South African Journal of Botany 178 (2025) 390–399

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

The invaded range of the tree fern *Sphaeropteris cooperi* is predicted to shrink in two southern hemisphere biodiversity hotspots

Megan L. van den Berg[a], Geethen Singh[a], Emily J. McCulloch-Jones[a,b], Mathieu Rouget[c], David M. Richardson[a], Tamara B. Robinson[a,*]

[a] *Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, 7600, South Africa*
[b] *South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa*
[c] *UMR PVBMT, CIRAD, 97410 Saint-Pierre, France*

ARTICLE INFO

Article History:
Received 3 October 2024
Revised 22 January 2025
Accepted 29 January 2025
Available online 6 February 2025

Edited by: Prof G.V. Cron

Keywords:
Climate change
Ensemble modelling
Niche dynamics
Plant invasions
South Africa
La Réunion Island
Cyatheaceae

ABSTRACT

Biological invasions are increasing globally, with species demonstrating differing responses to climate change in their native and invaded ranges. Investigating how alien species respond to climate change is important for planning management interventions. This study considered how the distribution of *Sphaeropteris cooperi* (Hook. ex F.Muell.) R.M.Tryon, a widely cultivated invasive tree fern with a broad climatic tolerance, could alter under climate change in two invaded southern hemisphere biodiversity hotspots: South Africa's Garden Route and La Réunion Island, Mascarene Archipelago. To determine the distributional changes of *S. cooperi* under future climate change scenarios, its niche dynamics were assessed in its native range (Australia) and two invaded southern hemisphere ranges using Schoener's statistic for niche overlap and principal component analyses. An ensemble modelling approach was used to predict the potential distribution of *S. cooperi* under future (2041–2070 and 2071–2100) carbon emission scenarios (SSP1-2.6 and SSP 5–8.5) using five global climate models. The results suggest that *S. cooperi* demonstrates some climatic niche overlap (17.6 %) between the Garden Route and its native range (Australia), but less overlap (3.7 %) was found between La Réunion Island and Australia. On La Réunion Island, little niche overlap together with niche expansion suggests that *S. cooperi* occupies niches not occupied in its native range, and that niche conservatism does not hold true for this location. Thus, under current climatic conditions, future spread may be anticipated in both the Garden Route and La Réunion Island. However, climatic conditions are shifting making it important to consider climate change when predicting how the range of this invader may change in the future. Species distribution models revealed that for both biodiversity hotspots, regardless of climatic scenario or the time frame considered, the range of *S. cooperi* is predicted to shrink, although the degree of decline is expected to vary with time and climate scenario.

1. Introduction

The global extent and impacts of biological invasions are increasing at an alarming rate (Pyšek et al., 2020; Seebens et al., 2021). Simultaneously, climate change is increasing in rate and severity (Lee and Romero, 2023). Understanding the interaction between biological invasions and climate change is crucial for developing effective management strategies. Although climate change generally heightens the risk of biological invasions, responses vary significantly by species and location (Zhu et al., 2007; Bradley et al., 2010; Bezeng et al., 2017; Heshmati et al., 2019; Shrestha and Shrestha, 2019; Nikkel et al., 2023), making it difficult to make broad predictions and generalizations (Ziska, 2023). This increased risk suggests that invasions may expand into previously unaffected areas, posing threats to native species (Bradley et al., 2009; Heshmati et al., 2019; Shrestha and Shrestha, 2019). Therefore, modelling changes in the distribution patterns of alien species under changing climatic conditions is crucial for understanding the drivers of invasion success, anticipating future changes, and informing management strategies (Chai et al., 2016; Rouget et al., 2016; Essl et al., 2020; Ricciardi et al., 2021). This is particularly important because prevention is more cost-effective than controlling biological invasions (Cuthbert et al., 2022).

Many studies have examined the impact of climate change on the distribution of alien plants (Shabani et al., 2018; Turbelin and Catford, 2021; Xian et al., 2023; Ángel-Vallejo et al., 2024; Kolanowska et al., 2024). These studies show that climate change can increase or decrease the potential distribution of invasive plants. For example,

---

* Corresponding author.
E-mail address: trobins@sun.ac.za (T.B. Robinson).

https://doi.org/10.1016/j.sajb.2025.01.046
0254-6299/

Bezeng et al. (2017) found that most (63.3 %) of the >150 invasive trees and shrubs included in their study are predicted to experience a decline in suitable climates in South Africa, while Shrestha et al. (2018) reported an increase in the distribution of most (75 %) invasive plants in Nepal. Similarly, Hoveka et al. (2016) reported that the five most damaging invasive aquatic plants are likely to expand their invaded ranges in South Africa under climate change. Similarly, it is unclear whether there are any discernible trends in the predictions of range shifts for alien ferns. This has not been specifically investigated, but McCulloch-Jones et al. (2023) showed that under current climatic conditions, there were no observable trends in the potential distribution of six different alien fern species. Compared to the number of studies on angiosperms and climate change, relatively few studies have explored the effects of climate change on alien ferns. Particularly, Kessler and Kluge (2022) highlight the difficulty of determining what factors constrain ferns, ultimately making it very challenging to understand how such constraints may in turn interact with a changing climate. Akomolafe and Rahmad (2018) reviewed fern invasions globally, highlighting a scarcity of studies considering how alien ferns may be affected by climate change.

The Australian tree fern, *Sphaeropteris cooperi* (Hook. ex F.Muell.) R.M.Tryon, has become invasive primarily due to its widespread use as an ornamental plant in horticulture (McCulloch-Jones et al., 2021). Its rapid growth and broad global distribution (indicating a potentially broad climatic tolerance) further facilitate its spread and establishment (Durand and Goldstein, 2001a; Crouch et al., 2011). Furthermore, the reproductive spores of *S. cooperi* are easily dispersed by wind and water, contributing to its invasive success (Akomolafe and Rahmad, 2018; Ricciardi et al., 2021). *Sphaeropteris cooperi* has successfully invaded multiple regions, including the Garden Route in South Africa (Baard and Kraaij, 2014; Jones et al., 2020), the Azores and Mascarene Archipelagos (Baret et al., 2006; Arosa et al., 2012), and Hawai'i (Medeiros et al., 1992; Daehler, 2009; Loope, 2011). In Hawai'i, negative impacts have been recorded where the species outcompetes native tree ferns (Durand and Goldstein, 2001a, b) and has disrupted natural ecosystems by altering leaf litter composition, soil nutrient cycling (Chau et al., 2012), and hence species assemblages (Medeiros et al., 1993). The impact of *S. cooperi* on native tree ferns and introduced ecosystems has not been assessed outside of Hawai'i.

The invasion history of *S. cooperi*, along with evidence of its negative impacts on invaded ecosystems, has resulted in the species being highlighted as a species of invasion concern (Baret et al., 2006; Robinson et al., 2010; McCulloch-Jones et al., 2023). As climate change is expected to alter species distributions (Bates and Bertelsmeier, 2021; Turbelin and Catford, 2021), further research is needed to understand the potential future distribution of this invasive tree fern in its invaded range. We consider two southern hemisphere regions: the Garden Route region of South Africa and La Réunion Island in the Mascarene Archipelago in the eastern Indian Ocean. Both regions have a high native biodiversity but are heavily invaded (Baret et al., 2006; Fenouillas et al., 2021; van Wilgen et al., 2023); both regions are also listed in the top ten most invaded regions globally (Turbelin et al., 2017). The Garden Route and La Réunion Island both contain large, formally protected areas which are rich in native biodiversity and are therefore global priorities for conservation and priority sites for invasive species management (Myers et al., 2000).

Invasions of *S. cooperi* have been noted both in, and outside the protected areas of the Garden Route and La Réunion Island. Therefore, it is vital to investigate the environmental niche of the species to provide a better understanding of its current and potential future distribution under climate change. Such information can support evidence-based management in and around protected areas where the spread of *S. cooperi* should be prevented or controlled. Accordingly, this study aimed to (1) determine the environmental niche of *S. cooperi* using its native and invaded ranges, and (2) predict its potential future distribution in the Garden Route and on La Réunion Island under future climate scenarios. Due to the wide tolerance of *S. cooperi* to both temperature and precipitation, we hypothesise that its invaded range will expand into areas that are predicted to become warmer and wetter under future climatic conditions.

2. Material and methods

2.1. Study regions

The Garden Route (23 331 km^2) is located on the southern coast of South Africa (Fig. 1). Mean annual rainfall varies (800–1100 mm) from east to west with the eastern side and higher elevations having higher rainfall (Baard and Kraaij, 2014). Temperatures are mild year-round (18–25 °C) due to the warming effect of the Agulhas current (Baard and Kraaij, 2014). La Réunion Island (2 512 km^2), part of the Mascarene Archipelago in the Indian Ocean (Fig. 1), has a warm climate also attributable to the surrounding warm ocean. The mean annual rainfall differs between the eastern and western sides of the island (500–5000 mm) due to the varied topography. The mean annual temperature ranges from 12 °C to 24 °C, depending on elevation (Jumeaux et al., 2011).

