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A horizon scanning approach to rapidly detect alien fern species through horticultural trade

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Abstract

Horticultural trade is a well-documented pathway of introduction for numerous invasive species globally, including ferns. In this study, we analysed trade in terrestrial true ferns (Polypodiophyta) in six anglophone countries: Canada (CA), the United States of America (US), Great Britain and Ireland (GB, for ease of reading), South Africa (ZA), Australia (AU), and New Zealand (NZ). The study provides an overview of fern trade and explored the relationship between trade and alien fern introductions with a view to better inform management interventions. Using a horizon scanning approach in consulting horticultural catalogues, we identified a total of 382 fern species currently traded by 148 traders in a period of just six months. International trade was observed in only three countries with most trade occurring at national scales and e-commerce was not the dominant mode of trade noted in this study, with a relatively higher proportion of species traded on-ground. Alien species accounted for more than 60 % of the total number of traded species in most countries except in AU and NZ, and a surprising number of species (11-14 species per country) known to be naturalised or invasive in their country of trade remain actively traded, with fewer species in CA (2) and AU (5). A total of 194 species noted in trade have not previously been recorded as alien in plant species inventories and did not have an invasion status assigned in their countries of trade. We identified 62 species of concern (i.e., potential future invaders) with *Dryopteris erythrosora*, *Anisocampium niponicum*, *Polystichum polyblepharum*, *Austroblechnum penna-marina* subsp. *penna-marina*, *Asplenium nidus*, *Dicksonia antarctica*, *Polypodium vulgare*, and *Adiantum raddianum* indicated as priority species for regulation in trade due to their high market presence. Citizen science records were noted for very few species of concern with only two records indicating the occurrence of two species in natural or semi-natural areas. This research constitutes one of few studies that have applied a horizon scanning approach using horticultural catalogues to identify alien species, and highlights the efficiency of this approach as a tool for the early detection of potentially invasive species.

Keywords: alien ferns, citizen science, horticultural catalogues, horizon scanning, novel records, pathways of introduction

Introduction

Horticultural trade is an important contributor to agricultural production and economic development but also forms one of the primary introduction pathways of alien plant species globally (van Kleunen et al. 2018). Horticultural trade promotes the continual introduction of species into areas outside of their native ranges which increases propagule pressure (Dehnen-Schmutz and Touza 2008; Simberloff 2009) and exacerbates the likelihood that an alien species will progress along the introduction-naturalisation-invasion continuum (*sensu* Richardson et al. 2000). Additionally, popular horticultural species generally have traits that also make them successful invaders, such as fast growth rates and resistance to disease (Kolar and Lodge 2001; Hulme 2015). The popularity of ornamental taxa in horticulture is also driven by consumer demand which may be linked to the discovery of new species (historically) or through the desires of horticultural fashions (Müller and Sukopp 2016; van Kleunen et al. 2018). Ferns are a good example of this – during the nineteenth century ferns flooded the market, most notably in Europe, in a period referred to as the ‘fern craze’ or ‘pteridomania’ (Allen 1969; Whittingham 2010). These terms were coined around the 1850’s and capture the fervor with which the public desired ferns and also the extent to which the taxon influenced fashions in art, design and ornamental decoration (Birkenhead 1897). The result being the introduction of some nine hundred species of alien fern to Britain for the purpose of cultivation during the 19th century alone (Smith 1896).

Marketing time has been directly linked to invasion success in multiple ornamental species (Dehnen-Schmutz et al. 2007a), including ferns (Pemberton and Liu 2009), where historically introduced species have extended time periods over which to invade, with long residence time being a known driver of invasion success (Wilson et al. 2007). The uses of ferns range from food through to medicine, but it is the ornamental value of ferns that largely underpins their direct economic importance (de Winter and Amoroso 2004; Srivastava et al. 2007). In 2003, ornamental fern production in the US was estimated around 150-300 million USD (de Winter and Amoroso 2004). The popularity of ferns in horticulture is driven by their aesthetic quality where they are used to enhance the scenic beauty of gardens, are popular indoor plants, and are commonly used for cut material in flower arrangements (Kawano 2015). To date, 157 species of ferns are documented as alien somewhere, the majority of which have been introduced for ornamental purposes (Jones et al. 2019). Popular ornamental ferns that have successfully invaded include, *Lygodium microphyllum* (Cav.) R.Br. in America (Goolsby 2004), *Angiopteris evecta* (G.Forst.) Hoffm. in the Tropics (Christenhusz and

Toivonen 2008), and *Sphaeropteris cooperi* (F.Muell.) R.M.Tryon in Hawaii (Palmer 2003) and their impacts range from the alteration of soil nutrient cycling to outcompeting native ferns and changing community structures (Medeiros et al. 1992; Durand and Goldstein 2001; Chau et al. 2013).

