. https://www.daf.qld.gov.au/__data/assets/pdf_file/0016/64042/african-boxthorn.pdf. Accessed: May 11, 2021
- Department of Agriculture, Water and the Environment (2021) Plant Species That Are Weeds. Australian Biosecurity Import Conditions–BICON. Australian Government Department of Agriculture and Water Resources. <https://bicon.agriculture.gov.au/BiconWeb4.0/>. Accessed: May 11, 2021
- Department of Environment and Natural Resources (2018) Declared Weeds in the Northern Territory. Northern Territory Government Department of Environment and Natural Resources. https://nt.gov.au/__data/assets/pdf_file/0016/252133/declared-weeds-in-the-nt.pdf. Accessed: June 26, 2019
- Department of Primary Industries and Regional Development (2019) *Lycium ferocissimum* Miers. Government of Western Australia Department of Primary Industries and Regional Development. <https://www.agric.wa.gov.au/organisms/103260>. Accessed: June 26, 2019
- Department of Primary Industries Parks Water and the Environment (2019) African Boxthorn Declared Weeds Index. Tasmanian Government Department of Primary Industries, Parks, Water and the Environment. <https://dpiiwe.tas.gov.au/invasive-species/weeds/weeds-index/declared-weeds-index/african-boxthorn>. Accessed: June 26, 2019
- Department of the Environment, Climate Change, Energy and Water (2009) ACT Weeds Strategy 2009–2019 Policy: Natural Environment. Canberra, ACT: Department of the Environment, Climate Change, Energy and Water. 36 p
- DiTomaso JM, Healy EA (2007) Weeds of California and Other Western States. Oakland, CA: University of California. 1808 p
- Dodson J (1974) Vegetation and climatic history near Lake Keilambete, western Victoria. *Aust J Bot* 22:709–717
- Driessen M (2011) Terrestrial mammals. Pages 93–100 in Harris S, Reid A, eds. Inner (West) Sister Island Scientific Expedition 2010. Hobart, TAS: Hamish Saunders Memorial Trust, New Zealand and Conservation Division Department of Primary Industries, Parks, Water and Environment (DPIIWE)
- Erkelenz PA (1993) Aspects of the ecology of African boxthorn, *Lycium ferocissimum*. Pages 368–371 in Proceedings of the 10th Australian Weeds Conference and 14th Asian Pacific Weed Science Society Conference. Brisbane, QLD: Weed Society of Queensland
- Erkelenz PA (1994) African boxthorn ecology in coastal areas. Page 3 in Carter RJ, ed. Managing weeds for landcare 1994: a workshop on protecting our land from invading weeds. Urrbrae, SA: Animal and Plant Control Commission and Crop Science Society of SA Inc.
- [EPPO] European and Mediterranean Plant Protection Organization (2020) EPPO Alert List–*Lycium ferocissimum*. https://www.eppo.int/ACTIVITIES/plant_quarantine/alert_list_plants/lycium_ferocissimum. Accessed: January 29, 2021
- [FAO] Food and Agriculture Organization of the United Nations (2007) Digital Soil Map of the World. Version 3.6. FAO–UN Land and Water Division (CBL). <http://www.fao.org/geonetwork/srv/en/main.home>. Accessed: June 27, 2019
- [FAO] Food and Agriculture Organization of the United Nations (2010) Land Use Systems of the World. Version 1.1. FAO–UN Land and Water Division (CBL). <http://www.fao.org/geonetwork/srv/en/main.home>. Accessed: June 27, 2019
- Fried G (2020) Premier signalement de *Lycium ferocissimum* Miers (Solanaceae) à l'état naturalisé en France (Aude). Centre de Ressources Espèces Exotiques Envahissantes. <http://especes-exotiques-envahissantes.fr/premier-signalement-de-lycium-ferocissimum-miers-solanaceae-a-letat-naturalise-en-france-aude>. Accessed: January 29, 2021