Both South Africa and La Réunion Island are high-biodiversity areas. The Garden Route encompasses the UNESCO Garden Route Biosphere Reserve which includes the Garden Route National Park (UNESCO, 2019) while La Réunion Island contains Réunion National Park and is part of the Western Indian Ocean Biodiversity hotpot (Myers et al. 2000). Both regions contain important indigenous forests. Despite being important biodiversity areas, both regions have a long history of biological invasions (Baret et al. 2006; van Wilgen

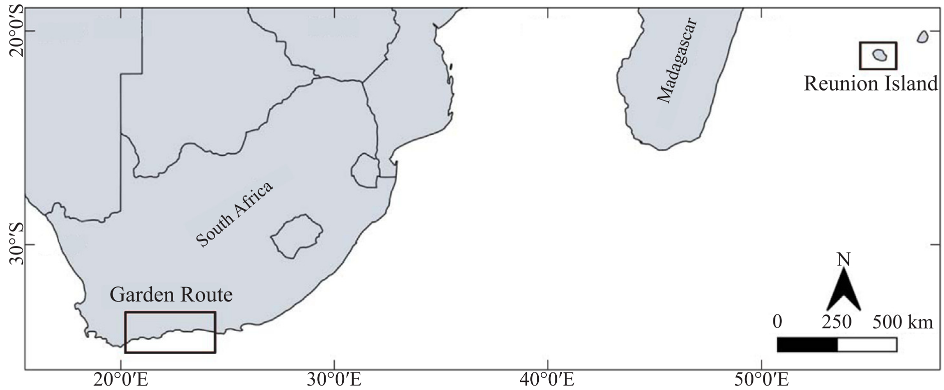

Fig. 1. Locations of the Garden Route in South Africa and La Réunion Island, Mascarene Archipelago, southern Indian Ocean.

et al. 2023) with both appearing on the top ten list of most invaded countries/territories globally (Turbelin et al. 2017).

2.2. Study species

The Australian tree fern (*Sphaeropteris cooperi* (Hook. ex F.Muell.) R.M.Tryon) is native to eastern Australia. Its taxonomy has been revised several times (Smith et al., 2006; Korall et al., 2007; Christenhusz and Chase, 2014; Schuettpelz et al., 2016) with synonyms including *Cyathea cooperi* (Hook. ex F.Muell.) Domin. and *Alsophila cooperi* F.Muell. all being used as accepted names over time. All species in the order Cyatheales are commonly referred to as 'tree ferns' due to their arborescent growth habit. *Sphaeropteris cooperi* is identified by the hairy reddish scales on the underside of the fronds and on the stem (caudex) (Crouch et al., 2011). The species tolerates a wide range of habitats; it grows in partial sun or shaded areas at altitudes ranging from 200 to 1000 m above sea level (Anderson et al., 1992; Durand and Goldstein, 2001b; Crouch et al., 2011).

2.3. Occurrence data processing

Occurrence data was obtained from the Global Biodiversity Information Facility (GBIF, 2024 GBIF Occurrence Download https://doi.org/10.15468/dl.rzw74k) by searching for "*Sphaeropteris cooperi* R.M. Tryon" which automatically includes ten recognised synonyms (Supplementary Table S1). Several exclusion criteria were applied: geospatial issues, absences, and fossil specimens. This resulted in 3 665 occurrence points. Records with an uncertainty of >25 000 m and records without an uncertainty measure were excluded (*n* = 549). To prevent false positives resulting from data derived from large databases (Maldonado et al., 2015), the occurrence data were cleaned using the R package *CoordinateCleaner* (Zizka et al., 2019, version 3.0.1) in R (R Core Team, 2024, version 4.3.3). Problems with locality data resulting from erroneous conversions between coordinate systems, rasterised data, and coordinates corresponding to country capitals, country centres, GBIF headquarters, and various botanical institutions were resolved by deleting spurious records. Records of planted ferns were removed after manually inspecting images associated with the records. These records were excluded because conditions for planted specimens are anthropogenically altered through gardening practices such as fertilizing, irrigation, protection from frost, and removal of competing vegetation.

The cleaned GBIF occurrence data were further supplemented by including records obtained from datasets of the *Conservatoire Botanique National de Mascarin* (Fenouillas et al., 2021) which were collected during surveys of alien plant species on La Réunion Island. These data were cleaned following the same methods applied to the GBIF data. Finally, the full dataset was spatially thinned to 1 km apart replicated 1000 times using the R package *spThin* (Aiello–Lammens et al., 2015, version 2.10-0) to reduce redundancy and the effects of sampling bias. The final number of occurrence points used for modelling was 1281.

2.4. Environmental predictors

2.4.1. Source of climate data

Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA) was chosen as the source of climate data (Karger et al., 2021) since it characterises precipitation patterns more accurately than WorldClim and shows improved predictive power (Bobrowski and Schickhoff, 2017; Karger et al., 2017).

2.4.2. Climatic variables

The climatic niche of scaly tree ferns has been shown to be predominantly characterised by high rainfall with little rainfall seasonality and minimum temperatures rarely dropping below freezing (Bickford and Laffan, 2006; Bystriakova et al., 2010; Kessler, 2010; McCulloch-Jones et al., 2023). As such and following McCulloch-Jones et al. (2023), annual mean temperature (BIO 1), temperature seasonality (BIO 4), mean temperature of the warmest quarter (BIO 10), mean temperature of the coldest quarter (BIO 11), precipitation seasonality (BIO 15), precipitation of the wettest quarter (BIO 16), and precipitation of the driest quarter (BIO 17) were chosen for inclusion in the modelling process. These variables were extracted from CHELSA at a resolution of 30 arc seconds (~1 km).

2.4.3. Current and future climatic conditions

Current climatic data used extended from 1981 to 2010. Five global climate models (GCMs) were downloaded from CHELSA and used to predict future climatic suitability for *S. cooperi* in the Garden Route and on La Réunion: GFDL-ESM4 (Dunne et al., 2020), IPSL-CM6A-LR (Boucher et al., 2020), MPI-ESM1-2-HR (Müller et al., 2018), MRI-ESM2-0 (Yukimoto et al., 2019), and UKESM1-0-LL (Mulcahy et al., 2022). The future projections were based on an optimistic (SSP1, Representative Concentration Pathway (RCP) 2.6) and pessimistic (SSP5, RCP 8.5) scenario for the near (2041–2070) and far future (2071–2100). The optimistic scenario assumes CO_2 emissions will remain constant until 2050 whereas the pessimistic scenario assumes that the current CO_2 emissions will double by 2050 (IPCC, 2023).

2.5. Niche dynamics

Species distribution models (SDMs) assume niche conservatism between input and modelled ranges (Wiens and Graham, 2005). This may be problematic for invasive species as they might not yet be at equilibrium (occur in all suitable climatic conditions) in their invaded range (Peterson and Vieglais, 2001). This drawback can be addressed by considering niche changes from native to invaded ranges (Liu et al., 2022). In this study, the R package *ecospat* was used to analyse ecological niche shift (di Cola et al., 2017, version 4.1.0). Specifically, the niche quantification tool was used to capture niche equivalency, similarity, and overlap between the native and invaded (southern hemisphere) regions of *S. cooperi*. Niche equivalency is used as a measure of niche overlap where occurrences from both ranges are randomly reallocated; niche similarity provides an indication of when niches were more similar than expected by chance (Warren et al., 2008). Niche overlap was determined using Schoener's statistic for niche overlap (D-index; Schoener, 1968) and Warren's similarity statistic (I-index; Warren et al., 2008) which both range from no overlap (0) to complete overlap (1).

$$D(p_x,\ p_y) = 1 - \frac{1}{2}\sum_i |p_{x,i} - p_{y,i}|, \tag{1}$$

$$I(p_x,\ p_y) = 1 - \frac{1}{2}H(p_x,\ p_y), \tag{2}$$

where p_x (or p_y) is the probability assigned by the model for population x (or y), $p_{x,i}$ (or $p_{y,i}$) is the probability assigned by the model for population x (or y) in cell i, and H is Hellinger's distance (van der Vaart, 2000):

$$H(p_x,\ p_y) = \sqrt{\sum_i \left(\sqrt{p_{x,i}} - \sqrt{p_{y,i}}\right)^2} \tag{3}$$

Overlap was further investigated by considering niche expansion, stability, and unfilling. Niche expansion refers to the species expanding to new environments in its invaded range, stability refers to the species occupying the same environments in its native and invaded ranges, and unfilling refers to the species only filling a portion of the niche in the invaded range (Pearman et al., 2008; Strubbe et al., 2013). Niches were further analysed using Principal Component Analysis (PCA) to compare niches in native and invaded ranges.