Over the last few decades the horticultural trade industry has changed significantly (Dehnen-Schmutz et al. 2010) and evolved to meet the ever-growing demand of the consumer (Dehnen-Schmutz et al. 2010). E-commerce, also known as online or internet trade, is a clear example of how trade has changed over the years and is a serious concern for biosecurity and alien species management as it encourages competitive pricing and quick access, and promotes the mass production and dissemination of numerous species at great distances across the globe (Humair et al. 2015). Furthermore, e-commerce may avoid certain biosecurity efforts as online traders generally do not have a locatable outlet store and the end destination of the product is difficult to predict, thus rendering regulation problematic (Kikillus et al. 2012; Beaury et al. 2021). Trade via e-commerce also expands the opportunity for global transactions (Lenda et al. 2014) and a greater degree of international trade has been strongly associated with higher numbers of invasive species (Westphal et al. 2008; Hulme 2009; Bradley et al. 2012; Seebens et al. 2015). On-ground trade (*sensu* McCulloch-Jones *et al.* 2021), on the other hand, also contributes to invasion success (Hulme et al. 2018). To supply demand, nurseries may harvest from wild populations, source species from dedicated breeders, or simply mass propagate species on-site. Mass production generally favours invasive species as their cultivation is often easier relative to native species and aliens thus commonly comprise the bulk of the market (Hulme et al. 2018). Although it is estimated that only 10 % of alien plant species are likely to escape cultivation (Williamson and Fitter 1996), it is the large number of species cultivated that warrants concern (Hulme 2012; Hulme et al. 2018). For instance, the total number of plant species in cultivation in Great Britain and New Zealand is estimated to be greater than the number of native species existing in the wild (Cubey et al. 2014; Hulme et al. 2018). In addition, commercial nurseries unfortunately often show weak compliance with regulations pertaining to alien or invasive species, and aliens continue to be stocked, propagated and sold regardless of their invasive potential and known negative environmental impacts (Hulme et al. 2018).

Over time, multiple tools have been developed as a means to anticipate and combat current or future invasions, for example, risk assessments (Kumschick et al. 2018) and impact classification frameworks (Blackburn et al. 2014). These tools are used to directly inform

mitigation efforts pre- and post-introduction (Latombe et al. 2017) and largely rely on understanding the biological, environmental and anthropogenic drivers of invasion success (Leung et al. 2012; Blackburn et al. 2014; Latombe et al. 2017; Kumschick et al. 2018). Introduced alien species (i.e., species transported into regions outside of their native range and not yet naturalised or invasive; Falk-Petersen et al. 2006; Blackburn et al. 2011) may remain undetected or unmanaged for extended periods of time as their distribution appears limited (Simberloff 2003). Consequently, they are only subjected to control efforts once invasion has already begun, which is the stage at which management is most challenging (Wilson et al. 2013). In light of this, early detection and rapid response (EDRR) is an essential process needed to slow the rate of introductions and reduce the impacts of invasive species (Reaser et al. 2020). Early detection is key to effectively direct pre-border management efforts and can be undertaken using multiple methods including visual detection of wild species, chemical detection, and horizon scanning using internet-based detection though automated or manual searches (Martinez et al. 2020). Horizon scanning is defined as the systematic examination of the threats and opportunities for invasive alien species introductions (Sutherland and Woodroof 2009; Roy et al. 2014) with the ultimate purpose to anticipate potentially problematic species and inform preventative action (Essl et al. 2015). Horizon scanning provides a powerful tool for early detection as it considers the pathways of introduction and allows for easy detection directly at the source (McGeoch et al. 2016; van Kleunen et al. 2018; Wilson et al. 2018). Work of this nature is however rare, with only a handful of studies (Humair et al. 2015; Novoa et al. 2017; Beaury et al. 2021) making use of trade information such as horticultural catalogues to identify the introduction of alien species. Another effective method of early detection includes the use of citizen science data which aims at detecting species distributions using information gathered by the public (Johnson et al. 2020).

The representation of ferns and their invasion status in plant species inventories is generally poor and so it is likely that many introduced alien ferns remain unrecorded (Jones et al. 2019). In addition, studies considering the relationship between trade and invasiveness in ferns are limited, but thus far have shown that market traits such as the selection of species from which multiple cultivars and variants can easily be developed, a high market presence and trade via e-commerce all drive establishment success (McCulloch-Jones *et al.* 2021). However, further studies are required to better inform country specific regulatory responses to current and future fern invasions that stem from trade. Considering that management

responses to newly introduced alien species may be delayed, and that information pertaining to the invasiveness of a species is not always readily available (Simberloff 2003), providing a means of early detection and classifying the invasion potential or invasion risk of a species is crucial in bettering alien species management (van Kleunen et al. 2010; Wilson et al. 2013; Essl et al. 2015). Accordingly, by using early detection techniques to develop an inventory of horticulturally traded ferns for six anglophone countries, this study aimed to identify per trade country, i) the dominant mode (e-commerce or on-ground) and scale (international or national) at which trade is taking place; ii) whether trade is dominated by native or alien fern species; iii) alien species for which no official records existed in plant species inventories and for which an invasion status has not previously been determined but which are being traded according to nursery catalogues (hereafter ‘novel records’ for ease of reference); and iv) species of concern as species with the status of introduced that have successfully invaded elsewhere which, arguably, should trigger regulatory and other management responses.

