

Assessing the invasion risk of traded alien ferns using species distribution models

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Abstract

Risk analysis plays a crucial role in regulating and managing alien and invasive species but can be time-consuming and costly. Alternatively, combining invasion and impact history with species distribution models offers a cost-effective and time-efficient approach to assess invasion risk and identify species for which a comprehensive risk analysis should take precedence. We conducted such an assessment for six traded alien fern species, determining their invasion risk in countries where they are traded. Four of the species (*Dicksonia antarctica*, *Dryopteris erythrosora*, *Lygodium japonicum*, and *Phlebodium aureum*) showed limited global distributions, while *Adiantum raddianum* and *Sphaeropteris cooperi* had broader distributions. *A. raddianum*, however, was the only species found to pose a high invasion risk in two known trade countries – the USA and Australia – and requires a complete risk analysis to determine the appropriate regulatory responses. *Dicksonia antarctica*, *Phlebodium aureum* (for New Zealand), and *Dryopteris erythrosora* (for the USA) posed a medium risk of invasion due to the lack of evidence of impacts, and a complete risk analysis is thus deemed less crucial for these species in these countries. For other species, suitable environments were not predicted in the countries where they are traded, thus the risk of invasion is low, and a complete risk analysis is not required. For species in countries where suitable environments are predicted but no trade information or presence data are available, risk assessments are recommended to better determine the risk posed. Despite the relatively limited potential global distribution of the studied ferns relative to other major plant invaders (e.g., *Pinus* spp. and *Acacia* spp.), their history of invasion, documented impacts in pristine environments, and high propagule pressure from trade warrants concern, possibly necessitating legislative and regulatory measures in environmentally suitable regions.

Keywords

early detection, environmental suitability, horticultural trade, invasion risk, MaxEnt, risk analysis

Introduction

The intentional or unintentional dispersal of species into areas outside of their native range is facilitated by various pathways of introduction which may be natural or human-mediated (Wilson et al. 2009). In particular, horticultural trade has been shown to be the primary source of introductions of invasive alien plants across the globe (Dehnen-Schmutz et al. 2007a; Dehnen-Schmutz and Touza 2008; Pyšek et al. 2011; Seebens et al. 2015; van Kleunen et al. 2018). Terrestrial true ferns (Polypodiophyta; hereafter ‘ferns’) have been a popular group in horticultural trade for centuries (Birkenhead 1897; Allen 1969; Whittingham 2010) and remain popular in trade today (de Winter and Amoroso 2003). Furthermore, various aspects of horticultural trade, such as a high market presence and trade via e-commerce, directly influence the invasion success of traded alien ferns (McCulloch-Jones et al. 2021). Many horticulturally popular ferns are successfully invading and negatively impacting various parts of the globe, for example, *Sphaeropteris cooperi* which has extensively invaded Hawaii and displaced native populations of the tree fern *Cibotium glaucum* (Chau et al. 2013); and *Lygodium japonicum* which is classified as a species of European Union concern (EU Commission 2022) and identified as an A1/A2 pest, requiring regulation and quarantine, by the European and Mediterranean Plant Protection Organization (OEPP/EPPO 2022).

The most cost-effective means of curbing invasions is through preventative action prior to introduction (IUCN 2000; Timmins and Braithwaite 2003; Hulme 2012; Larson et al. 2020; Martinez et al. 2020) or through early detection systems promoting rapid action post-introduction or following escape from confinement (Matthews et al. 2017; Reaser et al. 2020). Risk analysis is a comprehensive process used to determine the level of risk posed by invasive alien species and directly informs the appropriate management and regulatory response. In many countries these analyses are legally required for regulatory decisions regarding alien species, for example, in South Africa, the outcomes of risk analysis are used to determine whether a species is regulated and how (e.g., through trade restrictions or permitting) (Kumschick et al. 2020). Risk analysis is a systematic and robust evaluation that comprises various components, which can be grouped into four stages: hazard identification, risk assessment, risk management, and risk communication (Kumschick et al. 2020). However, as risk analysis is expensive and labour intensive, identifying species that should undergo this process is essential to best direct scarce resources. Risk assessments provide a time and cost-effective means to aid in the detection and anticipation of potentially problematic species that require attention and for which a complete risk analysis may be needed to inform regulation and legislation (Chai et al. 2016; Carboneras et al. 2018, Kumschick et al. 2020).

Risk assessments comprise the initial steps of risk analysis and generally consider the likelihood of invasion alongside consequence (negative environmental or socio-economic

impacts) (Kumschick et al. 2020). Although all risk assessments generally cover these aspects, they may comprise different components depending on the approach adopted (*sensu* Kumschick et al. 2020). Risk assessment approaches include: trait scoring (species traits are used to predict potential for harm), statistical approaches (a trait approach combined with statistical or machine learning to determine likelihood of invasion), decision trees (a tracking system of questions and answers designed to lead to a decision), rapid screening (a quick assessment performed on a large number of species for which limited information is available), detailed approaches (a targeted approach which most closely resembles a risk analysis, requiring a substantial amount of data, management considerations, and stakeholder perceptions), or mechanistic approaches (completed for smaller groups of species evaluating the likelihood of species surpassing invasion barriers, and determining their potential impact). Recent studies applying a mechanistic approach have used similar sets of criteria to assess the risk posed by alien species, namely, a history of invasion elsewhere, invasion status (i.e., introduced and not yet naturalised, naturalised, or invasive) in the region of interest, evidence of environmental or socio-economic impact in the invaded range, and climate or environmental suitability of the region of interest (Carboneras et al. 2018; Bayón and Vilà 2019; Reaser et al. 2020).

The consideration of the climatic or environmental suitability of the receiving region for the taxon in question can greatly enhance the predictive capacity of risk assessments (Beaumont et al. 2014; Chai et al. 2016; Matthews et al. 2017; Roy et al. 2018), and can be used to inform both preventative and reactive management responses. For example, species distribution models or climate matching techniques can detect habitats or regions that are suitable for a species, but where it does not yet occur or has not yet invaded – where preventative measures can be put in place – but can also help direct detection efforts to identify previously undetected populations in suitable habitats where reactive measures may be necessary.

