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Two decades of progress targeting boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*): a global review to inform eradication in Western Australia

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Review

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Abstract

Boneseed [*Chrysanthemoides monilifera* subsp. *monilifera* (L.) Norl.; syn. *Osteospermum moniliferum* subsp. *moniliferum* L.] is a perennial shrub native to the southwestern and southern coasts of South Africa. It was introduced to Australia in about 1852 and now represents a significant threat to natural ecosystems. Despite *C. monilifera* subsp. *monilifera* being listed as a Weed of National Significance, momentum on improving its management has dissipated at a national level, beginning in 2008 (when a national research initiative finished) and increasingly after 2013 (when funding for national coordination ceased). A recent synthesis of past management for *C. monilifera* subsp. *monilifera* and recommendations for guiding future priorities has rekindled interest in Western Australia. To complement this synthesis and to identify improvements for program efficiency and effectiveness, we reviewed research and management findings on this weed with a focus on the past two decades. We collated information across the ecology and biology of *C. monilifera* subsp. *monilifera*, and the near relative, bitou bush [*Chrysanthemoides monilifera* subsp. *rotunda* (DC.) J.C. Manning & Goldblatt; syn. *Osteospermum moniliferum* subsp. *rotundatum* (DC.)], as well as useful insight from *C. monilifera* subsp. *monilifera* management programs applied elsewhere. As part of this review, we assessed the classical biological control work that has been done on *C. monilifera* subsp. *monilifera*, focusing on likely explanations for why, despite nine agents and a naturalized fungus, biological control is not an effective management tool. Our synthesis suggests that for the limited populations with low-abundance plants in Western Australia, eradication from the state remains a realistic target. This objective, however, needs to build on the collated baseline of past management efforts and deploy a carefully planned management program over the coming two decades. Systematic surveillance using the latest techniques, combined with manual or herbicide removal and controlled burns where possible, remain the most suitable methods to deploy. The long-lived soil seedbank requires detailed monitoring following initial plant removals and long-term funding to ensure the sustained effort required to deliver the goal of eradication of *C. monilifera* subsp. *monilifera* in Western Australia.

Introduction

Boneseed [*Chrysanthemoides monilifera* subsp. *monilifera* (L.) Norl.; syn. *Osteospermum moniliferum* subsp. *moniliferum* L., Asteraceae], is a perennial shrub native to the southwestern and southern coasts of South Africa (Weiss et al. 2008). In Australia, *C. monilifera* subsp. *monilifera* was first recorded as an introduced plant in Sydney in 1852, from "MacLeay's garden" Melbourne, in 1858 (and subsequently grown in Melbourne suburbs as a garden plant), from Adelaide in 1892 at the West Terrace Cemetery, and from Ulverstone, Tasmania, in 1931 (Weiss et al. 1998). At the time, this shrub was mostly cultivated as an ornamental garden plant, but there may have been deliberate naturalization attempts in western Victoria in the You Yang Ranges and to stabilize coastal sand dunes between Nelson and Portland, Victoria (Weiss et al. 1998).

Currently, *C. monilifera* subsp. *monilifera* is widely distributed in southern Australia (Brougham et al. 2006). Its distribution in southeastern Australia covers an area from the Eyre Peninsula in South Australia to the Victorian–New South Wales border and extends from the coast to a significant way inland in some areas. Extensive infestations occur in South Australia's Mount Lofty Ranges and Murraylands and Victoria's Mornington Peninsula, Bellarine Peninsula, and the You Yang Ranges. In New South Wales, scattered infestations are present along the coast from Newcastle on the Central Coast to Moruya in the south. The majority of infestations are in the Sydney region, extending west into the Blue Mountains (Brougham et al. 2006).

Management Implications

Chrysanthemoides monilifera subsp. *monilifera* (syn. *Osteospermum moniliferum* subsp. *moniliferum*; boneseed) is a shrub native to the southwestern and southern coasts of South Africa. In Australia, *C. monilifera* subsp. *monilifera* was introduced in the 1850s and has spread extensively in the southeastern states of Victoria, South Australia, and Tasmania. The introduction of *C. monilifera* subsp. *monilifera* to Western Australia is thought to have happened almost a century later, and spread remains far more restricted. After *C. monilifera* subsp. *monilifera* was classified as a Weed of National Significance in Australia in 1999, detailed plans for its management were developed, drawing on a synthesis of available data at the time. This coordinated effort resulted in two detailed literature reviews being produced in 2006 and 2008. Since this time, research and management on *C. monilifera* subsp. *monilifera* has continued to generate new insight. In South Australia, containment lines are being applied, and more effective biological control may improve management outcomes. In Western Australia, a recent synthesis of past management has revealed that eradication remains a realistic target. All of these programs would benefit from an updated synthesis of relevant knowledge. Our review has brought together new information from the past two decades of research on the ecology, biology, and management of *C. monilifera* subsp. *monilifera*, with the specific goal of improving the chance of eradicating *C. monilifera* subsp. *monilifera* in Western Australia. A lack of detailed understanding of key ecological issues relating to management remains, including whether or not it is an obligate outcrossing taxon and the impacts of seed dispersal vectors in its non-native range. In contrast, understanding of its germination requirements and allelopathic effects and the effectiveness of management options, including fire and herbicides, have advanced. Regarding classical biological control, our review has revealed plausible explanations as to why the existing agents have not resulted in broadly effective management. Management of *C. monilifera* subsp. *monilifera* in southeastern Australia and New Zealand's South Island remains focused on containment where possible, some localized extirpations, and minimizing impact. Invasions elsewhere in the world remain largely unmanaged, but at the same time lack documented evidence of rapid invasion. Our synthesis supports retaining eradication as the management goal for *C. monilifera* subsp. *monilifera* in Western Australia via a mixed approach of manual removal, herbicide, and controlled burns where logistics permit.

In Tasmania, *C. monilifera* subsp. *monilifera* is concentrated around the fringes of inhabited areas and is mainly restricted to coastal and estuarine areas (Brougham et al. 2006). The disjunct distribution in Western Australia is more restricted in its range and abundance, found across multiple populations between Albany and Perth (Batchelor et al. 2023b, 2024).

Chrysanthemoides monilifera subsp. *monilifera* prefers winter rainfall regions, where it is found in a wide range of vegetation communities, including coastal dunes, estuarine areas, heath, mallee, woodland, and dry and wet sclerophyll forest (Brougham et al. 2006). *Chrysanthemoides monilifera* subsp. *monilifera* occurs on a range of soil types but does not tolerate water-logged soils (Muyt 2001). Seedlings emerge during winter, reaching reproductive maturity in the second year of growth. Flowering occurs from August to October, with fruiting following during September to November. Flowers are protandrous, with seeds usually produced by allogamy (Weiss et al. 2008). There is 1 seed per fruit, up to 6 seeds per inflorescence, and up to 50,000 seeds per plant, every year (Weiss et al. 1998). In Australia, birds are the primary dispersal vectors, although most seeds fall beneath the plant and either enter the seedbank or are consumed by rodents or ants. Seed longevity is highly variable and likely depends on local context, ranging from at least 3 yr (Weiss 1984) to more than 8 yr (French et al. 2024), 8.5 yr (Briden and McAlpine 2012), and 9 yr (L McMillan, personal communication). Mature plants are estimated to live 10 to 20 yr (Muyt 2001).

