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Over the Hedge: Assessment of the Invasiveness and Potential Distribution of the Barrier Plant, *Metrosideros excelsa* (Myrtaceae), in South Africa and Beyond

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ABSTRACT

Ornamental plants, including barrier or hedge plants, are important in horticulture. Occurring at the urban to natural barrier, plants are often conflict of interest species. Here, we study the invading ornamental barrier plant *Metrosideros excelsa* Soland ex Gaertn. (Myrtaceae) and determine the current and potential future distribution and the risk posed to South Africa. Roadside surveys were undertaken in the coastal regions of South Africa, yielding 1541 records. Most records are of large, planted trees, indicating a historical horticultural popularity. The 47 naturalising populations occur mostly in low-lying, seasonally wet coastal areas within the fynbos biome of South Africa. Globally coastal parts of southern Australia, Tasmania, southern Brazil, Uruguay, Argentina, a few scattered areas in the mountains of northern South America and along the Mediterranean are most suitable, while in South Africa, high environmental suitability was predicted along the southwest and south coast. Eradication of *M. excelsa* from South Africa is unlikely as the species is widespread, and since it is a popular hedge plant in coastal areas, biological control is advisable to minimise conflicts. The risk analysis for South Africa suggests that the species poses a high risk, has potential moderate environmental and minor socio-economic impacts and the taxon should be controlled as part of a national management programme. Countries in which *M. excelsa* is a popular ornamental tree and with similar climates and habitats to invaded areas in South Africa should consider prevention measures.

1 | Introduction

The horticultural trade is one of the most important pathways for the introduction and dissemination of invasive alien plants (IAPs) (Dehnen-Schmutz et al. 2007; Geerts et al. 2017; Saul et al. 2017; Hulme et al. 2018). This is reflected in national floras; for example, in Britain almost half of the ~2500 non-native species are horticultural introductions (Stace and Crawley 2015). Similarly, in South Africa, 296 species are escapees from cultivation from a total of 344 alien species with known pathways of introduction (Faulkner et al. 2016). In horticulture, species are often selected for traits such as fast growth, high plasticity, profuse flowering, and hardiness—traits that predispose these species to become invasive (Mgidi et al. 2007; Richardson and Rejmánek 2011; Datta et al. 2020). A subset of species with these traits are selected for specific functions, such as ground covers, shade trees, or barrier plants which, depending on the context, might enhance the probability of invasion.

Hedge or barrier plants provide an important function in delimiting gardens, or act as a windbreak, or both. Occurring on the edge of gardens, these plants are often less managed, and,

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particularly when bordering natural areas, might be more prone to escaping cultivation. For example, in South Africa, 428 plant species have been used as barrier plants, of which 62% are exotics, and of these, 26% are naturalised or invasive (Henderson 1983). Barrier plants are selected for fast growth, hardiness, and profuse flowering (which equates to higher propagule pressure), preselecting barrier plants for invasiveness (Henderson 1983). Furthermore, barrier plants are often nurtured to ensure survival and fast growth, after which longevity is the aim (Moodley et al. 2014). While for some species, environmental conditions can prevent invasion (Moodley et al. 2014), this is often not the case (Henderson 1983; Hails and Timms-Wilson 2007).

Species distribution models (SDMs) are widely used to predict areas of potential environmental suitability for alien species (Zimmermann et al. 2010). SDMs are correlative models that estimate the relationship between species occurrences and environmental variables, such as climate, soils, and land cover, to produce spatially explicit predictions of environmental suitability (Elith and Leathwick 2009; Peterson et al. 2011). In this way, SDMs help to address the Wallacean Shortfall in invasion biology, namely the lack of comprehensive knowledge on the distributions of invasive species (Lomolino 2004). This is particularly pertinent for invasive species where there may not have been enough time for a species to occupy the full extent of its potential range, or for novel introductions (Gallien et al. 2012). SDMs are widely used in invasion science for risk assessments, early detection and rapid response, and for control and management planning (Jarnevich et al. 2023; Sofaer et al. 2019). It is thus an easy and cost-effective method to rapidly gain information to inform risk analysis and identify areas that should be targeted for monitoring and management efforts, especially for countries with diverse climatic zones, like South Africa (Pěknicová and Berchová-Bímová 2016; Vicente et al. 2013). However, SDM outputs must be interpreted with caution, as they assume that species maintain their environmental tolerances across space and time, and that observed distributions reflect environmental limits rather than dispersal constraints or biotic interactions (Araújo and Peterson 2012).

South Africa has a long history of IAP introductions, many of which only became naturalised or invasive more recently (Richardson and Rejmánek 2011; Faulkner et al. 2020; Qongqo et al. 2022). Even though the Myrtaceae family has been introduced to South Africa centuries ago and widespread invasions have been recorded (Hickley et al. 2017; Hirsch et al. 2020), there has been a more recent wave of introductions of species from the genera *Metrosideros*, *Callistemon* and *Melaleuca* (Hickley et al. 2017; Jacobs et al. 2014, 2015; Matthys et al. 2022).