Species distribution modelling (SDM) is increasingly used to predict the potential distributions of alien species and identify sites that are climatically or environmentally suitable for them. These models have been extensively applied across various taxa from marine life to insects and terrestrial plants, and at various scales from local to global (Robinson et al. 2011; Kumar et al. 2015; Mainali et al. 2015; Santamarina et al. 2019; Lamelas-López et al. 2020; Venter et al. 2021). For alien ferns, SDMs have been adopted in only a small number of studies, most of which are at a fine spatial scale (i.e., at a country level or for regions within countries) (Goolsby 2004; Volin et al. 2004; Bystrakova et al. 2014; Akomolafe and Rahmad 2019). These studies have shown that alien ferns can expand their invaded ranges under present-day environmental conditions. For example, the distribution of an emergent invasive fern, *Cyclosorus afer* (H. Christ) Ching, is predicted to expand to an area of more than 25 000 km² across four states in Nigeria (Akomolafe and Rahmad 2018), and in Florida, the invasive fern, *Lygodium microphyllum* (Cav.) R.Br., could become widely established throughout the Everglades (Goolsby 2004; Volin et al. 2004).

Alien ferns are generally understudied and thus are poorly represented in official plant species inventories and in invasive alien plant regulatory lists. Therefore, to detect alien

fern species that have been introduced through trade, McCulloch-Jones et al. (2023) scanned horticultural catalogues for selected trading countries (Canada, the United States of America, the United Kingdom and the Republic of Ireland, South Africa, Australia, and New Zealand). They identified a total of 382 traded fern species and determined their invasion status in the countries in which they are traded, and success or failure of invasion elsewhere. This resulted in a list of 35 alien fern species that have a history of invasion elsewhere and that are introduced but not yet naturalised in the country in which they are traded. It was concluded that these species require SDMs to better assess their invasion risk and to determine the need for a complete risk analysis in countries where they are traded.

We selected six of these alien fern species and used SDMs to determine their potential global distribution. We subsequently considered the results of these models alongside information on the species' i) invasion status in the countries in which they are traded, ii) invasion history elsewhere, and iii) environmental or socio-economic impacts in their invaded range, to categorise each species, per trading country, in terms of the level of risk posed, and suggest the necessary response in terms of the need for risk analysis. We also indicate additional countries across the globe where the species are not yet known to occur and where risk assessment is necessary.

Methods

Study species

The six study species all have a history of invasion in numerous countries, are traded in several of the study countries (Canada, the United States of America, the United Kingdom and the Republic of Ireland, South Africa, Australia, and New Zealand), and have been introduced but are not yet naturalised or invasive in the countries where they are traded (McCulloch-Jones et al. 2023). The selected study species are further not associated with major taxonomic complexities and are not often mis-identified, issues that could lead to highly unreliable distribution data. For example, the fern *Polypodium vulgare* L. is fraught with considerable taxonomic issues (Hauffler et al. 1995) and consequently, the current distribution data for this species in the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) indicates an extensive occurrence in North America, yet the species *sensu stricto* is not known to occur there (in lit. Christopher Hauffler, 03 July 2022). Species identification errors may lead to under-or-over predictions in models and may shift predictions to favour the environmental suitability of the 'contaminating species'. This can further influence the practical applicability of the SDM (i.e., misinformed management suggestions) (Costa et al. 2015).

Modelling procedure

Maximum entropy modelling (MaxEnt) was used for the SDMs in this study as various analyses have proven MaxEnt to be a reliable predictive approach that often

outperforms other methods in terms of the accuracy of the predictions, particularly for those related to biological invasions (Elith et al. 2006; Merow et al. 2013; Mainali et al. 2015). Furthermore, MaxEnt is useful in that it uses presence data as well as formulated background data as a substitute for true absences – which are difficult to obtain due to the lack of systematic survey data – to forecast the distribution of species (Zaniewski et al. 2002; Phillips et al. 2004, 2006, 2009; Phillips and Dudík 2008; Merow et al. 2013; Fourcade et al. 2014). Below we have described the modelling procedure, but a more comprehensive account is provided in Suppl. material 1(1).

Collection and preparation of species occurrence records

When developing SDMs for alien species it is recommended to include occurrence records from both the native and introduced ranges (Jiménez-Valverde et al. 2011; Mainali et al. 2015; Barbet-Massin et al. 2018). Alien species are often not in equilibrium with their environment in their introduced range (and, in some cases, in their native range). Therefore, models that consider only the introduced range (or, in some cases, only the native range) can produce predictions that do not adequately estimate the potential introduced range of the species (Fernández and Hamilton 2015; Srivastava et al. 2019), and are thus less useful in the context of biological invasions. Accordingly, species occurrence records from the native and introduced ranges were used in this study to build the SDMs. Data for all species were obtained from the GBIF (see Suppl. material 1(2) for details). Searches for occurrence records were performed using the currently accepted species name (see Table 2) according to the GBIF taxonomic backbone (<https://doi.org/10.15468/39omei>). The searches yielded occurrence records listed under the currently accepted name of each species, as well as those listed under commonly applied synonyms. For example, the full dataset for *Sphaeropteris cooperi* (F.Muell.) R.M.Tryon contained results for synonyms including *Cyathea cooperi* (F.Muell.) Domin, *Cyathea brownii* var. *cooperi* (Hook. ex F.Muell.) Domin, and *Alsophila cooperi* F.Muell. The total number of occurrence records obtained per species ranged from 3 237 records to 18 996 records (Suppl. material 1(2)).

The quality of the occurrence records for each species was assessed using the packages Biogeo (Robertson et al. 2016) and CoordinateCleaner (Zizka et al. 2019) in R version 4.1.0 (R Core Team 2020). Records that were errors (i.e., records that fall into the sea), environmental outliers (i.e., records that were far away from the rest of the records in environmental space, such as records of ephemeral populations, individuals in cultivation, or where there are errors in the co-ordinates, see Robertson et al. 2016), and centroids (i.e., records at the centre of countries), as well as those that were missing co-ordinates were identified and removed. Duplicate records were removed to avoid pseudo-replication, as were records that were too imprecise for the analysis at 2.5 arc minutes (~4.5 km² at the equator). We subsequently mapped the occurrence records for each species to identify instances where occurrence records were severely clumped and where thinning would be required to account for sampling bias, however, none were identified. We further compared the maps of the downloaded occurrence records

with currently documented information regarding the range of each species to ensure that the full known range of each species was accounted for in the models, and to ensure that erroneous records were not retained during the cleaning process (for more details see Suppl. material 1(1)). The total number of occurrence records in the cleaned datasets for each species ranged from 886 to 3 356 records (Suppl. material 1(2)), which provided enough records for modelling (SDM predictions are generally regarded as not consistent if built using fewer than 30 occurrence records; Wisz et al. 2008).