Chrysanthemoides monilifera subsp. *monilifera*'s impact as a weed is most severe in natural ecosystems, and its presence is associated with the decline of flora and fauna in southeastern Australia. Grassy woodland, valley grassy forest, and lowland forest vegetation communities in Victoria are vulnerable to *C. monilifera* subsp. *monilifera* invasion, where dense infestations eliminated most native ground flora and prevented virtually all overstory regeneration (Muyt 2001). Dense, continuous canopy cover for *C. monilifera* subsp. *monilifera* has been recorded in areas of the You Yang Ranges (Adair and Holtkamp 1999), directly threatening the endangered orchid (*Pterostylis truncata* Fitzg.) (Adair et al. 2012; Bramwells 2003). The local extirpation of some 40 indigenous plant species within these ranges has been largely attributed to the local *C. monilifera* subsp. *monilifera* infestation (Blood 1987; Thomas et al. 2005). Moreover, removal of *C. monilifera* subsp. *monilifera* in a defined 109-ha area has coincided with an overall increase in koalas (*Phascolarctos cinereus*) and an expansion of their use of this habitat (Duffy 2020).

At the national level, *C. monilifera* subsp. *monilifera* (as well as bitou bush [*Chrysanthemoides monilifera* subsp. *rotunda* (DC.) J.C. Manning & Goldblatt; syn.: *Osteospermum moniliferum* subsp. *rotundatum* (DC.)]) was classified as a Weed of National Significance (WoNS) in 2000, due to the significant impacts it has on natural environments (ARMCANZ and ANZECC 2000). A national strategy was drafted for its management attempting to "arrest the spread and minimise the impact of *C. monilifera* subsp. *rotunda* and *C. monilifera* subsp. *monilifera* in natural ecosystems" (ARMCANZ and ANZECC 2000). The National Bitou and Boneseed Management Group was formed to implement the goals in the strategy. The strategy was revised in 2012 by the Australian Weeds Committee to progress the legacy of achievements by stakeholders under the previous strategy.

Unlike the *C. monilifera* subsp. *monilifera* invasion in the southeast of Australia, populations in Western Australia are often reasonably discrete and appear slow to spread. Some populations are also in areas where local conditions are well suited to detailed monitoring and large-scale management interventions. *Chrysanthemoides monilifera* subsp. *monilifera* in Western Australia became a declared plant in 1979 under the Agriculture and Related Resources Protection Act, 1976–1978 (Government Gazette of Western Australia, No. 4, 1980). In 2006, *C. monilifera* subsp. *monilifera* in Western Australia was reclassified as a plant not to be introduced to the state, with existing populations targeted for eradication (initially P1/P2, now Category C2). The current category prevents any sale, trade, or movement. Surveillance and management since that time has varied in effectiveness, particularly since 2013, when funding from the national WoNS program ceased (Batchelor et al. 2022).

There is a strong likelihood that a more coordinated, consistent, and systematic approach to surveillance could deliver greatly improved outcomes for *C. monilifera* subsp. *monilifera*

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management in Western Australia, as well as in other places where the plant is an introduced invader. To prepare for such management, two deliverables are required. First, an aggregated synthesis of past management and control efforts is required, detailing present and past population demographics for the weed. Until recently, this has not existed for Western Australia, because *C. monilifera* subsp. *monilifera* management has been done by multiple agencies without enduring overall coordination and has not been consistent in either space or time. A synthesis of these data as well as a full assessment of *C. monilifera* subsp. *monilifera* populations across the state has recently been completed (Batchelor et al. 2024). This insight will transform the ability of land managers in Western Australia to know *where* and *when* to act.

Second, an updated review of the literature covering *C. monilifera* subsp. *monilifera* management is essential to leverage existing understanding and identify knowledge gaps. This knowledge will help to inform *how* to act, particularly in regard to improving the efficiency and effectiveness of management. The reviews of Brougham et al. (2006) and Weiss et al. (2008) provided a comprehensive guide to the ecology and biology of *C. monilifera* subsp. *monilifera* and its management options in Australia as was best known at that time. The Brougham et al. (2006) review comprised six sections, providing detailed insight on ecology, biology, control and post-control restoration, and monitoring. It also featured case studies of *C. monilifera* subsp. *monilifera* control from South Australia, Tasmania, and Victoria. While there is strong overlap in content between the two publications, the Weiss et al. (2008) paper provides greater detail on the taxonomy, distribution (actual and potential), plant growth and development, dispersal and population dynamics, and legislative status.

Since these reviews, *C. monilifera* subsp. *monilifera* has remained a focus for much research in Australia and elsewhere. While most of this work has focused on *C. monilifera* subsp. *monilifera* as an introduced weed, further context from the native range can also provide relevant guidance for refining management. Here we review the past two decades of research on the ecology, biology, and management of *C. monilifera* subsp. *monilifera* to update the earlier work of Brougham et al. (2006) and Weiss et al. (2008) with the specific goal of guiding more efficient and effective management of *C. monilifera* subsp. *monilifera* in Western Australia specifically and elsewhere more generally.

Methods

We took two approaches to assembling content for this review. First, we consulted an extensive literature collection, including "gray" literature, that we have acquired through active searching for any publications on *Chrysanthemoides* over the past 20 yr (i.e., from when we started working on this genus; Scott 1996). Second, further literature on the biology, ecology, and management of *C. monilifera* subsp. *monilifera* since 2008 was systematically identified through keyword searches of Web of Science (webofscience.com), Google Scholar (scholar.google.com), and the standard Google search engine (google.com) using the following search strings: boneseed, *Chrysanthemoides*, *Chrysanthemoides monilifera*, *Osteospermum moniliferum*. This last name reflects a more recent taxonomic interpretation of *Chrysanthemoides* (synonymized in *Osteospermum*; Sadler et al. 2022) that has been accepted by the Plants of the World Online database and iNaturalist (POWO 2024) but is yet to be accepted by the Australian Plant Name Index published by the Council of Heads of Australasian Herbaria (https://chah.gov.au). For the purposes of this review, we have retained the use of *Chrysanthemoides monilifera* subsp. *monilifera*, based on the currently accepted name in the Australian Plant Census database (https://www.anbg.gov.au/cpbr/program/hc/hc-APC.html). Where relevant and to provide specific context, we referenced literature from before 2008. However, we have not sought to make this a thorough overview of all previous work on *C. monilifera* subsp. *monilifera*, given the earlier reviews covering this literature in detail (Brougham et al. 2006; Weiss et al. 2008). While this review focuses on *C. monilifera* subsp. *monilifera*, we also include literature on the closely related *C. monilifera* subsp. *rotunda* where it aids in the understanding of *C. monilifera* subsp. *monilifera* management.