2.6. Species distribution modelling

This study applied an ensemble approach using the R package *biomod2* (Thuiller et al., 2009, version 4.2-5–2). Random pseudo-absences were created in *biomod2* such that there were equal numbers of occurrence and pseudo-absence points (Barbet-Massin et al., 2012). Pseudo-absence runs were generated three times and then averaged with different points to improve model fit (Barbet-Massin et al., 2012). The algorithms used were artificial neural networks (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalised additive models (GAM), generalised boosted regression models (GBM), generalised linear models (GLM), multivariate adaptive regression splines (MARS), maximum entropy (MaxEnt), random forests (RF), species range envelopes (SRE), and extreme gradient boosting (XGBoost). Algorithms were cross validated using a block approach (Roberts et al., 2017, Supplementary Fig. S1). Since algorithms are sensitive to input hyper parameters (Hallgren et al., 2019), the *biomod2* tuning function was used to select the optimal parameter combinations. The best performing models were chosen according to the true skill statistic (TSS), and the sensitivity and specificity values (Table S2). Response curves are given per model in the supplementary material (Figs. S2, S3). The ensemble model was created by weighting the contribution of each individual model to the final output based on accuracy.

3. Results

3.1. Niche dynamics

3.1.1. Garden Route (invaded range) and Australia (native range)

The assessment of the invaded Garden Route niche showed some overlap with the native range of *S. cooperi* (17.57 % overlap according to the D-index and 39.44 % overlap according to the I-index; Figs. 2, S4, S5). The native Australian and invaded Garden Route niches were statistically equivalent (D: p = 0.5445; I: p = 0.2178) indicating that there was higher observed overlap than was expected by chance, with lower expansion and higher stability (D: p = 0.0198; I: p = 0.0199). The native range occupied the largest area in the PCA space indicating that the species occupied a wider range of climatic conditions in Australia when compared to the Garden Route (unfilling = 45.59 %, p = 0.0099).

3.1.2. La Réunion Island (invaded range) and Australia (native range)

The ecological niche of the species in the invaded La Réunion range exhibited limited overlap with its native Australian range (3.74 % overlap according to the D-index and 8.74 % overlap according to the I-index; Figs. 3, S4, S5), indicating that the environmental conditions occupied in La Réunion are quite different from those in Australia. However, niche equivalency tests showed no significant difference between the native and invaded niches (D: p = 0.5941, I: p = 0.2178), suggesting that despite the low overlap, the species in La Réunion occupies an environmental niche that is not significantly different from its native range. Niche similarity analysis supported this,

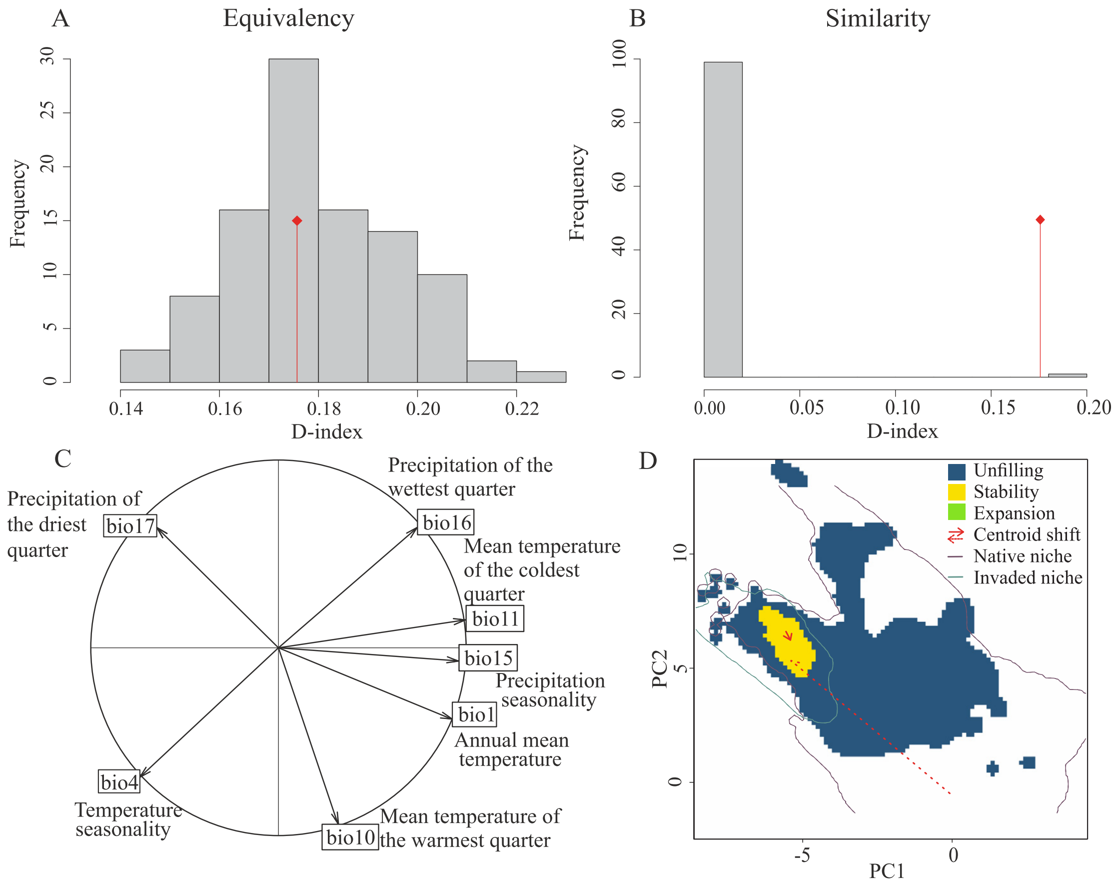

Fig. 2. The (A) equivalency (p = 0.5446) and (B) similarity (p = 0.0198) between Australia and the Garden Route niches of *Sphaeropteris cooperi*. The specific D-index (D = 0.1757) is indicated by the red line. (C) The correlation circle indicates that 92.18 % of the variance of the bioclimatic variables can be explained (axis 1 explains 60.1 % and axis 2 explains 32.08 % of the variance). (D) The PCA indicating the niche dynamics of unfilled, stable, and expanded niches are represented by blue, yellow, and green (not present), respectively. The grey shading shows the smoothed occurrence density with the red arrows indicating centroid shift in each niche (solid invaded, dashed native). The solid lines indicate the available suitable climate in each range.

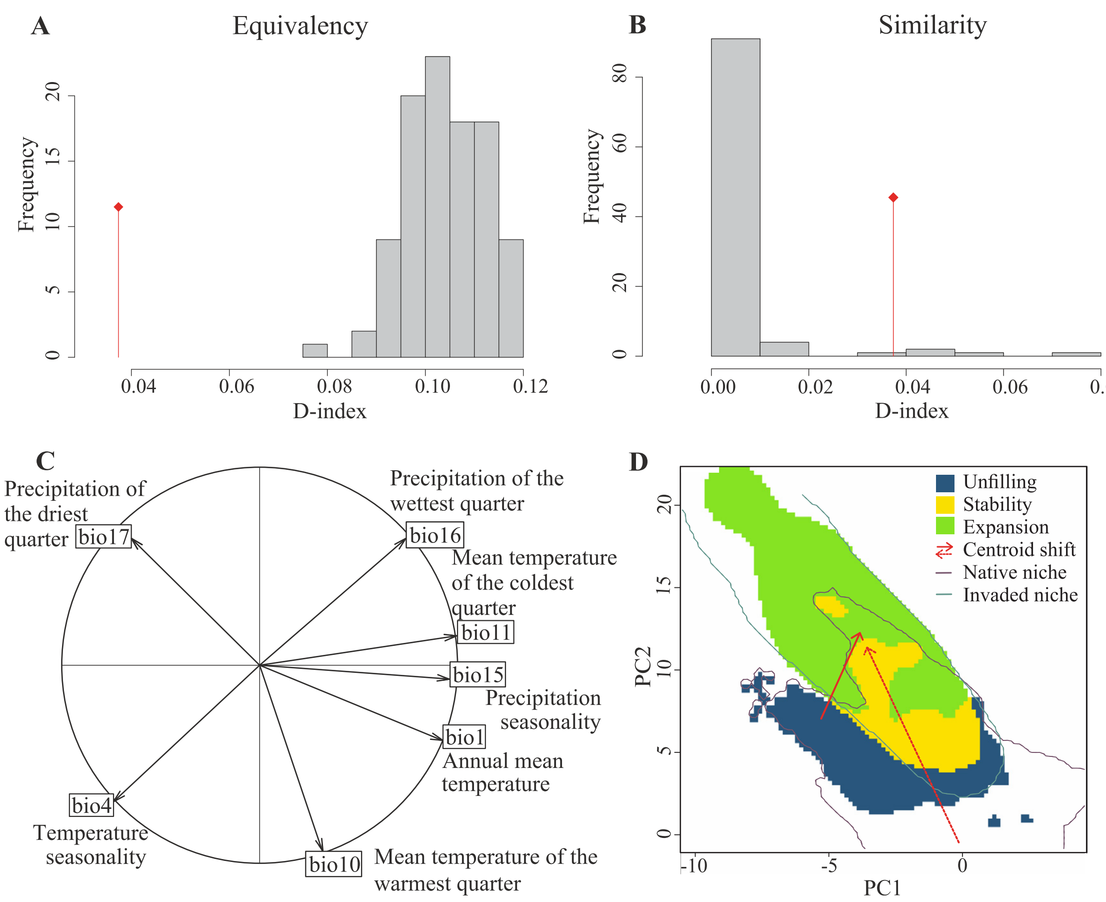

Fig. 3. The (A) equivalency (p = 1) and (B) similarity (p = 0.0495) between Australia and the La Réunion Island niches of *Sphaeropteris cooperi*. The specific D-index (D = 0.0374) is indicated by the red line. (C) The correlation circle indicates that 91.63 % of the variance of the bioclimatic variables can be explained (axis 1 explains 59.47 % and axis 2 explains 32.16 % of the variance). (D) PCA indicating the niche dynamics of unfilled, stable, and expanded niches are represented by blue, yellow, and green, respectively. The grey shading shows the smoothed occurrence density with the red arrows indicating centroid shift in each niche (solid invaded, dashed native). The solid lines indicate the available suitable climate in each range.

with borderline significant similarity (D: p = 0.0495), indicating that the invaded La Réunion niche is more similar to the native Australian niche than expected by random chance, though not perfectly aligned.