Selection and preparation of predictor variables

Although ferns are considered habitat specialists, as a group, they are known to have similar broad environmental preferences and generally select for wet habitats with moderate temperatures (i.e., avoiding temperature extremes) (Kessler 2010). Therefore, we used a standard set of predictors to model the distributions of all the selected fern species. The selection of candidate predictor variables was informed using a multi-pronged approach whereby we, i) considered the ecological requirements and limitations of ferns in general, namely, light exposure, temperature extremes and water availability (Kessler 2010); ii) considered the predictor variables that were highlighted as being important in studies that have performed species distribution modelling for ferns at global (Christenhusz and Toivonen 2008; Brummitt et al. 2016) or finer scales (Lehmann et al. 2002; Bystriakova et al. 2014; Akomolafe and Rahmad 2019); and iii) noted if the predictor variable is also considered as ‘state-of-the-art’ (SOA) – those that are commonly used in SDMs for plant species (Petitpierre et al. 2017). When the environmental niches of multiple species are to be modelled with a standard set of predictors, it is suggested that SOA variables are used to build SDMs to ensure transferability and reduce computing requirements (Petitpierre et al. 2017). Nine candidate predictor variables were ultimately selected (see Table 1 for further justification for the selection of these variables) to predict the global distribution of the six study species. The candidate predictors included one landscape variable, land cover, which was acquired from the ESA CCI Land Cover project (<http://maps.elie.ucl.ac.be/CCI/viewer/download.php>) (Suppl. material 1(3)), and eight bioclimatic variables, which were acquired from the WorldClim dataset (WorldClim 2.1; Fick and Hijmans 2017). Befittingly, seven of the candidate bioclimatic predictors were also SOA variables (Table 1). All variables were downloaded at or converted to a 2.5 arc-minute spatial resolution for the purpose of modelling.

Co-linearity can be detrimental to the accuracy of SDM predictions (Dormann et al. 2013; Petitpierre et al. 2017). Accordingly, for each species we used the Pearson correlation coefficient (‘cor’ function in R) to test for correlation amongst the candidate variables. In cases where variables were co-linear ($|>0.75|$, Dormann et al. 2008) we opted to retain variables that represented extremes. As a precautionary addition, we used univariate generalised additive models (GAMs) (see West et al. 2016), to determine the percentage deviance explained by each predictor, and ensured that all statistically significant variables were not excluded. GAMs were performed using the package *MuMin* (Barton 2023). Consequently, of the nine candidate predictor variables, seven

Table 1. Candidate predictor variables selected for modelling the potential distribution of the six alien fern species considered in this study.

Variable	Description	Data type	Motivation for selection with regards to ferns
Landscape variable			
Land Cover	Land cover map including 30 classes describing habitat and percentage canopy cover, e.g., tree cover, broadleaved, deciduous, closed (> 40 %); or tree cover, needle-leaved, evergreen, open (15–40 %) (full details, Suppl. material 1)	Categorical	Accounts for the habitat and light requirements of ferns. Although many species of fern can withstand full sun and occur in bare areas, ferns are most commonly associated with shaded habitats, often in woodlands and forests (Kessler 2010).
WorldClim bioclimatic variables			
Bio 1	Annual Mean Temperature (°C)	Continuous	An important predictor of fern richness and phylogenetic diversity at continental scales (Nagalingum et al. 2015). State-of-the-art-variable (SOA; Petitpierre et al. 2017) commonly used to predict the distribution of plant species.
Bio 4	Temperature Seasonality	Continuous	As for annual mean temperature. SOA.
Bio 10	Mean Temperature of the Warmest Quarter (°C)	Continuous	Representative of climatic extremes. Furthermore, although the global distribution of ferns is generally associated with warmer areas in the tropics (de Winter and Amoroso 2003) only a few species are adapted to extreme hot temperatures (Hevly 1963). SOA.
Bio 11	Mean Temperature of the Coldest Quarter (°C)	Continuous	Representative of climatic extremes. A limited number of fern species are adapted to survive sub-zero temperatures, and the majority of species do not show frond freezing tolerance (Fernández-Marín et al. 2021). SOA.
Bio 12	Annual precipitation (mm)	Continuous	The variable has been identified as one of the most important predictors of fern richness and phylogenetic diversity at continental scales (Nagalingum et al. 2015). Additionally, water is essential for sexual reproduction in ferns (Sharpe and Mehlreter 2010). SOA.
Bio 15	Precipitation seasonality (mm)	Continuous	As for annual precipitation. Additionally, fern occurrence and diversity are strongly associated with areas with many days of rain per year (Kessler 2010). SOA.
Bio 16	Precipitation of the Wettest Quarter (mm)	Continuous	As for precipitation seasonality. Representative of climatic extremes. SOA.
Bio 17	Precipitation of the Driest Quarter (mm)	Continuous	Representative of climatic extremes. The different life stages of ferns show varying levels of desiccation tolerance (López-Pozo et al. 2018), with approximately only 5–10 % of all fern species in the sporophyte form exhibiting desiccation tolerance (Hietz 2010).

(land cover, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation seasonality, precipitation of the wettest quarter, and precipitation of the driest quarter) were used to build SDMs for each of the six study species.

Background data generation

It has been recommended that the sites from which background records are selected should be unsuitable for the species, but should be near to the limit of what is suitable

(Jiménez-Valverde et al. 2011), and should be an intermediate distance from presence records (VanDerWal et al. 2009). Selecting background records in this way is more likely to result in SDMs that can correctly classify suitable from unsuitable sites (Jiménez-Valverde et al. 2011). Accordingly, background points for each species were selected from a restricted area that was, i) environmentally similar to sites where the species occurs, as identified using a map of the Köppen-Geiger climate zones (Kottek et al. 2006); and ii) within 500 km of the occurrence records based on the potential long-range wind and water dispersal of fern spores (Peck et al. 1990), but excluding areas within 5 km of the occurrence records as we assumed that while the organism has not been recorded at these sites, it likely occurs there (the majority of fern recruitment occurs within 2 m of the parent plants; Rose and Dassler 2017). Using a large number of randomly selected background records (e.g., 10 000 records) has been shown to greatly improve the predictive accuracy of MaxEnt models (Phillips and Dudík 2008; Barbet-Massin et al. 2012, 2018). Accordingly, we randomly selected 10 000 background points from the selected areas for each species, with one point per grid cell (i.e., no duplicates).