Results and Discussion

History of Chrysanthemoides monilifera *subsp.* monilifera *in Western Australia*

The first confirmed record of *C. monilifera* subsp. *monilifera* in Western Australia comes from a specimen collected by Brother Kissane on August 27, 1948, and lodged at the Western Australian Herbarium (PERTH 416444; AVH data). It was nearly three decades, however, before this specimen was formally determined to be *C. monilifera* subsp. *monilifera* (Gray 1976). The locality of the collection was recorded simply as "Armadale," but on the same day the collector also lodged a record for beard heath (*Leucopogon capitellatus* DC.) (PERTH 3004341; AVH data) with a location of "Cooliabberra Spring," which is either a winter-flowing creek within Bungendore Regional Park off the Albany Highway in Armadale or a private landholding adjacent to the park. Given the temporal proximity, it is very likely that the two records were from a similar area, which would place the first confirmed *C. monilifera* subsp. *monilifera* record for Western Australia near a well-known infestation that follows Neerigen Brook alongside the Albany Highway.

The number of residential properties found to have *C. monilifera* subsp. *monilifera* in the Perth hills and Narrogin (Batchelor et al. 2024) could suggest that at some point *C. monilifera* subsp. *monilifera* was available from plant nurseries. However, the plant has never been listed in any historical Western Australian nursery or seed catalog (J Viska, Australian Garden History Society, personal communication). Cherry (2010) noted that *C. monilifera* subsp. *monilifera* at Dardadine may have been introduced by teachers from South Australia, as this was the site of an old school. Given that the school closed in 1935, this would make that location Western Australia's earliest plantings, if true. We could not identify any other sources to further clarify the origins of *C. monilifera* subsp. *monilifera* in Western Australia, and the origin therefore remains unknown. Molecular studies would be a logical way to provide greater clarity on introduction pathways and timing, which in turn can inform improved management (Emmett et al. 2023).

Ecology and Biology

Genetics

Multiple genetic analyses that included the genus *Chrysanthemoides* have confirmed that *C. monilifera* subsp. *monilifera* is a well circumscribed and separate taxon from *C. monilifera* subsp. *rotunda* (Barker et al. 2005, 2009, 2015; Byrne et al. 2022; Emmett et al. 2023). The distribution of *C. monilifera* subsp. *monilifera* in its region of origin is relatively restricted and

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uncontroversial, occurring in the Western Cape Province of South Africa. There is evidence for *C. monilifera* subsp. *monilifera* hybridization with *C. monilifera* subsp. *rotunda* in Australia, where the two subspecies' distributions overlap in north coastal Victoria (Adair and Butler 2010; also herbarium collections MEL 1553294A, CANB 377051.1). There is no record of hybridization in Western Australia. In South Africa, these two *Chrysanthemoides monilifera* subspecies (i.e., *C. monilifera* subsp. *rotunda* and *C. monilifera* subsp. *monilifera*) are allopatric (Norlindh 1943).

Chrysanthemoides monilifera subsp. *rotunda* is an obligate outcrossing taxon (Gross et al. 2017; Scott et al. 2019b). This means that isolated plants do not produce seeds until another individual germinates nearby and flowers (i.e., subject to Allee effects due to pollination limitations). It is not known if *C. monilifera* subsp. *monilifera* is likewise obligately outcrossing, despite the mention of allogamy in Weiss et al. (2008). This trait needs to be determined, as it has significant implications for the management of *C. monilifera* subsp. *monilifera* introductions.

Seed Dispersal by Birds and Mammals

In South Africa, Knight (1988) recorded that 15 bird species visited *Chrysanthemoides monilifera* plants to feed on fruits, with the most frequent visitors being the sombre bulbul (*Andropadus importunus*), Cape bulbul (*Pycnonotus capensis*), and the Rameron pigeon (*Columba arquatrix*). Knight (1988) did not identify the subspecies of *Chrysanthemoides monilifera*, but we investigated the flora of his study location (Fernkloof Nature Reserve, Western Cape Province, 34.394°S, 19.265°E) and used its complete flora list with photos (https://www.fernkloof.org.za/index.php/all-plants/plant-families/item/osteospermum-moniliferum-subsp-moniliferum), confirming that the reserve only has *C. monilifera* subsp. *monilifera*.

Gosper (2003) reported on a detailed study of frugivores on *C. monilifera* subsp. *rotunda* from coastal New South Wales. Of the 22 bird species feeding on the fruit, the most frequent species were the pied currawong (*Strepera graculina*), Lewin's honeyeater (*Meliphaga lewinii*), silvereye (*Zosterops lateralis*), red-whiskered bulbul (*Pycnonotus jocosus*), yellow-faced honeyeater (*Lichenostomus chrysops*), and olive-backed oriole (*Oriolus sagittatus*) (Gosper 2003). Emus (*Dromaius novaehollandiae*) have been reported to consume fruit and may be the vectors responsible for long-distance dispersal (Brougham et al. 2006). While the viability of emu-egested seed has never been confirmed through formal experiments, dense clusters of *C. monilifera* subsp. *monilifera* seedlings have been observed germinating from emu scats (Batchelor et al. 2024).

An understanding of seed dispersal potential is critical to management of a bird-dispersed species such as *C. monilifera* subsp. *monilifera*. This relationship was studied by Mokotjomela et al. (2013a, 2013b, 2013c) as part of a broader study examining seed dispersal by frugivores in South Africa. The target plants in the study were two native [*C. monilifera* subsp. *monilifera* and African olive (*Olea europaea* subsp. *africana* Mill.)] and two non-native plant species [lantana (*Lantana camara* L.) and wooly nightshade (*Solanum mauritianum* Scopoli)] and the birds were the small species Cape white eye (*Zosterops capensis*), the medium-size Cape bulbul (*Pycnonotus capensis*), and the large speckled mousebird (*Colius striatus*). Flight distances corresponding with predicted seed gut retention times for *C. monilifera* subsp. *monilifera* were 9.4 km, 17.8 km, and 21.2 km for *Z. capensis*, *P. capensis*, and *C. striatus*, respectively. These maximum potential distances for seed dispersal, based on theoretical bird-ring recapture frequency and gut retention times, were much greater than that previously reported, which was on the order of 1 km (Mokotjomela et al. 2013c). While this study may suggest that very long distance dispersal events are theoretically possible for *C. monilifera* subsp. *monilifera*, their likelihood of occurrence in field-relevant conditions is another matter entirely.

Seed Predation by Birds and Mammals

Chrysanthemoides monilifera subsp. *monilifera* in its native habitat, South Africa, is harvested from plants and from the ground by Chacma baboons (*Papio ursinus*), but seeds do not survive ingestion (Knight 1988). Most seed is not dispersed but falls under the parent plant onto the ground (Knight 1988; Scott 1996), where seeds are subject to predation by rodents (Scott 1996).

In southeastern Australia, Gosper (2003) recorded *C. monilifera* subsp. *rotunda* seed predation by the parrots, crimson rosella (*Platycercus elegans*) and eastern rosella (*Platycercus eximius*), and the house sparrow (*Passer domesticus*). In contrast, *C. monilifera* subsp. *monilifera* is not exposed to seed predation by parrots, because the two types of organisms are geographically widely separated in Africa. *Chrysanthemoides monilifera* subsp. *monilifera* is restricted to the southwest Western Cape Province, whereas parrots are found in the northern parts of southern Africa (eight species in the family Psittacidae; Newman 1983). It is likely that rodent predation is the evolutionary driver producing a "bone" seed (i.e., round and hard).

