



Seed banking is more applicable to the preservation of tropical montane flora than previously assumed: A review and cloud forest case study

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ABSTRACT

The science is clear – significant reductions in tropical montane (TM) habitats are projected to occur by the end of this century. Urgent action is needed to build the resilience of TM flora and understand its adaptive capacity to climate change. Seed banking is the most widely employed *ex situ* conservation tool, providing insurance against plant species extinction and germplasm for associated research. However, tropical forest floras are grossly under-represented in seed banks due to historic assumptions and generalisations regarding collection, storage and germination of tropical forest seeds. In Australia, the Wet Tropics World Heritage Area of northeast Queensland contains tropical montane cloud forest (TMCF) in which > 70 endemic, seed-bearing species are at high risk of extinction. To mitigate this risk, we synthesised current seed science knowledge from TM plant communities around the world and examined what we know about collection, storage behaviour and germination of TM seeds. Included are our own preliminary investigations into seed banking of Australian TMCF flora. We argue that seed banking is applicable to more TM biodiversity than previously assumed and that a global effort to broaden *ex situ* conservation to include TM flora is needed. Making use of all the seed/gene banking tools available today, we call for a nationwide coordinated effort to establish a secure network of *ex situ* germplasm collections of Australian TMCF flora. Seed science research needed to inform and accelerate *ex situ* conservation of TMCF flora is also discussed.

1. Introduction

1.1. Seed banking and the tropical forest deficit

Ex situ conservation strategies preserve plants or plant germplasm away from the site of natural occurrence (Given, 1994). The most

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widely employed technique, known as seed banking, is the storage of seeds that are dried and deep-frozen in ‘conventional’ conservation seed banks (Li and Pritchard, 2009). Seed banking allows the preservation of high levels of plant genetic diversity at relatively low cost, in minimal space and for comparatively long periods (Potter et al., 2017). Seed collections safeguard against species extinction in the wild (Smith et al., 2003; Li and Pritchard, 2009; Liu et al., 2020), and they provide an immense resource for researching biological and physiological processes crucial to understanding how plant communities and ecosystems function, now and in the future (Hay and Probert, 2013; Martyn Yenson et al., 2021). Conventional seed banking relies on the following sequential steps:

1. *Collection*: wild seeds must be available, accessible, viable and genetically diverse.
2. *Drying*: seeds must tolerate drying to 15–20% equilibrium relative humidity (eRH) or ca. 3–7% moisture content (MC) to prevent fatal ice formation while in storage.
3. *Storing*: seeds must retain viability in storage at ca. -20°C .
4. *Recovering*: reliable germination protocols must produce healthy seedlings within a reasonable time period and, ultimately, mature plants (Smith et al., 2003; FAO, 2014; Pence et al., 2022).

In 2002, the Global Strategy for Plant Conservation called for representation of at least 75% of the world’s threatened plant species in seed banks (Sharrock, 2012), and decades of work have led to over 1750 seed banks globally and more than 50,000 species deposited (Walters and Pence, 2020). Efforts have focussed on ‘orthodox’ seeds that a) can tolerate the drying and freezing necessary for seed banking, and b) are easily accessible in dry or temperate regions (Wyse et al., 2018; Liu et al., 2020). In contrast, seeds of humid, tropical forest floras are currently under-represented in seed banks (Walters et al., 2013). This is due, in part, to the perceived challenges of collecting adequate genetic diversity of tropical forest species. For example, populations are often remote and access via road limited, individuals may be separated by large distances, fruits are often borne high in the canopy and flowering and fruiting is

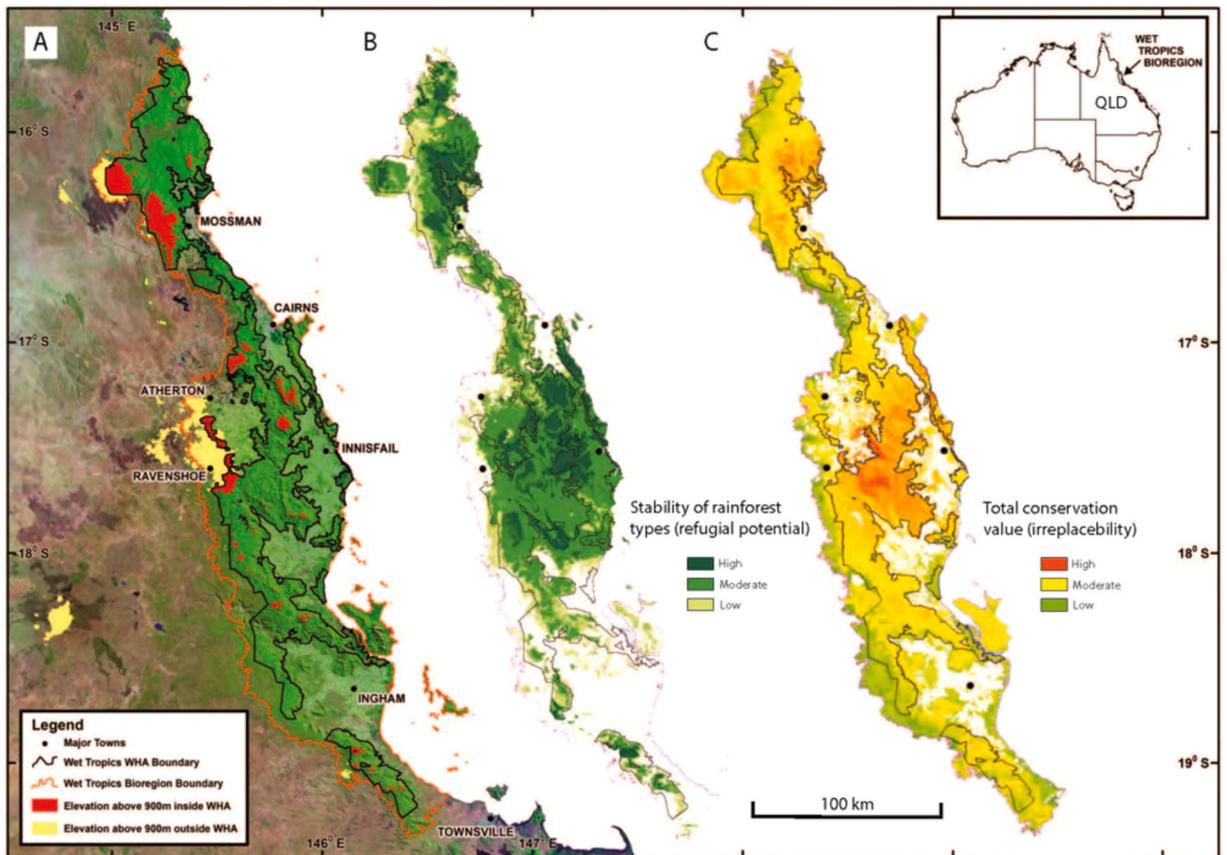


Fig. 1. Maps showing location of tropical montane cloud forest habitat in the Wet Tropics World Heritage Area of northeast Queensland (QLD), Australia. Map A: Areas > 900 m above sea level conserved within the Wet Tropics World Heritage Area (in red) and falling outside the World Heritage Area (in yellow). Map B: Relative stability of all types of rain forest in the Wet Tropics Bioregion. Dark colours represent areas predicted to be the most stable in all past and current climate scenarios (after WTMA, 2014, Fig. 11); The higher the stability, the greater potential the region has of being a refuge to species migrating due to climate change. Map C: Total conservation value (irreplaceability) based on number of species, median area of occurrence, number of endemic species and number of ancient angiosperm families (after WTMA, 2014, Fig. 8b); Note the moderate to high conservation value of areas > 900 m above sea level.

non-seasonal (Schmidt, 2000; Walters et al., 2013). In addition, historic assumptions and generalisations exist, based on a relatively small number of studied species, regarding low germinability of tropical forest seeds and their inability to tolerate drying and/or freezing (Berjak and Pammenter, 2008). Around 8% of seed plants are believed to produce desiccation-sensitive or ‘recalcitrant’ seeds (Wyse and Dickie, 2017), and the highest prevalence of recalcitrance is estimated to exist among woody species from evergreen rain forests (Tweddle et al., 2003; Wyse et al., 2018). Consequentially, tropical forests have never been a focus of seed banking efforts and there have even been calls to halt efforts to conserve tropical moist forest species via seed banking altogether (Wyse et al., 2018).

1.2. Climate vulnerable cloud forest flora

Tropical montane (TM) regions of evergreen forest that experience persistent, frequent or seasonal, low-level clouds give rise to TM cloud forest (TMCF) ecosystems. Distinctive climatic conditions in TMCF ecosystems have helped generate species-rich floras with especially high levels of beta diversity and endemism (Martin and Bellingham, 2016). The Wet Tropics World Heritage Area of northeast Queensland, Australia (the Wet Tropics Bioregion) includes TMCF at or above 900 m elevation (Fig. 1). These areas comprise a range of vegetation types, predominantly microphyll fern thickets and simple to complex notophyll vine forests, as per Webb and Tracey (1981), and are frequently immersed in clouds. Despite this, Australia’s TMCFs do not commonly appear in global TMCF assessments (Karger et al., 2021), diminishing their significance and limiting public awareness, appreciation and conservation of these extraordinary regions.

