



Tree ferns on the move: patterns of movement and current introduction status of Cyatheales species around the world

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Abstract Tree ferns (order Cyatheales) have been moved from their native ranges for more than two centuries, and the number of species introduced to new countries has recently increased rapidly. However, no comprehensive global list of alien tree ferns exists. Botanical garden collections and the Global Biodiversity Information Facility database were examined, and a systematic literature review was conducted to collect information on tree fern introduction dates, locations and impacts in non-native ranges. Overall, 158 species out of 795 Cyatheales species (c.

20%) were found to have been introduced. The earliest documented introduction occurred in 1789 when *Dicksonia arborescens* L'Hér. was moved from St Helena Island to the United Kingdom. Tree fern introductions are biased in favour of well-developed countries with historical exploration in regions with rich native tree fern floras. Five species have naturalised (*Alsophila australis* in Sri Lanka; *Alsophila speciosa* in Madagascar; *Sphaeropteris excelsa* in the United States of America; *Sphaeropteris medullaris* in Madeira (Portugal); and *Lophosoria quadripinnata* in Fiji, French Polynesia and the United States of America). Two species are invasive: *Sphaeropteris cooperi* in the Azores (Portugal), Hawaiian Is. (USA), Mauritius, Réunion Isl. (France) and South Africa; and *Dicksonia antarctica* in the Azores (Portugal) and Sri Lanka. The extensive history of tree-fern movement has radically altered the global distribution of the order Cyatheales, creating substantial invasion debt. The 151 alien (not yet naturalised) species represent a substantial capacity for future invasion. This list can inform monitoring of the distribution of already introduced species to support prevention of further invasions.

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Introduction

The first description of a Cyathea tree fern was by Linnaeus in 1735 in his *Species Plantarum* (von Linné & Salvius 1753), indicating a long history of interest in this order. Tree ferns have been collected since the 1700s and transported worldwide to meet the demand for both living specimens and spores (von Linné & Salvius 1753; Smith 1866). There was massive interest in the cultivation and symbolism of ferns in Europe during the mid-1800s; this has been termed called “pteridomania”, “fern fever” or the “fern craze” (Smith 1866; Jones 1987). During this time, finding new species was encouraged and the booming horticultural trade led to approximately 50 new species entering Britain each year (Smith 1866). Enclosed wood and glass miniature ‘Wardian cases’ enabled the transport of ferns out of their native tropical and subtropical regions to regions with vastly different climatic conditions (Ward 1842). Ferns were primarily collected from Australia, New Zealand, South America, and various islands in Central America (Smith 1866), and were traded around the world, largely for ornamental horticulture. Trade and interest in fern species was, and still is, supported by many resources, including books and more recently, gardening websites that provide detailed information about ferns and their cultivation (e.g., Smith 1866; Lowe 1867; Hibberd 1870; Jones 1987; Large & Braggins 2004). These resources and the insatiable demand for novelty in gardens have continued to drive the demand for non-native tree ferns.

Despite the sustained interest in describing and cultivating tree ferns, few studies have directly explored their invasion ecology (the potential for different taxa to naturalise and become invasive outside their native ranges). Since fern (and tree fern) introductions are ongoing (Unwin & Hunt 1997; McCulloch-Jones et al. 2021), there is increasing colonisation pressure (Lockwood et al. 2009) which is increasing the likelihood that tree fern invasions will increase in number and impact. Indeed, certain tree fern species have already become invasive in parts of the world (Medeiros et al. 1992; Arosa et al. 2012), resulting in negative impacts on native biodiversity and ecosystem functioning. For instance, *Sphaeropteris cooperi* is invasive on the Hawaiian Islands after being cultivated in public and private botanical gardens since the 1960s (Loope et al. 1992; Daehler 2009). It has

since spread into natural forests where it outcompetes native Hawaiian tree ferns and alters ecosystem functioning by changing the nutrient cycling of the soil (Medeiros et al. 1993; Durand & Goldstein 2001a, b; Chau et al. 2012).

Although several studies have explored the temporal trends in fern introductions and the reasons their movement (Daehler 2009; Loope 2011; van Kleunen et al. 2018; Jones et al. 2019, 2020; McCulloch-Jones et al. 2021), such information has yet to be collated and summarised at a global scale for tree ferns in particular. The most comprehensive inventory to date is from the Global Naturalised Alien Flora (GloNAF) database. The latest edition of GloNAF includes four naturalised and two invasive species in the order Cyathea (Davis et al. 2025) but provides no information on the overall number of introduced tree ferns or their earliest records of introduction. There is a need to document such information considering the lag-phase associated with many invasions (i.e., the extended time period between introduction and subsequent naturalisation and invasion (Crooks and Soulé 1999)), and the long history of fern introductions dating back to the late 1700s (Smith 1866).

This study provides the first systematic global review of tree fern introductions. It aimed to compile a list of tree fern species that have been moved out of their native ranges and to provide associated information such as introduction dates and introduction status. Documented impacts were collated and categorised using standardised schemes.

Methods

Data acquisition

Botanical gardens

Living collections of botanical gardens house important catalogued information (Rae 2008) and can provide insights into the movement of species. The network of botanical gardens, as documented in the Botanical Garden Conservation International (BGCI 2024) database, was consulted to extract information related to the movement and cultivation of tree ferns (Cyathea) in botanical gardens worldwide. Although BGCI contains data for 3,611 gardens, many did not disclose complete records of tree ferns.

Therefore, BCGI data were augmented by examining publicly available online catalogues (living specimens) of each botanical garden that indicated that they house tree ferns. Those without an online catalogue or with incomplete datasets (i.e., missing accession numbers or dates), were contacted individually for further information regarding their tree fern collections (Supplementary Information Table S1).

