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A review of Australian tree fern ecology in forest communities

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Abstract Australian forest ecosystems cover almost 16% of Australia's landmass. As the seventh-largest forested area worldwide, these forest ecosystems have largely evolved in the face of a changing climate and fire regime, drought and human land use practice. Australian tree ferns contribute to both the unique biodiversity of these forests and current forest product markets. We review the Australian tree fern literature including: the importance of tree ferns for other components of biodiversity; their response to disturbance such as fire and silviculture; and the management of tree ferns as a product for the horticultural market. Most studies focused on tree fern response to wildfire and clearfell burn and sow logging following management and horticultural industry changes. Survival and recruitment of tree ferns after a single fire/logging disturbance event found short-lived negative impacts. Studies of tree ferns over time include research on growth, with non-linear growth models found to best describe tree fern age; *Cyathea australis* grows 2.2 - 4.0 times faster than *Dicksonia antarctica* on average. Tree ferns perform a keystone function through habitat for epiphytes at the local scale, but it is unknown if this has an impact on biodiversity at the landscape scale. Our review found few studies on survival and recruitment following drought; multiple disturbance events such as repeated logging; and silvicultural techniques other than clearfell burn and sow. No studies had investigated the response of tree ferns to changing climate, invasive species, changes in fire frequency or effect of megafire. We conclude with recommendations for key areas of research including, future impacts due to changing climate, synecology, influence on forests, the impact of silvicultural techniques and the influence of megafires on survival.

Key words: disturbance, management, fire, silviculture, horticulture.

INTRODUCTION

Tree ferns are a worldwide group of ancient plants that dominate the order Cyatheales (Pryer *et al.* 2004). They are true ferns in that they are flowerless plants that reproduce by spores, which develop on the underside of the leaves or fronds, and exhibit 'circinate vernation' (Large & Braggins 2004). Tree ferns can have various growth forms. The term 'tree fern' describes the most common growth form, an arborescent growth which is a tall, erect rhizome (most notably in Cyatheaceae and Dicksoniaceae) known as the stem (or caudex).

Tree ferns are a major component of the understorey in tropical and temperate forests and perform important ecological roles (Tindale 1998; Dignan & Bren 2003; Ough & Murphy 2004). In temperate forests of southern Australia, they create a sheltered and moist forest floor (Ough 2001; Roberts *et al.* 2005), act as a nursery site for vascular plants (Ough & Murphy 1996; Ashton 2000; Bowkett 2011) and provide habitat for non-vascular plants and invertebrates (Garrett 1996; Roberts *et al.* 2005; Turner & Pharo 2005; Turner *et al.* 2006; Fountain-Jones *et al.* 2012). Like the majority of the rainforest species, tree ferns are shade tolerant when establishing in the understory of the mature forest but take advantage of gaps in the canopy from tree falls, wind damage and lightning strikes to increase their height and range (ABARES 2018).

The biogeographic distributions of tropical and temperate forests in Australia have been well described (Kirkpatrick *et al.* 1988; Wells & Hickey 1999; Ashton 2000; Corlett & Primack 2011). Knowledge of tree ferns in tropical forests in Australia is largely captured in the literature focused on taxonomy and distribution (Field 2020), with a few studies on tree fern conservation and ecology (e.g.

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Wallace 1981; Fensham 2007). Taxonomy is less of a focus in the temperate forest tree fern literature, with most taxonomic information found in field guides, and conservation management limited to a few species (Roberts *et al.* 2005; Peacock *et al.* 2013). Where tree ferns occur in temperate forests, they have been both a direct and indirect focus of research. Tree ferns have been included in research which has focused on areas harvested for timber extraction, areas burnt in either wildfire or regeneration burns (Ough 2001), and areas where tree ferns are harvested directly as a horticultural resource (Hickey 1994). Much of this research has been generated as a result of the requirement for research and monitoring of tree ferns as part of tree fern management plans of the southern states: Tasmania, Victoria and New South Wales (DNRE 2001; FPA 2017; OEH 2017). The Tasmanian Tree fern Management Plan (2017) is reviewed by the Tasmanian Forest Practices Authority (FPA) every 5 years and includes a summary of research projects to be undertaken before the next review (Tasmanian Tree fern Management Plan 2017, Appendix 2). The Tree fern Management Plan was presented to stakeholders (industry, government, environmental non-government organisations and researchers) and through this process, gaps in knowledge of tree fern ecology and management were found.

This paper reviews the Australian tree fern literature, aiming to provide a comprehensive review in the Australian context compared with systems elsewhere, noting where commonalities do and do not exist. More specifically, we review (i) the current state of knowledge and ecological role of tree ferns in temperate and tropical forests of Australia, (ii) the effects of production forestry management on tree ferns and (iii) a discussion of the gaps in knowledge in the ecology and management of tree ferns, with a focus on future climate change, reduced fire intervals and directions of future research.

METHODS

Literature was searched using scientific databases (Web of Science, Google Scholar), sourcing research from within reference lists of peer-reviewed publications and accessing technical reports from non-government and government departments. To find literature through scientific databases, we conducted searches including the word 'treefern' and/or 'tree fern', taxonomic rank (mainly genera, species and family, for example *Cyathea australis*; Dicksoniaceae), with words identified from topics: tropical, temperate, diversity, phylogeny, distribution, conservation, ecology, physiology, forest, forestry, habitat, food, substrate, epiphyte, keystone, weed, invasive, wildfire, fire, silviculture, forestry, forest, production, logging, clearfell, harvest, tropical, temperate, management and climate. A reference was only included if it (i) included a tree fern species found within Australia and (ii) contained information relevant to tree fern disturbance and ecology. The search terms 'tree fern' and 'tree-fern' alone resulted in 1973 and 5 peer-reviewed publications, respectively. Refining by the term: *Dicksonia* resulted in 65 peer-reviewed publications (of which 17 were relevant); *Cyathea* resulted in 176 papers (of which 18 were relevant); and *Todea barbara*, resulted in 15 papers (of which none were relevant; Appendix S1). Using reference lists of these peer-reviewed papers, and expert opinion, we found another 36 peer-reviewed papers. Twenty-seven technical and public reports, eight books and eight unpublished theses were also reviewed; many of these were only found in hardcopies collected by an author (PT) or in archives and not available online.

Although tree ferns are predominately found along the east coast of Australia, extending from the tropical forests of Far North Queensland, through subtropical forests in Queensland and New South Wales to the cool-temperate forests of Victoria and southern Tasmania, the majority of literature (peer-reviewed, reports and theses), as per keywords, has concentrated on cool-temperate forests of Tasmania and Victoria (Fig. 1). Despite having both the greatest tree fern species diversity in Australia and species of conservation concern, Far North Queensland tree ferns were poorly represented in the literature. The literature that concentrated on southern Australian temperate forests, focused mainly on two species, *Dicksonia antarctica* and *C. australis* (Fig. 1). Topics include: distribution (e.g. Neyland 1986), conservation status (e.g. Roberts *et al.* 2005); ecology and physiology (e.g. Hunt *et al.* 2002); influence on forest community (e.g. Garrett 1996; Ough & Murphy 1996; Ashton 2000; Roberts *et al.* 2005; Turner & Pharo 2005; Turner *et al.* 2006; Bowkett 2011; Fountain-Jones *et al.* 2012); and anthropogenic and natural disturbance (e.g. Ough & Murphy 2004; Turner *et al.* 2006; Blair *et al.* 2017). This bias also is reflected in the fact that the four species of tree fern managed for harvesting are from temperate southern Australian forests. These topics provide the framework for this literature review.

DIVERSITY, PHYLOGENY AND DISTRIBUTION

The ability of tree ferns to dominate forests from the ground through to the forest canopy has contributed to the species diversity and worldwide distribution of tree ferns (Large & Braggins 2004). Consisting of seven families with 13 genera and approximately 600 species, tree ferns span the temperate zones of the Northern and Southern Hemispheres especially in South Africa, Australia and New Zealand, while the greatest species richness is found in the subtropics and tropical areas (Kubitzki 1990; Korall *et al.* 2006; Korall & Pryer 2014). In Australia, tropical and temperate forest ecosystems occur from the coast to ~1300 m above sea level and within a broad latitudinal extent between −28°S and −43.7°S.

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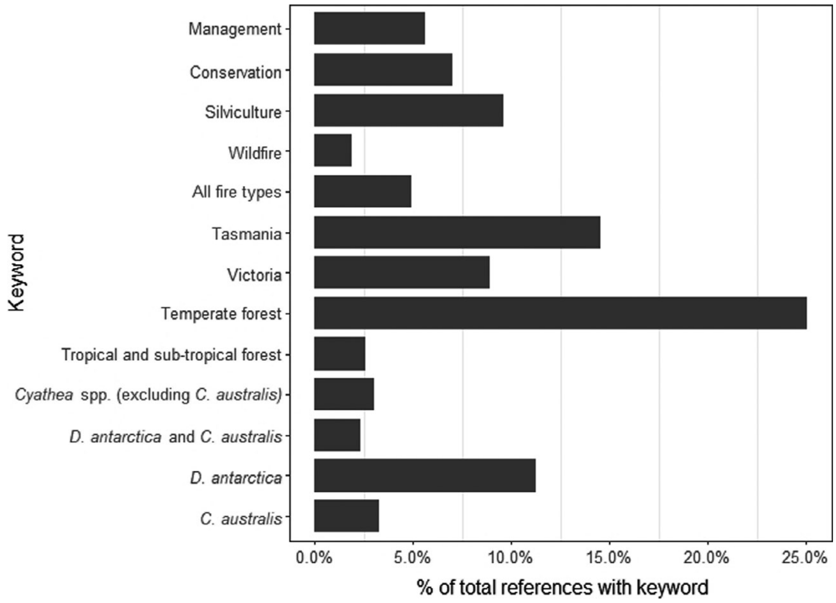

Fig. 1. The proportion (%) of the literature in which a main key word was found.