Furthermore, the analysis revealed significant niche dynamics in the invaded range, with 43.15 % of the La Réunion niche representing new environmental conditions not found in the native range, indicating substantial niche expansion (p = 0.0099). This suggests the species is adapting to novel environments in La Réunion. However, 56.85 % of the La Réunion niche remains consistent with the native range, reflecting significant stability (p = 0.0099) in its ecological preferences. Additionally, 13.74 % of the species' native niche remains unoccupied in the invaded range, indicating some degree of niche unfilling (p = 0.0099). Overall, these results suggest that while the species is adapting to new conditions in La Réunion, it is also maintaining its core ecological requirements from its native range, demonstrating both flexibility and niche conservation in the invaded range.

3.2. *Species distribution modelling*

3.2.1. *Model performance*

The individual models had varying levels of accuracy, but all the models performed relatively well overall (TSS > 79 %, Fig. S6). GBM and RF outperformed all remaining models (sensitivity and specificity >99 %) with a small standard deviation. MaxEnt was the worst performing model (sensitivity = 84.21 %; specificity = 79.77 %) with a large standard deviation indicating much variation between runs. ANN also had large standard deviation and a large difference between sensitivity (96.90 %) and specificity (87.27 %). Species range envelopes (SRE) showed high specificity but low sensitivity (sensitivity = 79.95 %; specificity = 98.72 %) indicating that it had a poor ability to predict true positives (species occurrences). In contrast, the ensemble model had relatively high model performance (sensitivity = 98.97 %; specificity = 96.68 %).

3.2.2. *Current suitable climate*

The projected current distribution of *S. cooperi* indicates that large parts of both the Garden Route and La Réunion Island have high climate suitability for this tree fern. Areas with low suitability generally occur where there is a high topographical complexity (i.e., mountainous areas) or at higher elevations (Fig. 4).

3.2.3. *Projected species range change*

For all global climate models, the extent of the projected range change for *S. cooperi* between the current and future projections was determined for both the near future (2041–2070) and far future (2071–2100). This was done for both an optimistic scenario (SSP1-2.6) and pessimistic scenario (SSP 5-8.5). For most models, most of the Garden Route remained suitable for *S cooperi* despite some decline in species range, although the extent of the decline differed with time and scenario (Figs. 5, 6; Tables S3, S4). Overall, the net species range is predicted to shrink under all global climate models. The only exception is under the optimistic scenario in the far future for the climate model MRI-ESM2-0; however, this is a small projected expansion (Garden Route: 0.168 %, La Réunion: 5.616 %). Despite an overall loss in range, there are areas of localised expansion in both

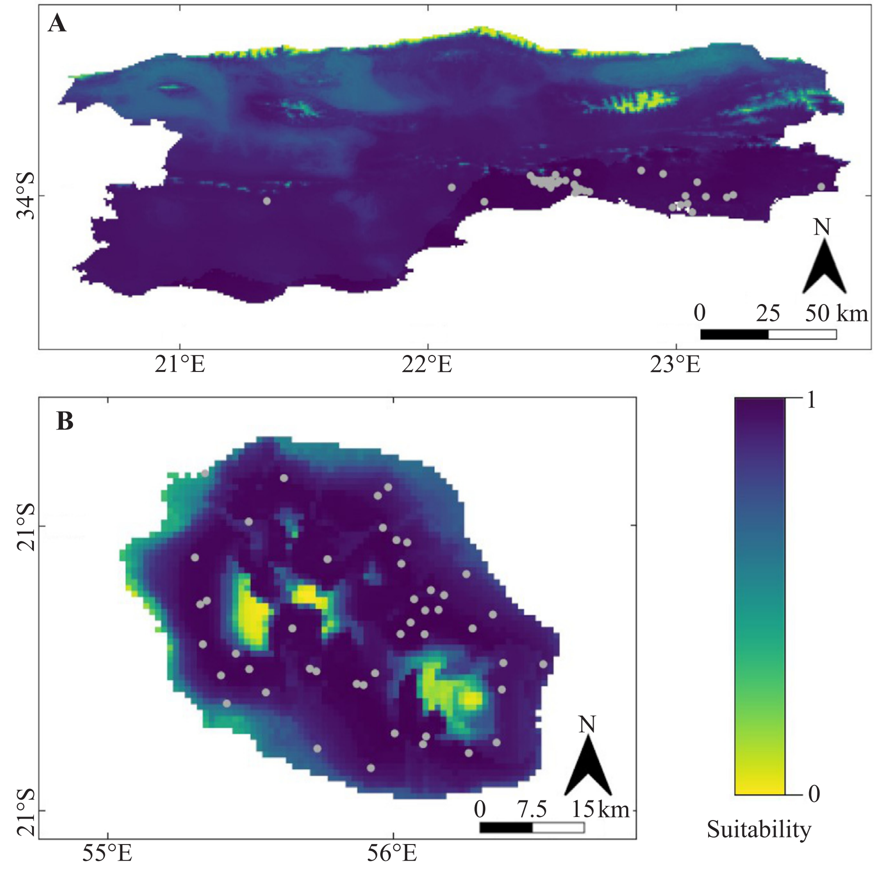

Fig. 4. Results of the ensemble model showing the climatic suitability of *Sphaeropteris cooperi* under current climatic conditions in (A) the Garden Route and on (B) La Réunion Island. A darker colour and a value closer to one, indicates a more suitable climate while a lighter colour and a value closer to zero, indicates a less suitable climate. The current occurrence data are indicated by the grey dots.

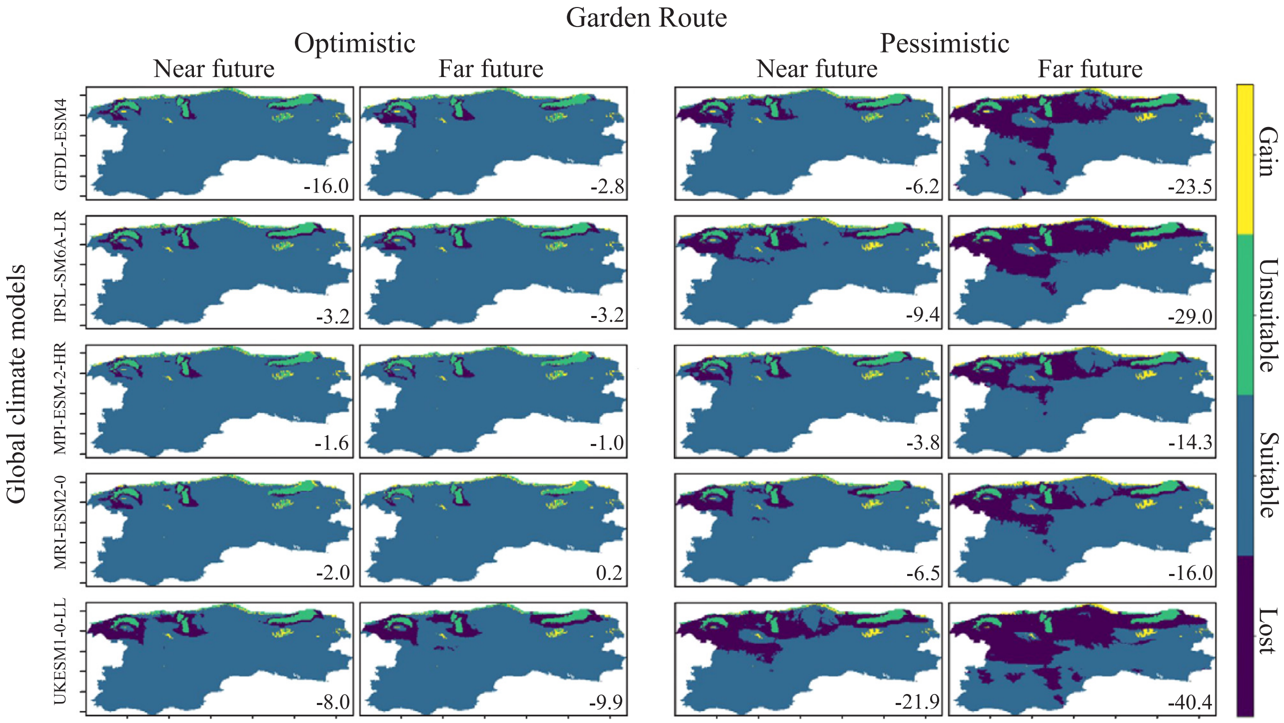

Fig. 5. The overall change in the range of *Sphaeropteris cooperi* for the Garden Route for all global climate models. Top to bottom: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM-2-HR, MRI-ESM2-0, and UKESM1-0-LL. Future climate scenarios are listed left to right with the optimistic (SSP1-2.6) and pessimistic scenarios (SSP5-8.5) in the near (2041–2070) and far (2071–2100) future. Colours indicate the gain (yellow), unsuitable (green), suitable (blue), and loss (purple) of areas climatically suitable for *S cooperi*. Species range change values are given in the bottom right corner of each map, indicating net gain (positive) or net loss (negative) in percent.