Databases

The Global Biodiversity Information Facility (GBIF) was also consulted as it holds important information from databases such as iNaturalist and government-funded vegetation surveys. A preliminary investigation revealed that many of the historic records detailing preserved specimens had discrepancies between the data recorded on GBIF and the information presented on the digitised herbarium sheets. These discrepancies were discussed with GBIF staff. As many of these discrepancies emanate from the host institutions, they must be changed by the individual institutions rather than by GBIF (A. Hahn, pers. comm. July 2025). As this is a complex process with an unclear timeframe, preserved specimens had to be excluded from this study. Cyatheales records were downloaded using the ‘rgbif’ package (Chamberlain et al. 2025) in R v4.4.1. The search yielded 193 484 records and 415 involved datasets (GBIF Occurrence 2025).

To complement this data on introduced tree ferns as well as determining invasion status (as per the primary sources, sensu Blackburn et al. 2011), other relevant databases were consulted. These included the Centre for Agriculture and Bioscience International (CABI) Compendium of Invasive Species, Global Naturalized Alien Flora (GloNAF), Global Register of Introduced and Invasive Species (GRIIS), and the Global Invasive Species Database (GISD). Missing information regarding invasion status, location and date were supplemented using regional checklists where possible.

Systematic literature review

A systematic literature review was also completed to record any information not captured in the databases. Google Scholar, Scopus and Web of Science were used to identify relevant papers. The following Boolean search string was used: (“tree fern*” OR

“treefern*” OR “arborescent fern*”) AND (“import*” OR “alien” OR “non-native” OR “non-indigenous” OR “introduced” OR “exotic” OR “invasive”). The combined searches resulted in a total of 4698 articles. These were screened to determine their relevance based on their titles and abstracts and 992 records were retained. For these records, the full text was read and if relevant it was retained. As this resulted in only 24 articles, a snowballing approach was adopted in which relevant in-text citations were also considered. Final inclusion was determined by reading the full text ($n=34$; Supplementary Information Table S2).

Data processing

Information extracted from all sources included the date of introduction, introduced regions, reason for introduction, and introduction status (i.e., alien (category B2 or higher in Table 1 of Blackburn et al. 2011), naturalised (category C3), invasive (category E) if possible. Taxonomy was then standardised and all tree ferns native to the focal region (i.e., the region covered by the publication or in which the botanical garden is located) were excluded from the database.

Standardising taxonomy

Due to the intense interest in tree ferns, 2000 names exist for roughly 800 species (e.g., Tryon 1970; Tryon and Tryon 1982; Holttum and Edwards 1983; Lelinger 1987; Schuettpelz and Pryer 2007; Schuettpelz et al. 2016; Dong & Zuo 2018). Therefore, collected records were standardised to follow the taxonomic treatment proposed by the Pteridophyte Phylogeny Group I (PPGI; Schuettpelz et al. 2016) and Dong & Zuo (2018) for families and followed by Plants of the World Online (POWO; <https://powo.science.kew.org/>) for species names. Accordingly, tree ferns are grouped into eight families and fourteen genera (Table 1). Names and authorities of all records were checked against all homotypic, heterotypic, and accepted infraspecific synonyms accepted by POWO and the most recently accepted name was used (Supplementary Information Table S3).

Some records were excluded due to insufficient information, or if the precise species was indeterminate as this resulted in an unknown native range and introduction status. The difficulty in identifying the species was due to the authority not being given in

Table 1 The Cyatheaales order contains eight recognised families, 14 genera and 795 accepted species (Schuettpehl et al. 2016; Dong & Zuo 2018) as well as the number of alien species by genus

Family	Genus	Number of species	Number of alien species
Cibotiaceae Korall	<i>Cibotium</i> Kaulf	10	9
Culcitaceae Pic.Serm	<i>Culcita</i> C.Presl	2	2
Cyatheaceae Kaulf	<i>Cyathea</i> Sm	322	32
	<i>Alsophila</i> R.Br	251	39
	<i>Sphaopteris</i> Bernh	106	32
	<i>Gymnosphaera</i> Blume	46	11
	<i>Dicksonia</i> L'Hér	31	19
Dicksoniaceae M.R.Schomb	<i>Calochlaena</i> (Maxon) M.D.Turner and R.A.White	5	5
	<i>Lophosoria</i> C.Presl	1	1
	<i>Loxosoma</i> R.Br. ex Hook	1	0
Loxsomataceae C.Presl	<i>Loxsomopsis</i> Christ	1	0
	<i>Metaxya</i> C.Presl	6	2
Metaxyaceae Pic.Serm	<i>Metaxya</i> C.Presl	6	2
Plagiogyriaceae Bower	<i>Plagiogyra</i> (Kunze) Mett	12	5
Thyrsopteridaceae C.Presl	<i>Thyrsopteris</i> Kunze	1	1

the record source. In such cases, different authorities indicated different species. For example, *Alsophila smithii* could either be *Alsophila smithii* (Hook.f.) R.M.Tryon or *Alsophila smithii* Trevis (which is a synonym of the accepted species *Sphaopteris glauca* (Blume) R.M.Tryon). Species with such unresolvable nomenclature were excluded (Supplementary Information Table S4). Varieties and hybrids were also excluded as the native range and invasion status of the parent species were unclear.

Excluding native species records

Detailed assessments were conducted to ensure that tree ferns recorded in their native ranges were excluded. Native ranges were checked against Plants of the World Online and raised to the country level. To this end, the United Nations list of countries was followed (<https://www.un.org/en/about-us/member-states>, accessed July 2025). Where ranges included islands, the island names were specified and in cases where they are island territories of mainland states, the country name was also provided. Records of species in their native range (at the country level) were excluded. Additionally, when records occurred in a poorly studied country or islands neighbouring the native range and habitat was continuous across the area, the records were accepted as possibly native and were excluded. Records of species native to a

country but non-native to a region within that country were also excluded. This conservative approach was taken to ensure that the list of introduced tree ferns was not artificially inflated by the inclusion of uncertain records. Excluded records can be found in Supplementary Information Table S2. Species with disjunct native ranges were assessed on an ad hoc basis to determine their status (native or introduced). This process resulted in an updated list of introduced tree ferns.