- Fukuda T, Yokoyama J, Ohashi H (2001) Phylogeny and biogeography of the genus *Lycium* (Solanaceae): inferences from chloroplast DNA sequences. *Mol Phylogeny Evol* 19:246–258
- Fuller M (1998) African Boxthorn (*Lycium ferocissimum*). Darwin, NT: Northern Territory of Australia, Department of Primary Production. Agnote No. 590. 2 p
- Galetto L, Bernardello G, Sosa CA (1998) The relationship between floral nectar composition and visitors in *Lycium* (Solanaceae) from Argentina and Chile: what does it reflect? *Flora* 193:303–314
- Gallego MJ (2012) *Lycium*. Pages 233–240 in Talavera S, Andrés C, Arista M, Fernández Piedra MP, Gallego MJ, Ortiz PL, Romero Zarco C, Salgueiro FJ, Silvestre S, Quintanar A, eds. Flora Iberica. Plantas vasculares de la Península Ibérica e Islas Baleares. Madrid, Spain: Madrid Real Jardín Botánico
- Gillham ME (1963) Some interactions of plants, rabbits and seabirds on South African islands. *J Ecol* 51:275–294
- [GBIF] Global Biodiversity Information Facility (2018) GBIF Occurrence Download. <https://doi.org/10.15468/dl.pbd67p>
- [GBIF] Global Biodiversity Information Facility (2020) GBIF Occurrence Download. <https://doi.org/10.15468/dl.8fg5z2>
- [GBIF] Global Biodiversity Information Facility (2021) GBIF Occurrence Download. <https://doi.org/10.15468/dl.wdq9mk>
- Government of South Australia (2004) Declared Plant Policy. African Boxthorn (*Lycium ferocissimum*). https://www.pir.sa.gov.au/__data/assets/pdf_file/0005/137291/African_boxthorn_policy.pdf. Accessed: June 26, 2019
- Green PS (1994) *Lycium*. Pages 297–298 in Orchard AE, Wilson AJG, eds. Flora of Australia. Volume 49, Oceanic Islands 1. Canberra, ACT: Australian Government Public Service Press
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Guiler E (1970) Observations on the Tasmanian Devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae) I. Numbers, home, range, movements and food in two populations. *Aust J Zool* 18:49–62
- Haegi L (1976) Taxonomic account of *Lycium* (Solanaceae) in Australia. *Aust J Bot* 24:669–679
- Hand R (2000) Contributions to the Flora of Cyprus I. *Willdenowia* 30:53–65
- Harris S, McKenny H (1999) Preservation Island, Furneaux Group: two hundred years of vegetation change. *Pap Proc R Soc Tasman* 133:85–102
- Hayes L, Fowler SV, Paynter Q, Groenteman R, Peterson P, Dodd S, Bellgard S (2013) Biocontrol of Weeds: Achievements to Date and Future Outlook. Lincoln, New Zealand: Manaaki Whenua Press, Landcare Research. Pp 375–385
- Heinsohn GE (1964) Ecology and Reproduction of the Tasmanian Bandicoots, *Perameles gunni* and *Isodon obesulus*. Berkeley, CA: University of California Press. 222 p
- Herbiguide (2015) African Boxthorn (*Lycium ferocissimum*) Miers. http://www.herbiguide.com.au/Descriptions/hg_African_Boxthorn.htm. Accessed: June 17, 2019
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Hoskin S (2006) Taranaki Boxthorn: Prickles and All. Puke Ariki. <https://terangiaoounui.pukeariki.com/all-stories/taranaki-stories/taranaki-boxthorn-prickles-and-all>. Accessed: June 26, 2019
- Humphries SE, Groves RH, Mitchell DS (1994) Plant invasions: homogenizing Australian ecosystems. Pages 149–170 in Kikkawa J, Moritz C, eds. Conservation Biology in Australia and Oceania. Chipping Norton, NSW: Surrey Beatty