MaxEnt models

All models were built using MaxEnt Version 3.4.4 (http://biodiversityinformatics.amnh.org/open_source/MaxEnt/; Phillips et al. 2004). In MaxEnt the choice of feature types and setting of the regularisation parameter (RM) are important considerations in the development of predictive models that involve transferal (i.e., when the potential distribution is estimated in a different time period or region than that where the data are from) (Phillips and Dudík 2008). Therefore, we modelled the distribution of the species using various features (e.g., hinge features only, and auto-features), and regularisation parameter settings, and monitored the impact on the predictions and model performance. The final, presented models were run using all features (auto-features), with the RM set to 1.5, which produced smoother, more ecologically plausible response curves (i.e., based on the general shapes of species-environment relationships – a typically smooth bell-shaped curve that does not have several minima or maxima; Austin 2007; Merow et al. 2013; Hannemann et al. 2016). SDMs produced using smoothed fitted functions have outperformed more complex models when modelling the distributions of alien species (Elith et al. 2010). Clamping was also used to avoid extrapolations of the SDM into novel environments.

All models were run using five-fold cross validation (as all records are used for training and testing in this method) and model performance was evaluated using multiple methods, i) evaluating the Area Under the Curve (AUC) statistic, ii) calculating the Continuous Boyce Index (CBI), iii) assessing the fitted response curves; iv) considering the sensibility of the model in terms of fern ecology (Austin 2007); and v) scrutinising the multivariate environmental similarity surface maps (MESS maps). The relative contribution of each environmental predictor in the model for each species was gauged using the Jack-knife test in MaxEnt which provides the percent contribution

of each variable to the model (Phillips et al. 2006). The potential global distribution of each species was mapped using QGIS 3.16.9, with the cleaned occurrence records used to produce the models for each species overlaid onto the prediction.

Risk assessment

Information on the invasion status of the study species per trade country and their invasion history (elsewhere) was taken from McCulloch-Jones et al. (2023) who largely obtained information from the global database of alien ferns (Jones et al. 2019) with updated data from published literature, herbarium records, and alien and invasive plant lists (e.g., the Global Register of Introduced and Invasive species; <https://griis.org/>). All study species have the status of introduced (i.e., present, but not yet naturalised, or invasive) in the trade countries, but their presence outside of captivity or cultivation is uncertain. To account for the history of invasion, species' invaded ranges were considered, while information on recorded impacts was obtained by searching the published and grey literature for evidence of environmental or socio-economic impacts of the study species in their invaded ranges (Table 2). We then closely scrutinised the SDM maps for instances where, i) suitable environments were available for the species in the trading countries (i.e., Canada, the United States of America, the United Kingdom and the Republic of Ireland, South Africa, Australia, and New Zealand), ii) where predictions indicated the possibility for expansion of the current range, and iii) where suitable habitat was predicted in regions outside of a species' current known range of occurrence. This information on invasion history, impact, and potential distribution was used to categorise species as per the level of risk posed, with each category aligned with a suggestion in terms of the requirement for risk analysis, namely, high risk- complete risk analysis needed; medium risk- risk analysis may be necessary, but not crucial, resources are better focussed on high risk species; and low risk- no further analysis necessary (see Table 3, as well as the decision tree presented in Suppl. material 1(4)). Lastly, we identified countries (or regions) other than the trading countries where suitable environments occur, but where the study species are not yet known to be present. Further work (research and subsequent risk assessment) is required in these regions in order to determine the risk posed, and whether risk analysis is required.

Results

Model performance

For all the models AUC values ranged between 0.76 and 0.95, indicating moderate to high performance, and the CBI values were > 0.97 indicating that predictions were consistent with the distribution of the occurrence records (Table 4). We noted few instances where occurrence records were found in areas that were predicted to have

Table 2. The six invasive alien fern species selected for the study, their native and invaded ranges, descriptions of the climates and habitats in which they occur, trading countries for which species distribution modelling is required according to McCulloch-Jones et al. (2023), and evidence obtained from the literature regarding the species' environmental or socio-economic impacts anywhere in their invaded ranges. CA– Canada, USA– United States of America, UK & RI– the United Kingdom and the Republic of Ireland (these were assessed jointly), ZA– South Africa, AU– Australia (AU), and NZ– New Zealand.

Species	Native range	Invaded range	Climate	Habitat	Trading countries in which species distribution modelling is required	Impact in invaded range
<i>Adiantum raddianum</i> C.Presl	Mexico to South America	Invaded Hawaii (Wilson 1996; DeMattos 2021), South Africa (Crouch et al. 2011; Jones et al. 2020), and parts of Europe (Keil et al. 2010)	Tropical and temperate	Herbaceous, terrestrial, lithophytic	CA, USA, AU	Displaces native species
<i>Dicksonia antarctica</i> Labill.	South-eastern Australia	Naturalised in the United Kingdom (Clement and Foster 1996) and Sri Lanka (Ranil et al. 2014), and has invaded São Miguel Island, Portugal (Arosa et al. 2012)	Temperate	Tree fern, terrestrial	CA, USA, NZ	None reported
<i>Dryopteris erythrosora</i> (D.C.Eaton) Kuntze	Eastern Asia	Naturalised in France and Belgium (Randall 2017) and is slowly but progressively invading various states of the USA (Rothfels et al. 2012; Umstead 2018; Wyatt 2020)	Temperate	Herbaceous, terrestrial	CA, USA, UK & RI, AU, NZ	None reported
<i>Lygodium japonicum</i> (Thunb.) Sw.	Asia	Invasive in south-eastern USA (Schmitz et al. 1997), Australia (Randall 2017), and South Africa (Jones et al. 2020)	Tropical and sub-tropical	Herbaceous, climbing	CA	Impacting the economic benefits of pine plantations and smothers indigenous vegetation
<i>Phlebodium aureum</i> (L.) J.Sm.	South-eastern USA, Caribbean, South America	Invasive in Australia, South Africa (Crouch et al. 2011; Jones et al. 2020), and Hawaii (Wilson 1996)	Tropical and sub-tropical	Herbaceous, epiphytic, terrestrial	NZ	None reported
<i>Sphaeropteris cooperi</i> (F.Muell.) R.M.Tryon	Eastern Australia	Invasive in Hawaii (Medeiros et al. 1992), South Africa (Jones et al. 2020), and New Zealand (Heenan et al. 2004)	Temperate, tropical, and sub-tropical	Tree fern, terrestrial	US, UK & RI	Displaces native species and changes soil and plant nutrient dynamics

Table 3. Categorisation of alien plant species in the horticultural trade in terms of the risk posed. The categorisation is based on three primary criteria: history of invasion, evidence of impact; and environmental suitability. Each level of risk is aligned with a suggestion in terms of the requirement for risk analysis. See also Suppl. material 1(4) for a decision tree tracking this process.