Seed Germination

Recent seed germination research on *C. monilifera* subsp. *monilifera* has focused on germination microclimates and chemical amendments to stimulate germination. *Chrysanthemoides monilifera* subsp. *monilifera* seeds germinated faster over a range of temperatures with the application of karrikins to harvested seeds, relative to control treatments (Reynolds et al. 2014). Their study also determined that seed imbibition was rapid (within 48 h) and that dormancy was physiological. Interestingly, germination was not inhibited by the hard, woody endocarp, and dormancy occurred in the winter months. Germination occurred over relatively low temperatures (10 to 20 C), characteristic of winter in southwest Western Australia and ceased at 35 C (Reynolds et al. 2014). In contrast, Batchelor et al. (2023b) found that germination of *C. monilifera* subsp. *monilifera* seeds was not enhanced by smoke water (containing karrikins), while gibberellic acid accelerated germination but did not increase overall germination percentage. Seeds appeared to have no afterripening phase, and seed desiccation did not increase the likelihood of endocarps fracturing (i.e., to initiate imbibition). Seeds were found to be vulnerable to direct flame exposure, even for short periods of 10 s, suggesting controlled burns may well lead to high mortality for seeds not protected deeper in the soil seedbank (Batchelor et al. 2023b).

Survival of *C. monilifera* subsp. *monilifera* and *C. monilifera* subsp. *rotunda* seeds was compared in controlled aging experiments performed at 45 C and 60% relative humidity (Schoeman et al. 2010). The number of days to lose 50% viability in *C. monilifera* subsp. *monilifera* and *C. monilifera* subsp. *rotunda* was 47 d and 16 d, respectively. The authors predicted that *C. monilifera* subsp. *monilifera* may have a long-lived seedbank and *C. monilifera* subsp. *rotunda* a more transient (<1 yr) seedbank (Schoeman et al. 2010). French et al. (2024) buried seeds of *C. monilifera* subsp. *monilifera* and *C. monilifera* subsp. *rotunda* at two locations and two depths and sampled regularly for 8 yr. Seed viability showed a rapid decline with time, although in excess of 10% of seeds were still alive at 8 yr at some sites. It is possible that edaphic factors, in particular duration of soil moisture, could

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explain the variation. Detailed field sampling of *C. monilifera* subsp. *rotunda* over more than a decade (Scott et al. 2019b) found that the soil seedbank of a non-native population in Kwinana, WA, appeared to have a seed longevity of approximately 7 yr. As the time since last known seed additions to the seedbank increased, it become increasingly difficult to measure seedbank viability, as it consisted of very few seeds (Scott et al. 2019b).

Biotic Resistance

Grazing using goats, sheep, or cattle is good at suppressing *C. monilifera* subsp. *monilifera*, but plants soon recovered once the grazers were removed, and there is the risk of seed dispersal via the grazing animals (Briden 2008). The Tasmanian distribution of *C. monilifera* subsp. *monilifera* is concentrated in cities and towns and is generally absent from the intervening rural areas. Scurr et al. (2008) hypothesized, and demonstrated by exclusion experiments, that grazing by wild macropods (especially Tasmanian pademelons [*Thylogale billardierii*]) and domesticated herbivores may be sufficient to prevent the spread of *C. monilifera* subsp. *monilifera*. This hypothesis could also explain the disparate distribution in Western Australia and needs to be further assessed.

Further supporting the role of native herbivores is the study of overabundant wallabies (mostly swamp wallaby [*Wallabia bicolor*], plus other grazing marsupials) in the Booderee National Park in southern New South Wales (Dexter et al. 2013). Grazing by wallabies inhibited the recruitment of *C. monilifera* subsp. *rotunda* following fire-induced recruitment events in 18 unfenced (browsed) plots, whereas healthy recruitment occurred in 16 fenced (unbrowsed) plots (Dexter et al. 2013).

Allelopathy

Understanding allelopathy is important, as it may have negative impacts on restoration efforts following *C. monilifera* subsp. *monilifera* removal. Field experience and anecdotal evidence indicate the likelihood that *Chrysanthemoides* species have allelopathic effects on other vegetation (Weiss et al. 2008). Vranjic et al. (2000) found that shoot and root biomass of coast wattle [*Acacia sophorae* (Labill.) R. Br.] was significantly lower for seedlings grown in *C. monilifera* subsp. *rotunda* soil than for those grown in *Acacia* soil. Our surveys of *C. monilifera* subsp. *rotunda* indicate that seeds were densest under the parent bush, but without germination unless the parent plant was dead for a few years (Scott et al. 2019b). Ens (2007) investigated the allelopathic effects of *C. monilifera* subsp. *rotunda* in a Ph.D thesis at Wollongong University and subsequently published that allelopathy in *C. monilifera* subsp. *rotunda* was a key mechanism driving the recruitment limitation of indigenous flora (Ens and French 2008; Ens et al. 2008, 2009a, 2009b, 2010).

A second Ph.D on allelopathy in *Chrysanthemoides* generated a series of papers on *C. monilifera* subsp. *monilifera* at Victoria University (Al Harun et al. 2014, 2015a, 2015b, 2015c). An initial experiment of aqueous solutions of ground-up *C. monilifera* subsp. *monilifera* plant parts (leaves, stem, roots) had no impact on germination of lettuce (*Lactuca sativa* L., Asteraceae), and little impact on germination of black wattle (*Acacia mearnsii* De Wild., Fabaceae), but inhibited growth and germination of rock isotome (*Isotoma axillaris* Lindl., Campanulaceae). The latter two species are found in the Australian environment where *C. monilifera* subsp. *monilifera* grows, whereas *L. sativa* is the usual bioassay for allelopathy studies (Al Harun et al. 2014).

A test of volatiles coming from *C. monilifera* subsp. *monilifera* stems, leaves, and roots, registered no impact on lettuce germination.

Table 1. Summary of methods used to control boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*) in Australia[a]

Type of control	Method	Specific details
Manual control	Hand pulling	*Chrysanthemoides monilifera* subsp. *monilifera* has a relative shallow root system and most plants can be pulled from the soil intact.
Chemical control	Cut stump	Plants are cut off at the base and herbicide is applied to the stump.
	Stem injection	Plants are drilled at the base of the trunk and herbicide is added to holes.
	Foliar spraying	Herbicide is applied to leaves and stems as a fine spray.
	Splatter gun	Spraying with large droplet size, suitable for targeting large plants, not often used against *C. monilifera* subsp. *monilifera*.
Mechanical control	Mechanical pulling	Heavy machinery is used to pull plants from the ground, with minimal disturbance to the soil. Suitable for agricultural areas and very large plants.
	Slashing	Suitable for non-natural areas, but stumps will resprout.
Fire	Effect on *C. monilifera* subsp. *monilifera*	Fire kills plants if entirely scorched. Fire will kill some seeds but stimulates mass germination.
	Control opportunities	If a bushfire burns a *C. monilifera* subsp. *monilifera*–infested area, be prepared for follow-up control of seedlings.
Biological control	Insects, mites, and pathogens	Nine biological control agents released between 1989 and 2006, none established on *C. monilifera* subsp. *monilifera* (Adair et al. 2012; Table 2).