At the family level, a Generalised Least Squares model was used to assess the role of native range size and the number of species on the number of introduced tree fern species, using the 'nlme' package in R (Pinheiro et al. 2025).

Assessing the impact of introduced tree ferns

The impacts of alien tree ferns were assessed following the International Union for Conservation of Nature's (IUCN) Environmental Impact Classification of Alien Taxa (EICAT; Blackburn et al. 2014) and Socio-economic Impact Classification of Alien Taxa (SEICAT; Bacher et al. 2018) schemes to determine the highest magnitude of impact in their non-native ranges. All data sources described above were searched for information on impact for all introduced species. Impact severity is categorised (in order of increasing impact severity) as minimal concern (MC),

minor (MN) moderate (MO), major (MR) or massive (MV) impact.

Convention on international trade in endangered species of wild Fauna and Flora

Alien species were checked against those protected by Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2025) to determine if species protected by CITES have been introduced outside of their native range.

Results

Species list

One hundred and fifty-eight species out of 795 tree fern species (c. 20%) are known to have been introduced outside of their native ranges (category B2 or higher in the Blackburn scheme); five are naturalised (category C3 in the Blackburn scheme) and two are invasive (category E in the Blackburn scheme), namely, *Dicksonia antarctica* and *Sphaeropteris cooperi* (Supplementary Information Tables S5, S6). Most families (88%) and genera (86%) were represented in the list of introduced tree ferns developed in this study, with only the Loxsomataceae family not represented. This family has only two genera, each containing one species, with no evidence of movement out of their native range. The largest family, Cyatheaceae, has the most alien species, including 39 species in the genus *Alsophila*, 32 in both *Cyathea* and *Sphaeropteris*, and 11 in *Gymnosphaera* (Table 1). However, when examining the relative proportions of alien species in relation to the total number of species in each genus, only 16% of *Alsophila* species have been recorded as introduced (Fig. 1). In fact, a significant increase in the number of alien species is seen with an increase in both the total number of species at the family level ($F=9.1$, $p=0.03$, coefficient=0.31) and the native range size of families ($F=8.1$, $p=0.04$, coefficient=0.11).

Almost all alien species (78%) are listed in Appendix II (CITES, 2025), indicating that trade might pose a risk to these species if not properly controlled (Supplementary Information Table S7). Appendix II also includes species that appear similar to species of conservation concern. No alien tree ferns were

listed on the other appendices, indicating that none are currently threatened with extinction (Appendix I) and inclusion has not been requested by a country or organisation already regulating trade (Appendix III).