Level of risk posed	Criteria	Requirement for risk analysis
High	Invasive or potentially invasive (i.e., invasive somewhere in the world) species for which suitable environments are available in the focus country, and for which impacts are known in its invaded range.	Complete risk analysis needed
Medium	Invasive or potentially invasive (i.e., invasive somewhere in the world) species for which suitable environments are available in the focus country, but for which no impacts have been recorded in its invaded range.	Risk analysis may be necessary, but resources are better focussed on high risk species
Low	Invasive or potentially invasive (i.e., invasive somewhere in the world) species, but for which no suitable environments exist in the focus country.	No further analysis necessary

Table 4. Model evaluation statistics for the SDMs for six selected fern species in trade. Results for both the Area Under the Curve (AUC) and Continuous Boyce Index (CBI) are shown.

Species	AUC	CBI
<i>Adiantum raddianum</i>	0.76	1
<i>Dicksonia antarctica</i>	0.88	1
<i>Dryopteris erythrosora</i>	0.88	0.97
<i>Lygodium japonicum</i>	0.85	1
<i>Phlebodium aureum</i>	0.91	1
<i>Sphaeropteris cooperi</i>	0.95	1

low suitability (*Dryopteris erythrosora* and *Sphaeropteris cooperi* in eastern USA, and *Dicksonia antarctica* along the British Isles and eastern USA). The MESS maps for each species indicated that the models did not extrapolate into novel environments. The vast majority of the response curves were plausible based on expectations of the general shapes of species-environment relationships (Suppl. material 1(5)). The response curves for two of the predictors, namely, temperature seasonality and precipitation seasonality did, however, appear slightly truncated or irregular in some of the models.

Variable contribution

The Jack-knife test of variable contribution showed that the most important predictor differed among the species, but land cover was the most important predictor for more than one species (*D. antarctica* and *P. aureum*) (Table 5). Mean temperature of the coldest quarter proved important for *A. raddianum*, precipitation of the wettest quarter for *D. erythrosora*, precipitation of the driest quarter for *L. japonicum*, and temperature seasonality for *S. cooperi*. Precipitation seasonality was the least important predictor for all species. On average, precipitation of the driest quarter and land cover contributed the most to the models.

Table 5. Average percent contribution of the environmental predictors used in the SDMs for each species. The most important predictor for each species is in bold.

	Land Cover	Temperature seasonality	Mean temperature of the warmest quarter	Mean temperature of the coldest quarter	Precipitation seasonality	Precipitation of the wettest quarter	Precipitation of the driest quarter
<i>Adiantum raddianum</i>	4.3	8.7	8	39.7	1	7.5	30.8
<i>Dicksonia antarctica</i>	67.4	14.5	12.7	0.2	0	0.2	5
<i>Dryopteris erythrosora</i>	9.4	7.1	18.4	3.7	0.1	39	22.3
<i>Lygodium japonicum</i>	9.4	15.1	0.6	1.3	0.2	17.9	55.5
<i>Plebodium aureum</i>	35	0.3	0.1	28.7	10.6	1.6	23.7
<i>Sphaeropteris cooperi</i>	17	25.1	12.6	21	0.1	9.3	14.9
Average contribution	23.8	11.8	8.7	15.8	2	11.7	25.3

Potential species distributions

The predicted potential global distributions for most species spanned relatively few continents, with the exception of *A. raddianum* and *S. cooperi* for which suitable environments were predicted over several continents and in a greater number of countries across the globe when compared to the other study species (Fig. 1). For these two species, relatively large areas of suitable environment were predicted in many countries outside of their current introduced ranges, including southern Brazil, central African countries, and Madagascar for *S. cooperi*, and the south-eastern coast of Australia, countries in east Africa and southern Asia, the Western United Kingdom and Ireland, and Madagascar for *A. raddianum*. For *L. japonicum*, relatively large areas of suitable environment were predicted in a few countries where the species does not occur, namely southern Brazil, Uruguay, and Paraguay. Based on our models, it appears that for the remaining species predicted environments beyond the current introduced ranges have a relatively low suitability and aren't particularly expansive (Fig. 1). These include Slovenia, Croatia, and Montenegro for *D. erythrosora*; southern Brazil and Taiwan for *D. antarctica*; and east Africa and southern China for *P. aureum*. In terms of potential range expansion in regions where the species already occur, suitable, unoccupied environments are available for *A. raddianum* in east-central Africa and along the coasts of Spain, Portugal, France, Australia, New Zealand, and South Africa; large parts of the north-eastern coast of South Africa for *S. cooperi*, and south-eastern USA for *L. japonicum*.

Requirement for risk analysis

Our literature search showed that environmental or socio-economic impacts have been recorded for three of the study species (*A. raddianum*, *L. japonicum* and *S. cooperi*;