The most well-known and species-rich tree fern families (over 470 species), the Cyatheaceae, comprises approximately 500 species (Large & Braggins 2004; Korall *et al.* 2006; Korall & Pryer 2014) and is generally found in the tropics, subtropics and southern temperate zones. Phylogenetic studies within Cyatheaceae have led to the recognition of three evolutionary lineages – *Sphaeropteris*, *Alsophila*, and *Cyathea* (Conant *et al.* 1994; Korall *et al.* 2006). The Cyatheaceae tend to have scales and hairs on the stem and fronds (leaves). It is the presence of scales, as well as the position of the sori, that are used to distinguish Cyatheaceae from Dicksoniaceae, the second most species-rich family of the Cyatheales order (Korall *et al.* 2006). Dicksoniaceae are characterised as having fronds with vein ends terminating in submarginal sori (Korall *et al.* 2006). Within the Dicksoniaceae, there are 40–45 species and six genera (Large & Braggins 2004; Korall *et al.* 2006; Korall & Pryer 2014), with a more restricted distribution including tropical America, Melanesia, New Caledonia, Juan Fernandez Islands, Fiji, Australia and New Zealand (McCarthy 1998). The diversity of tree ferns in Australia is greatest in tropical and subtropical forests in north-eastern Australia (Tindale 1998). The level of endemism in Australian tree ferns is high: twelve of the sixteen *Cyathea* species are endemic, including one hybrid (McCarthy 1998); all three species of *Dicksonia* are endemic (McCarthy 1998); and the final family of tree ferns, the Osmundaceae, consists of a single genus *Todea* and two species of which one, *T. barbara*, is found in Australia.

Evidence of tree ferns has been traced to the middle to late Jurassic (Jordan *et al.* 1996; Pryer *et al.* 2004; Pryer *et al.* 2004; Korall & Pryer 2014). The abundance and diversity of tree ferns has fluctuated over geological time (Nagalingum *et al.* 2002). Cool temperate taxa that dominated the treeless, cooler, drier climate disappeared after the last glacial maximum (~22 000 years ago; Singh *et al.* 1981). Before the last glacial maximum, *Cyathea* was the prevalent tree fern genus (Singh *et al.* 1981). In the present, *Dicksonia* is predominant, particularly in southern Australia. Up until the end of the last glacial period, climate dictated vegetation distribution, whereas since 65–45 Ka, when humans arrived in Australia, studies have shown human disturbance as having a higher impact on vegetation composition (Williams *et al.* 2006; Sniderman & Haberle 2012).

Currently, tree ferns are found in all Australian states and one territory. Queensland has the highest diversity of tree ferns with 15 native tree fern species, followed by eleven in New South Wales, seven in Victoria, five in Tasmania, two in the Australian Capital Territory (ACT), one (previously two) in South Australia (a relict population at Waterfall Creek as now extinct (Jones 1998)), one in Western Australia and none in the Northern Territory (Table 1).

There are three species of *Dicksonia* in Australia: *D. youngiae*, *D. herbetii* and *D. antarctica* (Fig. 2). *Dicksonia antarctica* is thought to have the largest population and distribution of any tree fern in Australia, with estimates in 2007 of 130 million stems in Tasmania alone (FPA 2011; FPA 2017; SOFR 2018). *Dicksonia antarctica* predominantly occurs in shady, wet gullies, primarily in wet sclerophyll forest or rainforest but also in some drier *Eucalyptus* forests

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Table 1. Australian native tree fern species (all data from Large and Braggins (2004) and the Atlas of Living Australia (2020); updated distributions and origins by Field (2020))

Species	Common name(s)	Maximum recorded height (m)	Maximum recorded frond length (m)	Distribution	Endemic
Dicksoniaceae – hairy tree ferns					
Dicksonia antarctica Labill.	Manfern, soft tree fern	15.0	4.5	Qld, NSW, ACT, Vic., Tas (SA now extinct)	Australia
Dicksonia herbertii W. Hill	Bristly tree fern	4.0	Unknown	Qld	Qld
Dicksonia youngiae C. Moore ex Baker	Bristly tree fern	5.0	Unknown	Qld, NSW	Australia
Cyatheaceae – scaly tree ferns					
Cyathea australis (R. Br.) Domin Domin subsp. *australis*	Rough tree fern	20.0	4.0	Qld, NSW, ACT, Vic., Tas	Australia
Cyathea baileyana (Domin) Domin	Wig tree fern	5.0	3.0	Qld	Qld
Cyathea brevipinna Baker ex Benth.		3.0	3.0	NSW	Lord Howe Island
Cyathea celebica Blume	na	6.0	5.0+	Qld, New Guinea, Indonesia	No
Cyathea cooperi (Hook. ex F. Muell.) Domin	Australian, lacy, scaly or Coopers' tree fern	12.0	6.0	Qld, NSW, Vic., WA (naturalised)	Australia
Cyathea cunninghamii Hook.f.	Gully or slender tree fern (Australia) Ponga or p_unui (New Zealand)	20.0	3.0+	Qld, NSW, Vic., Tas, New Zealand	No
Cyathea exilis Holttum	na	4.0	1.0	Qld	Qld
Cyathea feline (Roxb.) C.V. Morton	na	8.0+	4.0	Qld, Oceania, Asia	No
Cyathea howeana Domin	na	8.0	3.0	NSW	Lord Howe Island
Cyathea leichhardtiana (F. Muell.) Copel.	Prickly tree fern	7.0	3.0	Qld, NSW, Vic.	Australia
Cyathea macarthurii (F. Muell.) Baker	na	5.0	3.0	NSW	Lord Howe Island
Cyathea rebeccae (F. Muell.) Domin	Black tree fern	8.0	3.0	Qld	Qld
Cyathea robertsiana (F. Muell.) Domin	Lacy or slender tree fern	7.0	3.0	Qld	Qld
Cyathea robusta (C. Moore) Holttum	na	5.0	5.0	NSW	Lord Howe Island
Cyathea woollsiana (F. Muell.) Domin	na	6.0	2.5	Qld	Qld
Cyathea × marcescens N.A. Wakef.	Skirted tree fern	10.0	3.0–4.0	Vic., Tas	Australia
Osmundaceae					
Todea barbara (L.) T. Moore	Austral king fern, king fern	3.0	2.0	Qld, NSW, Vic., Tas, South Africa, Oceania	No

ACT, Australian Capital Territory; NSW, New South Wales; Qld, Queensland; SA, South Australia; Tas, Tasmania; Vic, Victoria.

where precipitation exceeds 600 mm and wet forest remnants persist in shaded and moist habitats (Neyland 1986). It can also occur as an extensive stand of tree fern understorey in tall wet *Eucalyptus* forests and mixed forests (Kirkpatrick 1991; Jones & Clemesha 1993; McCarthy 1998).

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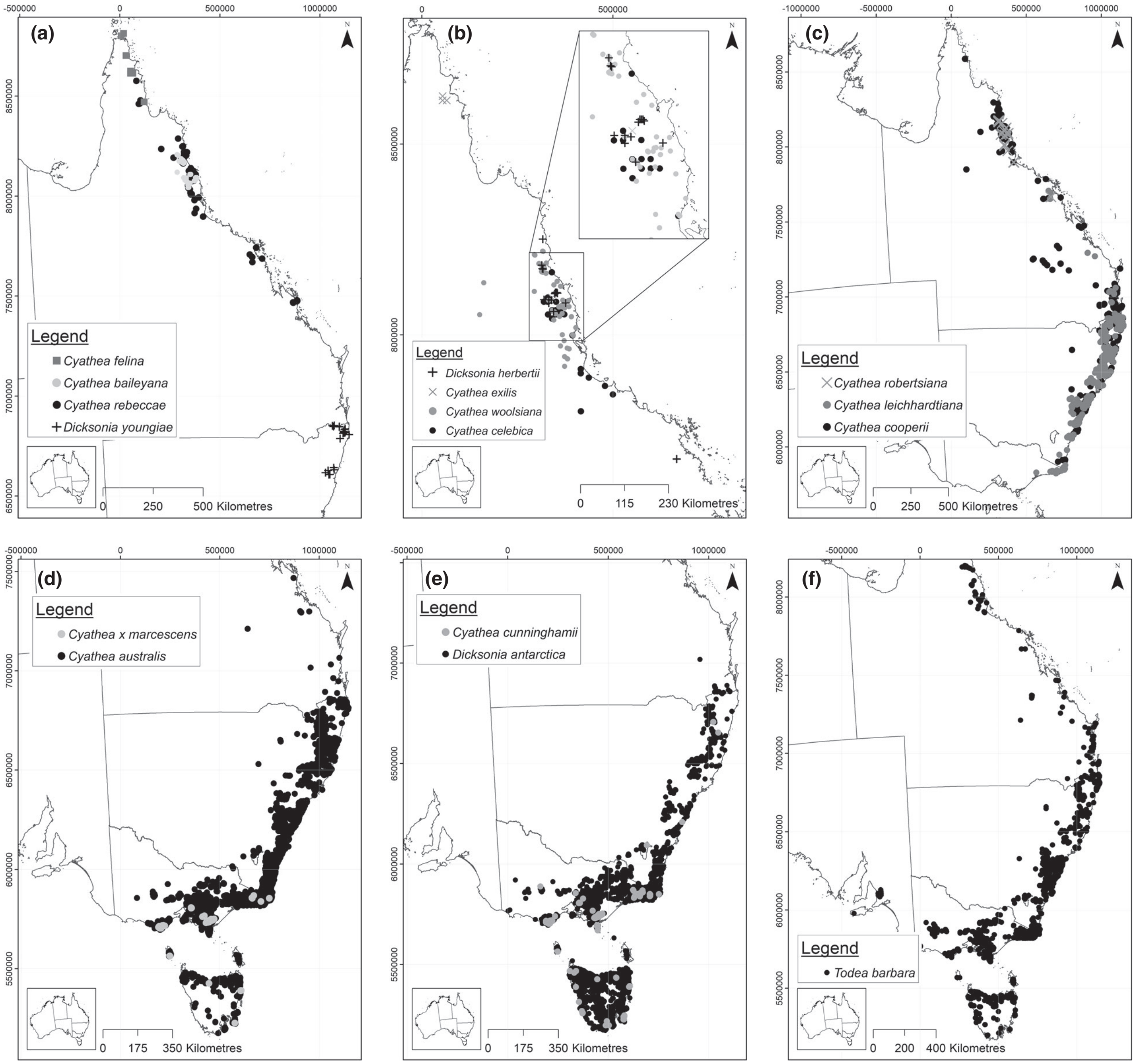