- Hussey BMJ, Keighery GJ, Dodd J, Lloyd SG, Cousens RD (2007) Western Weeds: A Guide to the Weeds of Western Australia. 2nd ed. Victoria Park, WA: Weeds Society of Western Australia. 254 p
- İlseven S, Baştaş M (2018) The place of Eucalyptus within the vegetation of Mesaoria Plain (Cyprus) and the views of vegetation geography lecturers. *Eurasia J Math Sci Technol Educ* 14:3381–3388
- Ireland KB, Hunter GC, Wood A, Delaisse C, Morin L (2019a) Evaluation of the rust fungus *Puccinia rapipes* for biological control of *Lycium ferocissimum* (African boxthorn) in Australia: life cycle, taxonomy and pathogenicity. *Fungal Biol* 123:811–823
- Ireland KB, Rafter M, Kumaran N, Raghu S, Morin L (2019b) Stakeholder survey reveals priorities for African boxthorn biocontrol research in Australia. *Biocontrol Sci Technol* 29:1123–1128

- Keighery G (2010) Weeds of the Nullarbor in Western Australia. *Western Australian Naturalist* 27:160–167
- Keighery GJ, Alford JJ, Longman V (2002) A vegetation survey of the islands of the Turquoise Coast from Dongara to Lancelin, south-western Australia. *Conserv Sci W Aust* 4:13–62
- Kent D, Taylor G (2010) Two new species of *Acizzia* Crawford (Hemiptera: Psyllidae) from the Solanaceae with a potential new economic pest of egg-plant, *Solanum melongena*. *Aust J Entomol* 49:73–81
- King K, Wallis R, Wallis A, Peucker A, Williams D (2015) Successful protection against canid predation on little penguins (*Eudyptula minor*) in Australia using Maremma guardian dogs: “the Warrnambool method.” *Int J Arts Sci* 8:139–150
- Köppen W (1936) Das geographische System der Klimate. Pages 1–44 in Köppen W, Geiger R, eds. *Handbuch der Klimatologie*. Berlin, Germany: Verlag von Gebrüder Borntraeger
- Kriticos DJ, Webber BL, Leriche A, Ota N, Macadam I, Bathols J, Scott JK (2012) CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol Evol* 3:53–64
- Kriticos DJ, Ireland KB, Morin L, Kumaran N, Rafter MA, Ota N, Raghu S (2021) Integrating ecoclimatic niche modelling methods into classical biological control programmes. *Biol Control*. 160:104667
- Lalas C, Jones PR, Jones J (1999) The design and use of a nest box for yellow-eyed penguins *Megadyptes antipodes*—a response to a conservation need. *Mar Ornithol* 27:199–204
- Lambert R (2015) Taranaki region—Changing the environment. Te Ara—the Encyclopedia of New Zealand. <http://www.TeAra.govt.nz/en/photograph/25277/boxthorn-hedges>. Accessed: June 25, 2019
- Lambinon J, Lewalle J (1986) *Lycium ferocissimum* Miers. Notes brèves sur certaines centuries distribuées dans le fascicule 21. Bulletin de la Société pour l'Echange des Plantes Vasculaires de l'Europe Occidentale et du Bassin Méditerranée 21:49–70
- Lavers JL (2014) Population status and threats to flesh-footed shearwaters (*Puffinus carneipes*) in South and Western Australia. *ICES J Mar Sci* 72:316–327
- Lawley EF, Lawley JJ, Page B (2005) Effects of African boxthorn removal on native vegetation and burrowing of short-tailed shearwaters on Althorpe Island, South Australia. *Trans R Soc S Aust* 129:111–115
- Lazzeri V, Mascia F, Sammartino F, Campus G, Caredda A, Carlesi V, Fois M, Gestri G, Mannocci M, Mazzoncini V, Cuenca Lombraña A, Santinelli M (2013) Novità floristiche per le regioni Sardegna e Toscana. *Acta Plantarum Notes* 2:42–78
- Lee AN (1978) Is African boxthorn a problem? *Qld Agric J* 104:533–537
- Levin RA, Bernardello G, Whiting C, Miller JS (2011) A new generic circumscription in tribe Lycieae (Solanaceae). *Taxon* 60:681–690