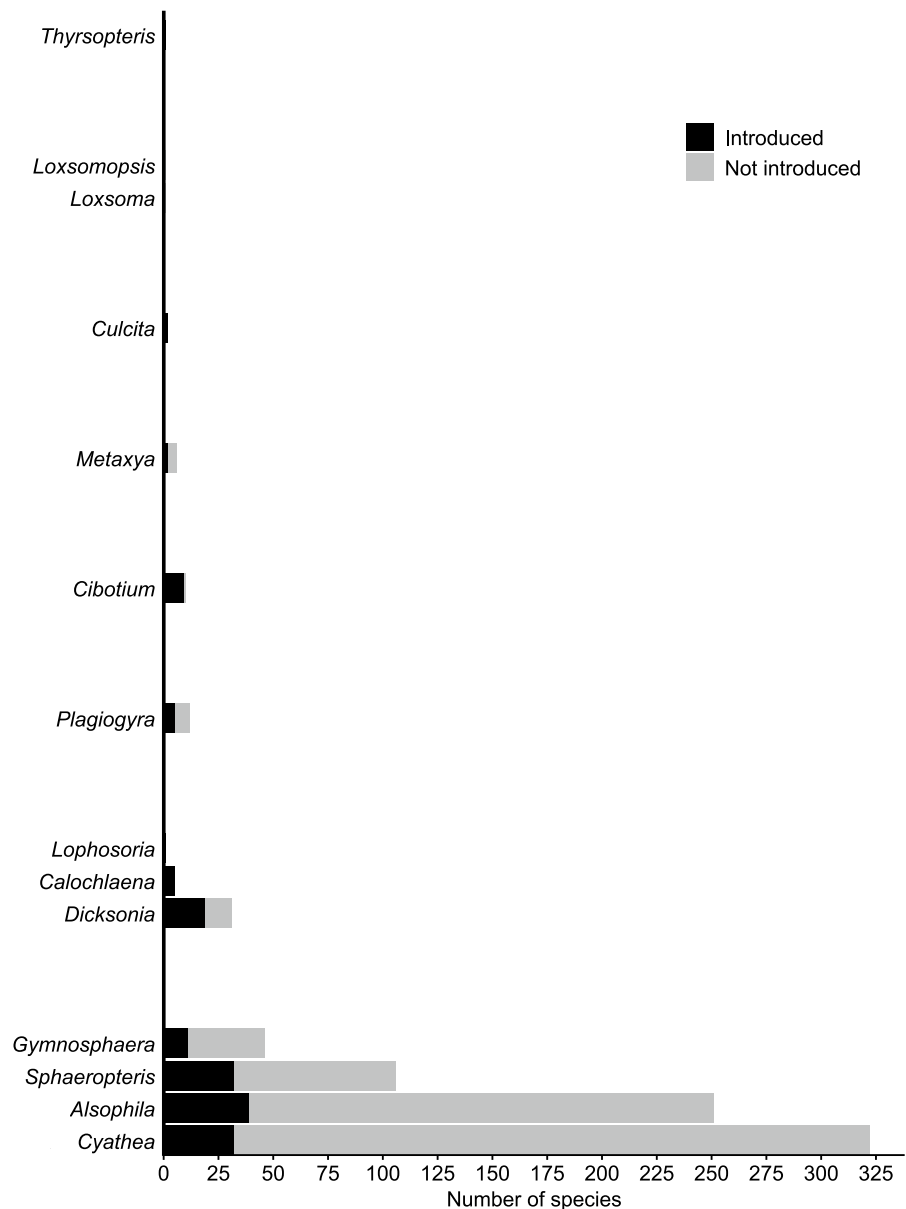
Introduction patterns

Most tree fern introductions were made for botanical garden collections and ornamental horticulture. These introductions were predominantly achieved by harvesting and transporting bare trunks. For instance, *Cibotium chamissoi* and *C. menziesii* were transported from Hawai'i to the American mainland as bare trunks, with root system and fronds removed (Drummond 1959). These specimens were reported to thrive when replanted. Nonetheless, in some instances mature, viable spores were also exported (Drummond 1959). Many resources (from the fern craze until present) provide details of cultivation and propagation techniques, further indicating their continued popularity and consequent introductions (Smith 1866; Adair 1878; Henderson 1881; Large & Braggins 2004).

Temporal patterns

There is a long history of tree fern transportation, starting in 1789 and continuing to the present (Fig. 2). There was an influx of tree fern species between 1830 and 1870 and another increase after 1950. Six of the eight genera were first moved out of their native range in the mid-1800s and early 1900s (Fig. 2c). The earliest record of a tree fern being moved from its native range was *Dicksonia arborescens* L'Hér. that was translocated from St Helena Island to the United Kingdom in 1789 (Smith 1866), followed by *Alsophila tricolor* (Colenso) R.M.Tryon which was moved from New Zealand to the United Kingdom in 1793. These earliest introductions happened between the UK and island territories administered by them. The number of tree fern species introduced outside their native ranges has grown rapidly since the 1960s with more tree ferns being moved in the recent past (since 1960) than over the previous 180 years (1780–1960). The highest number of new species introduced to new countries took place in the 1990s. The two invasive species (*Dicksonia antarctica* and *Sphaeropteris cooperi*) were increasingly recorded in new countries between 1990 and 2020 with specific peaks in

Fig. 1 Number of introduced (black) and non-introduced (grey) Cyatheales tree fern species. Genera are grouped by family (top to bottom): Thyrsopteridaceae, Loxsomataceae, Culcitaceae, Metaxyaceae, Plagiogyriaceae, Cibotiaceae, Dicksoniaceae, and Cyatheaceae



‘new-country’ introductions for *D. antarctica* in both the 1990s and 2010s while for *S. cooperi* the peak was in the 2010s.

Spatial patterns

The natural ranges of most Cyatheales tree ferns are predominantly in tropical and subtropical regions, particularly South America and islands in Oceania, Central America, the Indian Ocean, and the Pacific Islands (Fig. 3a). The countries from which

the highest number of native tree fern species have been moved to other countries are Indonesia (45), Brunei Darussalam (38), Colombia (26), Papua New Guinea (24) and Venezuela (20). It is worth noting that some countries in the Northern Hemisphere have tropical island territories with native tree ferns e.g., the United States of America (Hawaiian Is. – four native tree ferns) and the Russian Federation (Kuril Is. – one native tree fern). Some species are also found further from the equator in regions with cooler climates, resulting in more restricted ranges within