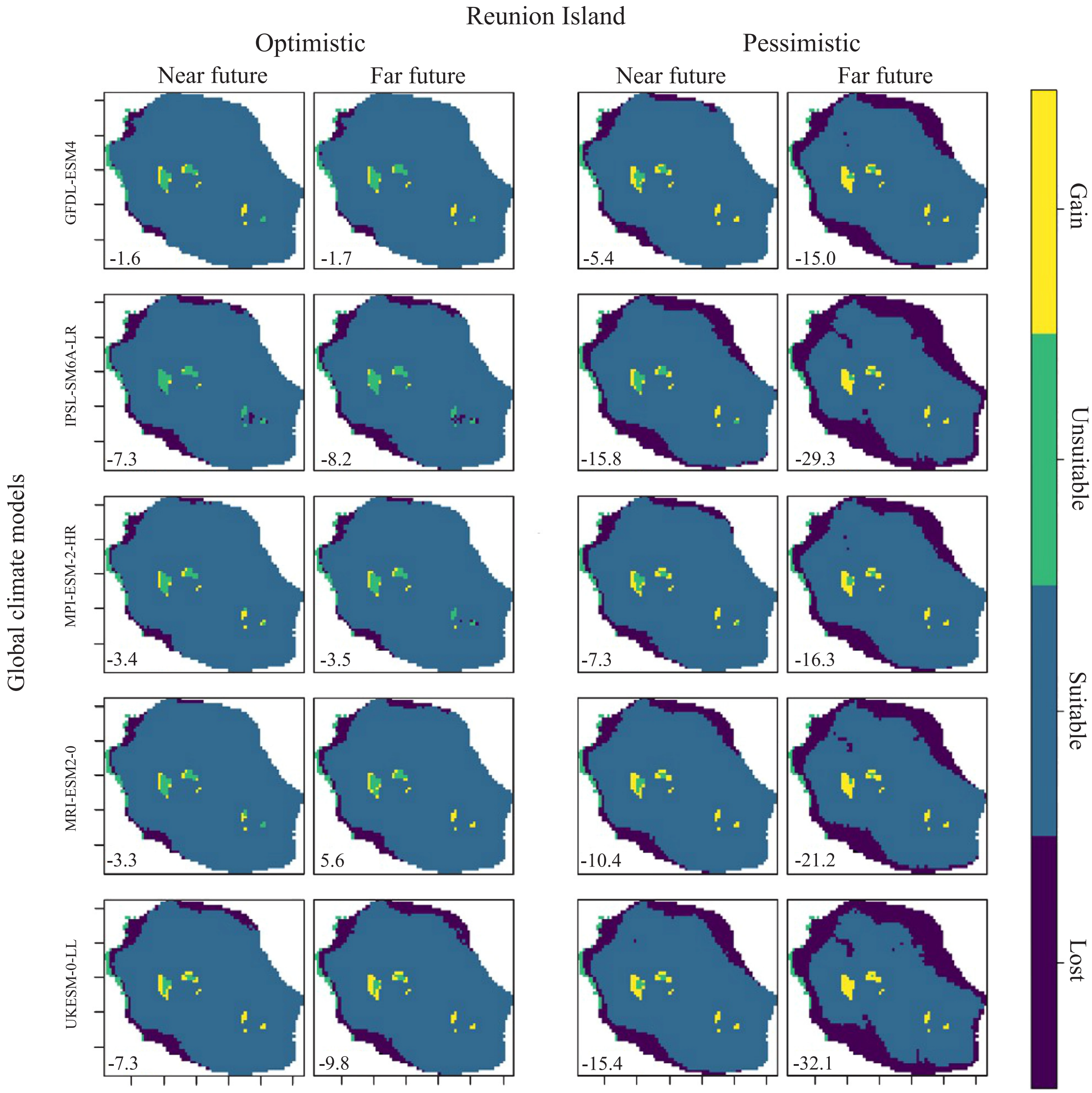

Fig. 6. The overall range change of *Sphaeropteris cooperi* for La Réunion Island for all global climate models. Top to bottom: GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM-2-HR, MRI-ESM2-0, and UKESM1-0-LL. Future climate scenarios are listed left to right with the optimistic (SSP1-2.6) and pessimistic scenarios (SSP5-8.5) in the near (2041−2070) and far (2071−2100) future. Colours indicate the gain (yellow), unsuitable (green), suitable (blue), and loss (purple) of areas climatically suitable for *S. cooperi*. Species range change values are given in the bottom right corner of each map, indicating net gain (positive) or net loss (negative) in percent.

regions, particularly in the north of the Garden Route and towards the centre of La Réunion Island.

4. Discussion

Sphaeropteris cooperi is an invasive tree fern that can outcompete native tree ferns, alter nutrient cycling, soil composition, and species assemblages (Durand and Goldstein, 2001a,b; Medeiros et al., 1993; Robinson et al., 2010; Chau et al., 2012). Therefore, understanding how the range of *S. cooperi* may change with a changing climate is important for informing management practices, especially in biodiversity hotspots. This study found that *S. cooperi* already occurs in almost all areas that are predicted to be suitable under current climatic conditions in the Garden Route. However, on La Réunion Island, the opposite is true with a relatively wide climatically suitable area not yet occupied by the species. This implies that *S. cooperi* has the potential to spread further on La Réunion Island under current conditions. However, in the near and far future, the species distribution models over both the invaded southern hemisphere regions suggest that the climatically suitable area for the species is likely to shrink under both optimistic and pessimistic climate change scenarios. These outcomes, likely driven by increased temperature and reduced precipitation, are in contrast to our original hypothesis.

With climate change accelerating and projected to become more severe (Lee and Romero, 2023), it is important to assess how invasive species will respond, especially as each invasion is context dependent. *Sphaeropteris cooperi* was presumably introduced to the Garden Route and La Réunion Island for ornamental horticulture (McCulloch-Jones et al., 2021) and has since spread widely within these regions (Baret et al., 2006; Baard and Kraaij, 2014; Fenouillas et al., 2021). Its current suitable climate extends towards the coastal areas of both the Garden Route and La Réunion Island with less suitable areas in the north for the Garden Route and in the centre of the island for La Réunion. The less suitable areas are predicted to increase in all five global climate models (GCMs) and under all climate change scenarios. Based on the expected range retraction, active management of this species is not recommended. However, due to the popularity of the species as an ornamental plant, areas with high anthropogenic activity (Vromans et al., 2010; Dupuy et al., 2020) may be most at risk of new invasive populations of *S. cooperi* establishing. Education drives could be a useful approach to minimising this risk, especially in communities living close to protected areas. In particular, labels indicating the risk posed by ornamental alien species sold in nurseries, can be an effective management technique (Humair et al., 2014). In the case of *S. cooperi*, such labels should highlight the risk associated with the large quantities of spores produced by this species (Durand and Goldstein, 2001a) and the fact that these can be widely spread by wind.

Niche dynamics are an important aspect to consider when predicting invasive species ranges, since they may indicate how adaptable a species is to different environmental niches. This study found that *S. cooperi* in the Garden Route has a broad overlap with its native range. The niche overlap is higher for the Garden Route than La Réunion, but neither is >50 %. This may indicate that *S. cooperi* is not present in all suitable climatic areas in the Garden Route. This could be because of dispersal barriers such as a lack of source populations or spores landing in unfavourable conditions for either the gametophyte or the sporophyte to establish (Schaefer, 2011). For La Réunion Island, there was less overlap with the native range and considerable expansion into niches that are not found in Australia. This could be due to factors in its native range that constrain the fundamental niche of this species and result in a compromised realised niche. For instance, tree ferns in Australia are eaten by deer which can prevent them from reaching maturity (Bennett, 2023), ultimately leading to unfilled niches in the native range and less overlap between native and invaded ranges. This highlights that biotic interactions such as herbivory, competition (or lack thereof) may be excluding *S. cooperi* from some climatically suitable niches.