[a]Adapted from Brougham et al. (2006) with updates.

A similar result occurred with *A. mearnsii* and strawflower [*Xerochrysum bracteatum* (Vent.) Tzyelev, Asteraceae] that grow in the same environment as *C. monilifera* subsp. *monilifera* (Al Harun et al. 2015a). Four phenolic compounds—catechins, *p*-coumaric acid, phloridzin, and ferulic acid—were identified from *C. monilifera* subsp. *monilifera* tissue out of the 13 tested (Al Harun et al. 2015c). Leachate from *C. monilifera* subsp. *monilifera* leaf litter inhibited germination in *X. bracteatum* and *I. axillaris*, but unidentified allelochemicals could still be the cause of the allelopathy observed (Al Harun et al. 2015c). Further experiments using litter alone, litter and soil, and soil alone did not reduce lettuce germination above 20%, indicating an effect (Al Harun et al. 2015b), albeit marginal in magnitude.

Management Options for Chrysanthemoides monilifera subsp. monilifera

The primary management tools that have been used to control *C. monilifera* subsp. *monilifera* infestations in Australia are manual weeding, controlled burns (i.e., fire), and herbicides (Table 1). For dense infestations, mechanical control can be deployed, but unless stumps are removed from the ground, there is a danger that plants will resprout. Classical biocontrol has also been pursued for *C. monilifera* subsp. *monilifera* in Australia, including new developments and insight in the last two decades.

Fire

Fire can successfully control *C. monilifera* subsp. *monilifera* by killing adult plants and near-surface seeds in the soil. When used as part of an integrated approach (e.g., fire followed by herbicide treatment and/or hand pulling of surviving plants), it is possible to extirpate *C. monilifera* subsp. *monilifera* via a controlled burn (i.e., lightly invaded, intact ecosystems; Melland and Preston 2008). Small-scale fire has been applied to *C. monilifera* subsp. *monilifera* in Western Australia in the past with good control outcomes (P Hennig, personal communication). For example, at one site in Manypeaks, a small fire over 20 to 30 m^2 in 2015 resulted in the emergence of ca. 250 seedlings the following year, which were subsequently controlled, and no plants have been observed since (P Hennig, personal communication). Lindenmayer et al. (2013) demonstrated that a too-frequent fire regime (<5-yr interval) led to the vegetation being dominated by bracken, likely as a result of overgrazing of *C. monilifera* subsp. *rotunda* and native plant species by wallabies (Dexter et al. 2013).

Herbicides

Much of the research on optimizing herbicide use on *C. monilifera* subsp. *monilifera* was done before 2008 and is summarized in Brougham et al. (2006) and Weiss et al. (2008). Little has been published on improving herbicide effectiveness for *C. monilifera* subsp. *monilifera* in the last 15 yr, indicating that there is no evidence to show approved herbicides being or becoming ineffective against *C. monilifera* subsp. *monilifera*. Herbicide remains an effective control solution for *C. monilifera* subsp. *monilifera*, particularly at higher plant densities.

Between 2006 and 2008, when large populations of *C. monilifera* subsp. *monilifera* were controlled in Western Australia, herbicide was applied to foliage or by cut-and-paint, with follow-up treatment the following year. Herbicides registered for use on *C. monilifera* subsp. *monilifera* in Western Australia include: 2,4-D amine, bromoxynil, glyphosate, metsulfuron, picloram plus 2,4-D, and metsulfuron plus glyphosate (Moore and Moore 2021).

Aerial spraying of herbicide has been used in eastern Australia against *C. monilifera* subsp. *rotunda* since 2005 and has been shown to be effective for control of large dense infestations (boom spraying) or individual plants (cone application) (Department of Planning and Environment NSW 2022; Toth and Winkler 2008). New application mechanisms that allow for targeted application via drones would be worth exploring for *C. monilifera* subsp. *monilifera*, as is being practiced for *C. monilifera* subsp. *rotunda* (Department of Planning and Environment NSW 2022), particularly if plants are identified in open yet inaccessible areas.

Biological Control

In South Africa, 113 phytophagous arthropods, 3 fungi, and 1 mycoplasm have been found associated with *C. monilifera*, with 46 taxa (mostly insects) having potential as biological control agents (Scott and Adair 1995; Weiss et al. 1998).

Nine potential agents (arthropod species) have been released in Australia, three potential agents (two insect and one fungus) were studied but not released, and one potential agent was found already established as part of a biological control program for *C. monilifera* subsp. *monilifera* and *C. monilifera* subsp. *rotunda* (Adair et al. 2012). Six of these species were approved for release to manage *C. monilifera* subsp. *monilifera*: three leaf beetles (*Chrysolina* spp.), seed fly (*Mesoclanis magnipalpis*), leaf-roller moth (*Tortrix* sp.), and leaf buckle mite (*Aceria* sp.) (Table 2). All except one species (buckle mite) failed to establish on *C. monilifera* subsp. *monilifera*, despite multiple releases (Downey et al. 2007; Morley 2010). One agent, the leaf buckle mite, is possibly established in Tasmania (Morley et al. 2012) and Victoria. It was recently observed in 2021 at Mount Eliza, Victoria, at a 2008 release site, but had only spread 25 m (Atlas of Living Australia, Biocontrol Hub; observation ID TM210214_01; https://biocollect.ala.org.au/biocontrolhub).

The release of *Tortrix* sp. in New Zealand to target introduced *C. monilifera* subsp. *monilifera* was initially thought to be unsuccessful, with only "patchy" establishment (Paynter et al. 2012) on the North Island and failure to establish on the South Island (Bownes 2022). By 2022, 11 yr postrelease, establishment was reported for the South Island, with indications of damage caused by the biological control agent (Bownes 2022).

An application to release boneseed rust (*Endophyllum osteospermi*) was not made due to the 2-yr life cycle making it extremely difficult to do testing and get the necessary supporting data (L Morin, personal communication). Another pathogen, *Austropleospora osteospermi* (syn.: *Hendersonia osteospermi*), is a leaf spot that somehow naturalized in Australia from southern Africa and is now widespread on *C. monilifera* subsp. *rotunda* in coastal New South Wales (Morin et al. 2010) but with no (or limited) demonstrated impact. Its host range is limited to *Chrysanthemoides* and close relatives, so it could be considered for use as a biological control agent against *C. monilifera* subsp. *monilifera* in Western Australia (Morin et al. 2010), but its absence from the state needs to first be confirmed.

As of 2012, there were no agents being actively researched in Australia (Adair et al. 2012). A lack of resourcing has resulted in no further *C. monilifera* subsp. *monilifera* biocontrol agent development since that time. The obvious question is why so many biocontrol agents have been worked up to a stage where they were approved for release, but have subsequently failed to establish on *C. monilifera* subsp. *monilifera*. Predation by native invertebrates appears to have hampered establishment or dispersal of *Chrysolina* spp. and *Tortrix* sp. (Adair et al. 2012). Other reasons could be a poor climate match or poor genetic match as part of the host-matching process.