Fig. 2. The distribution of tree ferns in Australia. (a) *Cyathea felina* is only found in eastern Cape York Peninsula in Queensland; *C. baileyana* is endemic to north-eastern Queensland; *C. rebeccae* occurs in northeastern and central eastern forest of Queensland; *Dicksonia youngiae* occurs in southeastern Queensland and northeastern New South Wales between the Mary and Clarence Rivers (McCarthy 1998). (b) *Dicksonia herbertii* occurs mainly in northeastern Queensland between the McLeod and Johnstone rivers (McCarthy 1998). There is an additional southern population in the ranges near Eungella; *C. exilis* is endemic to Cape York Peninsula, Queensland. As of 1998 only known from one vine-forest on sandstone (McCarthy 1998); *C. woollsiana* is endemic to coastal areas of north-east Queensland. Mostly between the Herbert and Bloomfield Rivers to an altitude of 1200 m; *C. celebica* occurs in northeastern Queensland on steep riverbanks and forest margins. Insert gives detail of boxed area; (c) *C. robertsiana* is endemic to north-eastern Queensland between the Herbert and Daintree Ranges at elevations of 300–1500 m. Also found in the Eungella Range; *C. leichhardtiana* occurs from central eastern Queensland to eastern Victoria (McCarthy 1998) with additional populations in the Bellenden Ker Range in northeastern Queensland; *C. cooperii* occurs in eastern Queensland and eastern NSW to 35°S (McCarthy 1998). It is also locally naturalised in south western Western Australia and possibly southern Victoria (not shown); (d) *C. australis* is endemic to south-east Queensland, eastern New South Wales, Australian Capital Territory, southern Victoria and Tasmania; *C. x marcescens* is a hybrid of *C. australis* and *C. cunninghamii* that occurs (not endemic) from the Otway Ranges to Gippsland, Victoria and in eastern Tasmania; (e) *C. cunninghamii* occurs in south-east Queensland, north-east New South Wales (only 1 or 2 possible locations), southern Victoria and Tasmania; *D. antarctica* occurs in south east Queensland, eastern New South Wales, Australian Capital Territory, southern Victoria and Tasmania; (f) *Todea barbara* occurs in south eastern South Australia, north eastern and south eastern Queensland, eastern New South Wales, Victoria, and Tasmania (including King Island).

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There are 12 species of the genus *Cyathea* on mainland Australia, with 11 of these species found in Queensland (4 are endemic; Table 1, Fig. 1). Four *Cyathea* species are recorded as endemic on Lord Howe Island: *C. brevipinna*, *C. howeana*, *C. macarthurii* and *C. robusta* (Table 1). The most abundant species, *C. australis*, is also the most widespread. *Cyathea australis* is more tolerant of drier microclimates than other tree fern species and can be found in mid to lower elevations where it is warmer and drier and distant from streams (Blair *et al.* 2017). In northern regions of Australia, *C. australis* can grow to elevations of 1200 m asl (McCarthy 1998). However, it is most prevalent in south-eastern Australia in wet eucalypt forest, extending into rainforest margins and dry sclerophyll forest.

Of all the tree ferns, *D. antarctica*, *C. australis*, *C. cunninghammii*, *C. leichardtiana*. *C. x marcescens* (*C. australis* * *C. cunninghamii*; de Salas & Baker 2019) and *C. cooperi* are most mentioned in the literature. The remaining Australian tree fern species have very little mention in the scientific literature except for descriptions in fern taxonomic texts, which may include a brief summary of ecology and distribution (e.g. Duncan & Isaac 1986; Jones & Clemesha 1993; Garrett 1996; McCarthy 1998; Large & Braggins 2004). The exception is *T. barbara*, which is common but not abundant and is typically found in sheltered riparian areas in tall open *Eucalyptus* forest (dry sclerophyll forest and/or remnant wet sclerophyll forest gullies) in Tasmanian coastal and hinterland regions (McCarthy 1998), south of the Great Dividing Range in Victoria (Walsh 1994), and less commonly in cool temperate rainforest gullies in both Tasmania and Victoria (Benson & McDougall 1993; Fig. 2). *Todea barbara* can extend from the coast up to elevations of 1000 m and tolerate rainfall above 1200 mm (Benson & McDougall 1993).

CONSERVATION STATUS

No tree ferns are listed as threatened under federal environmental legislation, but Tasmania, Victoria and Queensland have species listed in a threatened category under state legislation. The Tasmanian *Threatened Species Protection Act* 1995 lists *C. cunninghamii* as endangered and *C. x marcescens* as vulnerable (FPA 2011). Both species are listed as priority species requiring adequate consideration in the development of the reserve system (Commonwealth of Australia 1996b; DPIWE 1998). Most of the 22 known populations of *C. cunninghamii* are protected, either under conservation covenants as per the *Tasmanian Nature Conservation Act* 2002 or in formal reserves; of the 18 extant sites, four occur in streamside's close to public land available for forestry operations (Threatened Species Section 2011a). Four populations of *C. x marcescens* are known, with one of these populations found on a covenanted private land reserve (Threatened Species Section 2011b). The populations of both *C. cunninghamii* and *C. x marcescens* have been documented (Roberts *et al.* 2005; Peacock *et al.* 2013) and are considered to be at risk of decline due to climate change (Threatened Species Section 2011a,b). *C. x marcescens* is a sterile hybrid and recruitment is reliant on the presence of putative parents *C. australis* and *C. cunninghamii*. The three other species found in Tasmania, *D. antarctica*, *C. australis* and *T. barbara* are not listed as 'threatened'.

In Victoria, *C. cunninghamii* and *C. leichhardtiana* are recognised as 'vulnerable' under the *Flora and Fauna Guarantee Act* 1988. *Cyathea x marcescens* is not listed under the *Flora and Fauna Guarantee Act* 1988 but is prohibited from commercial harvest because of the likely damage to habitat during harvesting and likely confusion with the protected *C. cunninghamii*. *Todea barbara* is not listed as 'threatened' but collection is low in any one area, and some traders keep a limited number of artificially propagated *T. barbara* (DNRE 2001).

Of the twelve *Cyathea* species in Queensland, *C. celebica* and *C. cunninghamii* are 'near threatened', and *C. exilis* and *C. felina* are 'endangered' under the *Nature Conservation (Wildlife) Regulation* 2006. Little is known about the conservation, ecology and biology of these species. *Cyathea exilis* is only recorded at two localities, one of which is 1.5 km from a road and the other is remote. A draft recovery plan for *C. exilis* lists plant collection for horticulture as a threatening process (a threat mitigated by the ready availability of the species commercially) and damage to wild plants and associated habitat due to exotic wild pig trampling (Fensham 2007).

Cyathea spp. are listed as 'protected plants' under flora and fauna protection legislation in New South Wales (*Biodiversity & Conservation Act* 2016 – Schedule 1 and Schedule 6). Under this Act, *Cyathea* spp. cannot be picked, possessed, bought or sold for commercial purposes without a license. One moss species, *Calomnion complanatum*, grows on the stems of tree ferns (most commonly *D. antarctica* but also *Cyathea* species) and is protected under threatened species legislation in New South Wales (three localities) and Victoria (one locality). Where this moss is protected so are coexisting tree ferns (Meagher 1999; Downing *et al.* 2007). *Calomnion complanatum* has also been found recently in Tasmania on tree ferns and is postulated to be introduced due to its highly deciduous leaves and presence in tourist localities (Dalton 1998).

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ECOLOGY AND PHYSIOLOGY

Tree ferns are prolific spore producers (Nagalingum *et al.* 2002) and the viability of *D. antarctica* spores has been found to be up to 22 years in a laboratory (Lloyd & Klekowski 1970). There is limited literature on spore dispersal. Given that spores are wind dispersed (Tuomitso *et al.* 2003), tree ferns are limited in that: dispersal by tree fern fragments is unlikely; foundation from a single spore, while documented, must be followed by intragametophytic selfing to form a viable colony, which is difficult; species with only green spores have lower viability and tolerance to travelling than species with non-green spores (Muńoz *et al.* 2004). However, given time some tree ferns can disperse long distances, for example Noben *et al.* (2017) used sequence variation of family Dicksoniaceae to show that there was an evolutionary dispersal event between Melanesia to northern Australia 15–3 Ma.