Methods

Inventory of traded ferns

To develop a species inventory of traded ferns we closely followed the methods of McCulloch-Jones *et al.* (2021). We considered e-commerce and on-ground trade where on-ground trade included traders that had clearly identifiable geographic location for an outlet store that allowed for direct hand-to-hand trade, whereas e-commerce trade included online plant traders with no locatable outlet store. To ease our search efforts and avoid issues related to translation and linguistic constraints, we focussed our study on six anglophone countries known to have well-established ornamental plant trade networks (Dehnen-Schmutz et al. 2007b; Humair et al. 2015) namely, Canada (CA), the United States of America (US), Great Britain and Ireland (combined for ease of interpretation, and for simplicity, abbreviated as GB), South Africa (ZA), Australia (AU), and New Zealand (NZ). The approach followed to identify fern traders within the study countries, was rooted in EDDR, which implies a swift yet efficient approach (Reaser et al. 2020). Firstly, Google Maps (<https://www.Google.com/maps>) was searched, at a national scale, for plant traders using terms such as ‘plant nurseries South Africa’ or ‘ferns for sale Australia’. This approach provided websites for frequently searched-for or regularly visited plant traders, and as such, represented the most common or popular traders within a country, a method similar to that adopted by ‘Google trends’ (<https://www.trends.google.com/trends/>) (Vosen and Schmidt 2011). Google Maps only provides search results for traders with a locatable address or

coordinates and largely yielded results for on-ground traders. Thus, additional traders were searched for per country using Google Search (<https://www.google.com/search>), which yielded results for on-ground and e-commerce traders. Similarly, the immediate results provided through Google Search indicated frequently searched-for or regularly visited traders. Horticultural trade catalogues for 2019 or 2020 were considered to delimit currently traded species only and were obtained from traders either through their websites or via email request using a proforma email (Supplementary 1). Unfortunately, in some instances, correspondence with the traders was unsuccessful and catalogues for that trader could not be obtained. Search effort was guided by the principle behind species accumulation curves (Fisher et al. 1943; Soberón and Llorente 1993), whereby search effort was ceased when the cumulative number of recorded traders as a function of the cumulative search effort (~time) asymptoted. In other words, a slowed influx of information indicated sufficient representation by the sample. In keeping with the study approach rooted in EDRR and horizon scanning, the identified traders provided a sample of nurseries representative of the trade in ferns in each country, rather than an exhaustive inventory of nurseries and species. Data collection took place over a period of six months from August of 2019 to January of 2020. Statistics on global fern trade are challenging to obtain as data on fern production and sales are rarely published in census, a constraint noted in other studies on ferns in horticulture (de Winter and Amoroso 2004). As such this study recorded the presence of a species in the market but could not account for trade volumes and import or export data or routes. Nomenclature of species follows GBIF and is indicated in Supplementary 2, however, due to the taxonomic difficulties associated with ferns (Christenhusz and Chase 2014) and to ensure that no conspecific entities were duplicated in the database, additional sources were consulted to identify synonyms including the Germplasm Resources Information Network (GRIN; <https://npgsweb.ars-rin.gov/gringlobal/taxonomybrowse.aspx>), and the Catalogue of Life (CoL; <http://www.catalogueoflife.org/col/search/all>) which is linked to World Ferns (<https://www.worldplants.de/world-ferns/ferns-and-lycophytes-list>).

Mode and scale of trade

For each species and trader we recorded the mode of trade as e-commerce or on-ground. The mode of trade for a species was determined by the trader that offered that species. For example, if a species was offered on online only, the mode of trade for that species was recorded as e-commerce; if it was offered at an on-ground nursery only, the mode of trade for that species was recorded as on-ground; and if it was offered both online and by an on-ground

nursery, or if it was offered by an on-ground nursery with online sales facilities, the mode of trade for that species was recorded as both e-commerce and on-ground. As such, the total species counts per mode of trade contain duplicates. The scale of trade was recorded as international or national. For instance, terms such as ‘we ship globally’ were regarded as international trade; and ‘trading only in Australia’ as national trade. The species offered by each trader was then assigned a scale of trade (according to the trader), and therefore the total species counts per scale of trade, per country, contain duplicates. We then calculated the percentage of the total number of traders and the percentage of all traded fern species (respectively) per mode of trade and per scale of trade, per country.

Trade in native and alien species and species of concern

To establish whether a species is alien (non-native) to its trade country, the native range of each species was determined using CoL and GRIN. CoL and GRIN provided a descriptive means to determine the native range of a species and is described from a broad to narrow scale distribution, for example, “Native to: Northern America; Northern Mexico; Mexico; Sinaloa”. If the trade country fell within the native range of a species, the species was considered as native to that trade country. Species traded in countries which were outside of their native ranges were considered as alien to that trade country. To identify novel records of alien ferns, we determined if a species had been formally recorded as an alien in its country of trade according to plant species inventories and if an invasion status of introduced, naturalised or invasive had been assigned to that species within their countries of trade. For this purpose, we consulted various official plant species inventories that include alien plants at all scales, as well as those contained in published literature, for example, A Global Compendium of Weeds (Randall 2017), and the comprehensive database of 157 alien ferns produced by Jones et al. (2019); as well as online databases such as, the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/species/search>), World Ferns (<https://www.worldplants.de/world-ferns/ferns-and-lycophytes-list>), and the CABI Invasive Species Compendium (<https://www.cabi.org/isc>). See McCulloch-Jones *et al.* (2021) and Jones et al. (2019) for comprehensive lists of sources used. To ensure consistency, the invasion status of each species was re-evaluated and potentially modified according to the standard criteria of Falk-Petersen et al. (2006) and Blackburn et al. (2011). For example, if a species was listed as naturalised in a plant species inventory but later described as ‘spreading beyond the initial site of establishment’, the invasion status of that species was modified and recorded in this study as invasive, and if the species was described as exotic or adventive, but