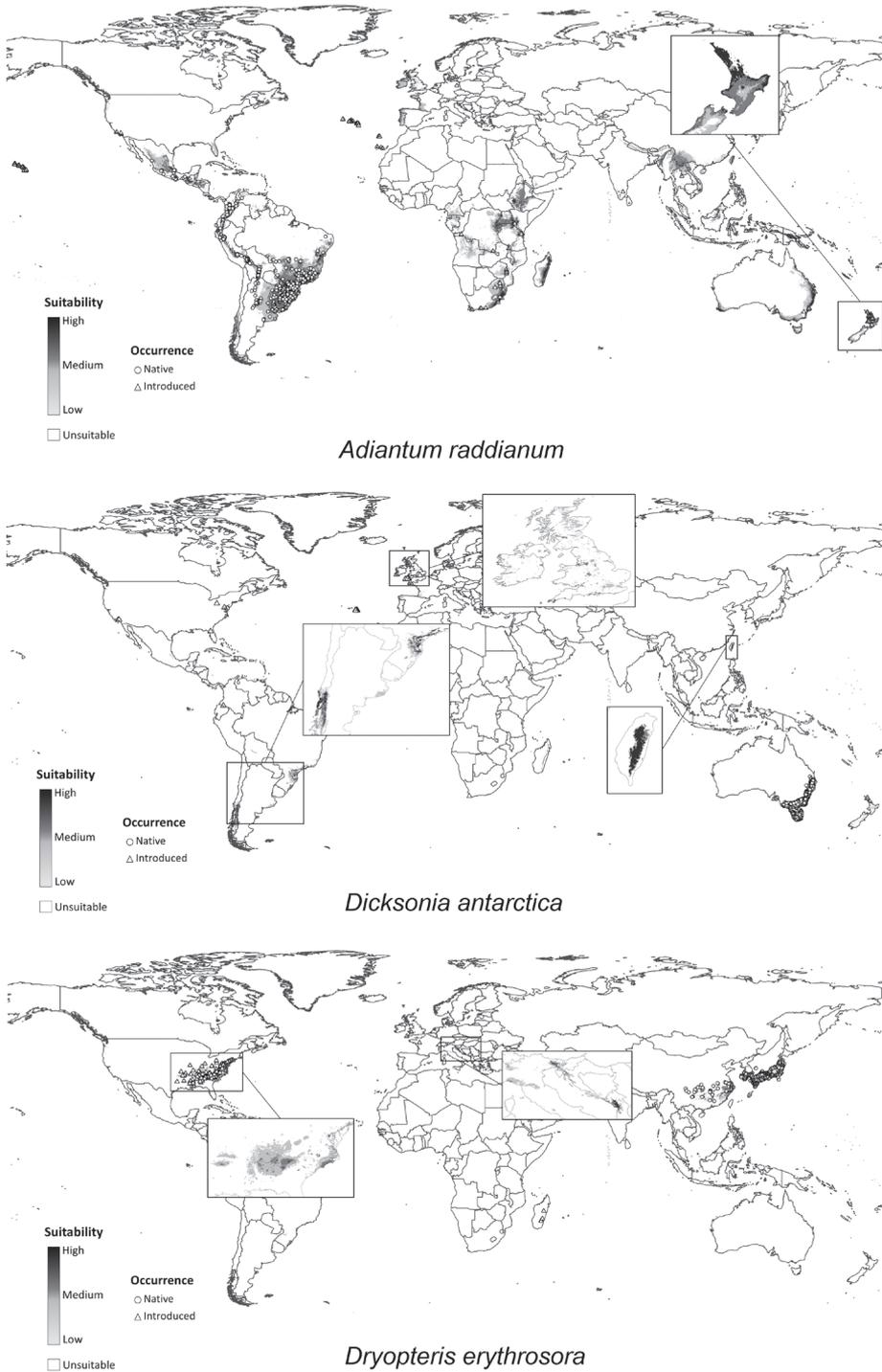


Figure 1. The global potential distribution of six invasive alien fern species as predicted by the species distribution models. In some instances, the identified suitable environments are not easily observed or have been superimposed with multiple species occurrence records. Insets have been used in these cases to improve visibility.

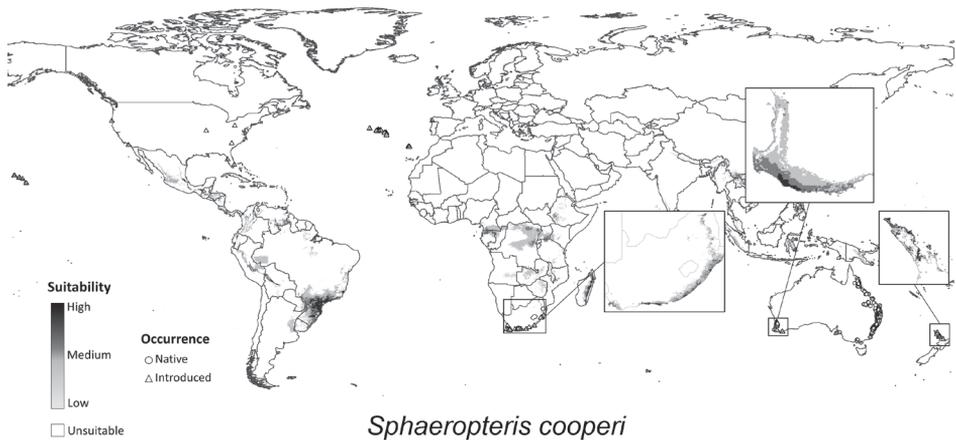
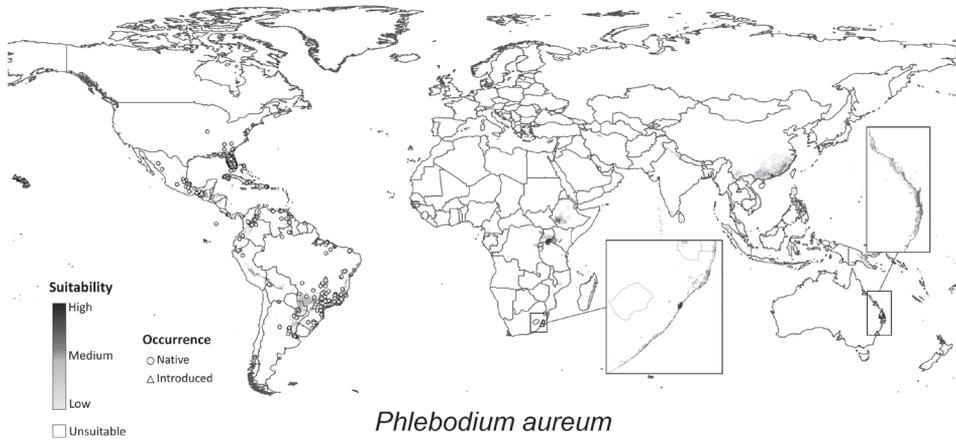
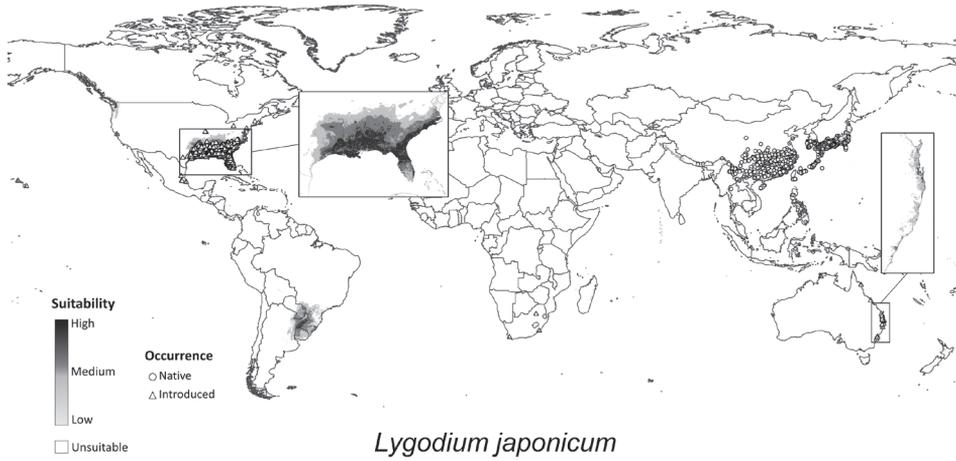


Figure 1. Continued.