Few studies have looked at germination of tree ferns and none of these been done *in situ*. Huckaby and Raghavan (1981) found germinating spore division patterns of *C. australis* and *C. cooperi* different to those of *D. antarctica* but did not detail germination longer than 10 days. One notable exception is research by Goller and Rybczyńksi (2007) who successfully cultured spores from *C. cooperi*, *C. australis* and *C. leichhardtiana*. Both *C. australis* and *C. cooperi* took 16 weeks to germinate and 12 months to reach reproductive capacity, while *C. leichhardtiana* took 6 weeks to germinate and only 6 months to become a sporophyte. Other laboratory work achieved successful germination of *D. antarctica* spores on agar jelly, burnt/unburnt soil, tree fern stems and decaying logs, with soil producing the greatest gametophyte development (Chuter *et al.* 2008). Water has been identified as a limiting factor for gametophyte germination and development (Chuter *et al.* 2008), becoming less of a limitation with sporophyte growth and being used very conservatively in *D. antarctica* at 1–2 m tall (Hunt *et al.* 2002).

Tree ferns can harvest water both through the soil and aerially through the stem (a root mantle) and fronds, which may explain the broad ecological range of the species from dry sclerophyll forest to riparian cool temperate rainforest (Garrett 1996; Large & Braggins 2004). The architecture of the frond plays an integral role in water capture (Hunt *et al.* 2002; Bowkett 2011). As a tree fern grows from the apex of the caudex, it sends out new fronds which funnel water along the frond down to the apex of the tree fern where it is captured by the aerial roots at the base of fronds and within the stem (Hunt *et al.* 2002). This aerial root system, combined with frond architecture and a great water storage capacity (Ashton 1986; Roberts *et al.* 2005), can help tree ferns withstand infrequent, severe drought events (Ashton 2000). Consistent with these natural conditions, Volkova *et al.* (2010) found that under controlled settings *D. antarctica* is more vulnerable to drought (water deficit) than *C. australis*; both species fare poorly despite being shaded but are resilient to short-term water stress and can restore physiology to surviving fronds and re-sprout following substantial frond loss (Volkova *et al.* 2010). The question of tree fern survival in a future with climate change and water stress (drought) has only been specifically addressed by Volkova *et al.* (2010).

Tree ferns are generally abundant in disturbance refuge sites such as watercourses and gullies (Dignan & Bren 2003). These sites provide a dependable water source, which facilitates spore dispersal, germination, and tree fern growth (Bowkett 2011) and a refuge from drying (hot) winds (Jones & Clemesha 1993). The tolerance of *D. antarctica* and *C. australis* to the low light levels of highly shaded and steep gullies (Dignan & Bren 2003; Bowkett 2011) is confirmed from laboratory (Volkova *et al.* 2009a,b) and field studies (Volkova *et al.* 2011). Comparing at a finer scale, the tolerance of light between the two tree fern species found mixed results. In the laboratory, *D. antarctica* has greater tolerance than *C. australis* to increased light levels (Volkova *et al.* 2009a). In the field, conditions based on eight mature stems of each of *D. antarctica* and *C. australis* along an exposure gradient (ranging from the edge of a wet forest coupe to a water course) found both species to be quite resilient. Results demonstrated seasonal acclimation and plasticity, with little differences in plant water status and photosynthetic parameters between the species, regardless of different origins or micro-site habitats (Volkova *et al.* 2011). In wet forests, *D. antarctica* was found to be more dominant than *C. australis* within 40 m of a watercourse where the natural light is low, beyond which light penetration gradually increases and so does the likelihood of *C. australis* (Dignan & Bren 2003). Volkova *et al.* (2011) concluded that with the lack of differences in photosynthetic performance between *C. australis* and *D. antarctica*, the habitat preferences of *C. australis* (e.g. Dignan & Bren 2003) are probably better described by water use efficiency at the leaf scale, related to the presence of leaf hairs only found on the abaxial surface of *C. australis* fronds. Leaf hairs are known to assist water absorption, protect against insolation and thought to reduce transpiration from boundary layers (Schreuder *et al.* 2001; Kessler *et al.* 2007). In addition to water availability, temperature has been found to affect tree fern growth and physiology; low temperatures are found to inhibit photosynthesis (Volkova *et al.* 2011). Brief exposure to increase in temperature (nine separate days over 34°C) caused heat stress and chlorosis in *C. cooperi*,

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yet general frond growth appeared unaffected (Doley 1983). Increase in temperature alone has no negative affect on photosynthesis of *D. antarctica*, but combined with irradiance, photosynthetic apparatus becomes damaged, suggesting that where shading is removed (e.g. via disturbance) competitive advantage and survival may decrease (Volkova *et al.* 2009b). *D. antarctica* is reported to tolerate temperature as low as −7°C, but there is no known specific optimum temperature range (Wrigley & Fagg 2013). These ecological and physiological studies found that tree ferns repair physiology quickly when water stressed, are temperature tolerant and use water efficiently. Therefore, we can infer that tree fern survival in a changing climate has a positive prospect.

Dicksonia antarctica frond lengths and stem heights are amongst the greatest recorded for Australian tree ferns (Bowkett 2011; Table 2). However, these data are not good indicators of tree fern ages or growth rates. *Dicksonia antarctica* stems may survive after falling over, even after complete severing of their link to the soil (Hunt *et al.* 2002). Tree ferns can live up to 50–250 years (100 and 193 years reported for *Dicksonia* species and 50 and 250 years reported for *Cyathea* species; Brock *et al.* 2016; Fedrigo *et al.* 2018) and have variable growth rates (Table 2). Short-term field-based studies reported growth rates for *D. antarctica* in Tasmania range from 30 to 50 mm year^{-1} (FPA 2011). In comparison, radiocarbon dating of the oldest material (from the base of the stem – an acceptable sampling area as verified by Fedrigo *et al.* 2018) of six samples found *D. antarctica* to have a highly variable average growth rate of 5.0–88.0 mm year^{-1} (Mueck *et al.* 1996). With data supporting non-linear growth models for both *D. antarctica* and *C. australis*, Blair *et al.* (2017) and Fedrigo *et al.* (2018), respectively, found that *C. australis* grew 2.2 times and four times faster than *D. antarctica* on average (Table 2), with *D. antarctica* outliving *C. australis*. Faster growth rates of taller tree ferns were attributed to available light by Blair *et al.* (2017), but Fedrigo *et al.* (2018) found no influence of light availability on growth rates, likely due to differing methodologies (see Fedrigo *et al.* 2018, Appendices S1–S4). Although differences of up to 12–14 mm year^{-1} were found in growth rates of *C. australis* and *D. antarctica* between the four locations studied by Blair *et al.* (2017), no reasons for differences in growth rates were given other than geographical location. Blair *et al.* (2017) found the biggest variable influencing growth rate after wildfire was the height of the stem at the time of fire. Other factors that have been reported to influence tree fern growth rates include precipitation, temperature, elevation and topography (Mueck *et al.* 1996; Bystriakova *et al.* 2011; Fedrigo *et al.* 2014, 2018; Blair *et al.* 2017).

INFLUENCE ON FOREST COMMUNITY

Forest communities with tree ferns in Australia are potentially at risk of invasion by exotic species, for example, blackberry *Rubus fruticosus* L. (WoNS 2012). Tree ferns, like exotic species, have a propensity for disturbance refuge sites such as watercourses and gullies, leaving tree ferns at risk of exotic species invasion. Australian tree fern species have historically been taken overseas (Arosa *et al.* 2012) and are currently legally sold overseas (DAWE 2020a). No tree fern species has been declared a weed risk within Australia. They have been declared weed risks elsewhere: *Cyathea cooperi* has become a threat to the native tree fern *Cibotium glaucum* on the Hawaii islands (Medeiros *et al.* 1992; Chau *et al.* 2012); *D. antarctica* has been declared an invasive species on the eastern part of Sao Miguel Island (Azores archipelago – Portugal; Arosa *et al.* 2012). For both species with no known elimination or control techniques, eradication from the islands is impossible and management is concentrating on eradication from priority habitats.

Tree ferns are important for the survival of other species including epiphytes (Chesterfield 1996; Roberts *et al.* 2005; Turner & Pharo 2005; Bowkett 2011), invertebrates (Fountain-Jones *et al.* 2012), and even as seedbed and nursery sites for trees (Chesterfield 1996; Bowkett 2011; FPA 2011). Since the early work by Ashton (1986) which examined the influence of tree ferns on associated vascular species in *Eucalyptus regnans* forests, there have been no studies in Australia that have tested the influence of tree fern leaf litter on ground vascular plant recruitment and/or function. Where high densities of tree ferns occur, the competitive shading effects recorded in New Zealand indigenous forests (Coomes *et al.* 2005; Brock *et al.* 2018) and older pine plantation forests (Forbes *et al.* 2016) may apply to tree ferns in Australian forests. For the most part, Australian studies have concentrated on tree ferns as habitat or food for animals and as substrates for epiphyte occurrence and persistence.