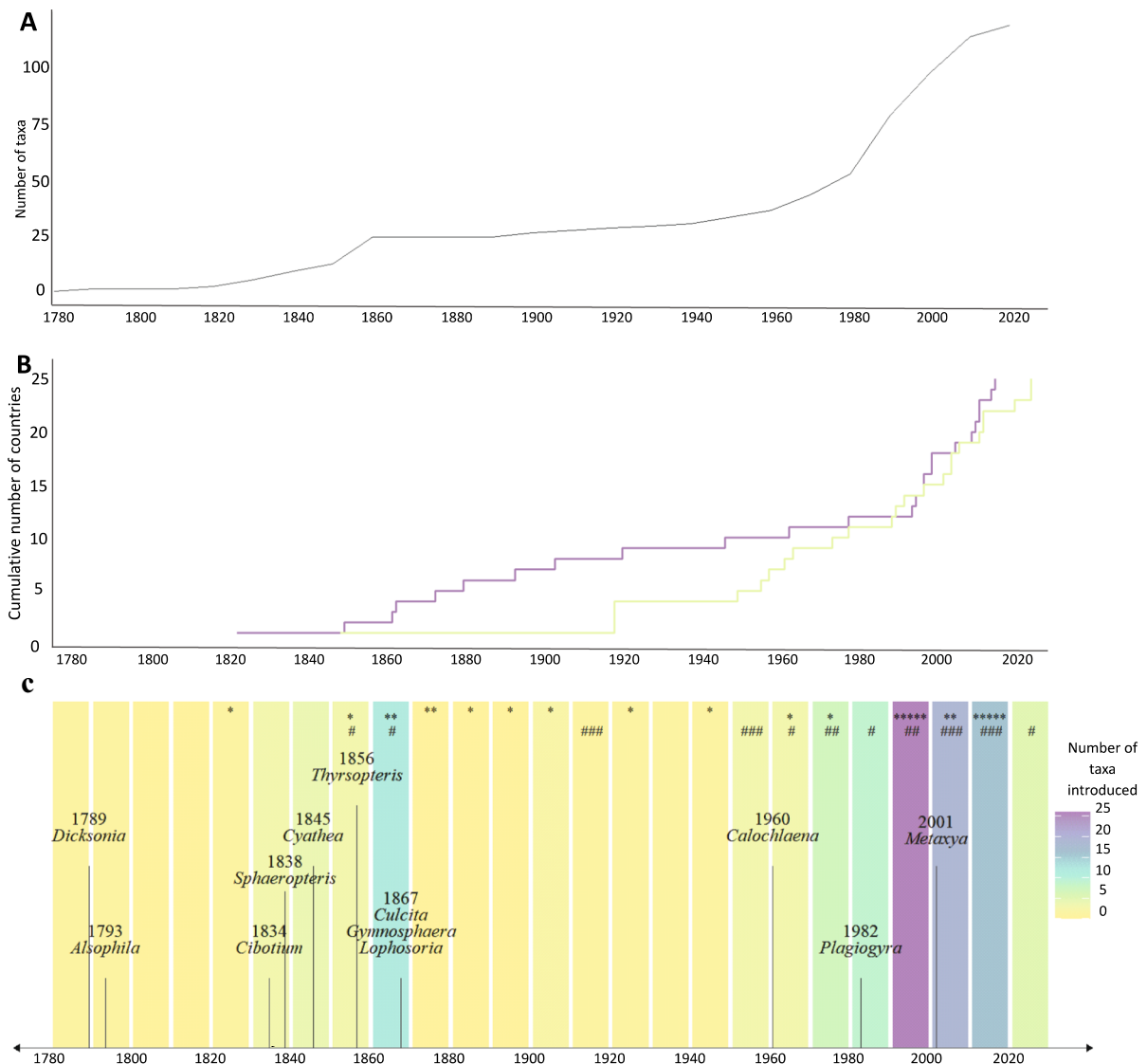


Fig. 2 **A** The cumulative number of times a tree fern was introduced to a country for the first time. **B** The cumulative number of introductions to new countries for each invasive species; *Dicksonia antarctica* is purple and *Sphaeropteris*

cooperi is green. **C** Timeline of first tree fern introductions to non-native countries. The colour of the bars indicates the number of countries tree ferns were introduced to for the first time. The first introduction of each genus is indicated

countries. For instance, *Thyrsopteris elegans* on the Juan Fernández Archipelago, Chile, and *Culcita macrocarpa* in Portugal, Spain, and their islands (the Azores, Maderia, and the Canary Is.).

Overall, tree ferns have been introduced to 54 countries. Introductions are biased in favour of Northern Hemisphere countries, and far fewer species have been introduced to Southern Hemisphere regions (Fig. 3b). Most alien tree ferns have been

reported in the United States of America (86 species). Other countries with many alien tree fern species are the UK (79), France (48), Australia (45), and Germany (34). Regions with fewer introduced species are predominantly in Africa, South America and various islands in Australasia. Many of these countries have received between one and ten alien tree ferns.

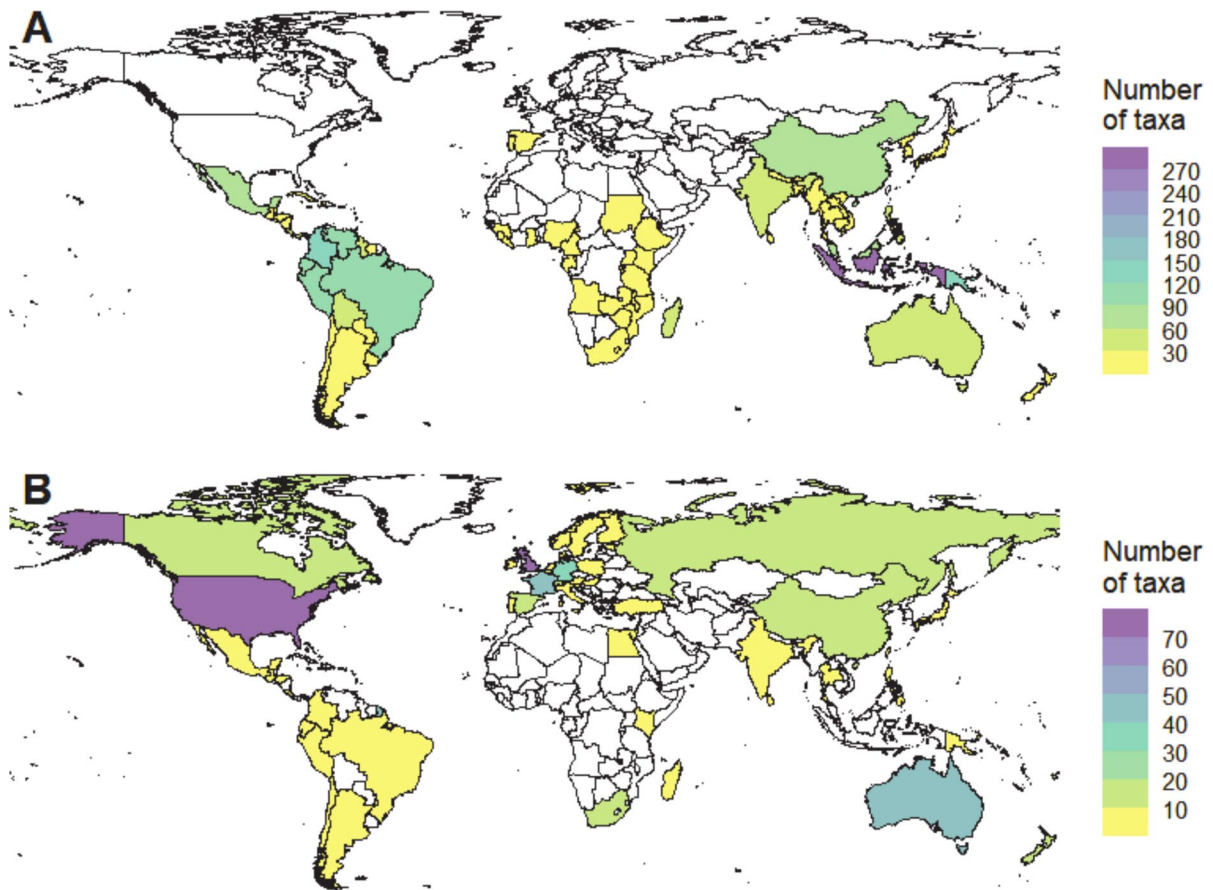


Fig. 3 Global species richness of tree ferns (order Cyatheaales). **A** The native ranges of all tree ferns with species richness for each country. **B** Alien ranges with species rich-

ness. Darker shading (purple) indicates more taxa per country while lighter shading (yellow) indicates fewer taxa