We now have a comprehensive knowledge of the genetics of the closely related *C. monilifera* subsp. *rotunda*, based on nuclear and chloroplast genomes, which has enabled us to identify the source population in South Africa for the single introduction(s) to Australia (Emmett et al. 2023). This work has identified a previous unsearched region in South Africa where potentially more suitable or specific biological control agents could be found. In contrast, *C. monilifera* subsp. *monilifera* has not been studied in relation to genetic variation or pollination syndromes, with only some glimpses of the genome where *C. monilifera* subsp. *monilifera* has been used as the outlier group in the study of *C. monilifera* subsp. *rotunda*.

An improvement in host–agent matching would be a possible outcome from such molecular work. All past agents were reared on Australian *C. monilifera* subsp. *monilifera* plants while in quarantine. However, the nutrient and physical status of plants in the field may have been very different from those used for agent rearing and testing in quarantine (e.g., not fertilized, greater leaf toughness). It seems unlikely that climate mismatch between invaded areas and regions where agent searching was conducted has played a role in the lack of success, at least in southeastern Australia. However, current climate-matching models (Adair et al. 2012) are inadequate, as projections extend implausibly into desert areas that are unlikely to be suitable for *C. monilifera* subsp. *monilifera*. If further agent searching was considered, it would be a priority to develop more robust process-based models to inform the agent development pipeline (Kriticos et al. 2021).

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Table 2. Biological control releases on boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*) in Australia[a]

Biological control agent	Biological control agent years released	Agent release events[b]	Establishment summary	Current status
Bitou tip moth (*Comostolopsis germana)*	1989–1998	37 (VIC, SA, TAS)	Did not establish—possibly due to predation or poor climate match	Established and widespread on *C. monilifera* subsp. *rotunda* but not *C. monilifera* subsp. *monilifera* in eastern Australia
Black boneseed leaf beetle (*Chrysolina scotti)*	1989–1996	18 (VIC), 1 (SA), 5 (NSW), 10 (TAS)	Did not establish—possibly due to predation	Not present in Australia
Blotched boneseed leaf beetle (*Chrysolina picturata)*	1992–1995	4 (VIC), 2 (TAS), 8 (NSW)	Did not establish—possibly due to predation	Not present in Australia
Painted boneseed beetle (*Chrysolina oberprieleri)*	1994–1995	7 (VIC), 2 (SA)	Did not establish—possibly due to predation	Not present in Australia
Lacy-winged seed fly (*Mesoclanis magnipalpis)*	1998–2000 and 2005 (onto *C. monilifera* subsp. *rotunda* and *C. monilifera* subsp. *monilifera*)	? (released onto *C. monilifera* subsp. *monilifera* hybrids in VIC and NSW)	Released onto *C. monilifera* subsp. *rotunda*, did not establish—small release numbers	Not present in Australia
Seed fly (*Mesoclanis polana)*	1998	0 (however, sampled on *C. monilifera* subsp. *monilifera*, where it overlaps with *C. monilifera* subsp. *rotunda*)	Did not establish—poor host match	Widespread and abundant on *C. monilifera* subsp. *rotunda* but not *C. monilifera* subsp. *monilifera* in eastern Australia
Boneseed leaf-roller moth (*Tortrix* sp.*)*	2000–2004	112 (VIC), >9 (NSW)	Did not establish— possibly due to predation and competition in larval stages	Established on *C. monilifera* subsp. *rotunda* but not *C. monilifera* subsp. *monilifera* in eastern Australia Established on *C. monilifera* subsp. *monilifera* in North and South Islands, New Zealand
Leaf buckle mite (*Aceria* sp.*)*	2008–2012	90 (VIC, SA, TAS)	At 12 mo after release, seen at 4 sites in VIC, 1 in TAS; not established in SA	Last presence survey in SA (2011), TAS (2012), and VIC (2021); 2012 survey (SA)—no agents found
Boneseed rust fungus (*Endophyllum osteospermi)*		n/a	n/a	Host-specificity testing abandoned—too difficult
Leaf spot fungus (Austropleospora osteospermi)	Naturalized in eastern Australia	n/a	South African species on *C. monilifera* subsp. *rotunda*	Established in NSW on *C. monilifera* subsp. *rotunda*, not observed on *C. monilifera* subsp. *monilifera* but Morin et al. (2010) demonstrates susceptibility in lab conditions

[a]Adapted from Brougham et al. (2006) and Adair et al. (2012) with updates.
[b]NSW, New South Wales; SA, South Australia; TAS, Tasmania; VIC, Victoria.

Integrated Control

Recent work on delivering more effective management outcomes for *C. monilifera* subsp. *rotunda* control has coalesced around a management approach involving spraying with herbicide, burning, then respraying (Lindenmayer et al. 2015; O'Loughlin et al. 2019). A similar approach is recommended to eliminate *C. monilifera* subsp. *monilifera* (Melland 2007; Melland and Preston 2008; Melland et al. 1999). At 6 to 12 mo before a fire, the infestation should be prepared by hand pulling and cutting *C. monilifera* subsp. *monilifera*, so as to provide fuel at ground level, otherwise a fire might be too patchy (Melland et al. 1999).

Fire in autumn at 250 to 300 C will kill *C. monilifera* subsp. *monilifera* plants and deplete the seedbank (Brougham et al. 2006). Management of *C. monilifera* subsp. *monilifera* is achieved when followed in 18 mo by herbicide treatment or hand pulling of surviving plants or new germinants. This approach works best at a density of under 1,000 seeds m^{-2} (i.e., a light infestation). For heavier seedbank densities (>1,000 seeds m^{-2}), fire treatments are only likely to produce lower population abundance rather than localized extirpation (Melland 2007; Melland and Preston 2008; Melland et al. 1999).

Detection

For management programs that are targeting localized extirpation or containment, improving detection of infestations and single plants for subsequent control is a priority. The role of citizen science in documenting new infestations, particularly via online reporting platforms (Howard et al. 2022), has increased significantly in the last two decades (e.g., Landscape South Australia 2020). Given that much of the control of *C. monilifera* subsp. *monilifera* across Australia is undertaken by community groups, online apps can be very effective tools.

New technologies have been applied to *C. monilifera* subsp. *monilifera* eradication programs to address the challenges of detecting rare plants in landscapes where operation is difficult due to access or terrain. Honey bee (*Apis mellifera*) hives were tested as potential aggregation tool for environmental DNA (eDNA; pollen in this case) to detect *C. monilifera* subsp. *monilifera* plants in an urban landscape (Batchelor et al. 2023a). A species-specific assay was developed and a proof-of-concept trial was successful using pollen collected from bees foraging in dense *C. monilifera* subsp. *monilifera* populations in South Australia. However, no *C. monilifera* subsp. *monilifera* DNA was detected when the

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method was applied to material from hive pollen traps situated near isolated *C. monilifera* subsp. *monilifera* plants in Western Australia (Batchelor et al. 2023a). It may be that other eDNA substrates (Bell et al. 2024) could be developed for *C. monilifera* subsp. *monilifera* using the same PCR assay.