Table 6. Requirement for risk analysis of species in the countries in which they are traded based on, i) their invasion history, ii) invasion status in the country (all introduced and not yet naturalised or invasive), iii) whether the species is known to have impacts in its alien range, and iv) the availability of suitable environments according to the species distribution models (see Table 1). Trading countries are CA – Canada (CA), USA – the United States of America, UK & RI – the United Kingdom and the Republic of Ireland (considered jointly), ZA – South Africa, AUS – Australia, and NZ – New Zealand.

Species	Country	Risk rating and requirement for risk analysis
<i>Adiantum raddianum</i>	CA	Low risk – no need for a risk analysis
	USA	High risk – needs a complete risk analysis
	AUS	High risk – needs a complete risk analysis
<i>Dicksonia antarctica</i>	CA	Low risk – no need for a risk analysis
	USA	Low risk – no need for a risk analysis
	NZ	Medium risk – risk analysis needed, but not immediately
<i>Dryopteris erythrosora</i>	CA	Low risk – no need for a risk analysis
	USA	Medium risk – risk analysis needed, but not immediately
	UK & RI	Low risk – no need for a risk analysis
	AUS	Low risk – no need for a risk analysis
	NZ	Low risk – no need for a risk analysis
<i>Lygodium japonicum</i>	CA	Low risk – no need for a risk analysis
<i>Phlebodium aureum</i>	NZ	Medium risk – risk analysis needed, but not immediately
<i>Sphaeropteris cooperi</i>	USA	Low risk – no need for a risk analysis
	UK & RI	Low risk – no need for a risk analysis

Table 2). *A. raddianum*, however, was the only species categorised as high risk for the countries in which it is traded. Suitable environments are available for this species in two of the countries in which it is traded (the USA and Australia), and given that the species has had negative impacts in its alien range, it needs a complete risk analysis for these countries. *D. antarctica* and *P. aureum* were categorised as a medium risk for New Zealand, and *D. erythrosora* a medium risk for the USA (Table 6) as suitable environments are available, but these species have no documented negative impacts. These species require a full risk analysis in these countries, but resources should first be focussed on high risk species. The remaining cases (various species-trade country combinations, see Table 6) were categorised low risk, as there was no suitable environment predicted in the countries of trade. A full risk analysis is not currently required in these cases, but low risk species cannot be considered as ‘safe’ for trade due to their histories of invasion elsewhere (see Table 2). It should be noted that the models for *S. cooperi* and *D. antarctica* may be under predicting in the USA (Fig. 1), and so the indication that these species be considered a low risk for the USA should be treated with caution. For three species, *A. raddianum*, *S. cooperi*, and *L. japonicum*, suitable environments were predicted in some countries where the species are not yet known to occur. Further work is required in these regions in order to determine the risk posed, and whether risk analysis is required, especially considering that these species are particularly popular in trade and introduction through this pathway is likely.

Discussion

A broad environmental and climatic tolerance is exhibited in many popular horticultural species (Dehnen-Schmutz et al. 2007b; Hulme 2011) and thus is an attribute that is also known to promote invasion success (Hulme 2015; van Kleunen et al. 2018). As such, we expected the popular ornamental alien ferns assessed in this study to have wide environmental tolerances and, consequently, wide potential global distributions. However, the predicted distributions for most of these species are relatively limited (spanning few continents and countries), with only *A. raddianum*, *S. cooperi*, and *L. japonicum* showing wider potential global distributions (as compared to the other study species) both in regions where they are already known to occur and beyond their current known range of occurrence. It is unlikely that the relatively limited distributions predicted for most species are due to issues with model performance as the evaluation statistics indicated that the models performed well. Rather, this may be attributed to the habitat specificity commonly associated with fern species (Mehltreter 2008; Kessler 2010), which aligns with the suggestion that alien ferns are unlikely to invade to the extent noted for some prominent angiosperm invaders (Jones et al. 2020).

Despite the satisfactory performance of the models, a few of the response curves were truncated and slightly abnormal, indicating that the occurrence records of some of the assessed species might not characterise their full fundamental niche (i.e., the full set of conditions in which a species can survive in the absence of biotic interactions; Peterson et al. 2011) (Rodríguez et al. 2019; Soberón and Peterson 2020). This, however, is common, as the realised niche (i.e., the set of conditions in which the species occurs in the presence of biotic interactions, Peterson et al. 2011) often forms a subset of the fundamental niche; or because the occurrence records do not span the entire geographical range of the taxon (i.e., they incompletely characterise the realised niche). The latter circumstance, however, was avoided in this study as we compared the downloaded occurrence records with currently documented information on the range of each species to ensure, as far as is possible, that all areas occupied were accounted for in the models.

Variables that contributed highly to the models reflected well the documented biological and environmental limitations typical for most fern species. The large contribution of precipitation variables, for example, was unsurprising as ferns generally require moist environments (Ferrer-Castán and Vetaas 2005; Karst et al. 2005; Kessler 2010; Sharpe and Mehltreter 2010), and as precipitation plays a role in determining fern species richness (Lehmann et al. 2002; Bickford and Laffan 2006; Moreno Saiz and Lobo 2008; Nagalingum et al. 2015). The reliance of ferns on water is considered a limitation in their evolution (Page 2002), and most likely explains why terrestrial ferns are deemed unlikely to invade to the same extent as some of the world's most aggressive invaders (see Lowe et al. 2000; Jones et al. 2019). Ferns exhibit poorly controlled evapotranspiration which restricts the degree of exposure they can withstand and limits them to areas of high precipitation and humidity (Page 2002; Sharpe et al. 2010). Accordingly, <10 % of fern species in their sporophyte form (the distinct frond producing form) exhibit

desiccation tolerance (Hietz 2010). Ferns rely on water to breed as sexual reproduction can only take place where free water is available to allow movement of the motile spermatozoids involved in fertilisation (Page 2002). In accordance with these requirements, precipitation of the driest quarter was, on average, an important predictor across species. Variables associated with temperature extremes also contributed to the models for some species, and in accordance with this, the majority of fern species cannot withstand frond freezing (Fernández-Marín et al. 2021). Mean temperature of the coldest quarter, for instance, was the most important predictor for *A. raddianum* and this tropical species generally selects for sheltered environments where frost is unlikely. In some instances, non-climatic variables (i.e., land cover) contributed most to the models and may be an indication of habitat specificity. For example, land cover was the most important predictor for *D. antarctica* and *P. aureum*, and these species displayed highly limited potential distributions in the models. Furthermore, in South Africa, *D. antarctica* has naturalised in the Cape Peninsula (Roux 2001; Crouch et al. 2011), but invasion has not yet occurred (Jones et al. 2020). This is suspected to be due to its slow growth rate and late age of reproductive maturity (~20 years) (Crouch et al. 2011), coupled with fragmentation of suitable forest habitat in the Western Cape (Roux 2001).