TM ecosystems, including TMCF regions, are highly threatened by climate change. This is due to a) steep environmental gradients that create geographically restricted habitat niches, b) reportedly narrow thermal tolerances of tropical species, and c) the secondary effects of the increasing altitude of cloud base formation (McJannet et al., 2008; Costion et al., 2015; Helmer et al., 2019; Karger et al., 2021). Recent climate models suggest greater rates of temperature rise at higher elevations compared to lower (Salinas et al., 2021), and changes in the reliability and quantity of precipitation in TMCF through reductions in cloudiness (Still et al., 1999; Foster, 2001; Hu and Riveros-Iregui, 2016). These factors increase the likelihood of longer drought periods and more frequent extreme temperatures, which are likely to significantly impact species adapted to consistent high-water availability and mild temperatures. Other potential challenges to TMCF flora include fires in previously fire-free environments (Asbjornsen and Wickel, 2009), loss of habitat with a suitable climate, lack of suitable alternative habitat to colonize, and dispersal, establishment and adaptation rates that are insufficient to track rates of change in climate × species interactions (Foster, 2001). As a result, we can expect altitudinal shifts in ranges and subsequent reshuffling of species and extinctions (Foster, 2001; Costion et al., 2015; Karger et al., 2021).

In Australian TMCF, the effects of climate change are expected to be felt before the end of this century (Williams et al., 2003; Costion et al., 2014). Costion et al. (2015) modelled changes in the distribution and extent of suitable habitat for 19 TMCF species and predicted declines of 17–100% of suitable habitat by 2040 (mean for all 19 species of 81%), and at least 46% by 2080 (mean for all 19 species of 95%). Rooble (2018) expanded on this work, modelling 37 species based on improved occurrence data from field surveys conducted in 2017–2019 and a mean habitat loss of 63% was predicted for all species by 2085. As a result of these startling findings, Costion et al. (2015) and Rooble (2018) strongly advocated for *ex situ* conservation action for Australian TMCF plant species with seed banking being the most practical and cost-effective option, if applicable.

1.3. Can we bank cloud forest plant species?

Driven by the pressing need to conserve TMCF plant biodiversity, we explore what evidence there is to support the challenges and assumptions that have led to the lack of seed banking efforts in tropical forests and how amenable TMCF might be to such activities. As literature on seed banking TMCF flora is lacking (Conservation Evidence database, 2022), we synthesise current seed science knowledge from other tropical forest and/or mountain plant communities around the world, where relevant (see search terms below). We examine what is known about the collection, storage behaviour and germination of seeds from these ecosystems and identify critical seed science research needed to advance *ex situ* conservation of TMCF flora. Search terms for this review included *tropical forest*, *tropical mountain/montane*, *subtropical mountain/montane*, *tropical mountain/montane forest/rainforest*, *tropical montane cloud forest* and *lower/upper cloud forest/rainforest*. Included are our own preliminary investigations into the suitability of seed banking for Australian TMCF flora, in the hope of raising awareness of the presence of TMCF in Australia. Our collecting, storage and research activities were carried out in line with internationally recognised seed banking protocols (Smith et al., 2003; Martyn Yenson et al., 2021), and resulting publications have been cited where possible. TMCF species considered ‘exceptional’ (*sensu* Pence et al., 2013) due to seed desiccation/freezing sensitivity or other plant/seed traits will require alternative approaches to ‘banking’ that are discussed. Not included in this review are studies of introduced species, or *ex situ* conservation via plant propagation and living collections.

2. A closer look at tropical montane cloud forests

2.1. Definitions, locations and climate

Ecological zonation in TM regions has been recognised by ecologists since the early 19th century (Humboldt and Bonpland, 2009), yet a globally acknowledged definition and delineation of TMCF remains lacking. The defining characteristic of TMCF – persistent cloud or fog at vegetation level (Ray, 2013) – is difficult to quantify without long-term observations (Mulligan, 2010). Maps based on ground-measured floristic or physiognomic characteristics have documented TMCF at small spatial scales, but accurate delineation of the global distribution is elusive because the term ‘cloud forest’ is not commonly or consistently used in national forest assessments

(Scatena et al., 2010). This is certainly the case in Australia where the term ‘cloud forest’ is rarely used, except by hydrologists (e.g., McJannet et al., 2006). Ecologists in Australia favour fine-scale tropical rainforest classification systems and maps that have been derived from decades of intensive study (e.g. Webb, 1959; Tracey and Webb, 1975; Tracey, 1982; WTMA, 2009). Other montane ecosystems in the world have not received this level of attention.

In the elevation-based definition and analysis of Aldrich et al. (1997) and Bubb et al. (2004), the total area of TCMF in the year 2000 was estimated at ca. 215 000 km² or 1.4% of the world’s tropical forests. By these calculations, ca. 43% of all remaining TCMF can be found in Asia and Oceania (including northern Australia), 41% in the Americas (including the Hawaiian archipelago) and 16% in Africa (Bruijnzeel et al., 2011). Using a hydro-climatic definition, Mulligan (2010) suggests that significantly cloud-affected forests may represent as much as 14.2% of all tropical forests.

Compared to other TM forests of the world, TCMFs are, on average, wetter (by 184 mm per year), cooler (by 4.2 °C), less seasonally variable and occupy more topographically exposed areas than other montane forests (Jarvis and Mulligan, 2010). Cloud forests also tend to be located closer to the coast (particularly in Asia and Australia), and at higher altitudes than montane forests not affected by clouds (Jarvis and Mulligan, 2010). The increase in the cloud immersion frequency at higher altitudes produces a progressively shorter vegetation with smaller leaves while providing important water and nutrient inputs to TCMF plants (Eller et al., 2020). Mt Bellenden Ker (1593 m a.s.l.) in Australia’s Wet Tropics Bioregion is the wettest place on the continent, with the summit weather station recording a mean annual rainfall of 7150 mm (Xu et al., 2014). Most of the rain falls during the ‘wet’ season (typically November – April), however, vegetation strips the clouds of moisture during the ‘dry’ season (May – September), which evens out seasonality (McJannet et al., 2008). The mean maximum/minimum air temperatures for summer and winter (1983 – 2012, 1488 m a.s.l.) were 22/16 and 15/11 °C, respectively (Stevens et al., unpublished).

2.2. Australia’s TCMF flora and our target species list

TMs are hotspots of biodiversity and endemism and Australia’s Wet Tropics Bioregion is no exception. A combination of topographic complexity and elevational amplitude has created environmental heterogeneity and high niche diversity. This has allowed for rapid speciation within some clades, persistence of relict taxa and habitat for immigrant taxa that are pre-adapted to high-elevation environmental conditions (Hoorn et al., 2013; Merckx et al., 2015; Noroozi et al., 2018). Formed predominantly from erosion-resistant Permian granites (Willmott, 2009), Australia’s TCMF are rich in plant taxa with strong Gondwanan links (e.g., Cunoniaceae, Elaeocarpaceae, Ericaceae and Proteaceae), including the northernmost stronghold of a number of southern cool temperate taxa (e.g. *Eucryphia*, *Acrotriche*, *Dracophyllum*), the southernmost occurrence of taxa common in New Guinea and south-east Asia (e.g. *Rhododendron*, *Cyrtandra*), and two endemic, monotypic genera (*Nothorites* and *Lenbrassia*). Other species, such as *Cryptocarya bellendenkerana* and *Tasmania* sp. Mt Bellenden Ker, are significant for exemplifying ancient flowering plant lineages (WTMA, 2014). Studies have found strong genetic structuring in plant taxa across Australia’s Wet Tropics Bioregion (Jones et al., 2010; Rossetto et al., 2009), some of which can be related to the relative geographic isolation of many of the peaks. The region is notable for species assemblages with low median area of occupancy, reflecting the already narrow ranges of taxa in these ‘sky island’ archipelagos and their correspondingly high conservation value (Mokany et al., 2014).

Conservation efforts begin with a target species list. We estimated that Australia’s TCMFs contain ca. 930 seed-bearing plant species (Zich et al., 2020), including ca. 70 – 80 endemics, all with a distributional range encompassing TM rainforest at elevations of ≥ 900 m a.s.l. From these we identified 85 target species warranting urgent conservation, including 74 seed-bearing angiosperms (Appendix 1). Eight of these seed-bearing species are currently listed as *Critically Endangered* under state species protection legislation, one is *Endangered*, and six are *Vulnerable* (Queensland Government, 2022; Appendix 1).

3. Collecting, storing and germinating TCMF seeds

3.1. Orthodox vs. exceptional seeds

Here we review the sequential seed banking steps and explore their application to TM flora. Accessible, high quality, non-dormant seeds with orthodox storage behaviour are currently the easiest form of plant germplasm to bank, and we will explore what proportion of TCMF flora falls into this category. In contrast, seed of ‘exceptional’ species require the application of a range of skills and technologies not always available in seed banks, due to limitations in resources and infrastructure, posing a challenge to banking such species (Pence, 2013). Pence et al. (2022) described four *exceptionality factors* (EFs), all of which have potential relevance to TCMF seed and will be examined:

- EF1. Seeds that are not produced/are extremely limited in quantity, viability and/or accessibility (see Section 3.2).
- EF2. ‘Recalcitrant’ or ‘desiccation-sensitive’ seeds that cannot survive drying to ca. 15% RH (see Section 3.3).
- EF3. ‘Intermediate’ seeds that are more tolerant of drying than recalcitrant seeds, but not as tolerant as orthodox seeds, and may also be freezing sensitive and unable to survive long-term at – 20 °C (see Section 3.3).
- EF4. Seeds that exhibit deep and complex dormancies, making their utilisation after banking difficult (see Section 3.4).