- Levin RA, Shak JR, Miller JS, Bernardello G, Venter AM (2007) Evolutionary relationships in tribe Lycieae (Solanaceae). *Acta Hort* 745:225–240
- Liefting LW, Weir BS, Pennycook SR, Clover GRG (2009) “*Candidatus Liberibacter solanacearum*,” associated with plants in the family Solanaceae. *Int J Syst Evol Microbiol* 59:2274–2276
- Lohr MT, Keighery G (2016) The status and distribution of alien plants on the islands of the south coast of Western Australia. *Conserv Sci W Aust* 10:1–43
- Martin TG, Campbell S, Grounds S (2006) Weeds of Australian rangelands. *Rangeland J* 28:3–26
- Matthews LJ (1982) Pasture weeds of New Zealand. Pages 387–394 in Holzner W, Numata M, eds. *Biology and Ecology of Weeds*. The Hague, Netherlands: Dr W. Junk Publishers
- McCulloch GA, Mauda EV, Chari LD, Martin GD, Gurdasani K, Morin L, Walter GH, Raghu S (2020) Genetic diversity and morphological variation in African boxthorn (*Lycium ferocissimum*)—characterising the target weed for biological control. *Biol Control* 143:104206
- Meikle RD (1985) *Flora of Cyprus*. Volume 2. London, UK: Bentham-Moxon Trust, Royal Botanic Gardens. 1136 p
- Miers J (1854) XX.—On the genus *Lycium*. *Ann Mag Nat Hist* 14:182–194
- Miller JS, Levin RA, Feliciano NM (2008) A tale of two continents: Baker's rule and the maintenance of self incompatibility in *Lycium* (Solanaceae). *Evolution* 62:1052–1065
- Minne L, Spies JJ, Venter HJT, Venter AM (1994) Breeding systems in some representatives of the genus *Lycium* (Solanaceae). *Bothalia* 24:107–110
- Mittermeier RA, Turner WR, Larsen FW, Brooks TM, Gascon C (2011) Global biodiversity conservation: the critical role of hotspots. Pages 3–22 in Zachos FE, Habel JC, eds. *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*. Berlin, Germany: Springer
- Moloney DJ (1982) A Comparison of the Behaviour and Ecology of the Tasmanian Bandicoots, *Perameles gunii* (Gray 1838) and *Isodon obesulus* (Shaw and Nodder 1797). Honours thesis. Hobart, TAS: University of Tasmania. 202 p
- Morin L, Scott JK (2012) *Asparagus asparagoides* (L.) Druce—bridal creeper. Pages 73–82 in Julien M, McFadyen R, Cullen J, eds. *Biological Control of Weeds in Australia*. Collingwood, VIC: CSIRO Publishing
- Morris MJ (1997) Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa. *Biol Control* 10:75–82
- Munyaneza JE (2012) Zebra chip disease of potato: biology, epidemiology, and management. *Am J Potato Res* 89:329–350
- Muyt A (2001) Bush Invaders of South-East Australia: A Guide to the Identification and Control of Environmental Weeds Found in South-East Australia. Meredith, VIC: R.G. & F.J. Richardson. 304 p
- Noble M, Adair R (2014) African boxthorn (*Lycium ferocissimum*) and its vertebrate relationships in Australia. *Plant Prot Q* 29:80–84
- Noble M, Adair R, Yen A (2014) African boxthorn (*Lycium ferocissimum*) and asset protection from a national perspective. Pages 231–234 in Baker M, ed. *Proceedings of the 19th Australasian Weeds Conference*. Hobart, TAS: Tasmanian Weed Society
- Noble MR, Rose M (2013) African Boxthorn National Best Practice Manual: Managing African Boxthorn (*Lycium ferocissimum*) in Australia. Devenport, TAS: Tasmanian Department of Primary Industries, Parks, Water and Environment. 76 p
- Nogales M, Delgado JD, Medina FM (1998) Shrikes, lizards and *Lycium intricatum* (Solanaceae) fruits: a case of indirect seed dispersal on an oceanic island (Aleganza, Canary Islands). *J Ecol* 86:866–871