no indication of establishment or spread was provided, the species was assigned the status of introduced. A history of successful invasion provides a useful indicator in determining the potential invasiveness of a species (Rejmánek et al. 2005; Gordon et al. 2010; Richardson and Rejmánek 2011). Accordingly, all species with the status of introduced were screened for records of naturalisation or invasion elsewhere (i.e., in regions outside of their country of trade) and species that have successfully naturalised or invaded elsewhere were flagged as potential future invaders (i.e., species of concern). For novel records that were also species of concern, we further investigated whether citizen science records existed for that species in its country of trade. We checked whether these records occurred in natural or semi-natural areas which would likely be indicative of escape from cultivation and thus potential successful establishment (i.e., naturalisation or invasion). GBIF was used to identify citizen science records as it is currently the largest collection of citizen science data available, and the most extensive species occurrence database in the world (Johnson et al. 2020). For each country of trade, we then calculated, i) the total number of fern species traded; ii) the average number of fern species offered per trader; iii) the number and percentage of traded fern species that were alien; iv) the number and percentage of traded alien fern species that are known to be naturalised or invasive; and v) the number and percentage of traded alien fern species that were identified as novel records in this study.

Results

Mode and scale of trade

Our search efforts identified a total of 382 fern species currently traded by 148 traders among the six countries considered in this study. In all countries, most traders traded at national scales, with international traders recorded only in the US, GB, and ZA (less than 5 % of traders across countries) (Fig. 1a). However, for these same countries, a relatively greater proportion of species were traded at international scales (approximately 10 % across countries; Fig. 1c) with the US showing the highest proportion (25 %). The mode of trade differed across the trade countries (Fig. 1b, d), where e-commerce traders dominated in GB, AU, and CA, and on-ground traders dominated in US and ZA, while it was equivalent in NZ (Fig. 1b). The proportion of species traded via e-commerce differed across countries, with the highest proportion in CA, and the least in ZA (Fig. 1d).

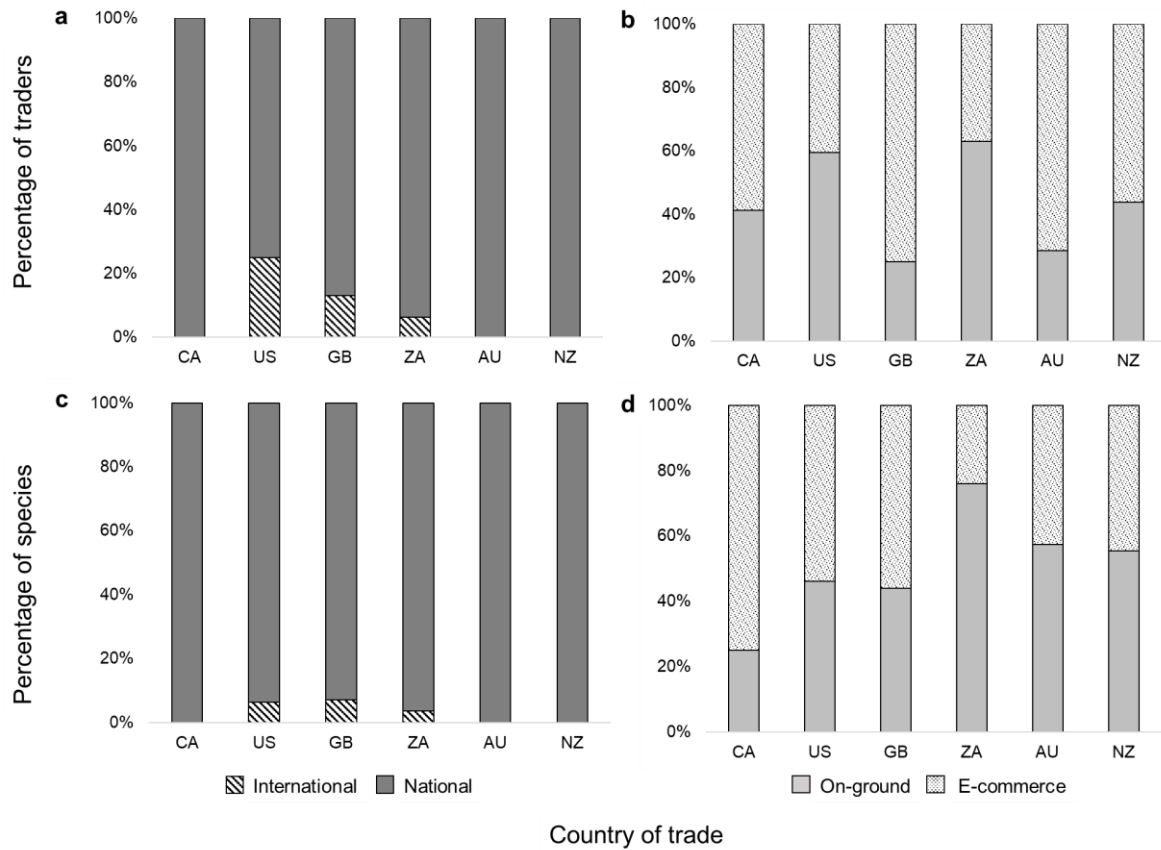


Figure 1 Prevalence of different (a, c) scales and (b, d) modes of trade expressed as proportions of the total number of traders and total number of species recorded per trade country. Treatment of species that were traded both on-ground and via e-commerce is detailed in the methods.