3.2. Sourcing and collecting seeds

One of the main goals of seed banking is to maximize genetic variation captured in collections to ensure that reintroduced

populations are self-sustaining and have the capacity for adaptive evolution (Kashimshetty et al., 2017 and studies therein). However, it can be difficult to obtain TM seed collections of this desired size and quality (Brown and Marshall, 1995; Kramer and Havens, 2009). Collecting is ideally guided by knowledge of a population's genetic structure (Sinclair and Hobbs, 2009), but this has been investigated in only a tiny fraction of TMCF species (e.g., Rico et al., 2022). Spatial separation is often used as a proxy for genetic diversity, however, population distributions in TM regions are also poorly known, and accessing a representative spatial sample is challenging. Very few species of the TM flora are accessible by road, particularly in the hazardous wet season when seed availability may be greatest (Zang et al., 2008). Limited access also makes it difficult to monitor seed maturation and dispersal. Additional challenges include a less distinct fruiting and seeding season relative to temperate ecosystems, separation of individuals by hundreds of metres or kilometres, difficulty in identifying and accessing tall canopy crowns, and highly variable flowering, fruiting and seed fill. Fruit ripening is often asynchronous which limits the number of mature seeds available for collection on a given day. Collection of fruits from the forest floor following natural ripening and abscission is a common practice for large-fruited, tropical tree genera (FAO, 2022). However, this practise can result in high levels of fungal contamination in the seed bank (causing seed viability to deteriorate quickly), and seeds may be empty / have been predated. There is also the risk of contamination from similar-looking seeds of nearby related species or from other individuals (Cochrane et al., 2021). High initial TMCF seed quality is important to maintain longevity in storage (see Section 4.2), particularly for exceptional seeds requiring cryo-storage (Ballesteros and Pence, 2019, see Section 4.1).

A study of seed harvesting strategies in tropical rainforest simulation trials suggested that collecting efforts can benefit from: a) collecting fewer seeds from each of a larger number of rare plants, b) sampling from peripheral, subdivided regions to help reduce costs and dangers associated with travelling deep into central regions of a population, and c) using predictive modelling of pollen dispersal when planning seed collection trips (Kashimshetty et al., 2017). Repeated sampling over time is another way to acquire genetically representative samples of rare species (Kramer and Havens, 2009; Guerrant et al., 2014), assuming time, resources and access to plants allow.

In preparation for TMCF collecting trips, we examined hundreds of TM herbarium voucher specimens held by the Australian National Herbarium (Canberra) and the Australian Tropical Herbarium (Cairns) for flowers, fruits and seeds. These vouchers indicated that mature seeds of up to 22 of our target Australian TMCF species (Appendix 1) are available throughout the year, with suggested peaks in May/June and December (Fig. 2). The April – June period is the start of the dry season and therefore also corresponds with greatest accessibility to the Wet Tropics Bioregion. Indeed, these are the months when the majority of seed collections were made between June 2019 and May 2021, plus an opportunistic and fruitful collecting trip in December 2020 (Fig. 2). Due to remoteness of collecting locations, it was not practical to monitor fruiting of the populations in detail, but observations were made at some sites revealing that fruit availability under an intact canopy was generally poor. Therefore, collections were made opportunistically within 200 m of the side of roads/paths, and from rock pavements and boulder outcrops where target species were known to occur. In total, we secured 93 seed collections, 25 of which were of 14 target species.

Appropriate post-harvest handling ensured that any viability loss prior to storage was avoided or kept to a minimum. While in the

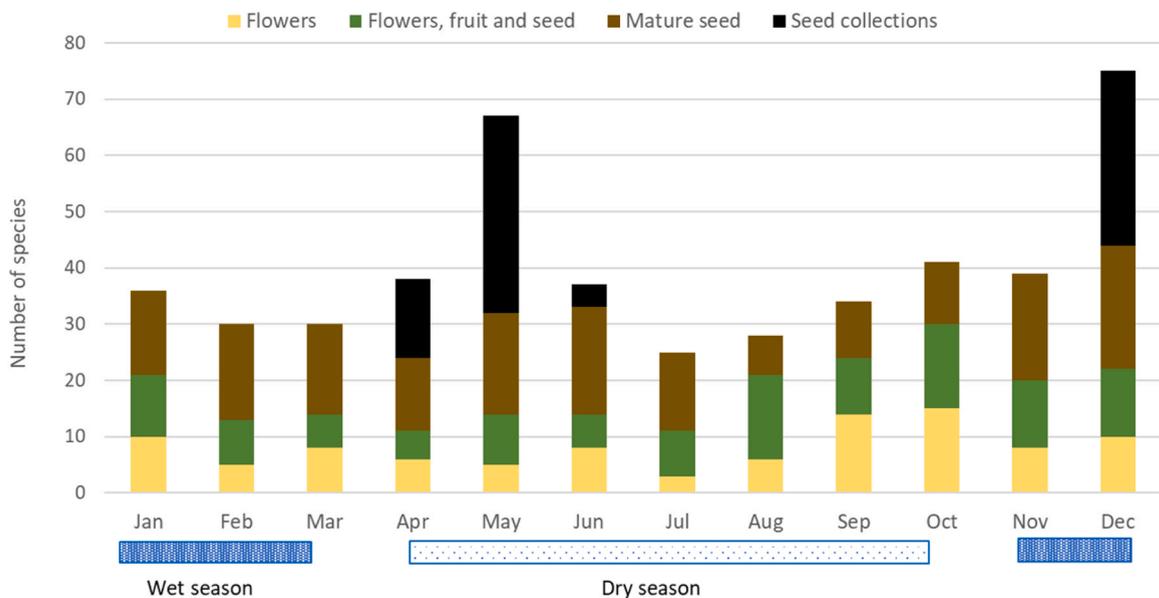


Fig. 2. Number of Australian TMCF species bearing flowers, fruits and/or mature seeds, and secured in *ex situ* storage. Flower (yellow), fruit (green) and mature seed (brown) data for 73 target TMCF species were derived from a few to dozens of herbarium specimen vouchers per species. Vouchers are held by the Australian National Herbarium (Canberra) and the Australian Tropical Herbarium (Cairns) and were collected between ca. 1930 and 2019. Seed collection data (black) were derived from the National Seed Bank (Canberra) and the Australian PlantBank (Mount Annan) from collections made between April 2019 and May 2021 and include 25 collections of 14 target species as well as numerous collections of non-target species. For a full list of target Australian TMCF species see Appendix 1.

field, fruits were kept cool in the shade or by placing them in a cooled, insulated container such as a Styrofoam box. Dry-fruited species were held in calico or paper bags for transport, while fleshy fruited species were held in breathable plastic bags. On arrival at the seed bank, dry-fruited species were placed directly in the drying room (ca. 15–20 °C, 15% RH). Fleshy-fruited species were held for 1–2 weeks in a fridge at ca. 15 °C but seeds were extracted as soon as possible to minimise viability loss (Martyen Yensen et al., 2021). Where collections were large enough (typically > 500 seeds), at least 500 seeds were stored for conservation, leaving the remaining seeds available for use in investigations of seed biology. Larger collections of > 1000 seeds were split 50/50 for conservation and research. Conservation collections were split between the Australian PlantBank (Mount Annan) and the National Seed Bank (Canberra) for insurance purposes and herbarium vouchers were lodged with the Australian Tropical Herbarium. Our ability to source and collect mature TMCF seed in large enough numbers for conservation and research demonstrates that seed banking of TMCF species is a possibility, with collecting success expected to increase with increasing experience, data and field campaigns.

3.3. Drying and freezing seed: seed storage behaviour

‘Seed storage behaviour’ refers to the response of seeds to the desiccation and sub-zero storage temperatures required for long term storage in a seed bank. We currently know the seed storage behaviour of very few TM species. Three main storage behaviour categories have been described: ‘recalcitrant’ seeds are sensitive to drying; ‘intermediate’ seeds are tolerant of at least some drying (but less than orthodox seeds), and sensitive to freezing; and ‘orthodox’ seeds are tolerant of both drying to low moisture content and freezing (Roberts, 1973; Hong and Ellis, 1996). However, seed storage behaviour might be best considered as a continuum subtended by extreme orthodoxy and the highest degree of recalcitrance (Berjak and Pammenter, 2008). Previous studies have reported a relatively high incidence of seed recalcitrance in the evergreen rainforest zone, particularly among trees and shrubs (Tweddle et al., 2003; Hamilton et al., 2013). Thus, a general assumption that most plants from warm, humid climates produce recalcitrant seeds has previously excluded many tropical plant communities from seed banking (Walters et al., 2013; Wyse and Dickie, 2018). However, a survey of the seed storage behaviour of Hawai’ian flora (ca. 280 taxa) reported that a high proportion of species produce orthodox seeds and less than 5% were recalcitrant (Weisenberger et al., 2008). Similarly, two studies of TM rainforest species in Thailand and Ecuador found orthodox or intermediate seed storage behaviour to be more prevalent than recalcitrant behaviour (Yu et al., 2008; Waiboonya et al., 2019).

In Australia, few TM rainforest species have been studied directly to determine their responses to drying and freezing, however, some data are available for related species. A recent study of 162 Australian subtropical and temperate rainforest species (including 58 species with a distribution that extended to TMCF and 44 species from genera that occur in TMCF), found the proportion of recalcitrant tree species to be high at 42% (Sommerville et al., 2021). However, compared to tree species, the seeds of shrubs and herbs were much

Table 1

Seed storage behaviour of 28 target Australian TMCF species: Genera containing target Australian TMCF species for which seed storage behaviour of one or more related species is known. Storage behaviour is categorised as: Orthodox: tolerant of drying and freezing (O), Intermediate: partially tolerant of drying and freezing (I) and Recalcitrant: sensitive to drying (R). This is a subset of a much larger table of known seed storage behaviour for Australian TM genera available as [Supplementary material](#). For a full list of target Australian TMCF species see [Appendix 1](#).