- [NSW DPI] New South Wales Department of Primary Industries (2019) African Boxthorn. NSW WeedWise. <https://weeds.dpi.nsw.gov.au/Weeds/AfricanBoxthorn>. Accessed: June 26, 2019
- Orange-bellied Parrot Recovery Team (2006) National Recovery Plan for the Orange-bellied Parrot (*Neophema chrysogaster*). Hobart, TAS: Department of Primary Industries and Water (DPIW). 53 p
- Parsons W, Cuthbertson EG (2001) *Noxious Weeds of Australia*. Melbourne, VIC: CSIRO Publishing. 698 p
- Perez Latorre AV, Yus Ramos R, Dana Sanchez E (2006) *Lycium ferocissimum* Miers in the Iberian Peninsula (Malaga, Espana). *Acta Bot Malac* 31:208–208
- Peyton J, Mountford O (2015) COST Action Short Term Scientific Mission—Lake Akrotiri, Cyprus. Wallingford, UK: NERC/Centre for Ecology & Hydrology. <http://nora.nerc.ac.uk/id/eprint/512985>. Accessed: June 28, 2019
- Phillips C (2014) A Field Report on *Lycium ferocissimum* (African Boxthorn) Eradication Excursions at the Beagle Islands in 2013 and 2014. Unpublished report to Department of Parks and Wildlife, Western Australia. 17 p
- Plant Health Australia (2017) Australian Plant Pest Database. Plant Health Australia. <http://appd.ala.org.au>. Accessed: February 2, 2017
- Pobke K (2007) Draft Recovery Plan for 23 Threatened Flora Taxa on Eyre Peninsula, South Australia 2007–2012. Adelaide, SA: Department for Environment and Heritage. 254 p
- Podda L, Santo A, Puddu S, Biagini L, Bacchetta G (2015) Germination eco-physiology of three invasive Solanaceae species in Sardinia (Italy). II International Plant Science Conference. 110th Congresso della Società Botanica Italiana. Pavia, Italy, September 14–17, 2015
- Popay I, Champion P, James T (2010) *An Illustrated Guide to Common Weeds of New Zealand*. 3rd ed. Christchurch, New Zealand: New Zealand Plant Protection Society. 416 p
- Purdie RW, Symon DE, Haegi L (1982) Solanaceae. Pages 64–65 in George AS, ed. *Flora of Australia*. Volume 29. Canberra, ACT: Australian Government Pulic Service Press
- Quin DG (1985) Observations on the diet of the southern brown bandicoot, *Isodon obesulus* (Marsupialia: Peramelidae), in southern Tasmania. *Aust Mammal* 11:15–25
- Randall RP (2017) *A Global Compendium of Weeds*. 3rd ed. Perth, Western Australia: R. P. Randall. 3654 p

- Roger E, Laffan SW, Ramp D (2007) Habitat selection by the common wombat (*Vombatus ursinus*) in disturbed environments: implications for the conservation of a “common” species. *Biol Conserv* 137:437–449
- Rutherford MC, Powrie LW, Husted LB (2014) Herbivore-driven land degradation: consequences for plant diversity and soil in arid subtropical thicket in south-eastern Africa. *Land Degrad Dev* 25:541–553
- Särkinen T, Bohs L, Olmstead RG, Knapp S (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evol Biol* 13:214
- Stevens PF (2019) Angiosperm Phylogeny website. Version 14. <http://www.mobot.org/MOBOT/research/APweb>. Accessed: June 13, 2019
- Taylor GA, Tennyson AJD (1999) Flora and fauna of Wooded Island, Inner Hauraki Gulf. *Tane* 37:91–98
- Taylor GS, Kent DS (2013) Potential economic pests of solanaceous crops: a new species of *Solanum*-feeding psyllid from Australia and first record from New Zealand of *Acizzia solanicola* (Hemiptera: Psyllidae). *Zootaxa* 3613:257–273
- Taylor RH (1968) Introduced mammals and islands: priorities for conservation and research. *Proceedings of the New Zealand Ecological Society* 15:61–67