Trade in native and alien species

The US, AU and GB were most active in trade in terms of total number of traded species (> 160 species each; Table 1). The average number of species offered per trader was highest in AU and GB and lowest in ZA (Table 1). Trade in alien ferns was prevalent across all countries, although the proportion of alien to native species traded differed. Alien species accounted for more than 60 % of the total number of traded species in GB, US, CA, and ZA but for less than that proportion in AU and NZ (Table 1). The number of fern species officially noted as naturalised or invasive that remain actively traded differed among countries with the fewest species noted for CA and AU and between 11 and 14 species noted for the remaining countries (Table 1 and 2). Thirty percent of the alien species traded in NZ constituted naturalised or invasive species.

Table 0.1 Characteristics of horticultural trade in terrestrial true ferns (Polypodiophyta) in six anglophone countries. ‘Novel records’ are alien species in a particular country of trade for which no official records existed in plant species inventories and for which an invasion status has not previously been determined.

	CA	US	GB	ZA	AU	NZ
Total number of species	87	196	161	62	163	101
Number (percentage) of species that are alien	56 (64 %)	129 (66 %)	142 (88 %)	42 (68 %)	88 (54 %)	46 (46 %)
Number (percentage) of alien species that are naturalised or invasive but remain in trade	2 (4 %)	12 (9 %)	12 (9 %)	11 (26 %)	5 (6 %)	14 (30 %)
Number (percentage) of alien species that are novel records	27 (48 %)	42 (34 %)	98 (70 %)	27 (63 %)	51 (58 %)	15 (33 %)
Number (percentage) of alien species identified in the current study as species of concern	22 (39 %)	25 (19 %)	30 (21 %)	10 (24 %)	29 (33 %)	14 (30 %)
Total number of traders identified	17	47	28	27	21	16
Average number (min, max) of species available per nursery	14 (1, 76)	12 (1, 84)	22 (1, 73)	6 (1, 48)	23 (1, 78)	15 (1, 58)

Novel records and species of concern

A total of 194 species noted in trade have not previously been recorded as alien in plant species inventories and did not have an invasion status assigned in their countries of trade. These novel records (Supplementary 3) constituted between 35 % and 70 % of the total number of alien fern species traded in each country (Table 1). GB had the highest total number of novel records, followed by AU and the US. A total of 62 species were identified as potential future invaders and flagged as species of concern. The highest numbers of species of concern were identified for GB, AU, the US, and CA (Table 3). Species of concern thus comprised between 20 % and 40 % of the total number of traded alien fern species per country (Table 1). Of the species of concern, 14 constituted novel records for AU and GB, with less than eight species for the remaining countries (Table 3). *Anisocampium niponicum* and *Dryopteris erythrosora* were highlighted as species of concern in all countries of trade except for ZA. A further 20 species of concern were noted in at least three or more countries, of which the following were also traded internationally: *Adiantum raddianum*, *Anisocampium niponicum*, *Davallia mariesii*, *Dicksonia antarctica*, *Dryopteris affinis*, *Microlepia strigose*, *Osmunda regalis*, *Polypodium vulgare*, and *Polystichum polyblepharum* (Table 3). Citizen science records existed for only three species of concern that were novel records according to this study, with only a single location record for each of the species: *Polystichum polyblepharum* was recorded in the Dandenong protected area near Boronia, Melbourne, AU (<https://www.gbif.org/occurrence/2988537693>); *Anisocampium niponicum* was recorded in a residential park or green area in Governors Bay, NZ (<https://www.gbif.org/occurrence/3044680348>; and *Platyserium superbum* was recorded on a roadside near the Walter Sisulu National Botanical Gardens, Krugersdorp, ZA (<https://www.gbif.org/occurrence/3058751749>).

Table 0.2 List of naturalised or invasive (indicated with an asterisk) species per country of trade that remain actively traded. These species should, if not already included, immediately be placed on lists of prohibited species in trade.

CA	US	GB	ZA	AU	NZ
<i>Asplenium scolopendrium</i> *	<i>Adiantum hispidulum</i> *	<i>Austroblechnum penna-marina</i> subsp. <i>penna-marina</i>	<i>Adiantum raddianum</i> *	<i>Cyrtomium falcatum</i> *	<i>Adiantum raddianum</i>
<i>Nephrolepis exaltata</i> *	<i>Arachniodes simplicior</i> *	<i>Cyathea dealbata</i> *	<i>Asplenium nidus</i> *	<i>Lygodium japonicum</i>	<i>Asplenium scolopendrium</i>
	<i>Cyrtomium falcatum</i> *	<i>Cyrtomium falcatum</i> *	<i>Cyathea australis</i> *	<i>Phlebodium aureum</i> *	<i>Athyrium filix-femina</i>
	<i>Cyrtomium falcatum</i>	<i>Dicksonia antarctica</i> *	<i>Cyrtomium falcatum</i> *	<i>Pteris cretica</i>	<i>Cyrtomium falcatum</i> *
	<i>Cyrtomium fortunei</i> *	<i>Matteuccia struthiopteris</i>	<i>Dicksonia antarctica</i>	<i>Pteris multifida</i> *	<i>Dryopteris affinis</i> *
	<i>Platycerium bifurcatum</i> *	<i>Onoclea sensibilis</i> *	<i>Nephrolepis cordifolia</i> *		<i>Dryopteris dilatata</i> *
	<i>Platycerium superbum</i> *	<i>Parablechnum cordatum</i>	<i>Nephrolepis exaltata</i> *		<i>Dryopteris filix-mas</i>
	<i>Pteris cretica</i> *	<i>Platycerium bifurcatum</i> *	<i>Phlebodium aureum</i> *		<i>Lomaria nuda</i>
	<i>Pteris ensiformis</i> *	<i>Polypodium vulgare</i> *	<i>Pityrogramma calomelanos</i> *		<i>Nephrolepis exaltata</i>
	<i>Pteris parkeri</i> *	<i>Polystichum munitum</i> *	<i>Platycerium bifurcatum</i> *		<i>Platycerium bifurcatum</i> *
	<i>Pteris tremula</i> *	<i>Pteris cretica</i> *	<i>Sphaeropteris cooperi</i> *		<i>Polystichum polyblepharum</i>
	<i>Woodwardia radicans</i> *	<i>Woodwardia radicans</i>			<i>Polystichum proliferum</i>
					<i>Polystichum setiferum</i>
					<i>Pteris cretica</i> *