Family	Genus	Spp. tested	No. O	No. I	No. R
Apocynaceae	<i>Parsonsia</i>	6	6	0	0
Araliaceae	<i>Hydrocotyle</i>	4	4	0	0
	<i>Polyscias</i>	3	2	1	0
	<i>Trachymene</i>	4	4	0	0
Araucariaceae	<i>Agathis</i>	4	2	1	1
Clusiaceae	<i>Garcinia</i>	11	2	0	9
Cunoniaceae	<i>Ackama</i>	1	1	0	0
	<i>Ceratopetalum</i>	2	1	1	0
	<i>Eucryphia</i>	1	1	0	0
Ebenaceae	<i>Diospyros</i>	32	21	2	9
Elaeocarpaceae	<i>Elaeocarpus</i>	4	0	0	4
Ericaceae	<i>Dracophyllum</i>	1	1	0	0
	<i>Leucopogon</i>	3	3	0	0
	<i>Rhododendron</i>	37	37	0	0
Lauraceae	<i>Cinnamomum</i>	9	1	1	7
	<i>Cryptocarya</i>	5	0	1	4
	<i>Endiandra</i>	2	0	0	2
	<i>Litsea</i>	4	0	0	4
Myrtaceae	<i>Leptospermum</i>	31	31	0	0
	<i>Ptilidostigma</i>	1	0	0	1
	<i>Rhodammia</i>	2	1	1	0
	<i>Syzygium</i>	12	0	0	12
Orchidaceae	<i>Dendrobium</i>	5	5	0	0
Piperaceae	<i>Peperomia</i>	7	7	0	0
Rubiaceae	<i>Psydrax</i>	1	1	0	0
Rutaceae	<i>Flindersia</i>	4	3	1	0
Sapotaceae	<i>Planchonella</i>	1	0	0	1
Solanaceae	<i>Solanum</i>	154	154	0	0

more likely to be desiccation tolerant (Sommerville et al., 2021).

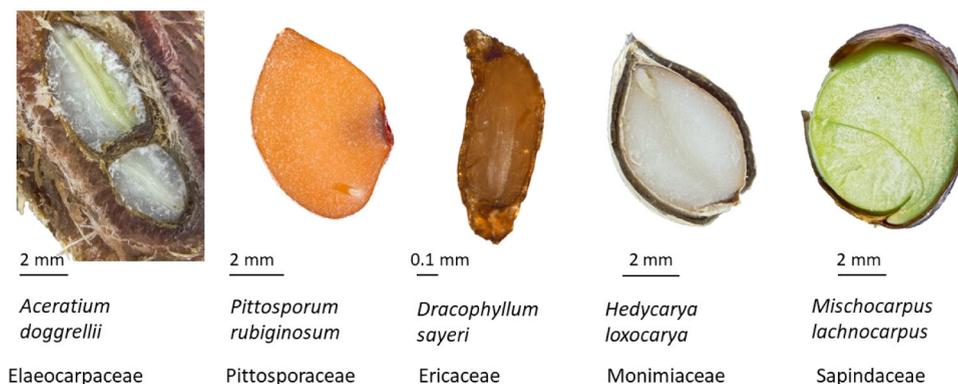
Wyse and Dickie (2018) reported that the storage behaviour of an untested species can often be predicted by that of other species in the same genus. Of 440 genera occurring in Australian TMCF, data on seed storage behaviour are available for at least one species from 272 genera (62%). For 192 of those genera (71%), all species tested so far have shown orthodox seed storage behaviour (Supplementary Material – Seed storage behaviour; a subset of this dataset, for 28 target TMCF genera, is shown in Table 1). On that basis, research is needed into the storage behaviour of 168 previously unstudied Australian TMCF genera, including 68 genera for which only 1 or 2 species have been studied to date (excluding mono- and bispecific genera). However, caution is required in using genus as a surrogate to determine storage behaviour unless several species with similar seed structure to the untested species have shown a consistent response (Sommerville et al., 2021). Wide differences in storage behaviour can occur among species in the same genus (Subbiah et al., 2019), particularly when those species have seeds with a different structure but also sometimes when they do not (Sommerville et al., 2021).

Accurately determining the seed storage behaviour for a species requires a series of germination tests on fresh seeds, seeds dried to different moisture contents, and seeds that have been dried and stored at a range of cool to sub-zero temperatures (Hong and Ellis, 1996). These tests can be significantly hampered by seed dormancy, an innate seed property that, *in situ*, prevents the germination of viable seeds until environmental conditions are favourable for seedling growth and establishment (Finch-Savage and Leubner-Metzger, 2006). The different types of dormancy are described in Baskin and Baskin (2004, 2021). For seeds with dormancy, each step to determining seed storage behaviour can take a considerable amount of time unless reliable techniques for alleviating or bypassing dormancy are known (see Section 3.3). In the absence of germination, a recently developed key may help to identify TMCF genera that are likely to be desiccation tolerant (Box 1). The response of those seeds to freezing can then be assessed using differential scanning calorimetry, a technique that involves lowering the temperature of a seed sample to $-150\text{ }^{\circ}\text{C}$ and back and observing any major endo- or exothermic reactions (e.g., Crane et al., 2006). Reactions occurring within the range of temperatures at which seeds are conventionally stored provide an indication of potentially freezing-sensitive or short-lived seeds (Mira et al., 2019).

In summary, it is likely that many of the shrub and herb species in Australian TMCF (i.e., the majority of our collections), as well as at least half of the tree species, will be tolerant of the desiccation required for ca. $-20\text{ }^{\circ}\text{C}$ storage. The high number of ‘intermediate’ Australian subtropical and temperate rainforest species (Sommerville et al., 2021), combined with similar findings in a study of tropical Hawai’ian species (Chau et al., 2019), suggest that more research will be needed to determine optimal storage temperatures of some TMCF seed. Meanwhile, advances in cryopreservation of diverse plant tissues that can be used as germplasm are providing alternative *ex situ* conservation options for recalcitrant and intermediate-seeded species (Section 4.1).

3.4. Utilising collections: seed germination

The effective management and utility of seed bank collections is dependent on the ability to germinate the seeds. Collection viability over time is measured via germination testing (Terry et al., 2003). Germination also enables collections to be used to regenerate plants for translocation (Crawford et al., 2021) and to replenish seed lots. Finally, germinable collections underpin seed-based research into optimising seed banking methods (Smith et al., 2003; Li and Pritchard, 2009; Hay and Probert, 2013; Liu et al., 2020; Martyn Yenson et al., 2021), and understanding the seed biology and ecology of plant communities (e.g., Satyanti et al., 2018; Hodges et al., 2021). Several studies report challenges in germinating seeds of species from TM zones citing high seed predation, limited seed longevity and long lag times to germination (Holl et al., 2000; Wenny, 2000; Athugala et al., 2021; Baskin et al., 2020). As



Box 1. A simple decision-making key to help rapidly assess the storage behaviour of tropical montane cloud forest (TMCF) seeds. For previously unstudied TMCF genera, and in the absence of germination, an indication of storage behaviour may be obtained by examining physical seed characteristics such as seed structure, the presence or absence of a woody endocarp, embryo colour, seed coat ratio and dry seed weight, following the recently developed key published by Sommerville et al. (2021). This key will provide a useful aid to quickly identifying TMCF species likely to be suitable for conventional seed banking and those likely to require alternative conservation measures. The images above illustrate some of the diversity in seed size and structure among previously unstudied TMCF seeds (*Aceratium doggrellii* image shows a longitudinal section of one endocarp containing two seeds).

discussed, seed dormancy can also be a hindrance to utilising collections unless the type of dormancy and techniques to alleviate it are known. A widely accepted criterion for dormancy is the inability of fresh seed to initiate and complete germination within 30 days of sowing (Baskin and Baskin, 2004). However, time to germination of TM rainforest species is variable. In Sommerville, Online Resource 1) et al. (2021), all 57 TMCF species achieved $\geq 59\%$ germination in laboratory test conditions, and 50 species achieved $\geq 70\%$ germination. However, only five of these species completed germination within 30 days and could be classified as non-dormant. Similarly, in a study of Sri Lankan TMCF species, only 25 out of a total of 80 completed germination within 30 days with no pre-treatment (Athugala et al., 2021).

We evaluated the presence or absence of dormancy among Australian TMCF species using seedling emergence data for 639 species (Zich et al., 2020; Supplementary Material - Time to germination). This included species restricted to TMCF and species that also occur at lower elevations. Data were derived from number of days to emergence of the first 1–6 seedlings from seeds sown in potting mix within two weeks of collection. We based our evaluation of this data on the following criteria: (i) where seedlings emerged in ≤ 40 days, seeds were likely non-dormant, (ii) where seedling emergence commenced after 40 + days, seeds were dormant, and (iii) where seedling emergence extended from < 40 days to several months or more, dormancy was deemed to be ‘variable’ and possibly related to the timing of seed collection. We also included unpublished germination data for five additional TMCF species following our own seed bank laboratory investigations (*Gahnia aspera* and *G. sieberiana* (Cyperaceae), *Linospadix palmerianus* (Arecaceae), *Tasmannia* sp. Mt Bellenden Ker (Winteraceae; Liyanage et al., 2022) and *Zieria alata* (Rutaceae). We categorised these species as described above but used radical emergence as the criterion for germination rather than seedling emergence from potting mix. Dormancy of 21 orchid species was assumed based on the minute, undifferentiated embryo. Of the total 665 species, 62.1% were classified as dormant (including 19.5% ‘variable’), and 37.9% as non-dormant. A subset of this dataset, representing 61 species largely restricted to 900 m a. s.l. or above, showed a lower proportion of dormant species (57.4%, including 6.6% ‘variable’). Thus, we expect 57–62% of Australian TMCF species to exhibit some degree of seed dormancy.