While *S. cooperi* may be adapted to disturbed habitats (Durand and Goldstein 2001a, b; Chau et al., 2012; Jones et al., 2019), it may not be as well adapted to a rapidly changing climate. For example, Daley (1983) found that brief elevated temperatures caused chlorosis then senescence in developing fronds, which may reduce the overall number of fronds that reach maturity and produce viable spores. However, the response of mature fronds to heat stress remains unexplored, especially in relation to the combined effects of changes in temperature and precipitation. Future work investigating these aspects of *S. cooperi* physiology would help to build a more comprehensive understanding of how this species may respond to future climate change. Nonetheless, the predictions of a declining range for *S. cooperi* in response to climate change are aligned with predictions that native tree fern richness will decrease in Brazil over the next 30 years due to climate change (de Gasper et al., 2021).

Efforts to manage *S. cooperi* in South Africa's Garden Route and on La Réunion Island should focus primarily on preventing invasions in protected areas. Since *S. cooperi* is widely grown in urban gardens in both regions, highly populated areas around protected areas may act as sources of propagules to launch invasions (McLean et al., 2017), especially as topographically complex area such as Garden Route National Park and Réunion National Park may provide suitable microhabitats for *S. cooperi* establishment and persistence (Kessler, 2010). This highlights the need for education drives that target communities in areas surrounding vulnerable protected areas.

Sphaeropteris cooperi is invasive in the Garden Route and on La Réunion Island where its potential negative effects, particularly on native tree ferns, have not yet been fully investigated. The niche dynamics of this species indicate that its niche is not stable, and the species could spread into unfilled climatic niches, especially on La Réunion Island. However, future climate change is expected to reduce the area of suitable conditions and restrict this species range in these biodiversity hotspots.

Funding

This work was supported by the research chair "Managing invasions in protected areas" held by TBR. This work was also supported by the European Union: Agricultural Fund for Rural Development (EAFRD), by the Conseil Départemental de La Réunion and by the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD).

Data statement

Data and associated code are available on Zenodo (https://zenodo.org/records/13884223).

Declaration of competing interest

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

CRediT authorship contribution statement

Megan L. van den Berg: Writing – original draft, Visualization, Methodology, Conceptualization. **Geethen Singh:** Writing – review & editing, Methodology. **Emily J. McCulloch-Jones:** Writing – review & editing, Conceptualization. **Mathieu Rouget:** Writing – review & editing, Methodology, Conceptualization. **David M. Richardson:** Writing – review & editing, Conceptualization. **Tamara B. Robinson:** Writing – review & editing, Funding acquisition, Conceptualization.

Acknowledgements

MLB gratefully acknowledges the Stellenbosch University Postgraduate Scholarship Programme for enabling her to complete this work. MLB also thanks Christopher Barnard for his input on the technical aspects of modelling. We thank two anonymous reviewers who helped to improve this work.

Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.sajb.2025.01.046.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B., Anderson, R.P., 2015. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38, 541–545. https://doi.org/10.1111/ecog.01132 version 2.10-0.

Akomolafe, G.F., Rahmad, Z.B., 2018. A review on global ferns invasions: mechanisms, management and control. J. Res. For. Wildl. Environ. 10, 42–54. http://www.ajol.info/index.php/jrfwe.

Anderson, S.J., Stone, C.P., Higashino, P.K., 1992. Distribution and spread of alien plants in Kipahulu Valley, Haleakala National Park, above 2,300 ft elevation. In: Stone, C.P., Smith, C.W., Tunison, J.T. (Eds.), Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. University of Hawaii Press, Honolulu.

Ángel-Vallejo, M.C., Aguirre-Acosta, N., Rodríguez-Rey, G.T., García-Marín, E.J., Álvarez-Mejía, L.M., Feuillet-Hurtado, C., 2024. Distribution models in invasive plants with climatic niche expansion: a case study of *Ulex europaeus* L. in Colombian Andes. Biol. Invasions 26, 1919–1930. https://doi.org/10.1007/s10530-024-03285-7.

Arosa, M.L., Ceia, R.S., Quintanilla, L.G., Ramos, J.A., 2012. The tree fern *Dicksonia antarctica* invades two habitats of European conservation priority in São Miguel Island. Azores. Biol. Invasions 14, 1317–1323. https://doi.org/10.1007/s10530-011-0166-9.

Baard, J.A., Kraaij, T., 2014. Alien flora of the Garden Route National Park, South Africa. S. Afr. J. Bot. 94, 51–63. https://doi.org/10.1016/j.sajb.2014.05.010.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Baret, S., Rouget, M., Richardson, D.M., Lavergne, C., Egoh, B., Dupont, J., Strasberg, D., 2006. Current distribution and potential extent of the most invasive alien plant species on La Reunion (Indian Ocean, Mascarene Islands). Ecol. Soc. Aust. 31, 747–758. https://doi.org/10.1111/j.1442-9993.2006.01636.x.

Bates, O.K., Bertelsmeier, C., 2021. Climatic niche shifts in introduced species. Curr. Biol. 31, R1252–R1266. https://doi.org/10.1016/j.cub.2021.08.035.

Bennett, A., 2023. Assessment of tree fern browsing by introduced Sambar Deer in south-eastern Australia. Ecol. Manage. Restor. 24, 137–144. https://doi.org/10.1111/emr.12582.

Bezeng, B.S., Morales-Castilla, I., van der Bank, M., Yessoufou, K., Daru, B.H., Davies, T.J., 2017. Climate change may reduce the spread of non-native species. Ecosphere 8, e01694. https://doi.org/10.1002/ecs2.1694.

Bickford, S.A., Laffan, S.W., 2006. Multi-extent analysis of the relationship between pteridophyte species richness and climate. Glob. Ecol. Biogeogr. 15, 588–601. https://doi.org/10.1111/j.1466-8238.2006.00250.x.

Bobrowski, M., Schickhoff, U., 2017. Why input matters: selection of climate data sets for modelling the potential distribution of a treeline species in the Himalayan region. Ecol. Model. 359, 92–102. https://doi.org/10.1016/j.ecolmodel.2017.05.021.

Boucher, O., Servonnat, J., Albright, A.L., Aumont, O., Balkanski, Y., Bastrikov, V., Bekki, S., Bonnet, R., Bony, S., Bopp, L., Braconnot, P., 2020. Presentation and evaluation of the IPSL-CM6A-LR climate model. J. Adv. Model. Earth Syst. 12, e2019MS002010. https://doi.org/10.1029/2019MS002010.

Bradley, B.A., Wilcove, D.S., Oppenheimer, M., 2009. Climate change increases risk of plant invasion in the Eastern United States. Biol. Invasions 12, 1855–1872. https://doi.org/10.1007/s10530-009-9597-y.

Bradley, B.A., Blumenthal, D.M., Wilcove, D.S., Ziska, L.H., 2010. Predicting plant invasions in an era of global change. Trends Ecol. Evol. 25, 310–318. https://doi.org/10.1016/j.tree.2009.12.003.

Bystriakova, N., Schneider, H., Coomes, D., 2010. Evolution of the climatic niche in scaly tree ferns (Cyatheaceae, Polypodiopsida). Bot. J. Linn. Soc. 165, 1–19. https://doi.org/10.1111/j.1095-8339.2010.01092.x.

Chai, S.L., Zhang, J., Nixon, A., Nielsen, S., 2016. Using risk assessment and habitat suitability models to prioritise invasive species for management in a changing climate. PLoS One 11, e0165292. https://doi.org/10.1371/journal.pone.0165292.

Chau, M.M., Walker, L.R., Mehltreter, K., 2012. An invasive tree fern alters soil and plant nutrient dynamics in Hawaii. Biol. Invasions 15, 355–370. https://doi.org/10.1007/s10530-0120291-0.

Christenhusz, M.J.M., Chase, M.W., 2014. Trends and concepts in fern classification. Ann. Bot. 113, 571–594. https://doi.org/10.1093/aob/mct299.

Crouch, N., Klopper, R., Burrows, J., Burrows, S., 2011. Ferns of Southern Africa: A Comprehensive Guide. Struik Nature, Cape Town.

Cuthbert, R.N., Diagne, C., Hudgins, E.J., Turbelin, A., Ahmed, D.A., Albert, C., Bodey, T.W., Briski, E., Essl, F., Haubrock, P.J., Gozlan, R.E., 2022. Biological invasion costs reveal insufficient proactive management worldwide. Sci. Total Environ. 819, 153404. https://doi.org/10.1016/j.scitotenv.2022.153404.

Daehler, C.C., 2009. Short lag times for invasive tropical plants: evidence from experimental plantings in Hawai'i. PLoS One 4, e4462. https://doi.org/10.1371/journal.pone.0004462.