Habitat or food for fauna

Tree ferns, both alive and dead, provide habitat and food for several fauna species. Sooty owls (*Tyto tenebricosa*) in Victoria were modelled to be more likely found in forest associated with *C. australis* and *D. antarctica* (Loyn *et al.* 2001). Platypus (*Ornithorhynchus anatinus*) have used the fibrous roots from the stem of tree ferns to line their nests (Munks *et al.* 2004), and the ringtail possum (*Pseudocheirus peregrinus*) has been noted as using fibrous roots to line a drey (S. A. Munks pers. comm., 2020). Dead tree fern stems provide habitat for invertebrates (e.g.

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Table 2. Growth rate (mm $year^{-1}$) for tree ferns based on Australian studies

Species	Location	Annual precipitation (mm per annum) and annual temperature (°C)	Method	Growth rate (mm $year^{-1}$)	Sample size	Reference
Todea barbara	Victoria	na	Unknown	600.0	Unknown	DNRE (2001)†
Cyathea australis	Western Port, Victoria	750–900 mm per annum (1880–1977) ~22–7°C	Frond spacing	105.0	5	Ferwerda *et al.* (1981)
C. australis	Ferntree Gully NP, Victoria	na	Regrowth after fire	113.0	6	Ferwerda *et al.* (1981)
Dicksonia antarctica	Hobart nursery	na	Frond length	350.0–500.0	Unknown	M. Garrett as cited in Neyland (1986)
D. antarctica	Tasmania	na	Regrowth after fire	460.0	33	Neyland (1986)
D. antarctica	Toolangi, Victoria	na	Radiocarbon dating	5.0–88.0	5	Mueck *et al.* (1996)
C. australis			Radiocarbon dating	22.0–38.0	2	
D. antarctica	Florentine, Styx and Plenty, Tasmania	>1000 mm per annum	Regrowth after fire (15-, 28- and 41-year regrowth)	178.0 (15-year-old sites) 260.0 (28-year-old sites) 310.0 (41-year-old sites)	20	Chuter (2003)
D. antarctica	Tasmania	na	Unknown	30.0 (0–1 m tall) 50.0 (1–2 m)	Unknown	FPA (2011)
C. cunninghamii		na	In a garden	300.0	Unknown	FPA (2011)‡
D. antarctica	Wayatinah, Tasmania	na	Regrowth after fire (10-year regrowth)	265.0	Unknown	Peacock and Duncan (2021)
			Caudex growth (undisturbed control site)	275.0	Unknown	
C. australis	Central Highlands, Victoria	1194–1393 mm per annum	Regrowth after fire. Linear random effects modelling	73.0 (±22)	163	Blair *et al.* (2017)§
D. antarctica			Regrowth after fire. Linear random effects modelling	33.0 (±12)	172	Blair *et al.* (2017)§
C. australis	Central Highlands, Victoria	600–2000 mm per annum 5.4–14.2°C	Radiocarbon dating and non-linear modelling	92.7	12 (radiocarbon dating) 44 (non-linear modelling)	Fedrigo *et al.* (2018)¶
D. antarctica			Radiocarbon dating and non-linear modelling	22.7	12 (radiocarbon dating) 347 (non-linear modelling)	Fedrigo *et al.* (2018)††

†Based on pers. comm from P. Bostock.
‡Based on pers. comm. from M. Garrett.
§Absolute growth rates from linear random effects models on sampled individuals with different initial sizes. Fedrigo *et al.* (2018) calculated non-linear relative growth rates (RGR) of Blair *et al.* (2017) tree ferns (see Appendix 8 Figure S9 of Fedrigo *et al.* 2018).
¶For ferns >0.23 and <4.36 m $Age_{C.australis} = 7.8139372e^{0.0043036 \times height}$ (height in cm).
††For ferns >0.56 and <4.25 m $Age_{D.antarctica} = 29.57e^{0.004814 \times height}$ (height in cm).

insects, spiders, millipedes, minute land snails, isopods and amphipods) (Ogle *et al.* 2000). For instance, native bees (*Amphylaeus morosus*) nest in dead stems of both *C. australis* (Spessa *et al.* 2000) and *D. antarctica* (DNRE 2001). Fauna also provide habitat for tree ferns, for example when the superb

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lyrebird (*Menura novaehollandiae*) forages on steep slopes in Victoria it makes available bare ground suitable for *C. australis* prothalli development (Ashton & Bassett 1997).

Deleterious effects to tree ferns by faunal grazing does not appear to be an issue in Australia (or at least does not get a mention in any literature) but is an issue elsewhere. For example, in New Zealand, exotic species such as the common brushtail possum *Trichosurus vulpecula*, (imported from Australia), rats, mice and red deer (Gaxiola *et al.* 2008), graze tree ferns. Possums especially have heavily grazed on several tree fern species, which has resulted in the loss of the largest emergent trees and led to their replacement by smaller diameter stems and tree ferns (Bystriakova *et al.* 2011). In Australia, the mountain brushtail possum (*Trichosurus caninus*) feeds on tree ferns in forests, with *D. antarctica* and *C. australis* also potentially acting as hosts for food sources such as fungi eaten by *T. caninus* (Lindenmayer *et al.* 1994). Crimson rosellas (*Platycercus elegans*) feed on tree fern spores (DNRE 2001) and rufous fantails (*Rhipidura rufifrons*) have been observed foraging on invertebrates in the fronds and around tree ferns (DNRE 2001).

Overall, Australian studies anecdotally record interactions between tree ferns and fauna and concentrate on the presence or absence of fauna in tree fern dominated forests as opposed to looking at the impact and/or association of fauna on the tree fern itself. One exception is Fountain-Jones *et al.* (2012) who examined beetles on the fronds and stems of *D. antarctica* and concluded that the beetle populations observed appear to be of low pest potential.

Substrate for epiphytes

Together, tree ferns and their epiphytic species in wet eucalypt forests play a key role in the ecology of forests through habitat provision, rainfall funnelling and moisture retention (Scott 1994). In Australia, there are many studies that consider epiphytes on tree ferns (Appendix S2) in terms of position (Roberts *et al.* 2005; Floyed & Gibson 2006), abundance (Roberts *et al.* 2005; Floyed & Gibson 2006) and use as nursery sites for new growth (Chesterfield 1996; Bowkett 2011). In fact, tree ferns are seen as keystone species in the Victorian Tree-fern Management Plan (DNRE 2001), principally because once stems exceed 1.5–2 m, they are often unique substrates for epiphytes such as orchids, ferns and bryophytes. Vascular plant epiphytes account for 9% of all vascular plant species (Zotz 2013) with greater diversity at tropical latitudes compared to temperate latitudes (Zotz 2005; Wagner *et al.* 2015). The wet tropics of Australia is an area with the greatest richness of epiphytic species in Australia (Sanger & Kirkpatrick 2015), yet there are few studies on epiphytes on tree ferns in Australian tropical forests (Wallace 1981; Cummings *et al.* 2006; Frieberg & Turton 2007; Sanger & Kirkpatrick 2015; Sanger & Kirkpatrick 2017a,b,c). Of these few studies, only Wallace (1981) mentions tree ferns with epiphytes and in one situation – *Cyathea* hosting the epiphyte *Fieldia australis*. Most of the Australian studies of epiphytes on tree ferns come from temperate forests and these consider both vascular and non-vascular plants (Wallace 1981; Ashton 1986; Chesterfield 1996; Ashton 2000; Roberts *et al.* 2003, 2005; Turner & Pharo 2005; Bowkett 2011; Black 2013).

Epiphytes are sensitive to microclimate factors such as humidity, light and wind, which can all be impacted by disturbance events (FPA 2011). Older and less disturbed tree fern stems are likely to have a greater epiphytic species richness and diversity than younger tree ferns found on more actively managed sites (Ashton 1986; FPA 2011; Blair *et al.* 2017). Microclimate variation of different regions on a tree fern stem has been shown to influence bryophyte and vascular plant species associations and epiphyte growth rates (Ashton 1986; Leitch 1997; Bowkett 2011).

The abundance and diversity of epiphytes increases with tree fern size. As tree ferns grow so does the root mantle of the stem, and the increased surface area and reduced or elevated tree fern skirt enables the establishment of a greater number of epiphytes compared to shorter tree ferns with a dense light-restricting skirt (Bowkett 2011; Blair *et al.* 2017; Roberts *et al.* 2005; Page & Brownsey 1986). Two main areas of the stem have been identified as the main zones occupied by epiphytes: the lower stem closest to the ground is dominated by obligate hygrophytic vascular plant epiphytes (Bowkett 2011), and the upper zone closest to the apex of the stem is colonised by obligate epiphytes tolerant of a more desiccated environment (Bowkett 2011). Similar zonal separation is found for bryophytes (Leitch 1997; Sinclair 2012).

One of the most frequently studied species of tree ferns, in terms of supporting epiphytes, is *D. antarctica* (Appendix S2). Studies have found up to 20 fern species and 106 bryophyte species epiphytic on upright stems of *D. antarctica,* and 83 species of bryophyte (40 mosses and 43 liverworts) on fallen stems of *D. antarctica* (Appendix S2). In comparison, *C. cunninghamii* was found to have 64 species of fern or bryophyte in Tasmania (Roberts *et al.* 2005) and *C. australis* 21 species of bryophyte, of which 54% were also found on *D. antarctic*a (Sinclair 2012; Appendix S2). Whilst many bryophyte species are epiphytic on *D. antarctica*, an increase in number of stems does not equate to greater bryophyte (liverwort) species richness (Turner *et al.* 2006).