The incidence of dormancy is known to vary considerably among different tropical habitats (Fig. 3). A global dataset compiled by Baskin and Baskin (2014) reported that 52% of species in tropical/subtropical evergreen rainforests exhibit dormancy ($n = 2265$), as do 57% of species in tropical/subtropical semi-evergreen forests ($n = 1423$). These data are comparable to the estimated proportion of dormancy in Australian TMCF. A comparatively higher proportion of dormancy was reported in TM mixed habitats (83%; ‘mixed’ meaning both wet and dry TM habitats; $n = 485$). However, this likely reflects the inclusion of species from the drier, leeward side of mountains and not just the wetter, windward side where TMCF habitats typically occur. A study of dormancy in the TM zone in the Hawai’i Islands that includes both dry and wet habitats found 90% of 29 species exhibited dormancy (Baskin et al., 2020). In comparison, only 69% of 80 species from Sri Lankan TMCF regions exhibited dormancy (Athugala et al., 2021) and of 10 endangered tree species in Mexican TMCF, 6 exhibited dormancy (Toledo-Aceves, 2017).

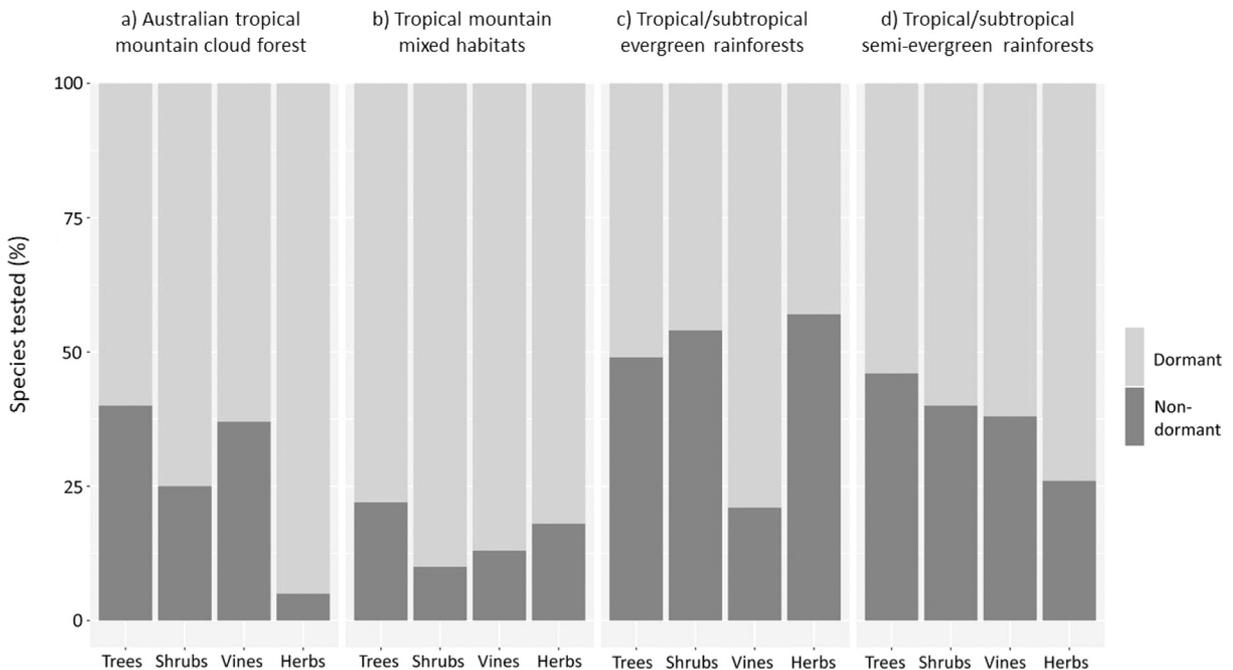


Fig. 3. Seed dormancy in Australian TMCF compared to other tropical/subtropical habitats: Proportion (%) of tree, shrub, vine and herb species with dormant seeds in a) Australian TMCF ($n = 457, 117, 81$ and 41 spp. for trees, shrubs, vines and herbs respectively), compared to global datasets compiled for b) TM mixed (both wet and dry) habitats ($n = 207, 157, 24$ and 97 spp.), c) tropical/subtropical evergreen rainforest ($n = 2058, 107, 70$ and 30 spp.) and d) tropical/subtropical semi-evergreen forest ($n = 1120, 103, 61$ and 139 spp.). Australian data were derived from Zich et al. (2020); global datasets were compiled by Baskin and Baskin (2014).

The proportion of species exhibiting seed dormancy can also vary with plant growth form. Our data for Australian TCMF indicate a much higher proportion of dormancy in herbs (95%) than in trees, shrubs or vines (60%, 75% and 63% respectively; Fig. 3a). We also see this trend in tropical/subtropical semi-evergreen rainforests globally (Fig. 3d). However, the majority of dormancy in TM mixed habitats and tropical/subtropical evergreen rainforests is seen in shrubs and vines respectively (Fig. 3b, c).

While these data suggest that more than half of the seed-producing TCMF flora possess seed dormancy, our laboratory-based studies have shown that dormancy, in at least some species, can be overcome using relatively simple treatments. Precision nicking alleviated both morpho-physiological and physiological dormancy of *Tasmannia* (Winteraceae) and *Acronychia* (Rutaceae) species (Liyanage et al., 2020, 2022). *Gahnia sieberiana* (Cyperaceae) required a scarification pre-treatment to assist with radical emergence, prior to application of Gibberellic Acid to overcome what was likely physiological dormancy (G. Liyanage, unpublished data). Seeds of *Lebrassia australiana* appeared to cycle in and out of dormancy (Hoyle et al., 2023) and this is in accordance with 'variable' dormancy of *L. australiana* that we determined from seedling emergence data (Supplementary Material – Time to germination). The ability to achieve useful percentages of germination varies between alpine mountain seed collections of the same species (Hoyle et al., 2014; Satyanti et al., 2019), and within-species variation warrants further investigation in TCMF seed lots. For example, we reported non-dormant *Abrophyllum ornans* seeds and dormancy cycling of *Dracophyllum sayeri* seeds (Hoyle et al., 2023), and neither of these findings are consistent with the seedling emergence data (Supplementary Material – Time to germination).

4. Research needed to inform and accelerate seed banking TCMF flora

The evolutionary history, uniqueness and vulnerability of TCMF flora are well studied, particularly in Australia (WTMA, 2014; Costion et al., 2015; Merckx et al., 2015; Noroozi et al., 2018; Karger et al., 2021). However, there remains a need to study the seed biology and ecology of TCMF flora to increase our power to predict which species are most vulnerable to climate change and where to focus our conservation efforts. Seed banking activities provide opportunities, infrastructure and seeds for the associated research. Common data collection across TCMFs would facilitate effective seed banking and enable cross-site comparisons of how TCMFs are responding to drivers of climate change. Here, we identify key gaps in our understanding of factors limiting collecting, storing and utilising TCMF seeds that necessitate further research.

4.1. Conserving exceptional species

As discussed, factors relating to the quantity, accessibility, longevity, desiccation tolerance and germination of seeds can hamper their *ex situ* conservation. For TCMF species found to be exceptional, determining their *exceptionality factor* (Pence et al., 2022; see Section 3.1) will be important. Species considered exceptional due to limited seed quantity and accessibility (EF1) and/or limited germinability (EF4) may be re-classified as non-exceptional based on new discoveries or technologies in the future (Pence et al., 2022), opening the door to seed banking greater TCMF biodiversity. Research that uncovers germination requirements of EF4 species is discussed in Section 4.3. To inform more efficient collecting protocols we propose researching the reproductive phenology of target TCMF species (Luna-Nieves et al., 2017). Collecting efforts may also benefit from knowledge of the species' pollen dispersal biology and using this in predictive modelling of collecting trips (Kashimshetty et al., 2017). The decreasing costs and increased efficiency of genomic studies support their addition to TCMF conservation workflows to inform extinction risk assessment evaluations and help target collecting efforts (Rossetto et al., 2021).

TCMF species considered exceptional due to seed desiccation (EF2) or freezing sensitivity (EF3) will require alternative approaches to banking. Cryopreservation is a storage option that involves rapidly freezing plant germplasm, usually in liquid nitrogen ($-196\text{ }^{\circ}\text{C}$) or its vapour (-130 to $-192\text{ }^{\circ}\text{C}$), which limits the formation of ice crystals within cells that can cause lethal damage (Berjak and Pammenter, 2008). Since many recalcitrant seeds are too large to be cooled this way (Berjak et al., 2011), cryopreservation of seed embryonic axes was a significant breakthrough (Normah et al., 1986) that may need exploring for large-seeded TCMF species. Cryopreservation is also safe and effective for conserving other germplasm such as dormant buds, spores, pollen, shoot tips and gametophytes, with a growing number of studies indicating that viability can be maintained over at least 2–3 decades (Pence et al., 2020). The fast-tracking of conservation efforts for exceptional TCMF species must include the latest techniques for selection of appropriate germplasm to conserve *ex situ* (Bremner et al., 2021). For example, for TCMF tree species, additional cryopreserved collections of pollen warrant investigation to optimise genetic diversity.

However, unlike conventional seed banking, plant cryopreservation (or gene banking) does not have a universal formula that can be applied to a wide range of plant taxa and/or tissues. Developing new, species-specific cryopreservation protocols, and in-vitro techniques that support them (Pence, 2011), will be critical for securing desiccation sensitive TCMF flora. Avenues of investigation need to include degree of desiccation, length of germplasm exposure to cryoprotective agents, and preculture and recovery environment (Bettoni et al., 2021). Successful cryopreservation of tropical flora to date includes species in the Rutaceae (Malik et al., 2012), Arecaceae (Sopade et al., 2010), Amaryllidaceae (Pammenter et al., 2007) and Loganiaceae (Berjak et al., 2011) due to efforts to reduce excision damage, lower metabolic activity and increase totipotency of small axis sections (Pammenter and Berjak, 2014).