Daley, D., 1983. Chlorosis in a tree fern (*Cyathea cooperi*) induced by brief heat stress. Aust. J. Bot. 31, 23–33. https://doi.org/10.1071/BT9830023.

de Gasper, A.L., Grittz, G.S., Russi, C.H., Schwartz, C.E., Rodrigues, A.V., 2021. Expected impacts of climate change on tree ferns distribution and diversity patterns in subtropical Atlantic Forest. Perspect. Ecol. Conserv. 19, 369–378. https://doi.org/10.1016/j.pecon.2021.03.007.

di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F.T., d'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., 2017. ecospat: an R package to support spatial analyses and modelling of species niches and distributions. Ecography 40,. https://doi.org/10.1111/ecog.02671 version 4.1.0.

Dunne, J.P., Horowitz, L.W., Adcroft, A.J., Ginoux, P., Held, I.M., John, J.G., Krasting, J.P., Malyshev, S., Naik, V., Paulot, F., Shevliakova, E., 2020. The GFDL Earth System Model version 4.1 (GFDL-ESM 4.1): overall coupled model description and simulation characteristics. J. Adv. Model. Earth Syst. 12, e2019MS002015.

Dupuy, S., Gaetano, R., Le Mézo, L., 2020. Mapping land cover on Reunion Island in 2017 using satellite imagery and geospatial ground data. Data Br. 28, 104934. https://doi.org/10.1016/j.dib.2019.104934.

Durand, L., Goldstein, G., 2001a. Growth, leaf characteristics, and spore production in native and invasive tree ferns in Hawaii. Am. Fern J. 91, 25–35. https://doi.org/10.1640/0002-8444(2001)091[0025:GLCASP]2.0.CO;2.

Durand, L., Goldstein, G., 2001b. Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126, 345–354. https://doi.org/10.1007/s004420000535.

Essl, F., Lenzner, B., Bacher, S., Bailey, S., Capinha, C., Daehler, C., Dullinger, S., Genovesi, P., Hui, C., Hulme, P.E., Jeschke, J.M., 2020. Drivers of future alien species impacts: an expert-based assessment. Glob. Change Biol. 26, 4880–4893. https://doi.org/10.1111/gcb.15199.

Fenouillas, P., Ah-Peng, C., Amy, E., Bracco, I., Dafreville, S., Gosset, M., Ingrassia, F., Lavergne, C., Lequette, B., Notter, J.C., Pausé, J.M., 2021. Quantifying invasion degree by alien plants species in Reunion Island. Austral. Ecol. 46, 1025–1037. https://doi.org/10.1111/aec.13048.

GBIF.org (16 February 2024) GBIF occurrence download https://doi.org/10.15468/dl.rzw74k

Hallgren, W., Santana, F., Low-Choy, S., Zhao, Y., Mackey, B., 2019. Species distribution models can be highly sensitive to algorithm configuration. Ecol. Model. 408, 108719. https://doi.org/10.1016/j.ecolmodel.2019.108719.

Heshmati, I., Khorasani, N., Shams-Esfandabad, B., Riazi, B., 2019. Forthcoming risk of *Prosopis juliflora* global invasion triggered by climate change: implications for environmental monitoring and risk assessment. Environ. Monit. Assess. 191, 72. https://doi.org/10.1007/s10661-018-7154-9.

Hoveka, L., Bezeng, B., Yessoufou, K., Boatwright, J., Bank, M., 2016. Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa. S. Afr. J. Bot. 102, 33–38. https://doi.org/10.1016/J.SAJB.2015.07.017.

Humair, F., Siegrist, M., Kueffer, C., 2014. Working with the horticultural industry to limit invasion risks: the Swiss experience. EPPO Bull. 44, 232–238. https://doi.org/10.1111/epp.12113.

Jones, E.J., Kraaij, T., Fritz, H., Moodley, D., 2019. A global assessment of terrestrial alien ferns (Polypodiophyta): species' traits as drivers of naturalisation and invasion. Biol. Invasions 21, 861–873. https://doi.org/10.1007/s10530-018-1866-1.

Jones, E.J., Kraaij, T., Guerbois, C., Moodley, D., 2020. An assessment of the invasion status of terrestrial alien ferns (Polypodiophyta) in South Africa. S. Afr. J. Bot. 131, 64–73. https://doi.org/10.1016/j.sajb.2020.02.008.

Jumeaux, G., Quetelard, H., Roy, D., 2011. *Météo France, Sainte-Clotilde, Réunion Atlas climatique de La Réunion*. 1−25.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the Earth's land surface areas. Sci. Data 4, 170122. https://doi.org/10.1038/sdata.2017.122.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2021. Climatologies at high resolution for the Earth's land surface areas. Environ. Data. https://doi.org/10.16904/envidat.228.v2.1.

Kessler, M., 2010. Biogeography of ferns. In: Mehltreter, K., Walker, L.R., Sharpe, J. (Eds.), Fern Ecology. Cambridge University Press, Cambridge, pp. 22–60. https://doi.org/10.1017/CBO9780511844898.003.

Kessler, M., Kluge, J., 2022. Mountain ferns: what determines their elevational ranges and how will they respond to climate change? Am. Fern J. 112, 285–302. https://doi.org/10.1640/0002-8444-112.4.285.

Kolanowska, M., Rewicz, A., Ackerman, J.D., 2024. Climate change will likely facilitate invasion of Asian orchid *Eulophia graminea* into new areas. Biol. Invasions 26, 1969–1983. https://doi.org/10.1007/s10530-024-03290-w.

Korall, P., Conant, D.S., Metzgar, J.S., Schneider, H., Pryer, K.M., 2007. A molecular phylogeny of scaly tree ferns (Cyatheaceae). Am. J. Bot. 94, 873–886. https://doi.org/10.3732/ajb.94.5.873.

Lee, H., Romero, J., 2023. Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel On Climate Change. IPCC, Geneva, Switzerland. https://doi.org/10.59327/IPCC/AR6-9789291691647.

Liu, C., Wolter, C., Courchamp, F., Roura-Pascual, N., Jeschke, J.M., 2022. Biological invasions reveal how niche change affects the transferability of species distribution models. Ecology 103, e3719. https://doi.org/10.1002/ecy.3719.

Loope, L., 2011. Hawaiian Islands: invasions. In: Simberloff, D., Rejmánek, M. (Eds.), Encyclopedia of Biological Invasions. University of California Press, Berkeley and Los Angeles, pp. 309–319.

Maldonado, C., Molina, C.I., Zizka, A., Persson, C., Taylor, C.M., Albán, J., Chilquillo, E., Rønsted, N., Antonelli, A., 2015. Estimating species diversity and distribution in the era of Big Data: to what extent can we trust public databases? Glob. Ecol. Biogeogr. 24, 973–984. https://doi.org/10.1111/geb.12326.

McCulloch-Jones, E., Kraaij, T., Crouch, N., Fritz, H., 2021. The effect of horticultural trade on establishment success in alien terrestrial true ferns (Polypodiophyta). Biol. Invasions 23, 3583–3596. https://doi.org/10.1007/s10530-021-02599-0.

McCulloch-Jones, E., Kraaij, T., Crouch, N., Faulkner, K.T., 2023. Assessing the invasion risk of traded alien ferns using species distribution models. NeoBiota 87, 161–189. https://doi.org/10.3897/neobiota.87.101104.

McLean, P., Gallien, L., Wilson, J.R., Gaertner, M., Richardson, D.M., 2017. Small urban centres as launching sites for plant invasions in natural areas: insights from South Africa. Biol. Invasions 19, 3541–3555. https://doi.org/10.1007/s10530-017-1600-4.

Medeiros, A.C., Loope, L.L., Flynn, T., Anderson, S.J., Cuddihy, L.W., Wilson, K.A., 1992. Notes on the status of an invasive Australian tree fern (*Cyathea cooperi*) in Hawaiian rain forests. Am. Fern J. 82, 27–33. https://doi.org/10.2307/1547758.

Medeiros, A.C., Loope, L.L., Anderson, S.J., 1993. Differential colonization by epiphytes on native (*Cibotium* spp.) and alien (*Cyathea cooperi*) tree ferns in a Hawaiian rain forest. Selbyana 14, 71–74. https://www.jstor.org/stable/41760419.

Mulcahy, J.P., Jones, C.G., Rumbold, S.T., Kuhlbrodt, T., Dittus, A.J., Blockley, E.W., Yool, A., Walton, J., Hardacre, C., Andrews, T., Bodas-Salcedo, A., 2022. UKESM1. 1: development and evaluation of an updated configuration of the UK Earth System Model. Geosci. Model Dev. Discuss. 1–45. https://doi.org/10.5194/gmd-16-1569-2023.

Müller, W.A., Jungclaus, J.H., Mauritsen, T., Baehr, J., Bittner, M., Budich, R., Bunzel, F., Esch, M., Ghosh, R., Haak, H., Ilyina, T., 2018. A higher-resolution version of the Max Planck Institute earth system model (MPI-ESM1. 2-HR). J. Adv. Model. Earth Syst. 10, 1383–1413. https://doi.org/10.1029/2017MS001217.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nikkel, E., Clements, D.R., Anderson, D., Williams, J.L., 2023. Regional habitat suitability for aquatic and terrestrial invasive plant species may expand or contract with climate change. Biol. Invasions 25, 3805–3822. https://doi.org/10.1093/aobpla/plu078.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2008. Niche dynamics in space and time. Trends Ecol. Evol. 23, 149–158. https://doi.org/10.1016/j.tree.2007.11.005.