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D. antarctica has been described as having a more luxuriant bryophyte community than *C. australis*, despite a relatively similar substrate thickness (Ashton 1986; Duck 2017). *D. antarctica* is a particularly good host for epiphytes because the fibrous lower stem root mantle grades into the soil, creating an alternative litter free micro-habitat for epiphytes that would otherwise perish in the deep litter (Roberts *et al.* 2005). The persistent frond base and aerial roots of both *Dicksonia* and *Cyathea* species typically create a substrate with good moisture retaining abilities (Beever 1984; Ashton 1986; Leitch 1997) and a surface more conducive to epiphyte growth than most woody host species (Hassall & Kirkpatrick 1985; Page & Brownsey 1986). Furthermore, the upper stem of *C. australis* has persistent stipe bases or scars that are not welcoming to rhizomatous species (Garrett 1996). Only one study has documented epiphytes on *T. barbara* (Benson & McDougall 1993).

DISTURBANCE – FIRE AND FORESTRY

A major focus of Australian tree fern literature has been the impact of disturbance, which includes snow fall (Fedrigo *et al.* 2018) and light/gap creation (Ashton 2000; Dignan & Bren 2003), with the majority focusing on fire (unmanaged and managed) and forestry (harvesting and reforestation; Ough & Ross 1992; Hickey 1994; Murphy & Ough 1997; Ough & Murphy 1999; Ough & Murphy 2004; Lindenmayer & Ough 2006; Bowd *et al.* 2018).

Land clearance and timber harvesting have been a major disturbance factor since European colonisation. Australia's forest cover is estimated to have reduced from 30% when Europeans arrived (Barson *et al.* 2000), predominantly in the early 19th century, to a current 17% (ABARES 2018). A proportion of the remaining forests (22%) have been subject to harvesting and reforestation activities (ABARES 2018). Despite the considerable reduction in forest area since European settlement and ongoing forestry activity, tree ferns remain widely distributed in the forests of eastern Australia (Large & Braggins 2004). Many of the ecological studies investigating tree ferns and disturbance have concentrated on a handful of tree fern species (the most common being *D. antarctica*, *C. australis* and *T. barbara*). These studies have mainly been done in forests subjected to production forestry in southern Australia. Tree ferns are also observed to survive in modified forestry environments such as exotic pine and eucalypt plantations.

Fire has the capacity to damage the external root system of tree ferns, as well as the stem and the apex from which fronds grow (Peacock & Duncan 1995a). High-intensity fires have the potential to kill tree ferns, whilst a tree fern can regenerate after low-intensity fires where the apex is protected. In fact, tree ferns can be the first vascular plant species to regenerate after low-intensity wildfire (Ough 2001). However, most epiphytes that grow on tree ferns are unlikely to survive a fire and population recovery occurs through re-colonisation (Hickey 1994; Turner & Pharo 2005).

Water stress or desiccation is one of the main factors that contributes to mortality of tree ferns after fire, due to the increased exposure to wind and sun (FPA 2011; Blair *et al.* 2017). The plants that survive the fire often have decreased health due to the lack of a protective forest canopy, which makes them more susceptible to climate extremes, such as high summer temperature, winter frosts and snowfalls (FPA 2011; Blair *et al.* 2017; Fedrigo *et al.* 2018).

The effects of wildfire on tree ferns differ to those of a high-intensity regeneration burn (Hickey & Savva 1992) as part of forest clear-fell burn and sow silviculture (Cunningham 1960). Tree ferns, bryophytes and other vascular plants (particularly epiphytic ferns) are more negatively affected by clearfell logging followed by regeneration burning than by natural wildfire (Cremer & Mount 1965; Cunningham & Cremer 1965; Hickey 1994; Ough 2001; Turner & Kirkpatrick 2009; Appendix S2). During a wildfire, particularly a lower intensity wildfire, tree ferns are standing at the time of disturbance and the sensitive stem and apex are above the ground, so tree ferns regularly survive the fire (Ough & Ross 1992; Ough & Murphy 1999; Ough 2001; Ough & Murphy 2004). However, during a timber harvesting operation, tree ferns are regularly knocked over (e.g. Chesterfield 1996), so the sensitive stem and apex are closer to the ground and more likely to be burnt intensely and so not survive the fire (Browning *et al.* 2010). The health of remaining tree ferns may continue to decline for several months to years after logging due to the change in microclimate associated with the loss of forest cover (Ough & Murphy 2004; Blair *et al.* 2017).

In some cases, harvesting of forests can occur after wildfire, known as salvage harvesting. The salvage harvest of native trees (e.g. permitted in Victoria since the 1930s) has historically been assumed to have little impact on the populations of *C. australis* and *D. antarctica* (Lindenmayer & Ough 2006). However, studies have shown that populations of both species decline after salvage logging post-wildfire or clearfelling (Lindenmayer & Ough 2006; Blair *et al.* 2017; Bowd *et al.* 2018). The frequency of tree ferns, including *D. antarctica* and *C. australis*, has been found to be significantly less in salvage logged sites than undisturbed sites (Blair *et al.* 2017; Bowd *et al.* 2018) with some salvage logged sites containing no records of common species such as *D. antarctica* (Bowd *et al.* 2018).

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Most of the studies that consider the impact of timber harvesting on tree ferns examine clearfall operations followed by a high intensity burn. These studies show that under this type of silviculture typically 15–30% of tree ferns survive (Tasmania – Barker 1988; Hickey 1994; Chuter 2003; Peacock 2003; and Victoria – Chesterfield 1996; Harris 2004; Ough & Murphy 1996; Ough & Murphy 2004) (Appendix S2), with one study finding only 5% of tree fern stems in plots pre-harvest were standing one year after a clearfell, burn and sow treatment (Ough & Murphy 2004). However, there is a difference between tree fern species in how they respond to harvest. *C. australis* is less likely to regenerate after being uprooted than *D. antarctica* (Garrett 1996; Ough & Murphy 2004; Blair *et al.* 2017) and is subsequently less common post-logging than post-wildfire (Ough & Ross 1992; Ough & Murphy 1999; Ough 2001; Ough & Murphy 2004). One study found that 6 years after harvesting and regeneration burning there was approximately one third fewer *C. australis* stems than *D. antarctica* stems (Ough & Murphy 2004). In Tasmania, *C. cunninghamii* and *C. x marcescens* are unlikely to be directly affect by logging as they are often located within riparian zones along watercourses, which are largely protected through prescribed reservation (FPA 2011) in the Forest Practices Code (FPA 2015). In timber production landscapes, informal and formal streamside reserves are excluded from production forestry and provide protection for all tree fern species (FPA 2015; FPA 2017).

The few studies that have looked at the long-term effects of both wildfire and logging disturbance on survival and recruitment of tree ferns have found similar results (Turner 2003; Sinclair 2012). In Tasmanian wet forests regenerating from wildfire or clearfell, burn and sow silviculture, there was no difference in fallen *D. antarctica* cover between the disturbance types 30 years after the disturbance occurred (Turner & Kirkpatrick 2009). Using a chronosequence design and comparing younger forest (1–18 years) regenerating from clearfell burn and sow silviculture, the 30-year-old sites of Turner and Kirkpatrick (2009), and old growth (>110 years) mixed forest regenerating from wildfire, Turner *et al.* (2011) found that *D. antarctica* basal area was 2.3 times greater in middle-aged forests and 53 times greater in old-growth forest indicating that in the long-term, recovery to pre-fire densities is possible. *C. australis* has also been shown to be less common post-logging than post-wildfire (Ough & Ross 1992; Ough & Murphy 1999; Ough 2001; Ough & Murphy 2004). The response of *T. barbara* to fire is unknown, but it is a vigorous coloniser of cleared sites (Duncan & Isaac 1986; Benson & McDougall 1993).

TREE FERN HARVESTING AND MANAGEMENT

In Australia, four species of tree fern are sought after for the commercial market. The most common is *D. antarctica* (Tasmania, Victoria and New South Wales) with smaller numbers of *C. australis* (Victoria and New South Wales), *T. barbara* (Victoria and New South Wales) and *C. cooperi* (New South Wales). The stem of *D. antarctica* is made of a mass of roots facilitating successful transport and transplant of the live stem from its natural site to suburban gardens (Garrett 1996; Large & Braggins 2004). *C. australis* does not have a root mantle akin to *D. antarctica*, which makes the live trees harder to transplant, although it is still attempted (Large & Braggins 2004). While *C. cooperi* can only be grown from spores (Harvey & Fagg 2012), it is popular as it grows faster and is hardier than *D. antarctica* and *C. australis*. There are very little available data on the tree fern horticulture and export industries except in the grey literature.

In 1994, the Australian Government placed a moratorium on all exports of native *D. antarctica* stems, regardless of point of origin (Unwin & Hunt 1997). Prior to this, Tasmanian tree ferns outside of legislated reserves, conservation areas and national parks were unprotected (Neyland 1988), while on mainland Australia tree ferns were only protected by the relevant state's flora and fauna legislation.