Detection of isolated plants in heterogeneous landscapes is also being widely addressed using drone-based remote-sensing methods. These methods were applied to detecting low-density *C. monilifera* subsp. *monilifera* plants in Western Australia with mixed success (Batchelor et al. 2023b). Both visible and multispectral band imagery were stitched into an orthomosaic for subsequent image classification based on pixel reflectance values. The models ended up with high performance metrics but unacceptably high type II error, a likely artifact of insufficient training imagery from Western Australia to develop the model (images from high-density *C. monilifera* subsp. *monilifera* populations in South Australia were used, which likely created model transferability issues; Batchelor et al. 2023b). Similar drone-based methods for plant detection have recently been developed for *C. monilifera* subsp. *rotunda* (Amarasingam et al. 2024). There may be learning opportunities to adapt this model for *C. monilifera* subsp. *monilifera*. However, habitat differences mean that *C. monilifera* subsp. *monilifera* is frequently found in environments with a tree overstory (as opposed to the often-open dune environments occupied by introduced *C. monilifera* subsp. *rotunda*), making the issue of image processing and analysis (i.e., orthomosaic vs. single-image workflows) an important consideration.

Lessons Learned from Management Elsewhere

Management in Southeastern Australia

While Western Australia has been in the enviable position of being able to maintain an eradication goal for *C. monilifera* subsp. *monilifera* across the entire state, Victoria, South Australia, and Tasmania (where *C. monilifera* subsp. *monilifera* is abundant) are mostly focusing on containment or asset protection. In 2014, the Eastern Australia Boneseed Eradication Project was working across southern and western New South Wales and eastern Victoria to eradicate all known infestations of *C. monilifera* subsp. *monilifera* from the former state and seeking to establish a new national containment line on the New South Wales border in a strategic, cross-jurisdictional effort (Martin 2013). This effort, combined with the South Coast Bitou Bush Task Force and relevant stakeholders, implemented the national southern *C. monilifera* subsp. *rotunda* containment line at Tuross Head, NSW, to prevent *C. monilifera* subsp. *rotunda* from spreading south and hybridizing with *C. monilifera* subsp. *monilifera* spreading up from Victoria (Cherry 2010; Cherry et al. 2006).

South Australia has a declared plant policy for *C. monilifera* subsp. *monilifera* under the Landscape South Australia Act 2019, which as of 2021 aimed to *eradicate C. monilifera* subsp. *monilifera* from the Northern, Yorke, and Eyre Peninsula and South Australian Arid Lands, *contain C. monilifera* subsp. *monilifera* in the Murraylands and Riverland and Limestone Coast (via destruction of outlier populations and the Murray-Coorong Boneseed Containment Zone), and *asset protect* in the Hills and Fleurieu and Green Adelaide areas. More recently, it has been accepted that it will not be feasible to eradicate *C. monilifera* subsp. *monilifera* from the Northern and Yorke region, which has moved to a *contain* approach (D Hughes, Landscape South Australia, personal communication). The Kangaroo Island and Alintjara Wiluranara regions are still free of *C. monilifera* subsp. *monilifera* (Government of South Australia 2021; J Walter, Landscape South Australia, personal communication).

In Tasmania, *C. monilifera* subsp. *monilifera* is a declared weed under the Biosecurity Act 2019. Eradication remains the stated aim in the northwest, where all *C. monilifera* subsp. *monilifera* has been controlled and local land managers are engaged (Cherry 2010; Department of Natural Resources and Environment Tasmania 2011). In the south and northeast, all outlier populations are listed as control priorities, and containment lines are maintained around core infestations to prevent further spread to areas known to be free (or in the process of becoming free) of *C. monilifera* subsp. *monilifera* (Cherry 2010; Department of Natural Resources and Environment Tasmania 2011). We note that these plans are now more than a decade old and we were not able to confirm that an active coordinated program is still in place.

Chrysanthemoides monilifera subsp. *monilifera* is listed as a noxious weed (Schedule 2) in Victoria under the Catchment and Land Protections Act 1994 and was identified as an environmental weed with typically significant impacts and a "high" risk rating by White et al. (2018). In Victoria, there is regional level variation as to whether the weed is regionally prohibited or regionally controlled. What action is taken is often undertaken by community Landcare groups. Currently, *C. monilifera* subsp. *monilifera* is listed for local eradication in the East Gippsland, North Central, and North East regions, whereas the weed is managed by prevention of growth and spread, particularly around high-value conservation areas, in the Corangamite, Glenelg Hopkins, Goulburn, Port Phillip and Westernport, and West Gippsland regions. Control in the Wimmera and Mallee regions was initially focused on eradication but has now transitioned to regional control only. At Port Phillip and Westernport, there appear to be ongoing eradication efforts and asset protection targeting a hybrid *C. monilifera* subsp. *rotunda*–*C. monilifera* subsp. *monilifera* population.

Across all southeastern states in Australia, the methods being deployed for *C. monilifera* subsp. *monilifera* management remain consistent with those outlined in previous guidelines (e.g., Brougham et al. 2006). The failure of classical biological control agents to establish in Australia has meant that manual control, herbicide treatments, managed burns, and occasionally mechanical control are the dominant approaches deployed, often in combination.

We were unable to confirm any records of *C. monilifera* subsp. *monilifera* from Norfolk Island, a small Australian territory in the Pacific Ocean, as reported by Mariotti and Zappa (2022). Rather, this report appears to be a misidentification of *C. monilifera* subsp. *rotunda*, which was recently noted as a new record for the remote island (Martoni et al. 2023). The infestation was first documented in 2011 under a large Norfolk Island pine tree [*Araucaria heterophylla* (Sailsb.) Franco] and spread from a small area (ca. 2 m^2) to cover more than 100 m^2 at its peak in around 2021 (T Patel, Norfolk Island Regional Council, personal communication). The infestation has been actively managed in recent years with the main infestation mechanically mulched and individual plants that had established on the nearby coastal cliffs being hand weeded (T Patel, Norfolk Island Regional Council, personal communication). Learning from *C. monilifera* subsp. *rotunda* eradications in Western Australia (Scott et al. 2019a) and Queensland (Cherry et al. 2008) is of clear relevance for a successful eradication of *C. monilifera* subsp. *rotunda* on Norfolk Island.

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Management in New Zealand

Chrysanthemoides monilifera subsp. *monilifera* is also a non-native invasive weed in New Zealand. It was first recorded in 1870 and after a very long lag phase became prominent in the 1990s (Briden 2008). Invasion initially was localized to urban areas, but now occurs in a wide range of native vegetation and situations from dunes to islands (Briden 2008). The strategy in New Zealand is to have surveillance and weed-led control to find and eradicate new infestations and a site-led approach to manage large infestations in valuable ecosystems.

The range of control methods—manual, herbicide, mechanical, and biological control—used in New Zealand are similar to the controls outlined in the *Boneseed Management Manual* (Brougham et al. 2006; Table 1). An additional control method used in New Zealand is the "mechanical shredder," a mechanical mulcher mounted in an all-terrain vehicle with rubber tracks (Briden 2008). Biological control activities have recently been revived, with the redistribution of *Tortrix* sp. encouraged now that it is established in the South Island (Bownes 2022).