Naturalised and invasive tree fern patterns

Five species are naturalised, namely, *Alsophila australis* in Sri Lanka; *Alsophila speciosa* in Madagascar; *Sphaeropteris excelsa* in the United States of America; *Sphaeropteris medullaris* in Madeira (Portugal); and *Lophosoria quadripinnata* in Fiji, French Polynesia, and the United States of America). Only two tree fern species have been recorded as invasive, namely, *Dicksonia antarctica* (Azores, (Portugal) and Sri Lanka) and *Sphaeropteris cooperi* (Azores, Hawaiian Is. (USA), Mauritius, La Réunion Isl. (France), and South Africa) (Fig. 4). Additionally, *Dicksonia antarctica* is naturalised in Maderia while *Sphaeropteris cooperi* is naturalised in Madeira and New Zealand. *Sphaeropteris cooperi* is considered naturalised in the western part of Australia (Keighery

and Longman 2004; Donoghue and Turner 2022). However, since it is native to the eastern part of Australia, it was considered extra-limital and counted as native in this assessment.

Impacts of introduced tree ferns

The impact of alien tree ferns is understudied in their alien ranges, resulting in data deficient EICAT and SEICAT assessments for all species except *S. cooperi* (Supplementary Information Table S8). *Sphaeropteris cooperi* was found to have moderate environmental impacts (with high confidence, based on the highest impacts in its invaded ranges). This score was based on the competition with native species (Durand & Goldstein 2001a, b), forming hybrids in captivity (Holttum 1984), and altering the chemical

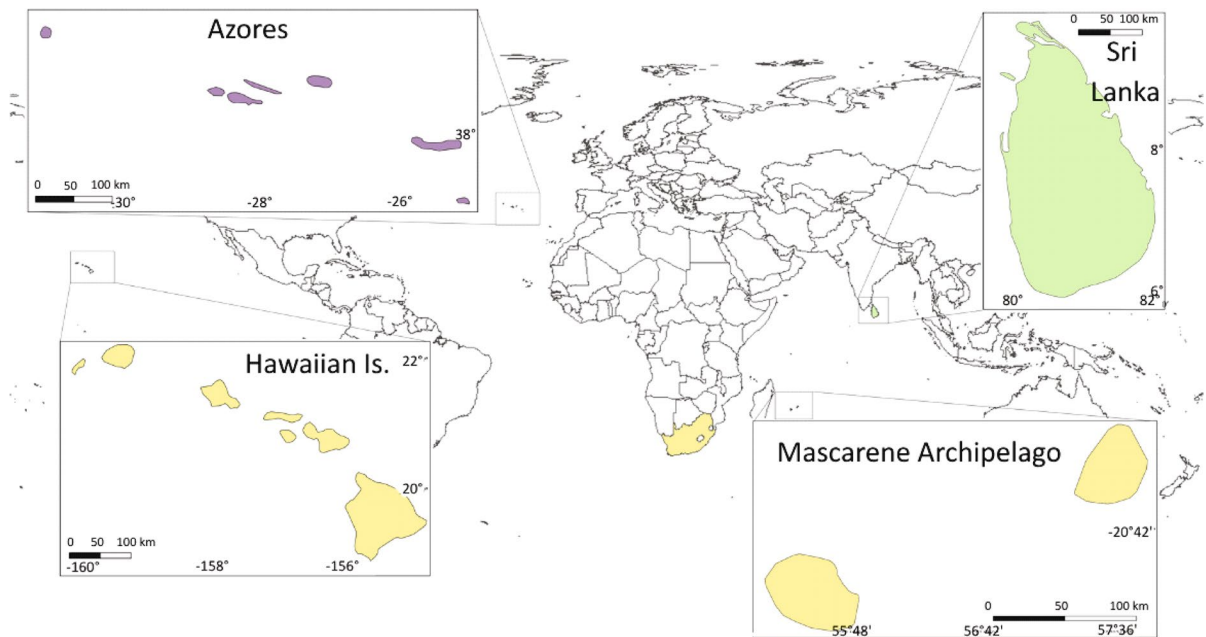


Fig. 4 Regions where the tree ferns *Dicksonia antarctica* (green) and *Sphaeropteris cooperi* (yellow) are invasive with purple indicating where both species are invasive

composition (Chau et al. 2012) and structure (Medeiros et al. 1992, 1993) of invaded ecosystems. However, no information is available on the socio-economic impact of *S. cooperi* in its invaded ranges.

Although the other tree ferns were data deficient in both EICAT and SEICAT assessments, there are several positive socio-economic impacts associated with tree ferns in both their native and introduced ranges. For instance, *D. antarctica* is harvested and traded locally and internationally in its native range (Tasmanian Forest Practices Authority 2022). Tree ferns are also economically important in Mexico, where the adventitious roots of *Alsophila firma* (Baker) D.S.Conant, *Cyathea fulva* (Martens & Galeotti) Fée, and *Cyathea tuerckheimii* Maxon are harvested to make garden ornaments (Eleutério & Pérez-Salicrú 2006).