Table 0.3 Traded fern species with the status of introduced in their trade country that are deemed to be of concern given their status of naturalised or invasive elsewhere and are thus potential future invaders. The list includes alien species already recorded as introduced in plant species inventories and novel records of alien species identified from nursery catalogues in this study (indicated with an asterisk). Internationally traded species are further shown.

Species [#]	Country of trade					Internationally traded
<i>Adiantum caudatum</i>	AU		GB*			
<i>Adiantum hispidulum</i>			GB			✓
<i>Adiantum macrophyllum</i>				US		
<i>Adiantum pedatum</i>			GB	NZ		✓
<i>Adiantum raddianum</i>	AU	CA		US		✓
<i>Adiantum tenerum</i>	AU					
<i>Anisocampium niponicum</i>	AU	CA	GB	NZ*	US	✓
<i>Asplenium aethiopicum</i>	AU					
<i>Asplenium bulbiferum</i>	AU		GB		US	ZA*
<i>Asplenium ceterach</i>				NZ*		
<i>Asplenium nidus</i>		CA*	GB	NZ	US	
<i>Asplenium scolopendrium</i>	AU	CA				✓
<i>Athyrium filix-femina</i>	AU					
<i>Athyrium otophorum</i>	AU*	CA	GB*		US*	✓
<i>Austroblechnum penna-marina</i> subsp. <i>penna-marina</i>	AU	CA		NZ	US*	
<i>Blechnum occidentale</i>					US	ZA*
<i>Ceterach officinarum</i>			GB			
<i>Christella dentata</i>			GB*			✓
<i>Cyathea australis</i>			GB*	NZ		
<i>Cyrtomium falcatum</i>		CA*				✓
<i>Cyrtomium fortunei</i>	AU*	CA	GB			
<i>Cystopteris fragilis</i>	AU					
<i>Davallia bullata</i>						ZA*
<i>Davallia canariensis</i>			GB			
<i>Davallia fejeensis</i>	AU			NZ	US	
<i>Davallia mariesii</i>	AU*		GB*		US*	✓
<i>Dennstaedtia punctilobula</i>			GB			✓
<i>Deparia petersenii</i>	AU	CA*				
<i>Dicksonia antarctica</i>		CA		NZ	US	✓
<i>Dicksonia fibrosa</i>	AU	CA	GB*			ZA
<i>Drynaria rigidula</i>						ZA*
<i>Dryopteris affinis</i>	AU*	CA*			US	✓
<i>Dryopteris atrata</i>		CA				
<i>Dryopteris cycadina</i>	AU*		GB*		US	
<i>Dryopteris dilatata</i>	AU*	CA			US	
<i>Dryopteris erythrosora</i>	AU*	CA	GB	NZ	US	✓
<i>Dryopteris filix-mas</i>	AU*					
<i>Hypolepis punctata</i>	AU					
<i>Lomaria nuda</i>			GB*			
<i>Lygodium japonicum</i>		CA				
<i>Matteuccia struthiopteris</i>				NZ		✓
<i>Microlepia strigosa</i>			GB		US	ZA*
<i>Nephrolepis exaltata</i>	AU		GB*			✓
<i>Nephrolepis hirsutula</i>			GB			
<i>Onoclea sensibilis</i>	AU*					✓
<i>Onychium japonicum</i>					US	
<i>Osmunda regalis</i>		CA			US	ZA
<i>Parablechnum cordatum</i>					US*	
<i>Phlebodium aureum</i>			GB*	NZ		✓
<i>Phymatosorus scolopendria</i>			GB*		US	✓
<i>Platycterium superbum</i>						ZA*
<i>Polypodium vulgare</i>	AU*	CA			US	✓
<i>Polystichum braunii</i>				NZ*		
<i>Polystichum luctuosum</i>	AU*	CA		NZ*	US	
<i>Polystichum munitum</i>	AU*					✓
<i>Polystichum polyblepharum</i>	AU*	CA	GB*		US	✓
<i>Polystichum setiferum</i>		CA		NZ	US	
<i>Pteris ensiformis</i>			GB*			ZA*
<i>Pteris parkeri</i>			GB*			ZA*
<i>Pteris tremula</i>			GB			
<i>Sphaeropteris cooperi</i>			GB			✓
<i>Woodwardia orientalis</i>	AU*	CA*	GB*		US	

[#]Species authorities are provided in Supplementary 2.