The New Zealand experience is that the effort required for control decreases over time. Most effort is required in the first 1 to 3 yr with the removal of large plants and control of seedlings. After 5 to 6 yr, the ongoing seedbank is much reduced, and ongoing maintenance takes little effort (Briden 2008). However, this approach does not consider the impact of fire. A *C. monilifera* subsp. *monilifera* infestation cleared 8.5 yr previously had a massive germination of seeds from the soil seedbank following a fire (Briden and McAlpine 2012). There is also evidence that soil disturbance and canopy removal stimulate germination of *C. monilifera* subsp. *monilifera* seeds over native plants, indicating that any form of disturbance to an ecosystem will favor germination of *C. monilifera* subsp. *monilifera* (McAlpine et al. 2009). Howell (2012) assessed 10 yr of progress towards environmental weed eradication in New Zealand. His sample of 90 eradication programs included 2 on *C. monilifera* subsp. *monilifera* that had made zero progress. The main conclusion of this work was that to succeed with any weed eradication, it pays to start few programs and to focus on those most likely to succeed.

Management Elsewhere (Chile, United States, and Europe)

Atala et al. (2023) describe the impact on local species diversity of *C. monilifera* in Valparaíso, Chile, without identifying the subspecies involved. Numerous photos are available online of the study area showing flowers and fruits (Fundación RA Philippi de Estudios Naturales 2024), which enables us to conclude that the subspecies is most likely *C. monilifera* subsp. *monilifera*. The invasion is attributed to the introduction as an ornamental plant to the Quinta Vergara Park in Viña del Mar, Chile, from which it escaped cultivation and spread to inland dunes of the Valparaíso region (Atala et al. 2023). We could not find any evidence of management for this invasion and would suggest that further work to confirm identification would be prudent.

Similarly, there does not appear to be active management of *C. monilifera* subsp. *monilifera* in California, USA, where it is cultivated as a garden plant and naturalized, but reportedly infrequently escapes and/or rarely persists in the flora (Brusati et al. 2014; Strother 2006).

Chrysanthemoides monilifera subsp. *monilifera* is recorded from multiple areas across Europe, including France (Channel Islands, Saint Raphaël, Théoule sur Mer) Monaco, Italy (Sicily, Ventimiglia), Gibraltar, and Andorra (Bock 2024; Greuter 2006; Mariotti and Zappa 2022). We were not able to obtain independent verification of the report from Andorra. This location, given its high altitude and winter climate, seems an unlikely spot for *C. monilifera* subsp. *monilifera* to establish. In Italy, Mariotti and Zappa (2022) report that the Sicilian population of *C. monilifera* subsp. *monilifera* has been eradicated and that the Ventimiglia introduction took place in 1869 via seeds planted at the Hanbury Botanic Gardens. The Ventimiglia population was reported as naturalized in 1996 as part of the first survey to assess the status of non-native plants of the area.

Occasional reports of "boneseed" being introduced to Saint Helena, a remote island in the South Atlantic Ocean, are likely a misreported occurrence based on common name confusions. The closely related St. Helena boneseed (*Osteospermum sanctae-helenae* Norl.), an endemic to Saint Helena, is also sometimes referred to as simply 'boneseed' (Cronk 1987).

Updated Insight to Guide Chrysanthemoides monilifera *subsp.* monilifera *Management*

In the nearly four decades since *C. monilifera* subsp. *monilifera* was first targeted for control in Western Australia, management outcomes have had mixed success. Existing ecological knowledge has generally been sufficient to guide effective management choices, particularly with sparsely distributed plants. However, if eradication is going to be achieved in the state, a step change in management will be required over a considerable duration. The recent assessment of past management and current distribution (Batchelor et al. 2024) provides a robust platform for launching a management program in Western Australia. This review has delivered additional complementary insight across four areas that could help to further improve the program in Western Australia, as well as *C. monilifera* subsp. *monilifera* management programs elsewhere.

First, the origins and introduction pathway for *C. monilifera* subsp. *monilifera* in Western Australia remain unclear. Improving understanding in this regard, particularly if combined with insight across the full Australian and South African *C. monilifera* subsp. *monilifera* distribution, would help to guide genetically informed native range surveys for classical biological control agents. It is important to note that classical biological control remains an unfeasible management option for Western Australia, particularly given the lack of any notable effectiveness elsewhere and the difficulty of maintaining agent presence with the very low ongoing abundance of mature plants. More generally, however, the recently reported positive impacts of *Tortrix* on New Zealand *C. monilifera* subsp. *monilifera* suggest there may be benefit in reevaluating this agent failure elsewhere where containment or minimizing impact is a management goal (e.g., southeastern Australia).

Second, improved knowledge on the ecology and biology of *C. monilifera* subsp. *monilifera* has reinforced that currently deployed control methods remain the most effective for use in an eradication program for Western Australia. Important knowledge gaps remain with respect to determining whether *C. monilifera* subsp. *monilifera* is capable of self-fertilization (autogamy), and the full cohort of dispersal agents across the introduced range. Both emus and the currently controlled non-native starlings (*Sturnus vulgaris*) could challenge the working assumption that a 500-m buffer zone (based on dispersal kernels) is adequate to inform population delimitation in Western Australia (Batchelor et al. 2024). Some ecological knowledge gaps have also been addressed to provide management insight. Failure to completely extinguish the soil seedbank remains the biggest threat to a successful eradication campaign (Panetta 2004). Ten years would be a minimum time frame to actively manage a *C. monilifera* subsp. *monilifera* seedbank, with 15 yr as a more conservative duration likely necessary for eradication programs. Evidence for using chemical amendments to accelerate seedbank depletion is inconclusive, yet fire appears to cause significant seed mortality.

Third, insight from active programs suggests that a combination of manual, chemical, and fire-based control, with mechanical removal for large infestations, is still optimal for *C. monilifera* subsp. *monilifera* management in Western Australia. This knowledge could also be applied to overseas introductions where active management seems absent. An opportunity to eradicate *C. monilifera* subsp. *monilifera* before it has spread widely, particularly in areas with Mediterranean climates, appears to be worth prioritizing, even if confirmed identifications found the introduction to be another taxon of non-native *Chrysanthemoides*.

Finally, novel detection techniques for isolated plants in heterogenous or hard to access landscapes could transform the likelihood of achieving successful eradication of *C. monilifera* subsp. *monilifera* in Western Australia. Such techniques are equally applicable to maintaining containment lines for introduced *C. monilifera* subsp. *monilifera* elsewhere. While initial attempts to develop eDNA and drone-based remote-sensing methods to detect *C. monilifera* subsp. *monilifera* were not successful, they generated promising insights that could be further refined in future work.

This synthesis from invasions in Australia's southeastern states and elsewhere overseas, combined with updated ecological knowledge of the local weed context, suggests that *C. monilifera* subsp. *monilifera* continues to represent a significant weed threat to natural ecosystems in Western Australia. Integrating knowledge obtained from this literature review with a collated baseline of past management efforts (Batchelor et al. 2024) to produce robust and enduring management programs will give land managers the best chance of achieving their eradication objectives.

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