In 1999, the Australian Government passed the *Environment Protection & Biodiversity Conservation* Act 1999 (EPBC Act). This provided a legal framework for wildlife trade, which included protecting and managing tree fern harvesting and redistribution nationally and internationally. Tree fern harvesting and conservation is also managed through the *National Forest Policy Statements* (Commonwealth of Australia 1995), the *National Strategy for Ecologically Sustainable Development* (Commonwealth of Australia 1992), the *National Strategy for the Conservation of Australia's Biological Diversity* (Commonwealth of Australia 1996a) and state-based *Regional Forest Agreements* (RFA). There are 10 RFAs across four states: Victoria has five RFAs, New South Wales (3), Western Australia (1) and Tasmania (1) (DAWE 2020a). *C. australis* is also listed on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and has additional protections and regulations with regard to international trade. Under provisions of the *EPBC Act* 1999, the harvest and export of tree ferns for commercial purposes must come from an approved source, for example Wildlife Trade Operations. There are currently (as of August 2019) two approved Wildlife Trade Operations for *D. antarctica* and one for *C. australis* in Australia, both from Victorian nurseries (DAWE 2020b). Tree fern management

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Table 3. Summary of current tree fern or flora management plans in Australia

State	Species listed in plans	Type of land	Permits or licence needed	Permits approved	Tags needed	Permit exemptions	Regulating body	Plan *year of commencement
Tas	*Dicksonia antarctica*	Public and private	Yes – Forest Practices Plan (FPP)	12 in 2017–2018 financial year	Yes – since 2002	Small scale harvesting of up to six *D. antarctica* per year for personal use	Forest Practices Authority	*Tasmanian Treefern Management Plan* (FPA 2017) *2001
Vic.	*D. antarctica*, *Cyathea australis*, and *Todea barbara*	Private and limited public (areas being permanently cleared)	Yes – *Flora and Fauna Guarantee* Act permit, additional permit maybe needed from local council; Tree-fern Farm plan to selectively harvest treeferns	Unknown	Yes – since 2002	Unknown	Department of Environment, land, Water and Planning	*Victorian Tree Fern Management Plan* (DNRE 2001) *2001
NSW	*D. antarctica*, *C. australis*, *C. cunninghamii*, *C. cooperii* and *T. barbara*	Private and limited public	Yes – Wild harvester, approved harvester or grower licence depending on species	40 since 2008	Yes – since 2000s	Unknown	Office of Environment and Heritage	*NSW Whole Plant Sustainable Management Plan* (OEH 2017) *2013 Before 2013, tree fern management came under the 'Cut flower management plan'
Qld	*C. celebica*, *C. cunninghamii*, *C. exillis*, *C. feline*, *D. antarctica*, *D. youngiae*, *D. herbertii*	Public and private	Yes – Protected Plant Harvest Licence [PPHL] and Protected Plant Growing Licence [PPGL]	None since 2017	Unknown	Regulation do not apply to taking of plants not 'in the wild'. Plantations are not considered in the wild	Department of Environment and Heritage Protection	*Management Plan for Protected Plants in Queensland 2014–2019* (DEHP 2013)
WA	None	Unknown	Unknown	None	Unknown	Unknown	Department of Biodiversity, Conservation and Attractions	*Management of commercial harvesting of protected flora in Western Australia 2018–2023* (DBCA 2018) *2013
ACT	Unknown	Unknown						
SA	Unknown	Unknown						
NT	No native tree ferns in NT	Unknown						

ACT, Australian Capital Territory; NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; Tas, Tasmania; Vic., Victoria.

plans vary from state to state (Table 3). The two most detailed plans are from Tasmania (FPA 2017) and Victoria (DNRE 2001). New South Wales, Queensland and Western Australia all have general flora management plans rather than ones specifically for tree ferns.

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Key threatening processes identified in the *EPBC Act* 1999 for tree fern conservation include: land clearance; loss of climatic habitat caused by anthropogenic emissions of greenhouse gases; forestry operations (e.g. impacts such as inappropriate logging and regeneration burning in adjacent coupes and upstream activities influencing downstream sediment, deposition and scouring). Forestry operations are of great conservation concern in southern Australian states, whereas in Queensland illegal collection and damage to habitat are the focus.

Under the Tasmanian and Victorian Tree Fern Management Plans, all harvested tree ferns must be tagged at point of harvest with a tag issued by the Forest Practices Authority (FPA) (in Tasmania) and Department of Environment, Land, Water and Planning (in Victoria). The tags were also introduced in New South Wales in the 2000s by the Office of Environment and Heritage (OEH) (Table 3). In Tasmania, the funds collected from tag sales are used for the implementation, monitoring and enforcement of the Tasmanian Tree Fern Management Plan (2017) and for research into the sustainable management of tree ferns (e.g. this review). In New South Wales, a fee is also required to obtain the tags, but it only covers the cost of the tag. The exception is for *T. barbara* which is a high-risk species, so a higher tag fee is required to decrease the incentive to harvest and encourage the use of plants from cultivated sources instead (OEH 2017). Any profit made from tag sales in New South Wales is used to support OEH research and compliance activities. In Victoria, there are no fees associated with the tags.

As there is free trade under the Australian Constitution between States, the lack of uniformity of legal control systems for tree fern sale is a problem. Tasmania can utilise biosecurity controls to restrict import of mainland tree ferns for sale in the local market. Hence, under Tasmania's *Forest Practices* Act 1985 anyone harvesting or trading in tree ferns without a tag attached to the stem can be liable to prosecution and severe financial penalties if found guilty. This is much more difficult to enforce in mainland States due to the movement of tree ferns between States and differences in tag requirements.

Most tree ferns are legally extracted from native forests through silviculture (FPA 2017), although there is minor farming in the form of seedling production (Vulcz *et al.* 2002). While it has been assumed that the majority of *D. antarctica* harvesting occurs in Tasmania (DNRE 2001), records of tags issued between 2002 and 2019 indicate that Victoria harvests the largest number of tree ferns (Fig. 3). The average number of tree ferns harvested in Tasmania (largely *D. antarctica*) since 2002 is 29 262/year compared to 58 958/year in Barwon South West, Victoria, 3800/year in Gippsland, Victoria and 2410/year in New South Wales (Table 4). Records do not indicate where the tree fern markets are, but given the number of tags issued, a large portion of the harvested tree ferns must be going overseas.

No published studies have investigated the biodiversity and ecology at sites before and after a tree fern harvest, although two unpublished datasets attempted this (FPA unpub. data, Peacock & Duncan 2021). These two studies remain unpublished because they encountered difficulties including: control sites were burnt; burnt sites were not burnt to expectations; tree ferns could not be found for repeated measures; and poor replication. The lack of long-term data following the fate of individual tree ferns has been highlighted as a priority elsewhere (Brock *et al.* 2016).

Given the ecological role that tree ferns play in forests, there is a risk that exporting tree ferns could spread pests in other areas. One of the only studies to consider this found beetles both on the fronds and the stems of *D. antarctica* but concluded that the beetle populations observed appear to be of low pest potential with regard to export management of tree ferns (Fountain-Jones *et al.* 2012). This result may reflect current practices for tree fern harvesting, which include removal of all live and dead fronds and leaf-litter in the crown before exportation, with the aim that tree fern stems should be relatively insect-free when they reach the market.

KEY FINDINGS

A review of the New Zealand tree fern literature from the last 100 years was recently published (Brock *et al.* 2016). The key findings from this review were: tree fern establishment is favoured by canopy removal, in both space and time; tree ferns dominate early and mid-successional forests and, when abundant, alter successional pathways of vascular plant species communities. When considering all the published data describing the ecology of tree ferns throughout their range, the literature is most comprehensive for New Zealand, where tree ferns are prevalent. Whilst also prevalent and important in Australia, no similar summary exists, something the current review has aimed to rectify.

Overall, we found that approximately 75% of the literature about tree ferns in Australia is not easily sourced. This is highlighted by a search that found only 41% of the possible peer-reviewed literature is picked up through scientific databases (Appendix S3). A large proportion of the relevant literature is grey literature (39%) and is held in collections that are not easily accessible or searchable, for example institute collections, public sector reports and university theses (although many universities are

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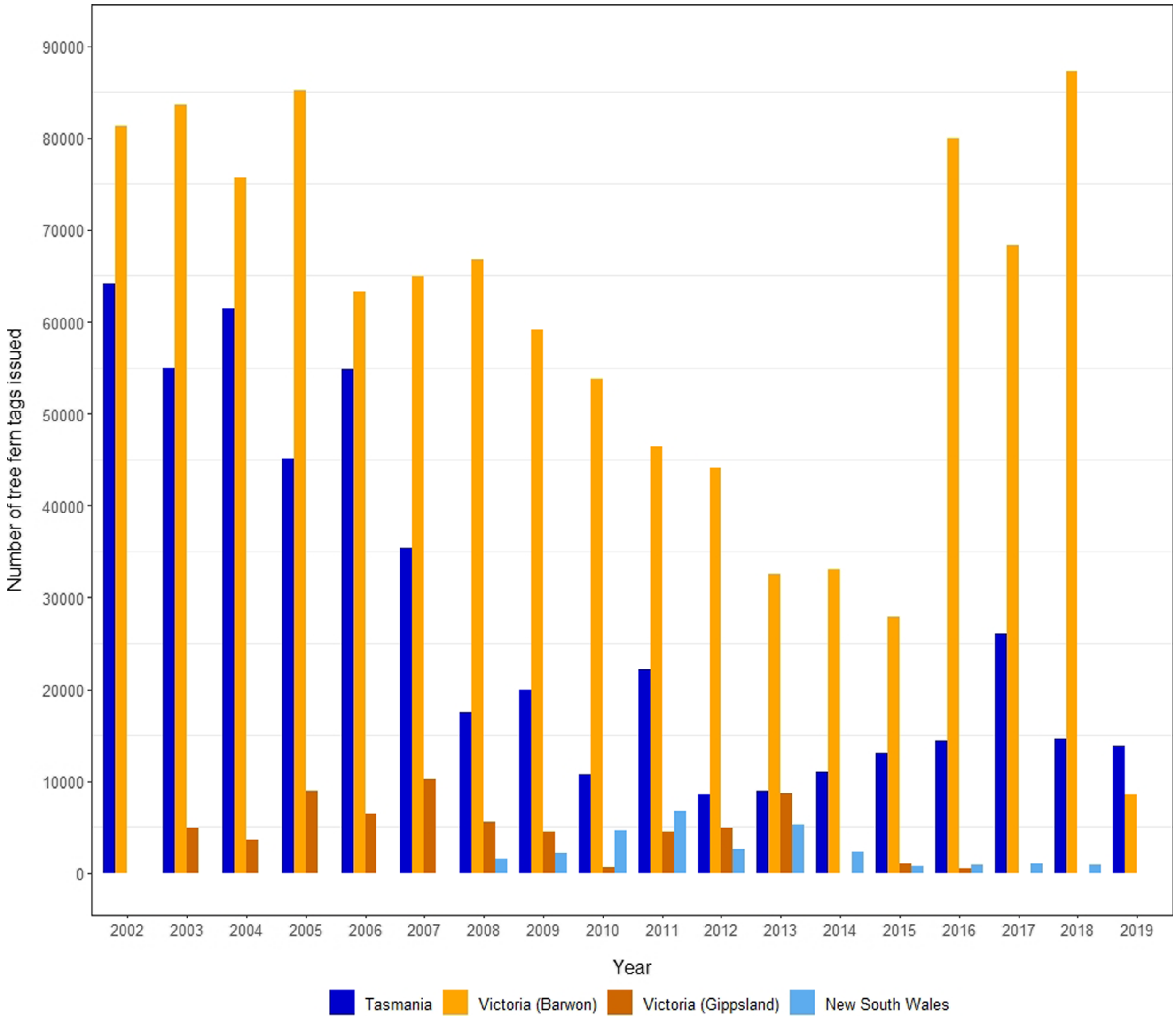