Peterson, A.T., Vieglais, D.A., 2001. Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem: a new approach to ecological niche modeling, based on new tools drawn from biodiversity informatics, is applied to the challenge of predicting potential species' invasions. BioScience 51, 363–371. https://doi.org/10.1641/0006-3568(2001)051[0363:PSIUEN]2.0.CO;2.

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., Jeschke, J.M., Kühn, I., Liebhold, A.M., Mandrak, N.E., Meyerson, L.A., Pauchard, A., Pergl, J., Roy, H.E., Seebens, H., Simberloff, D., van Kleunen, M., Vilà, M., Wingfield, M.J., Richardson, D.M., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95, 1511–1534. https://doi.org/10.1111/brv.12627.

R. Core Team, 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Angel Food Cake", Vienna, Austria.. Version 4.3.3 https://www.R-project.org/.

Ricciardi, A., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.C., Dick, J.T.A., Hulme, P.E., Iacarella, J.C., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., Meyerson, L., Pyšek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Vilá, M., Wardle, D.A., 2021. Four priority areas to advance invasion science in the face of rapid environmental change. Environ. Rev. 29, 119–141. https://doi.org/10.1139/er-2020-0088.

Roberts, D., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40, 913–929. https://doi.org/10.1111/ECOG.02881.

Robinson, R.C., Sheffield, E., Sharpe, J.M., 2010. Problem ferns: their impact and management. In: Mehltreter, K., Walker, L.R., Sharpe, J.M. (Eds.), Fern Ecology. Cambridge University Press, pp. 255–322.

Rouget, M., Robertson, M.P., Wilson, J.R.U., Hui, C., Essl, F., Renteria, J.L., Richardson, D.M., 2016. Invasion debt—quantifying future biological invasions. Divers. Distrib. 22, 445–456. https://doi.org/10.1111/ddi.12408.

Schuettpelz, E., Schneider, H., Smith, A.R., Hovenkamp, P., Prado, J., Rouhan, G., Salino, A., Sundue, M., Almeida, T.E., Parris, B., Sessa, E.B., Field, A.R., de Gasper, A.L., Rothfels, C.J., Windham, M.D., Lehnert, M., Dauphin, B., Ebihara, A., Lehtonen, S., Schwartsburd, P.B., Metzgar, J., Zhang, L.B., Kuo, L.Y., Brownsey, P.J., Kato, M., Arana, M.D., Assis, F.C., Barker, M.S., Barrington, D.S., Chang, H.M., Chang, Y.H., Chao, Y.S., Chen, C.W., Chen, D.K., Chiou, W.L., de Oliveira Dittrich, V.A., Duan, Y.F., Dubuisson, J.Y., Farrar, D.R., Fawcett, S., Gabriel y Galán, J.M., de Araújo Góes-Neto, L.A., Grant, J.R., Grusz, A.L., Haufler, C., Hauk, W., He, H., Hennequin, S., Hirai, R.Y., Huiet, L., Kessler, M., Korall, P., Labiak, P.H., Larsson, A., León, B., Li, C.X., Li, F.W., Link-Pérez, M., Liu, H.M., Lu, N.T., Meza-Torres, E.I., Miao, X.Y., Moran, R., Mynssen, C.M., Nagalingum, N., Øllgaard, B., Paul, A.M., Jovani, J.B., Perrie, L.R., Ponce, M., Ranker, T.A., Schulz, C., Shinohara, W., Shmakov, A., Sigel, E.M., de Souza, F.S., Sylvestre, L., da, S., Testo, W., Triana-Moreno, L.A., Tsutsumi, C., Tuomisto, H., Valdespino, I.A., Vasco, A., Viveros, R.S., Weakley, A., Wei, R., Weststrand, S., Wolf, P.G., Yatskievych, G., Xu, X.G., Yan, Y.H., Zhang, L., Zhang, X.C., Zhou, X.M., 2016. A community-derived classification for extant lycophytes and ferns. J. Syst. Evol. 54, 563–603. https://doi.org/10.1111/JSE.12229.

Schaefer, H., 2011. Dispersal limitation or habitat quality–what shapes the distribution ranges of ferns. In: Fontaneto, D., Hortal, J. (Eds.), Biogeography of Microscopic Organisms: is Everything Small everywhere?. Horizon Scientific Press, Norwich, pp. 234–243.

Schoener, T.W., 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726. https://doi.org/10.2307/1935534.

Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P.E., Van Kleunen, M., Kühn, I., Jeschke, J.M., 2021. Projecting the continental accumulation of alien species through to 2050. Glob. Change Biol. 27, 970–982. https://doi.org/10.1111/GCB.15333.

Shabani, F., Kumar, L., Ahmadi, M., 2018. Assessing accuracy methods of species distribution models: AUC, specificity, sensitivity and the true skill statistic (TSS). Glob. J. Hum. Soc. Sci.: B 18, 7–18.

Shrestha, U., Sharma, K., Devkota, A., Siwakoti, M., Shrestha, B., 2018. Potential impact of climate change on the distribution of six invasive alien plants in Nepal. Ecol. Indic. 95, 99–107. https://doi.org/10.1016/J.ECOLIND.2018.07.009.

Shrestha, U.B., Shrestha, B.B., 2019. Climate change amplifies plant invasion hotspots in Nepal. Divers Distrib. 25, 1599–1612. https://doi.org/10.1111/ddi.12963.

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. Taxon 55, 705–731. https://doi.org/10.2307/25065646.

Strubbe, D., Broennimann, O., Chiron, F., Matthysen, E., 2013. Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob. Ecol. Biogeogr. 22, 962–970. https://doi.org/10.1111/geb.12050.

Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD - A platform for ensemble forecasting of species distributions. Ecography 32, 369–373. https://doi.org/10.1111/J.16000587.2008.05742.X version 4.2-5-2.

Turbelin, A.J., Malamud, B.D., Francis, R.A., 2017. Mapping the global state of invasive alien species: patterns of invasion and policy responses. Glob. Ecol. Biogeogr. 26, 78–92. https://doi.org/10.1111/geb.12517.

Turbelin, A., Catford, J.A., 2021. Invasive plants and climate change. In: Letcher, T.M. (Ed.), Climate Change. Elsevier pp, pp. 15–539. https://doi.org/10.1016/C2019-0-01498-7.

United Nations Educational, 2019. Scientific and Cultural Organization (UNESCO), 2019. Garden Route Biosphere Reserve. South Africa. United Nations Educational, Scientific and Cultural Organization.

van der Vaart, A.W., 2000. Asymptotic Statistics. Cambridge University Press.

van Wilgen, N.J., Faulkner, K.T., Robinson, T.B., South, J., Beckett, H., Janion-Scheepers, C., Measey, J., Midgley, G.F., Richardson, D.M., 2023. Climate change and biological invasions in South Africa. In: Ziska, L.H. (Ed.), Invasive Species and Global Climate Change, CAB International, pp. 158–187. https://doi.org/10.1079/9781800621459.0009.

Vromans, D.C., Maree, K.S., Holness, S., Job, N., Brown, A.E., 2010. The Garden Route Biodiversity Sector Plan for the George, Knysna and Bitou Municipalities. Supporting land-Use Planning and Decision-Making in Critical Biodiversity Areas and Ecological Support Areas for Sustainable Development. Garden Route Initiative. South African National Parks, Knysna.

Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36, 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431.

Xian, X., Zhao, H., Wang, R., Huang, H., Chen, B., Zhang, G., Liu, W., Wan, F., 2023. Climate change has increased the global threats posed by three ragweeds (*Ambrosia* L.) in the Anthropocene. Sci. Total Environ. 859, 160252. https://doi.org/10.1016/j.scitotenv.2022.160252.

Yukimoto, S., Kawai, H., Koshiro, T., Oshima, N., Yoshida, K., Urakawa, S., Tsujino, H., Deushi, M., Tanaka, T., Hosaka, M., Yabu, S., 2019. The Meteorological Research Institute Earth System Model version 2.0, MRI-ESM2. 0: description and basic evaluation of the physical component. J. Meteorol. Soc. Jpn. Ser. II. 97, 931–965.

Zhu, L., Osbert, J.S., Sang, W., Li, Z., Ma, K., 2007. Predicting the spatial distribution of an invasive plant species (*Eupatorium adenophorum*) in China. Landsc. Ecol. 22, 1143–1154. https://doi.org/10.1007/s10980-007-9096-4.

Ziska, L.H., 2023. Communicating the dynamic complexities of climate, ecology and invasive species. In: Ziska, L.H. (Ed.), Invasive Species and Global Climate Change. CAB International, Wallingford, pp. 9–21.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., 2019. CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. Methods Ecol. Evol. 10, 744–751. https://doi.org/10.1111/2041-210X.13152 version 3.0.1.