Discussion

Tree ferns have been transported from their native ranges predominantly for botanical garden collections and ornamental horticulture. One hundred and fifty-eight tree fern species are known to have been

introduced to areas outside their native ranges. Five of these are naturalised and two are invasive (*Dicksonia antarctica* and *Sphaeropteris cooperi*). The spatial and temporal patterns of these introductions have interesting trends. Introductions are predominantly biased towards developed countries and show a moderate increase in 1865 followed by a sharp increase in the 1990s. The environmental and socio-economic impacts of tree ferns are severely understudied; impacts have been documented for only one species (*S. cooperi*) while all others are data deficient.

Taxonomic trends of alien tree ferns

Most tree fern families and almost all genera are represented in this list of alien tree ferns, only the family Loxsomataceae is not represented. The absence of introductions from this family is likely because the family has only two species, both with restricted native ranges. For the remaining families a general pattern of increasing numbers of alien species is seen with increasing family size and extent of the associated native range. Most stark is the finding that most alien species are from the largest family, Cyatheaceae. This family has over 700 species and a native range

that encompasses most tropical, subtropical and some temperate regions globally, highlighting that a diversity of species and broad environmental requirements can predispose high demand for horticulturally important taxa. It is important to note that once the issues in the preserved GBIF specimen data have been resolved, the preserved specimens may hold information that might expand the global list of alien tree ferns.

Interestingly, most alien tree ferns are listed in CITES Appendix II. This indicates that trade may pose a threat to these species if not properly controlled to prevent over-exploitation (CITES 2025). As such, controlling trade could achieve multiple conservation aims—protecting native populations from overexploitation and reducing the propagule pressure of these species in their introduced ranges.

Introduction patterns

Botanical gardens aim to expand their collections to form living collections of plants for research and education (Middleton & Breed 2010). However, botanical gardens also form an introduction pathway for species which can become naturalised and invasive (Hulme 2011; van Kleunen et al. 2018). For instance, *Dicksonia antarctica* is thought to have been introduced to Sri Lanka by a botanical garden, from where it spread to downwind forests (Ranil et al. 2014). Another introduction pathway for invasive plants is ornamental horticulture (van Kleunen et al. 2018). In this situation, preference is often given to taxa with traits that are beneficial in horticulture; unfortunately, many of the same traits also inadvertently promote naturalisation and invasion (Guo et al. 2019). For instance, the invasive *S. cooperi* exhibits fast growth, ease of cultivation, and wide climatic tolerance. While these traits are favourable in horticulture, they are also markers for invasion success (Guo et al. 2019). This species also has many available cultivars ‘Brentwood’, ‘Cinnamon’, ‘Highland Lace’, ‘Red Dwarf’, ‘Revolvulum’, and ‘Robusta’ (Bezonsa et al. 1994; Large & Braggins 2004; Yansura & Hoshizaki 2012). Taken together, its popularity in horticulture has clearly contributed to its naturalization and subsequent invasion.

The movement of tree ferns from their native ranges has been facilitated in a variety of ways. For instance, Hawaiian tree ferns were transported to Los Angeles as bare trunks with no fronds or roots

(Drummond 1959). These tree ferns (of the genus *Cibotium*) were able to establish and thrive in their new range. Other tree fern genera cannot be transported in this way and need to be moved either as whole plants or as spores. Initially, whole tree ferns were transported in sealed protective Wardian cases (Ward 1842) which allowed for the unintentional introduction of associated ‘stowaway’ species such as bryophytes, pests and diseases. For instance, it is speculated that after the addition of living tree ferns to various European greenhouses, bryophytes and some tree ferns native to Australia and New Zealand appeared as accidental introductions (France 2019). Spores are easier to transport but are more difficult to cultivate, although many resources supply simple instructions to this end (Hibberd 1870; Kleinschmidt 1952). Many publications in the 1800s attest to the popularity of tree ferns in horticulture. For example, nursery catalogues from the 1800s advertise *Alsophila australis* (listed under its synonym *Cyathea australis*) for sale in its native Australia (Guilfoyle 1866), and a mature *D. antarctica* specimen in the UK for sale “for want of space” (Moore 1885).

Tree fern introductions have increased steadily since the fern craze began in the 1800s, with a notable dip between 1870 and 1960. The timing of this decline roughly corresponds with the death of Sir William Hooker. Hooker, the first curator of the Royal Botanical Gardens Kew, was a key facilitator of botanical explorations and had a particular interest in ferns, liverworts and mosses (Hooker 1859; Hooker & Baker 1874). He was instrumental in driving botanical collections, resulting in many specimens (both living and preserved) being transported from their native ranges to Kew. The tempo of tree fern introductions declined after Hooker’s death in 1865. Introductions increased again after the 1970s, presumably as a result of increasing globalisation and resulting connectivity (van Kleunen et al. 2015), a trend also seen in alien birds (Dyer et al. 2017).

Tree ferns have been introduced to 54 countries with a general pattern of more developed countries receiving more tree ferns. The USA has the highest number of known alien tree fern species, followed by the UK, France, Australia, Germany and Czechia. These are developed countries with adequate resources to transport and cultivate tree ferns. Colonial links also contribute to the general pattern of developed countries having more alien flora and

introduced tree ferns (Lenzner et al. 2022). At the height of the fern craze, many tree ferns were transported from colonies back to colonising countries. For instance, the UK colonised Australia, South Africa, and India (among several others), contributing to the high proportion of introduced tree ferns in these countries (they have 43, 11 and 4 alien species, respectively). Another reason for this pattern may be that developed countries are over-represented in the data, potentially due to more available resources documenting collections in botanical gardens. In contrast, countries with only one introduced species (such as Chile, the Democratic Republic of Congo, Ecuador, Madagascar, Peru and Thailand) are less well-developed and have native tree ferns. Countries with many native tree ferns generally have fewer alien tree ferns, whereas countries with few native tree ferns have many introduced tree ferns. For instance, the USA only has five native tree ferns, but these are found on the Hawaiian Islands rather than the mainland. Australia is an exception; it has 33 native tree ferns but 43 introduced species. This is potentially due to Australia being close to the many island countries of Oceania with high native tree fern richness, allowing for easier movement between countries.