Requirements to conserve desiccation sensitive species *ex situ* are being progressively understood and workflows developed to fast-track these efforts and increase the diversity of species in seed / gene banks (Bremner et al., 2021). For TCMF flora, strong networking between seed and gene banks is needed and could be facilitated by the online *Exceptional Plant Conservation Network* (<https://cinnatizoo.org/epcn>; Pence et al., 2020). We encourage sharing information on exceptional TCMF species to focus attention, facilitate collaboration and progress research. The material costs of starting a small cryopreservation program within an existing laboratory are relatively low (Abeli et al., 2019; Pence, 2013; Werden et al., 2020), and cryopreserved collections of wild plant germplasm are

increasingly being created within seed banks and botanic gardens across Australia (Offord et al., 2021), and globally (Breman et al., 2021). Lastly, although beyond the scope of this review, conservation of exceptional species often relies heavily on living plant collections (Breman et al., 2021). Living collections of TCMF plant species are needed, in conjunction with seed banking, including research into TCMF species propagation and horticulture.

4.2. Seed longevity and persistence

Once in seed bank storage, the longevity of orthodox TCMF seed accessions will have implications for their management. Collections of species with relatively short longevity will need to be monitored for viability and replenished more often than those that are relatively long lived. We propose comparative longevity studies (or the controlled ageing test, CAT) that involve artificially ageing seeds (Walters et al., 2005; Newton et al., 2014; Hay et al., 2022), to enable us to rank the potential longevity of TCMF species in seed bank storage relative to seeds of other ecosystems. Like alpine mountain seeds elsewhere in the world, seeds from the cool, wet Australian Alps were found to be relatively short-lived and overall shorter-lived than Australian plants in general (Satyanti et al., 2018). In contrast, seeds from hot, dry environments are generally longer lived than those from cool, wet conditions (Probert et al., 2009; Merritt et al., 2014). TCMFs are wetter and cooler than cloudless TM forests of the world (Jarvis and Mulligan, 2010), therefore we might expect TCMF seeds to be overall shorter lived than those of the lowland flora or those of other TM forests, but perhaps not as short-lived as alpine mountain seeds. Using 20 + years of real-time seed storage viability data, Chau et al. (2019) investigated *ex situ* seed longevity of 295 Hawai'ian species. To maximise viability of stored seeds, the authors recommended re-collection intervals of < 5 years for only 45 species tested, compared to re-collection intervals of ≥ 10 years for 123 species tested (Chau et al., 2019). The determination of three species with re-collection intervals > 20 years, despite having freeze-sensitive seeds and being stored at 5 °C, supports the use of seed banking even for species that cannot be conventionally stored (Chau et al., 2019). An indication of longevity and recommended re-collection intervals for TCMF seed would help confirm the efficiency of seed banking, even if only to prevent extinctions in the short to medium term, until alternative storage conditions are discovered/developed.

Seed burial experiments provide insight into seed persistence in the soil (Long et al., 2008; Bekker et al., 2003) and may also be related to longevity of TCMF seeds in storage. In the past, tropical rainforest species were thought to have short-lived soil seed banks, but this was on the assumption that most rainforest species produced recalcitrant seeds (Tweddle et al., 2003). In fact, soil seed banks have been reported in montane cloud forest in Mexico (Williams-Linera, 1993; Alvarez-Aquino et al., 2005) and Costa Rica (Lawton and Putz, 1988), Hawai'ian montane rainforest (Drake, 1993) and TM rainforest of South China (Zang et al., 2008), but whether they were transient or persistent was not addressed. Decades-long persistence in the soil seed bank may be common in large-seeded tropical pioneers and unrelated to regeneration requirements (Dalling and Brown, 2008). The persistence of seeds in the field can correlate positively with their longevity in controlled ageing tests and controlled storage conditions (Long et al., 2015), but this is not always the case (Walters et al., 2005). We propose seed burial studies to better understand the ability of TCMF flora to form persistent soil seed banks, and to investigate the relationship between the *in situ* persistence and *ex situ* longevity of TCMF seed. The prevalence of dormancy among TCMF species may indicate their potential to survive *in situ* in the soil seed bank (Long et al., 2015), or during *ex situ* storage, and warrants investigation (Baskin and Baskin, 1989; Saatkamp et al., 2011). Similarly, a light requirement for germination, and/or any defence mechanisms against decay or predation, may also contribute to TCMF seed persistence (Grime et al., 1981; Benvenuti, 1995; Long et al., 2015; Milberg et al., 2000).

4.3. Germination strategies, now and in the future

Regeneration from seeds is critical for plant species persistence in the landscape under future climate scenarios (Walck et al., 2011). This is particularly true in mountain environments where upward migration to cooler, wetter refuges may be the best option for survival (Pauli et al., 2012; Auld et al., 2022). Current predictions for the persistence of the Australian TCMF habitat assume that the current niche occupied by each species is essential for its survival (Costion et al., 2015; Roebler, 2018). In fact, we know very little about how environmental factors influence the regeneration and distribution of seed-bearing TCMF plant species, or which species are most at risk of regeneration failure in the future. The main factors controlling germination are temperature, moisture and light (Baskin and Baskin, 2014), and *ex situ* investigations permit the control and manipulation of variables with the benefit of not being confounded by field conditions such as predation, fungal infestation and extreme weather events. We propose researching the current breadth of TCMF species' germination niches in relation to these factors, to inform target species for seed banking and to guide modelling of species distribution under climate change (Fernandez-Pascual et al., 2015; Sampayo-Maldonado et al., 2021).

Temperature is one of the most important bioclimatic elements in determining the response of seeds to climate change (Walck et al., 2011), particularly the distribution of tropical forest species (Nakao and Cardoso, 2016). Temperature drives local adaptation and phenotypic plasticity in germination traits, as well as the physiological processes of dormancy loss (Fernandez-Pascual et al., 2015). Previously, tropical species were thought to be more susceptible to climate warming than higher latitude species based on the assumption that they tolerate a narrower range of temperatures (Ghalambor et al., 2006). This susceptibility to temperature increase is related to seeds already experiencing temperatures close to their upper germination limits (Sentinella et al., 2020). By 2070, over half of the tropical species studied (79/142) are predicted to experience temperatures exceeding their optimum germination temperatures, with some even exceeding their maximum germination temperature (Sentinella et al., 2020). However, Sentinella et al. (2020) used data mainly from lowland biomes, and more research is needed to understand susceptibility of higher altitude tropical plant species to climate warming. New temperatures under climate change may not match those that currently alleviate dormancy and/or elicit germination of TCMF seeds. This mismatch is expected to alter recruitment in alpine mountain regions (Mondoni et al., 2012; Hoyle

et al., 2013), but we are not aware of similar TM studies. Seeds also possess a thermal memory (via phenotypic plasticity) that incorporates information from past thermal history e.g., temperatures experienced by the reproducing plant since seedling establishment. Work is needed to investigate the thermal memory of TMCF seeds and to incorporate this into climate change simulations. There is evidence that thermal memory may allow seeds to adjust their germination phenology to climate changes, even if warming goes beyond the current thermal thresholds (Fernandez-Pascual et al., 2019).

As mentioned, TMCFs are likely to be sensitive to predicted reductions in precipitation, increased periods of drought and changes in the height of the cloud base (Foster, 2001; Hu and Riveros-Iregui, 2016). Despite this, we found very few studies into the effect of rainfall/soil moisture on germination in wet TM regions. In Hawai'i, changes in emergence of *Metrosideros polymorpha* (Myrtaceae) seedlings along a precipitation gradient suggested that even moderate drying could significantly reduce recruitment, and that even trees with high dispersal abilities can show significant changes in drought tolerance across their geographical range (Barton et al., 2020). Different concentrations of Polyethylene Glycol (PEG) are commonly used to apply drought stress to seeds in the laboratory. Using PEG, Daws et al. (2008) concluded that response to drought stress was related to seed size in neotropical pioneer species. Small-seeded species (seed mass < 2 mg) were thought to germinate only in comparatively moist microsites such as small canopy gaps, which may reduce the risk of drought-induced mortality. Conversely, large-seeded species were able to germinate in the drier environment of large gaps, where they benefitted from enhanced seedling growth in a high irradiance environment (Daws et al., 2008). Similarly, short-term rainless periods delayed germination of small-seeded Dipterocarpaceae species native to wet tropical rainforest in Borneo compared to large-seeded species, suggesting that under more frequent or longer rainless periods large-seeded species would have a germination advantage over small-seeded species (O'Brien et al., 2013). However, final germination declined by an average of 39.4% for all species when seeds were watered at six-day intervals compared to daily, and days to germination increased by 76.5% (O'Brien et al., 2013). Precipitation manipulation experiments on TMCF seeds would help to remedy the scarcity of such studies in tropical systems (Wu et al., 2011). Long-term perspectives of climate change can only be verified by long-term experiments, but only a few long-term experiments (> 10 years) exist (Beier et al., 2012). Precipitation manipulation experiments in TMCF will need to apply manipulations relevant for future climate change scenarios, run for at least 10 years (Beier et al., 2012), and alter precipitation timing, frequency and intensity (Wu et al., 2011).