Fig. 3. The number of tree fern tags issued by Tasmania, Victoria (Barwon and Gippsland) and New South Wales from 2002 to present. The New South Wales tag numbers are only available from 2008 to present; Barwon data is by financial year from 2002 to 2015 and then annually from 2015 – present; and Tasmania data is by financial year only. A total of 4239 tags between 2003 and 2019 in Gippsland have been issued, and in the Barwon region up to 20 000 tags per year could be for trees <50 cm. In Tasmania tags are issued in two different categories >30 and <30 cm; both are included in these totals. *Source*: Victoria (DNRE, unpubl. data); New South Wales (OEH, unpubl. data); Tasmania (FPA annual reports 2003–2019; 2019 data is up to 30th April 2020).

now publishing theses electronically). Accessibility and peer-reviewed publishing of grey literature needs to be addressed to ensure ongoing verification of knowledge gaps.

The majority of Australian tree fern literature is centred in the temperate forests of Tasmania and Victoria (Fig. 1). This is mainly due to tree fern harvesting and management in the southern Australian states requiring research and monitoring of tree ferns. Most studies focused on tree fern response to wildfire and clearfell burn and sow logging following management and horticultural industry changes. Tree ferns are long-lived; longevity in forests is fundamental for the existence and persistence of many epiphytic species. Survival and recruitment after single fire/logging disturbance found short-lived negative impacts. Tree ferns are more negatively affected by clearfell logging followed by regeneration burning than by natural wildfire, but after >110 years recovery to pre-fire densities is possible after a single fire/logging disturbance.

From the literature, the resilience of tree ferns to short-term drought conditions, and ability to restore frond physiology and resprout quickly after disturbance, may mean tree ferns will respond positively to longer climate fluctuations, more frequent fire events

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Table 4. Comparison of the number of tags issued for harvested tree ferns for the last 5 years in Tasmania, Victoria and New South Wales

State	2015	2016	2017	2018	2019 (to June)
Tasmania	12 191	14 722	16 804	18 776	13 030
Victoria	28 847	80 500	68 282	87 235	8500
New South Wales – all tree ferns	824	951	1030	871	0
New South Wales – *D. antarctica* only	824	75	10	15	0

The majority of the tags issued in Victoria from 2014 onwards were in the Barwon South West region compared to the Gippsland region which over the period 2014–2019 issued a total of 1507 tags (unpub. data DNRE 2019). New South Wales tags have been issued for *Dicksonia antarctica*, *Cyathea cooperi*, *C. australis*, and *Todea barbara* since 2008. The table indicates total number of tree fern tags issued in a year and the total of *D. antarctica* only (unpub. data, OEH 2019). The tags are also issued for different licence types from 2008-present: picker (10), grower (13), wild harvest (16) and salvage harvest (1) (unpub. data, OEH 2019). Note these data use different wording of the licence types from the New South Wales Whole Plant Management Plan (OEH 2017).

and intensive browsing. However, as the literature is dominated by studies of temperate tree fern species and single disturbance events, forecasting findings to all tree ferns and multiple disturbance events may not be appropriate. More frequent fire events could have a negative impact on the survival of the species more vulnerable to desiccation and susceptible to frequent disturbance: the late successional epiphytic vascular and non-vascular plants, and facultative nursery rainforest species.

GAPS IN KNOWLEDGE

Brock *et al.* (2016) reports on topics in New Zealand that have not been investigated in Australia. There is potential to build upon Brock *et al.* (2016) and investigate Australian issues such as: the influence of tree fern leaf litter and shading on the recruitment of rainforest vascular plant species in different forest types (e.g. Dearden & Wardle 2008; Bystriakova *et al.* 2011; Forbes *et al.* 2016); and recruitment and survival of tree ferns over time (Ogden *et al.* 1997; Smale *et al.* 1997; Bystriakova *et al.* 2011). Long-term data are lacking for tree ferns in Australia, and there are few studies looking into tree fern age. Short-term growth responses and lack of environmental data can lead to misleading assumptions about environmental factors (Blair *et al.* 2017; Fedrigo *et al.* 2018). While radiocarbon dating is one solution, it is expensive, contains uncertainties in age estimates and is not reflective of the entire disturbance history at a site (Fedrigo *et al.* 2018). Radiocarbon dating is best used in conjunction with dendrochronological techniques; however, suitable shrub and tree species for dendrochronology are not always available (Fedrigo *et al.* 2018).

We found gaps in knowledge relating to key-threatening processes that may affect tree ferns into the future, including the potential of negative impacts to populations and conservation due to: climate change; frequent fire; invasive species; and commercial demand. There are currently no specific studies that have modelled tree fern future distribution or response to climate change. Only one study, Volkova *et al.* (2010), directly considered the ecology and biology of tree ferns with a change in climate. Speculation based on Volkova *et al.* (2010), the other studies revised in the *Ecology and physiology* section of this review, and preliminary analyses (initial results using B1 and A2 emission scenarios; Donoghue and Turner in prep.), indicates the ecology and biology of tree ferns will respond positively to climate change.

Studies that included fire only looked at a single wildfire, or clearfell burn and sow logging event. They did not consider the long-term resilience of tree ferns, or their epiphytes, to more frequent fires, megafires, repeated logging events, or many different disturbance events. Godfree *et al.* (2021) in an analysis of hotspot data of fires found fire sensitive rainforest species (epiphytes) may face decline. Given the keystone role of tree ferns as hosts for epiphytic species, and the lack of knowledge on that role at a landscape scale, there is a strong need for research on the impact of future megafires to tree ferns in the broader landscape.

The impact to tree ferns by introduced vertebrate herbivores (found to damage tree ferns and cause forest assemblage transition [Brock *et al.* 2016]) has not been studied in Australia. Tree fern die off where ungulates are abundant has been recorded in New Zealand (Mark *et al.* 1991). In Tasmania, European fallow deer (*Dama dama*) are predicted to increase, both locally in abundance and range extension (Potts *et al.* 2015), and at present, the impact to tree ferns is unknown.

In terms of overseas exportation of tree ferns, there are no freely available data on the number of tree ferns being exported or to where they are being sent. While this is of little conservation concern to some species (e.g. *D. antarctica* is abundant and widespread; FPA 2017), it is of conservation concern where plant

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collection for horticulture is listed as a threatening process (e.g. *C. exilis* in Queensland). Queensland is the area with the greatest tree fern species diversity and largest number of threatened tree fern species. However, there is little published on the tree ferns of conservation concern in tropical/subtropical forests of Queensland (Fig. 1). More research needs to be done on Queensland tree fern species to provide a complete picture of the ecology and abundance of tree ferns in Australia, enabling more detailed and useful management plans to be developed, for the conservation of tree fern biological diversity.

Conservation and management of tree ferns in temperate forests subject to silvicultural practices dominates the tree fern literature (Fig. 1; Appendix S1). Despite this, gaps in knowledge remain, for example the sustainability of silvicultural practices other than clearfell burn and sow logging, such as effects on tree ferns of harvesting and reforestation in drier forests under silvicultural systems. Given the important ecological role of tree ferns at the local scale (particularly as a host to epiphytes; Appendix S2), their susceptibility to disturbance such as repeated fire, their importance commercially to timber harvesting, and the conservation concern of tree ferns in tropical ecosystems, it is important that research into tree fern ecology continues.

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AUTHOR CONTRIBUTIONS

Shavawn Donoghue: Data curation (equal); Investigation (equal); Methodology (equal); Validation (equal); Writing-original draft (equal); Writing-review & editing (equal). **Perpetua Anne Mary Turner:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Validation (equal); Writing-original draft (equal); Writing-review & editing (equal).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Literature search.
Appendix S2. Species richness of tree fern epiphytes in Australia, recorded in the literature.
Appendix S3. Effects of disturbance (wildfire and/or silviculture) on tree ferns.

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