- Taylor RJ (1993) Observations on the behavior and ecology of the common wombat *Vombatus ursinus* in northeast Tasmania. *Aust Mammal* 16:1–7
- Thinakaran J, Horton DR, Rodney Cooper W, Jensen AS, Wohleb CH, Dahan J, Mustafa T, Karasev AV, Munyaneza JE (2017) Association of potato psyllid (*Bactericera cockerelli*; Hemiptera: Trioziidae) with *Lycium* spp. (Solanaceae) in potato growing regions of Washington, Idaho, and Oregon. *Am J Potato Res* 94:490–499
- Timmins SM, Mackenzie TW (1995) Weeds in New Zealand Protected Natural Areas Database. Department of Conservation Technical Series No. 8. <http://www.doc.govt.nz/Documents/science-and-technical/docts08.pdf>. Accessed: June 14, 2019
- Timmins SM, Williams PA (1991) Weed numbers in New Zealand’s forest and scrub reserves. *NZ J Ecol* 15:153–162
- Todd SW (2000) Patterns of seed production and shrub association in two palatable Karoo shrub species under contrasting land use intensities. *Afr J Range Forage Sci* 17:22–26
- [USDA–NRCS] U.S. Department of Agriculture–Natural Resources Conservation Service (2019) *Lycium ferocissimum* Miers, African Boxthorn. <http://plants.usda.gov/core/profile?symbol=LYFE4#>. Accessed: June 17, 2019
- van der Vyver ML, Cowling RM, Campbell EE, Difford M (2012) Active restoration of woody canopy dominants in degraded South African semi-arid thicket is neither ecologically nor economically feasible. *Appl Veg Sci* 15:26–34
- Venter AM (2000) Taxonomy of the Genus *Lycium* L. (Solanaceae) in Africa. Ph.D dissertation. Bloemfontein, South Africa: University of the Orange Free State. 273 p
- Vereijssen J, Smith GR, Weintraub PG (2018) *Bactericera cockerelli* (Hemiptera: Trioziidae) and *Candidatus Liberibacter solanacearum* in potatoes in New Zealand: biology, transmission, and implications for management. *J Integr Pest Manag* 9:13
- Veth P, Ward I, Manne T, Ulm S, Ditchfield K, Dortch J, Hook F, Petchey F, Hogg A, Questiaux D, Demuro M, Arnold L, Spooner N, Levchenko V, Skippington J, *et al.* (2017) Early human occupation of a maritime desert, Barrow Island, North-West Australia. *Qua Sci Rev* 168:19–29
- Webb CJ, Sykes WR, Garnock-Jones PJ (1988) Flora of New Zealand. Volume 4, Naturalised Pteridophytes, Gymnosperms, Dicotyledons. Christchurch, New Zealand: Botany Division, Department of Scientific and Industrial Research. 1365 p
- Welman WG (1993) Solanaceae. Page 617 in Arnold TH, De Wet BC, eds. *Plants of Southern Africa: Names and Distribution* (Memoirs of the Botanical Survey of South Africa No. 62). Pretoria: National Botanical Institute
- Welman WG (2003) Solanaceae. *Strelitzia* 14:913–918
- Western Australian Herbarium (1998–) *Lycium ferocissimum* Miers. FloraBase—The Western Australian Flora. Department of Biodiversity, Conservation and Attractions. <https://florabase.dpaw.wa.gov.au/browse/profile/6968> Accessed: May 11, 2021
- Wishart S (2018) African Boxthorn. New Zealand Geographic. <https://www.nzgeo.com/stories/african-boxthorn-lycium-ferocissimum>. Accessed: June 26, 2019
- Zann RA (1994) Reproduction in a zebra finch colony in south-eastern Australia: the significance of monogamy, precocial breeding and multiple broods in a highly mobile species. *Emu—Austral Ornithology* 94:285–299
- Ziegler K, Hopkins K (2011) Furneaux Islands—Boxthorn Control. Hobart, TAS: Friends of Bass Strait Islands–Wildcare. 8 p