In TMCF, where rainfall or water availability is high throughout the year and there is little seasonal variation in temperature, light may be the main driver of germination. Light-sensitive species utilise light to indicate conditions suitable for germination (Pearson et al., 2003), with light controlling the induction, maintenance and release of seed dormancy via hormone metabolism and signalling (Yan and Chen, 2020; Yang et al., 2020). In TM regions, an absolute light requirement for germination, or greater germination in high light compared to low, has been reported for species in wet forests (Everham et al., 1996) and rain forests (Zang et al., 2008). Restoration efforts in Costa Rican TM forest reported low germination of small-seeded tree species due to reduced light beneath the canopy (Sady et al., 2010). Light/dark studies provide some information on the germination requirements of species, but the forest floor does not consist of simply open sun and full shade. The denser the leaf canopy and leaf litter, the lower the ratio of red to far-red light (R:FR) experienced by seeds, and there is evidence that this inhibits germination of multiple Brazilian tropical rainforest species (Valio and Scarpa, 2001). There are also reports of species-specific R:FR for maximum germination in TM regions (Vieira et al., 2018) and tropical rain forests (Vázquez-Yanes and Orozco-Segovia, 1990). The ratio of R to FR light is particularly interesting in TMCF since far-red light is affected by water vapour in the atmosphere such that the R:FR increases as atmospheric water content increases (Górski, 1976; Reinhardt et al., 2010). In the future, predicted reduction in atmospheric moisture and cloud immersion in TMCF (Still et al., 1999; Hu and Riveros-Iregui, 2016; Helmer et al., 2019), may lead to a reduction in R:FR below the canopy. We investigated germination of six TMCF species in relation to light quality and found that, while species exhibited wide variation in germination response to a R:FR gradient, all six showed acclimation potential to changes in light quality under climate change (Hoyle et al., 2023). Following on from germination, investigation into the impact of light quality on TMCF seedling establishment and growth is warranted. For example, tropical pioneer species are understood to persist as small seedlings for a long time before taking advantage of a canopy gap and growing rapidly (Swaine and Whitmore, 1988), which may be in response to changes in R:FR.

Single-factor experiments can be informative but may not adequately illustrate the germination response of species under interacting effects of climate change. For example, germination response to light is expected to be correlated with other environmental factors in Amazon forests (Aud and Ferraz, 2012). To date, multiple-factor manipulation experiments have largely been limited to herbaceous ecosystems in mid-to-high latitudes in the northern hemisphere, and experiments in low latitude, woody and tropical systems such as TMCF are much needed (Wu et al., 2011). To inform such investigations, it will be essential to collect long-term, site-specific TMCF microclimate data. As part of our investigations in Australia's Wet Tropics Bioregion, Singh Ramesh et al. (2022) collected understory microclimate data between January 2020 and December 2022, including soil temperature (ca. -10 cm below ground in the location of the soil seed bank), and air temperature (ca. +15 cm above ground in the location of seedlings) at 20 sites ranging from 40 to 1550 m a.s.l. Soils in lowlands were cooler than air, and soils in the highest mountaintop site were almost tracking, or were much higher, than air temperatures, based on long-term averages. These observations suggest that the temperature offsets between the soil and air are potentially much more important than free soil or air temperatures in driving ecological processes such as germination and seedling establishment in these sites (Singh Ramesh et al., Unpublished), and warrant further investigation. In the laboratory, a daily temperature amplitude of at least 6 °C was important for optimal germination of an Australian TMCF endemic (*Dracophyllum sayeri*), and soil temperature data collected *in situ* suggested that such temperature variation only occurs during summer months under a closed canopy (Stevens et al., Unpublished). Insight into the time and place of *in situ* germination provides a valuable starting point for *ex situ* germination trials and for predicting species persistence and distribution under future climates. Identifying the ecological drivers of within-species variation in germination is also important, particularly when seed germination expectations are not consistently met. Lastly, microclimate data could inform TMCF mapping, modelling of vegetation dynamics and be incorporated

into conservation and management plans at various spatial scales (Bruijnzeel et al., 2011).

4.4. Seed trait data collection and analysis

A major priority in seed science research today is uncovering how seed traits influence seed *ex situ* conservation, ecological functions and sustainable use (Jiménez-Alfaro et al., 2016; Saatkamp et al., 2019). We propose research into TCMF seed traits relating to their morphology (e.g., seed mass, seed coat thickness, embryo to seed size ratio) and physiology (e.g., storage behaviour, germination requirements, dormancy type) that will allow us to rapidly identify difficult to bank and climate vulnerable species. For example, research focused on linking TCMF seed traits to seed bank storage behaviour could potentially yield many new trait-based insights to inform *ex situ* conservation (Daws et al., 2006; Joshi et al., 2015; Sommerville et al., 2021). TCMF seed trait data could also be used to prioritise species most at risk and accelerate TCMF seed banking in regions with low capabilities and/or little current action. A study on seed and germination functional traits for 48 species from threatened Amazon TM flora provided support to restorationists and conservation biologists to better manage seed collection, storage and germination, with expected reduced costs and increased seedling establishment success (Zanetti et al., 2020). In the future, the selection of TCMF species with climate-resilient regeneration traits will be essential for future-proof TCMF restoration (Christmann and Menor, 2021), therefore, understanding how TCMF seed traits map to seed functions is critical.

Several seed traits including seed mass, dormancy prevalence and type, and light requirement for germination, appear to be dominated by different values in tropical versus temperate regions (see studies in Visscher et al., 2022). However, Visscher et al. (2022) highlighted a geographical bias in available data towards temperate zone species which may undermine analyses. For example, tropical species represent only 22% of the data on post-dispersal embryo growth currently available. In addition, within tropical species there exists a bias towards studies of woody species and often multiple species of the same genus, resulting in a very poor representation of tropical diversity (Visscher et al., 2022). The fact that few examples of clinal variation in trees come from the tropics likely reflects a bias in research sites and not the absence of such intraspecific variation in the tropics (Barton et al., 2020). For widespread TCMF species that drive community interactions and ecosystem dynamics, it is likely that clinal variation will be important for predicting which populations and species are most vulnerable to climate change (Barton et al., 2020).

We propose the collection and consolidation of TCMF seed trait data, and the creation of a TCMF seed trait dataset (e.g., Ordóñez-Parra et al., 2022), which could then populate national and global databases such as Austraits (Falster et al., 2021) and SeedArc (<http://unioviado.es/seedarc/>) respectively. Seed trait data generated by seed banking activities are already informing predictions regarding tropical plants under climate change (Sentinella et al., 2020), however, TCMF data are needed to help verify current patterns among tropical seed traits and perform truly global analyses in the future.

5. Conclusions

The science is clear – significant reductions in TCMF are projected to occur by the end of this century. Urgent action is needed to build the resilience of TCMF flora and research its adaptive capacity in the face of climate change. Here, we have reviewed the literature and undertaken preliminary investigations to explore how amenable TCMF is to *ex situ* conservation via seed banking. The term ‘cloud forest’ is a useful, broadscale term to describe tropical, high elevation communities of flora that experience regular cloud cover, and their common threats. While the function and name of the *ex situ* seed bank may vary (e.g., genebank, germplasm bank, biobank), the concept and purpose remain the same—using controlled environments to preserve a broad diversity of viable plant germplasm for immediate and future use (Bremner et al., 2021). We have begun to address the lack of TCMF plant germplasm in *ex situ* storage and TCMF seed biology and ecology knowledge. We have also demonstrated that, as we move away from historic assumptions and generalisations and towards investigating individual plant species and their seed traits, seed banking is a worthwhile approach to conserving more TCMF biodiversity than previously assumed:

- We were able to make 93 viable seed collections in Australian TCMF within three years. The majority of these were made opportunistically, not too far from roads/paths, and at the start of the dry season when the forest was most accessible. Appropriate post-harvest handling ensured that viability loss was avoided or kept to a minimum and collecting success is expected to increase with experience, data and field campaigns.
- More than 70% of the Australian TCMF genera studied to date have desiccation tolerant seeds that can be stored using conventional seed banking techniques. This includes many of the shrub and herb species, and at least half of the tree species. These proportions may increase as the storage behaviour of previously unstudied genera is explored. The global literature for seed storage behaviour continues to grow and is mobilised in databases (e.g., Liu et al., 2019), enabling regional assessments of multiple taxa (Walters, 2003; Sommerville et al., 2018; Teixeira et al., 2017).
- Advances in cryobiotechnologies will provide alternative storage options for recalcitrant-seeded TCMF species, including storage of other plant germplasm such as dormant buds, spores, pollen, shoot tips and gametophytes. For seeds that are freezing sensitive or short-lived at -20°C , relatively simple alterations to conventional seed banking methods (such as storage at 5°C) may facilitate conservation. To ensure safe storage, new approaches to classifying seed storage behaviour can be applied to the study of TCMF seeds.
- Approximately 60% of Australian TCMF species can be expected to exhibit seed dormancy, particularly herbaceous species. However, once uncovered, treatments to alleviate or bypass seed dormancy in TCMF species can be relatively easy to apply.

Reliable germination protocols will facilitate seed use and monitoring of seed viability over time while delivering healthy seedlings for propagation.

- Seed banking activities will provide opportunities, infrastructure and seeds for research. In addition to investigating the storage behaviour and germination requirements of target TCMF species, research into their reproductive phenology, pollen dispersal biology, genomic sequence, cryopreservation, longevity and innate germination strategies will all inform and accelerate TCMF seed banking. Seed morphological and physiological trait-based insights will likely allow us to rapidly identify difficult to bank and climate vulnerable species.

Australia's TCMF is restricted to one of the most effectively regulated and managed protected areas in the world (Weber et al., 2021). Combined with the opportunities highlighted here, Australia's TCMF may be one of limited examples where an integrated strategy of both *in situ* and *ex situ* conservation and research activities (Li and Pritchard, 2009; Volis and Blecher, 2010) leads the way in mitigating species extinction and provides evidence-based advice to policy makers and land managers. We call for a nationwide coordinated effort to establish a secure network of *ex situ* germplasm collections of Australian TCMF flora and to continue the associated research described here. We note the collaborative plant conservation efforts in Hawai'i (Werden et al., 2020) and argue that this approach is applicable to Australian TCMF flora. Work in Hawai'i owes part of its effectiveness to alliances formed with a suite of organizations and stakeholders. Within Australia, organizations such as the *Australian Seed Bank Partnership* (ASBP, 2023) could facilitate collaboration between existing partner botanical institutions, seed scientists and conservation and restoration experts to ensure that resources and expertise are used in a strategic, efficient and effective manner to secure TCMF flora *ex situ*.