Discussion

Mode and scale of trade

Our results provided an overview of fern trade in six anglophone countries by distinguishing the countries that are most active in trade, the mode via which ferns are being traded and at what scales. The countries trading in the largest number of fern species were the US, AU and GB. Similarly, these countries were highlighted as dominant in the trade of various angiosperm species on eBay.com (Humair et al. 2015). Contrary to expectation, trade via e-commerce was not the prevailing mode of trade identified in this study and only three of the studied countries (US, GB, and ZA) traded in ferns internationally. Although up to 60 % of the traders in each country had online platforms, a relatively higher proportion (up to 80 %) of species were traded on-ground. Conversely, some other popular ornamental plant groupings such as cacti (Novoa et al. 2017) and orchids (Hinsley et al. 2016) are more extensively traded via e-commerce. One may assume that e-commerce is linked to trade over vast distances (Lenda et al. 2014; Humair et al. 2015), and that e-commerce thus relates with the degree of trade at international scales. Our findings that e-commerce and international trade did not dominate the trade market are thus aligned. Although a wider scale of trade may be generally more concerning in how it can facilitate long-distance dispersal of alien species (Levine and D'Antonio 2003; Westphal et al. 2008; Hulme 2009; Lenda et al. 2014), the dominance of trade in ferns at local scales coupled with the prevalence of on-ground trade likely increases propagule pressure at local scales (Dehnen-Schmutz and Touza 2008). This phenomenon is well known to facilitate invasion in various plant taxa (Lockwood et al. 2005; Simberloff 2009).

We postulate that the limited extent of e-commerce and international trade noted for ferns in this study may be attributed to biological limitations of the taxon. Due to the temperature dependent longevity of fern spores, species that are traded as spore may be difficult to transport as they require specific forms of storage for successful passage (Ballesteros et al. 2011, 2019). Negative effects are most evident after extended exposure periods (Ballesteros et al. 2011) and modern transport technology should, in-theory, be efficient enough to avoid such issues. The sporophyte life phase may likewise be sensitive to temperature fluctuations during transport. For example, the leather leaf fern, *Rumohra adiantiformis*, is a widely traded species that can be shipped at a broader temperature range than other ferns, but it still is reported to be very sensitive to chilling injury, high temperatures or temperature fluctuations that lead to condensation (PPECB 2006). Transportation of this species from

South Africa to other countries of import entails a minimum of two weeks for shipping; during this time period conditions must be carefully monitored as deterioration of the plant will begin shortly after exposure to unfavorable conditions (PPECB 2006). Considering that this species has a wider tolerance than most ferns, it is reasonable to assume that, to avoid shipping losses, most traded species are propagated on site and traded on-ground. In addition, given that ferns can be difficult to propagate from spores, one may assume that trade is almost exclusively in sporophytes. Since some countries (e.g., NZ) have strict regulations against importing most live plant material, this would also probably severely limit international trade.

Trade in alien species

Alien ferns clearly dominated the market with at least 64 % of fern species offered in trade being alien in four of the six study countries. NZ and AU were exceptions, trading in relatively equal proportions of native and alien ferns, suggesting interest in native fern species or more efficient regulation. In line with this, a recent study conducted in Australia highlighted a positive shift in public perceptions towards the use of native plant species in residential gardens (Shaw et al. 2018). The preference for native or alien species is likely dependent on various country-specific variables, for example, cultural, legal, economic, or environmental factors which will determine the availability or richness of species offered by traders (Westphal et al. 2008; Singh and Johari 2018). These factors may also determine the scale at which trade can take place. The US, for example, has a strong horticultural economy and a diffuse trade market (i.e., an innovative market that readily adopts new products or services) which permits the country to expand their connectivity to the international market and avoid the seasonal nature of sales (Dehnen-Schmutz et al. 2010). Accordingly, the US was the strongest internationally trading country identified in this study. Greater degrees of international trade have been directly linked to a higher incidence of invasive alien species occurrence (Westphal et al. 2008). Similarly, the countries in this study that were active in international trade also traded in the highest proportions of alien fern species. Countries that trade internationally may facilitate alien species introductions across the globe through the contribution of their native species to the trade market. This phenomenon has been highlighted in previous studies where the inclusion of native ornamental species in the trade market in Brazil is considered to increase the pool of potentially invasive alien species for other countries (Dehnen-Schmutz et al. 2010).

NZ and AU are considered world-leaders in biosecurity implementation (Meyerson and Reaser 2002; Simberloff 2009) and have been successful in reducing the rate of alien species introductions through the adoption of a ‘whitelist’ approach, whereby species not yet cleared for import require evaluation through an official weed risk assessment (Auld 2012; Hulme et al. 2018). In line with this, amongst our study countries, NZ and AU presented with the lowest proportions of alien ferns in trade. Countries that adopt ‘blacklist’ approaches – whereby any species not listed may be freely imported – have generally shown to be less successful in curtailing invasive species introductions (Simberloff 2006; Hulme et al. 2018). Such countries include various European countries (Essl et al. 2011), the US (Beaury et al. 2021), and ZA (van Wilgen et al. 2017). In line with this, GB, the US and ZA traded in relatively high proportions of alien ferns in this study. Moreover, a surprisingly high number of fern species that are officially noted as naturalised or invasive remain actively traded in all countries except CA and AU (Table 2). These species should immediately be included in lists of species that are prohibited in trade, for example, the National Pest Plant Accord List in NZ or the Alien and Invasive Species Regulations of the National Environmental Management: Biodiversity Act (10/2004) in SA. In cases where these species may already be included in legislative lists an increased effort to monitor industry compliance is necessary. Despite the differences observed between countries with whitelist versus blacklist approaches to regulation, within a global context, our six study countries are deemed to have relatively strong regulatory legislation in place (Turbelin et al. 2017). One may assume that the number of alien and invasive fern species that are traded may be more pronounced in countries that we have not considered, where lesser or no regulatory systems exist. Countries that are most active in trade, but especially those with a high native fern diversity that also trade in high proportions of alien fern species should be particularly cognizant of potential trade impacts, as these countries are likely more susceptible to invasion (Westphal et al. 2008; Fitzgerald et al. 2016; Yu et al. 2018).