This over-representation of some countries is countered by the under-representation of others. For instance, several Chinese botanical gardens are listed on the BGCI database but do not have publicly accessible catalogues of their living collection. This may be due to differences in culture, language, and resources. Thus, a potential bias exists in that perhaps only botanical gardens with enough resources to publish publicly accessible catalogues were captured in this study. Additionally, the number of gardens included in this study were not reflective of country size. For instance, Chile is more than twice the size of Germany but only one Chilean botanical garden responded to requests for information, compared with three botanical gardens in Germany which had open access catalogues. Thus, the abovementioned factors may have led to the disproportionate representation of some countries in the current dataset.

Impacts of introduced tree ferns

Scant information is available on the impact of introduced tree ferns. This is problematic as there are 158 alien species worldwide, five of which are

naturalised. A lack of data meant that ecological and socio-economic impacts could be assessed for only 0.6% of introduced tree ferns. Impacts of the one species with sufficient data, (*Sphaeropteris cooperi*) have only been studied in Hawai'i where it has negative environmental impacts at individual, population and potentially community levels. This species supports fewer epiphytes than native tree ferns, alters nutrient cycling and outcompetes the native tree fern *Cibotium glaucum* (Durand & Goldstein 2001a, b; Chau et al. 2012). The impact of this species needs to be assessed in the rest of its introduced range to determine its full range of potential impacts. More research is needed to identify the potential environmental impacts of other introduced tree ferns in their non-native ranges. The negative socio-economic impacts have yet to be investigated for any introduced tree fern. This knowledge gap is a priority for research. However, given their popularity in ornamental horticulture, the benefits (positive impacts) of tree ferns should also be considered. The export of wild-harvested *D. antarctica* specimens as well as nursery-propagated individuals supports a large industry in Australia (Unwin & Hunt 1997). Between 2002 and 2007, 315 721 specimens were harvested in Tasmania (Tasmanian Forest Practices Authority 2022). On Réunion Island, having tree ferns in residential gardens is culturally important, but cultivating native tree ferns is difficult. For this reason, the easily cultivated and fast-growing *S. cooperi* is preferentially planted (M. Rouget, pers. obs.). Overall, tree ferns fall into the category of "conflict-generating invasive species" (sensu Zengeya et al. 2017) as they add economic value but may have negative environmental impacts.

Managing tree fern introductions

Effective management of biological invasions requires access to accurate and up-to-date information. Invasive species databases (such as GloNAF and GISD) must have current invasion status if they are to improve management practices. However, many issues were noted in such databases. For instance, *Sphaeropteris lepifera* is listed as an alien species in Taiwan on GloNAF (under its synonym *Cyathea lepifera*; van Kleunen et al. 2019), but this is the native range of this species (POWO 2025, <https://powo.science.kew.org/>; accessed 24 March 2025). Moreover, *D. antarctica* is not listed in the Global

Invasive Species Database while *S. cooperi* is still listed under its synonym *Cyathea cooperi* (GISD 2025; <http://www.iucngisd.org/gisd/speciesname/Cyathea+cooperi>, accessed 24 March 2025). Making the latest information available on these platforms could support improved management outcomes.

Prevention is the most cost-effective intervention in the management of biological invasions, followed by early-detection and rapid response (Kim et al. 2006; Cuthbert et al. 2022). However, certain species are socio-economically important which thwarts efforts aimed at prevention or complete removal. In such cases, a concerted effort is required to find common ground between governments, the ornamental horticulture industry, and consumers (Hulme et al. 2018). While banning the sale of problematic species may be possible in some instances, where the sale of impactful species such as *S. cooperi* is allowed, it should be supplemented with outreach programs to highlight the potential negative impacts of planting this species. Alternatively, the use of native species should be encouraged, thereby supporting both conservation and local livelihoods. In areas where tree ferns are already introduced, new incursions should be identified and controlled quickly to prevent further spread. Once established or invasive, the manual removal of tree ferns is required to control spread. However, certain tree ferns can resprout and thus a species-specific approach is required. Some options exist for effective chemical control of *S. cooperi*. For example, Motooka et al. (2003) found that *S. cooperi* is effectively treated with dicamba and 2,4-D. Follow-up surveys must be undertaken to determine the long-term effectiveness of these control methods under different environmental conditions.

The high introduction effort documented in this study has generated a substantial invasion debt (sensu Rouget et al. 2016) for alien tree ferns in many parts of the world, particularly since the traits that make some tree fern species popular in ornamental horticulture overlap with traits associated with a high risk of invasiveness in plants (McCulloch-Jones et al. 2021). For instance, *S. cooperi* grows fast and is considered a weed in the fern houses at the Kew Gardens (Holtum 1984). With the rapidly increasing trend of newly introduced tree ferns over the last 80 years and the 158 alien species highlighted in this study, it is possible that more tree fern species may become naturalised or invasive. However, this may be moderated

as climate change is expected to alter temperature and rainfall patterns, which could facilitate invasions in some areas (Kunwar et al. 2025) but inhibit them in others (de Gasper et al. 2021).

This study demonstrates that there is continued global interest in tree ferns with introductions ongoing, despite increasing recognition of the impacts of plant invasions (Roiloa et al. 2020) and the implementation of regulations (such as CITES and the Convention on Biological Diversity (CBD 2022)). With five naturalised and two invasive species, it is suggested that many of the tree fern species that have already been introduced could become naturalised or invasive in the future. As climate change could facilitate or impede this process (Kunwar et al. 2025), monitoring the status of alien tree ferns is imperative. The list produced in this study offers a baseline upon which future monitoring of tree ferns can be founded.

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Data availability All data associated with this paper can be found at <https://doi.org/10.5281/zenodo.17540623>.

Declarations

Conflict of 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.

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