With this review and case study we hope to have challenged assumptions, raised awareness of the presence of TCMF in Australia and inspired the integration of TCMF seeds into existing and proposed seed banking. Effective seed banks must be equipped to make use of all the seed/gene banking tools available, and push research boundaries, to stem the loss of TCMF species diversity. A global effort to broaden *ex situ* conservation beyond 'conventional' seed banking for all TM flora is needed and collaborations between seed banks, cryobanks and botanic gardens will be crucial to ensure that no species is left behind.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix 1

Vascular plant species restricted to Australian TCMF (12 ferns and lycophytes, 2 gymnosperms, 74 angiosperms). Species conservation status under State (Queensland Nature Conservation Act, 1992) and Federal (Environmental Protection and Biodiversity Conservation Act, 1999) legislation is indicated: Extinct in the wild (X), Critically Endangered (CR), Endangered (E), Vulnerable (V), Near Threatened (NT). Angiosperm families that represent ancient, early diverging lineages are in bold. Nomenclature and family assignment follow the Queensland Plant Census (Brown, 2021). NB. *Micromyrtus delicata* occurs in high altitude heath but is not found in forest

Species	Family	Queensland Nature Conservation Act (1992)	Environment Protection and Biodiversity Conservation Act (1999)
Ferns and Lycophytes			
<i>Hymenophyllum whitei</i> Goy	Hymenophyllaceae	CR	X
<i>Lastreopsis grayi</i> D.L.Jones	Dryopteridaceae		
<i>Lastreopsis tinaroensis</i> Tindale	Dryopteridaceae		
<i>Lindsaea terrae-reginae</i> K.U.Kramer	Lindsaeaceae	E	
<i>Oreogrammitis albosetosae</i> (F.M.Bailey) Parris	Grammitidaceae	V	

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Species	Family	Queensland Nature Conservation Act (1992)	Environment Protection and Biodiversity Conservation Act (1999)
<i>Oreogrammitis leonardii</i> (Parris) Parris	Grammitidaceae	V	
<i>Oreogrammitis reinwardtii</i> Blume	Grammitidaceae	V	V
<i>Oreogrammitis wurunuran</i> (Parris) Parris	Grammitidaceae		
<i>Phlegmariurus creber</i> (Alderw.) A.R.Field & Bostock	Lycopodiaceae	CR	E
<i>Phlegmariurus delbrueckii</i> (Herter) A.R.Field & Bostock	Lycopodiaceae	V	V
<i>Phlegmariurus lockyeri</i> (D.L.Jones & B.Gray) A.R. Field & Bostock	Lycopodiaceae	V	V
<i>Tomophyllum walleri</i> (Maiden & Betche) Parris	Polypodiaceae	V	V
Gymnosperms			
<i>Agathis atropurpurea</i> B.Hyland	Araucariaceae		
<i>Pectinopitys ladei</i> (F.M.Bailey) C.N.Page	Podocarpaceae	NT	
Angiosperms			
<i>Ackama</i> sp. Bellenden Ker (W.Sayer 45) Qld Herbarium	Cunoniaceae		
<i>Acrotriche baileyana</i> (Domin) J.M.Powell	Ericaceae	NT	
<i>Aidia gyropetala</i> A.J.Ford & Halford	Rubiaceae		
<i>Austromuellera valida</i> B.Hyland	Proteaceae	V	
<i>Boea kinneari</i> (F.Muell.) B.L.Burt	Gesneriaceae	E	
<i>Bubbia whiteana</i> A.C.Sm.	Winteraceae	V	
<i>Bulbophyllum lilianiae</i> Rendle	Orchidaceae		
<i>Bulbophyllum wadsworthii</i> Dockrill	Orchidaceae		
<i>Bulbophyllum windsorensense</i> B.Gray & D.L.Jones	Orchidaceae	V	
<i>Ceratopetalum corymbosum</i> C.T.White	Cunoniaceae	V	
<i>Ceratopetalum hylandii</i> Rozefelds & R.W.Barnes	Cunoniaceae		
<i>Cinnamomum propinquum</i> F.M.Bailey	Lauraceae	V	
<i>Cryptocarya bellendenkerana</i> B.Hyland	Lauraceae		
<i>Dendrobium brevicauda</i> (D.L.Jones & M.A.Clem.) M. A.Clem. & D.L.Jones	Orchidaceae		
<i>Dendrobium carrii</i> Rupp & C.T.White	Orchidaceae		
<i>Dendrobium finniganense</i> D.L.Jones	Orchidaceae		
<i>Diospyros granitica</i> Jessup	Ebenaceae	NT	
<i>Dracophyllum sayeri</i> F.Muell.	Ericaceae	V	
<i>Elaeocarpus carbinensis</i> J.N.Gagul & Crayn	Elaeocarpaceae		
<i>Elaeocarpus hylobroma</i> Y.Baba & Crayn	Elaeocarpaceae		
<i>Elaeocarpus linsmithii</i> Guymer	Elaeocarpaceae		
<i>Endiandra jonesii</i> B.Hyland	Lauraceae	V	
<i>Eucryphia wilkiei</i> B.Hyland	Cunoniaceae	CR	
<i>Flindersia oppositifolia</i> (F.Muell.) T.G.Hartley & Jessup	Rutaceae	V	
<i>Garcinia brassii</i> C.T.White	Clusiaceae		
<i>Gynochthodes constipata</i> (Halford & A.J.Ford) Razafim. & B.Bremer	Rubiaceae		
<i>Gynochthodes podistra</i> (Halford & A.J.Ford) Razafim. & B.Bremer	Rubiaceae		
<i>Helicia lewisensis</i> Foreman	Proteaceae	V	
<i>Hollandaea porphyrocarpa</i> A.J.Ford & P.H.Weston	Proteaceae	CR	
<i>Hydrocotyle miranda</i> A.R.Bean & Henwood	Araliaceae		
<i>Hypsophila halleyana</i> F.Muell.	Celastraceae		
<i>Leionema ellipticum</i> Paul G. Wilson	Rutaceae	V	
<i>Lenbrassia australiana</i> (C.T.White) G.W.Gillett var. <i>australiana</i>	Gesneriaceae		
<i>Leptospermum wooroonoran</i> F.M.Bailey	Myrtaceae		
<i>Leucopogon malayanus</i> subsp. <i>novoguineensis</i> (Sleumer) Pedley	Ericaceae		
<i>Linospadix apetirolatus</i> Dowe & A.K.Irvine	Arecaceae		
<i>Liparis fleckeri</i> Nicholls	Orchidaceae		
<i>Litsea granitica</i> B.Hyland	Lauraceae	V	
<i>Micromyrtus delicata</i> A.R.Bean	Myrtaceae	E	
<i>Nothorites megacarpus</i> (A.S.George & B.Hyland) P. H.Weston & A.R.Mast	Proteaceae		
<i>Octarrhena pusilla</i> (F.M.Bailey) M.A.Clem. & D.L. Jones	Orchidaceae		
<i>Parsonia bartlensis</i> J.B.Williams	Apocynaceae	V	
<i>Peperomia hunteriana</i> P.I.Forst.	Piperaceae		
<i>Phaleria biflora</i> (C.T.White) Herber	Thymelaeaceae	V	V
<i>Piliostigma sessile</i> N.Snow	Myrtaceae		
<i>Pleioluma ferruginea</i> Jessup	Sapotaceae		
<i>Polyosma globosa</i> A.R.Bean & P.I.Forst.	Escalloniaceae		

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Species	Family	Queensland Nature Conservation Act (1992)	Environment Protection and Biodiversity Conservation Act (1999)
<i>Polyosma nigrescens</i> A.R.Bean & P.I.Forst.	Escalloniaceae		
<i>Polyosma reducta</i> F.Muell.	Escalloniaceae		
<i>Polyscias bellendenkerensis</i> (F.M.Bailey) Philipson	Araliaceae	V	V
<i>Polyscias willmottii</i> (F.Muell.) Philipson	Araliaceae		
<i>Prostanthera albohirta</i> C.T.White	Lamiaceae	CR	CR
<i>Prostanthera athertoniana</i> B.J.Conn & T.C.Wilson	Lamiaceae	CR	
<i>Psychrax montigena</i> S.T.Reynolds & R.J.F.Hend.	Rubiaceae		
<i>Rhodamnia longisepala</i> N.Snow & A.J.Ford	Myrtaceae	CR	
<i>Rhododendron lochiaie</i> F.Muell.	Ericaceae		
<i>Rhododendron viriosum</i> Craven	Ericaceae		
<i>Sersalisia sessiliflora</i> (C.T.White) Aubrév.	Sapotaceae		
<i>Solanum dimorphispinum</i> C.T.White	Solanaceae		
<i>Solanum eminens</i> A.R.Bean	Solanaceae		
<i>Symplocos bullata</i> Jessup	Symplocaceae		
<i>Symplocos graniticola</i> Jessup	Symplocaceae	V	
<i>Symplocos oresbia</i> Jessup	Symplocaceae	NT	
<i>Symplocos wooronooran</i> Jessup	Symplocaceae	NT	
<i>Syzygium fratris</i> Craven	Myrtaceae	CR	
<i>Tasmania</i> sp. Mt Bellenden Ker (J.R.Clarkson 6571) Qld Herbarium	Winteraceae		
<i>Trachymene geraniifolia</i> F.M.Bailey	Araliaceae	NT	
<i>Trochocarpa bellendenkerensis</i> Domin	Ericaceae		
<i>Uromyrtus metrosideros</i> (F.M.Bailey) A.J.Scott	Myrtaceae		
<i>Wendlandia connata</i> C.T.White	Rubiaceae	NT	
<i>Zieria alata</i> Duretto & P.I.Forst.	Rutaceae	CR	
<i>Zieria madida</i> Duretto & P.I.Forst.	Rutaceae	CR	

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e026](https://doi.org/10.1016/j.gecco.2023.e026).

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