Although many ferns can colonise disturbed and altered habitats (Murakami et al. 2005; Walker and Sharpe 2010), typical fern habitat is characterised by wet, shady, undisturbed forests (Kessler 2010). For example, in their native range *A. raddianum* commonly favours shaded earth banks in forest (Crouch et al. 2011; Jones et al. 2020); *P. aureum* occurs in forest canopies, but also in the lower strata of the forest (Smith 1993); and *D. antarctica* is one of the dominant understorey species of wet evergreen forests (Ough and Murphy 1996). Similarly in their invaded range, alien ferns have generally been found to largely occur in sites associated with other invaders, close to water, and most often in forest systems or in an urban/forest matrix, for example in South Africa (Jones et al. 2020), Hawaii (Chau et al. 2013), and India (Morajkar et al. 2015). Although intact forests generally display some resistance to invasion (Fine 2002; Green et al. 2004; Levine et al. 2004), various shade-tolerant and often late successional species do show the capability to invade these environments (Martin et al. 2009). Ferns are a prime example of such species (Kessler 2010; Sharpe and Mehltreter 2010): in just over six years *L. microphyllum* (a climbing fern) formed dense mats covering large swathes of remote intact forests in Florida, USA (Volin et al. 2004). Similarly, the related climbing fern *L. japonicum* (modelled here) displays comparable behaviour where it invades in northern Florida (Lott et al. 2003). Some of the other alien ferns considered in this study have been shown to outcompete native species and change forest community structure in their invaded range. For example, *D. antarctica* has invaded two European Union conservation priority habitats on São Miguel Island where eradication is now deemed impossible (Arosa et al. 2012), and *A. raddianum* has replaced populations of the native fern *Adiantum capillus-veneris* L. in Hawaii, USA (Wilson 1996). It is their selection for, and evidence of impacts in some unaltered environments, such as forests, that warrants concern despite their relatively limited potential global extent for invasion.

The consideration of environmental suitability in conjunction with the invasion status of a species and the knowledge of their invasion and impact history has enabled us to classify the study species in terms of the invasion risk they pose in the countries in which they are traded, and thus get an indication of whether they require a complete risk analysis. The USA, Australia, and New Zealand show the greatest potential for invasions by these traded alien ferns, with suitable environments available for at least four of the six study species which now constitute medium or high risk species that require risk analysis. The USA is of particular concern, as this country already has extensive documentations of fern invasions and is a prominent trader in alien fern species (McCulloch-Jones et al. 2023). For example, in the USA, the Florida Exotic Pest Plant Council's 2019 List of Invasive Plant Species lists seven fern species as invaders that are changing community structures or ecological functions, or hybridizing with native species (FLEPPC 2019). Furthermore, in Georgia, USA, five alien ferns have recently been documented as spreading beyond their sites of introduction (Wyatt 2020), including *D. erythrosora* (modelled here) which was first noted outside of cultivation just 13 years ago (Simpson et al. 2008). According to our study, Georgia and its surrounding areas are environmentally suitable for this species, but the area available for range expansion is closely confined to its current invaded range (which spans a large area of south-eastern USA, excluding Florida). Similarly, New Zealand also has a history of multiple fern invasions (Brownsey 1980; Brownsey and Perrie 2014; Perrie et al. 2019) and there are suitable environments available in New Zealand for three of the study species, namely *D. antarctica*, *L. japonicum*, and *S. cooperi*, but these have a relatively limited potential range, and moderately suitable environments.

The USA, Australia, and New Zealand are most in need of trade regulations, specifically for the species identified as medium and high risk to prevent the occurrence of, or increase in, invasions. As official regulation is contingent on risk analysis, this study provides crucial information by identifying species that require risk analysis. Efforts to detect and manage escaped populations are necessary as suitable environments are available and invasive populations may remain undetected in these countries. Furthermore, countries that possess suitable environments, but lack documented occurrences of these species should conduct risk assessments. Based on the assessment outcomes, they can determine whether it is necessary to perform risk analysis and implement trade regulations to prevent future invasions. It is important to note that all species considered in this study are highly popular in trade and introduction via this pathway is thus likely (McCulloch-Jones et al. 2021). We suggest that key habitats (e.g., moist, shaded environments) that occur close to, or as a matrix with, urban areas are prioritised for efforts to locate undetected populations as this is where fern invasions most commonly occur. Trading countries for which the majority of species were categorised as a low risk (i.e., Canada and the United Kingdom and the Republic of Ireland) are under a lower potential threat of invasion and the current response arguably need not be as aggressive (i.e., risk analyses are not indicated, and trade bans are likely unnecessary). Importantly, the suggested categorisation of the study species should be revised periodically, given changes in land-use and climate, and as the occurrence and environmental data available for modelling could improve with time as further resources become available.

Conclusion

This study is the first to model the potential global distribution of multiple invasive alien fern species, identifying countries susceptible to invasion and informing the need for risk analyses. The models reveal relatively limited potential global distributions for these ferns compared to other major invaders, but their association with undisturbed habitats, such as forests, and their documented impacts in such habitats raises concern. The projections of environmental suitability have allowed us to complete risk assessments for the studied species to inform their requirement for risk analyses in the countries in which they are traded, thus initiating the early stages of management action. The USA, Australia, and New Zealand stand out as potential hotspots for invasion by traded alien ferns, necessitating management interventions and on-ground population detection for high or medium risk species. This risk assessment approach serves as a valuable management tool, highlighting focal species for each trade country and supporting efficient resource allocation in alien species management and regulation.

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Supplementary material I

Supplementary information

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Data type: docx

Explanation note: (1): Comprehensive methods on the modelling procedure applied in the study. The sub-sections are divided as in the main text to improve readability; (2): The total number of occurrence records for each study species obtained from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) and the number of occurrence records available for modelling post-data cleaning; (3): A breakdown of the land cover variable which was acquired from the ESA CCI Land Cover project (<http://maps.elie.ucl.ac.be/CCI/viewer/download.php>). Left aligned numbers and land cover types are main categories, and right aligned numbers and land cover types are sub-categories; (4): Decision tree used for categorising the priority of species for risk analysis (after Bayón and Vilà 2019) in trading countries. All species are present in the trading countries considered and all are invasive somewhere in the world – hence ‘yes’ is the only possible response for the first two questions of the decision tree; (5): Response curves for the SDMs for each study species. Curves show how each environmental variable affects the Maxent prediction and how the predicted probability of presence changes each environmental variable is varied, keeping all other environmental variables at their average sample value.

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