Novel records and species of concern

Our research constitutes one of very few studies (Humair et al. 2015; Beaury et al. 2021) that have applied a horizon scanning approach using horticultural catalogues to identify records of alien species that have previously gone undetected in plant species inventories. We identified 194 such novel records of alien fern species (assigned the status of introduced in this study), evidencing that consultation of horticultural catalogues constitutes a very efficient method for the early detection of alien species (Essl et al. 2015; Humair et al. 2015; van Kleunen et al.

2018), compared to results obtained through consultation of official plant species inventories which produced few species with the status of introduced (Jones et al. 2019). Furthermore we detected significantly more alien species at a country scale, for example, official plant species inventories accounted for 15 alien fern species in ZA and 22 in the US (Jones et al. 2019), whereas we detected 42 alien fern species in ZA and 129 in the US. In developing a list of alien species per country of trade and determining the invasion status of each species we were able to identify species of concern that constitute candidates for formal risk assessment and post-border control interventions such as sales restrictions in their countries of trade as a means to try and limit their propagule pressure.

Our study highlighted 62 species with the status of introduced in their trade country that were deemed to be of concern given their history of invasion elsewhere (i.e., potential future invaders), and which should form the focal species for regulation and management in their respective countries of trade – and potentially wider in other countries to which they are bioclimatically adapted. Bioclimatic or niche distribution modelling can assist to identify where the most problematic traded species pose a high invasion threat (Thuiller et al. 2005; Jiménez-Valverde et al. 2011; Srivastava et al. 2019). Of the 62 species of concern identified, we recommend that the following species be prioritised for management (and niche distribution modelling) based on their high market presence (sold by more than 20 nurseries) as noted in McCulloch-Jones *et al.* (2021), namely, *Dryopteris erythrosora*, *Anisocampium niponicum*, *Polystichum polyblepharum*, *Austroblechnum penna-marina* subsp. *penna-marina*, *Asplenium nidus*, *Dicksonia antarctica*, *Polypodium vulgare*, and *Adiantum raddianum* (species are listed in order of priority). Policies should target prevention of introduction of species of concern through four primary types of regulations, i) pre-border control through import restrictions; ii) banning of plant sales post-introduction; iii) implementing ‘codes of conduct’ for the horticultural industry; and iv) public awareness as a means of informing the consumer and instigating behavioral change and consumer trends (Shaw et al. 2017; Hulme et al. 2018). Furthermore, regular screening of horticultural catalogues is recommended to directly inform and update regulatory responses (e.g., blacklists and whitelists).

Citizen science has been highlighted as a successful tool in monitoring biological invasions and detecting novel records of introduction (Johnson et al. 2020), most specifically because the data can account for habitats often missed in traditional survey approaches (Sheard et al. 2020). We consulted citizen science records with the aim to establish whether novel records

of introduction identified in this study that were also flagged as species of concern, have potentially already escaped outside of cultivation, and thus naturalised or invaded. Only three species were noted with a single record each and only two of the species records appear to occur in natural or semi-natural areas. Having noted so few records is encouraging if it suggests that the naturalisation of these species is slow. However, it may also be due to ferns comprising a cryptic taxonomic group with species that are not as easily detected or keenly followed by the general public as some more noticeable or attractive flowering plants. This then suggests that citizen science is not (yet) an effective means of detecting novel introductions of alien ferns. Interestingly, however, two of the species detected by citizen science, namely *Polystichum polyblepharum* in AU and *Anisocampium niponicum* in NZ, are particularly concerning due to their high market presence noted in McCulloch-Jones *et al.* (2021). As market presence has been shown to be an important driver of invasiveness in angiosperms (Dehnen-Schmutz *et al.* 2007a) and ferns (McCulloch-Jones *et al.* 2021), these two species form strong candidates for proactive management actions including pre-border control, mitigation of introduction, and incursion response.

Conclusion

Our study provides an overview of fern trade in six anglophone countries and found that international trade in ferns appears limited, and with higher degrees of on-ground trade occurring relative to e-commerce. We suspect this to be linked to biological limitations of ferns, specifically temperature sensitivities that make them poor candidates for extended transit. This research constitutes one of few studies that have adopted a horizon scanning using horticultural catalogues to identify novel records of alien species. This is particularly important for alien ferns as they are cryptic and often underrepresented in plant species inventories and in citizen science data repositories. The adopted approach allowed for relatively rapid identification of 194 novel records of alien ferns in the six countries studied and seemed more efficient at detecting alien species than consultation of official plant species inventories only. Considering the six study countries represent a subset of countries trading in ferns across the globe, and that we assessed a sample of traders rather than a comprehensive list, it is reasonable to assume that numerous species of alien fern introduced through horticultural trade remain undetected. Alien ferns (relative to native ferns) dominated the market in most countries and several species known to be naturalised or invasive remain actively traded and should, if not already included, immediately be placed on lists of species

prohibited in trade. The other 62 species of concern and the eight prioritised species should form the focal species for regulation and management in their respective countries of trade.

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