Metrosideros excelsa Soland ex Gaertn. (Myrtaceae) is extensively cultivated across the world and was introduced to South Africa in the 1940s (Dawson and Heenan 2010; Dawson 2014). *Metrosideros excelsa* is a tall, evergreen, coastal tree native to the temperate zone of northern New Zealand (Arkins et al. 1999; Bergin and Hosking 2006; Bylsma et al. 2014) and has become invasive in the United States of America, Australia, and parts of New Zealand outside of its native range (Bylsma et al. 2014; Dawson 2014; Mitcalfe 2002) due to widespread plantings and repeated introductions (Groenteman et al. 2015). It also occurs in, but has not been recorded as invasive, in Hawaii, Spain, England, Ireland, Norfolk Island, and Japan (Bergin and Hosking 2006; Bylsma et al. 2014; Dawson 2014; Dawson et al. 2010; Dawson and Heenan 2010; Harris 2002). However, understanding the invasion dynamics of *M. excelsa* is largely lacking, that while another wetland invader of the Myrtaceae family, *Melaleuca quinquenervia* (Cav.) S.T. Blake, is a notorious invader globally and a recent invader in South Africa (Watt et al. 2009; van Wyk and Jacobs 2015).

Metrosideros excelsa has been widely promoted and cultivated in coastal areas within the fynbos biome of South Africa (Richardson and Rejmánek 1999). In the 1990s, *M. excelsa* already formed dense monospecific stands and was considered a problematic invader on moist fynbos soils (Henderson 1998; Richardson and Rejmánek 1999). The many seeds, due to up to 40000 flowers on a single tree (Bylsma et al. 2014; Kraaij et al. 2024), suggests that it may overcome habitat limitations (Richardson and Rejmánek 1999; Rejmánek et al. 2005) and once established, may show high plasticity for a range of conditions (Atkinson 2004; Bergin and Hosking 2006; Bylsma et al. 2014; Clarkson 1990). However, *M. excelsa* seeds require high moisture and light for germination, which may hinder invasion (Clarkson 1990; Schmidt-Adam 1999; Rejmánek et al. 2005). Moreover, limited resprouting after fire suggests that even low severity ('safe') burning may be a useful control method (Kraaij et al. 2024). Despite these potentially mitigating factors, whether *M. excelsa* is widespread or has the potential to become a widespread invader in South Africa still needs to be determined to accurately inform legislation (Nel et al. 2004). Furthermore, the risk of invasion needs to be quantified as to inform management efforts (Panetta and Lawes 2005).

One such risk analysis method is the Risk Analysis of Alien Taxa framework (RAAT) based on the Environmental Impact Classification for Alien Taxa (EICAT) and the Socio-Economic Impact Classification for Alien Taxa (SEICAT; Bacher et al. 2018). The RAAT is a formal, evidence-based scheme to quantify the impacts and benefits of alien species that is particularly useful for potential conflict of interest species (Kumschick et al. 2020). Currently, *M. excelsa* is listed as an eradication target (Category 1a; South African National Environmental: Biodiversity Act (Act 10 of 2004) (NEM:BA)). However, whether *M. excelsa* is already too widespread to be an eradication target is unknown. Furthermore, it is not clear whether *M. excelsa* is an invader of natural fynbos in coastal areas only.

In this study, we aim to determine the current and potential distribution of *M. excelsa* in South Africa and quantify its invasion risk. Specifically, we (i) establish, through roadside surveys, the current distribution, demographics, and habitat preferences of *M. excelsa* in South Africa, (ii) model the potential distribution of *M. excelsa* at a global scale, (iii) assess the risk of *M. excelsa* becoming a more widespread and problematic invader in South Africa, and (iv) provide management and legislative recommendations.

2 | Methods

2.1 | Study Species

Metrosideros excelsa is a single or multi-stemmed shrub or tree of up to 25 m tall with a gnarly growth habit (Bylsma et al. 2014). Flowering occurs from middle December to early January (i.e., southern hemisphere summer) in its native range, after which

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dry capsule clusters form which can persist for up to a year on the tree (Bergin and Hosking 2006). In the native range, *M. excelsa* naturally occurs within about a kilometre from the coast (Bergin and Hosking 2006; Bylsma et al. 2014). *Metrosideros excelsa* was introduced to South Africa during the 1940s to the windy coastal areas of the Fynbos biome as an alternative windbreak and hedging plant for *Leptospermum laevigatum*, which had become invasive.

2.2 | Introduction History and Current Distribution in South Africa

A list of all South African occurrence records for *M. excelsa* was compiled from the Plants of Southern Africa database (POSA/BRAHMS) (http://posa.sanbi.org/sanbi/Explore), the Global Biodiversity Information Facility (GBIF.org 2025), the Southern African Plant Invaders Atlas (Henderson 2007; Henderson and Wilson 2017) and a project page on iNaturalist (https://www.inaturalist.org/projects/new-zealand-christmas-tree).

Roadside surveys were done during 2019 and 2020 to visit all known localities and survey surrounding areas to quantify the current distribution and abundance of *M. excelsa* in South Africa. Potential suitable coastal areas, i.e., free of severe frost, with moist, peaty soils (Bergin and Hosking 2006; Bylsma et al. 2014; Rejmánek et al. 2005; Sakai and Wardle 1978), but without occurrence records, were also surveyed. Roads along the edges of cities and towns were surveyed as well as selected roads within urban areas, with a bias towards those that were close to (< three kilometres) natural areas and in potentially suitable habitat (Rew et al. 2006) for a total of 4059 km unique roadside surveyed. A consistent search effort (approx. 2 h) was afforded to large towns or suburbs (Marco et al. 2010). Only publicly accessible roads were surveyed (Starr et al. 2005). Speeds driven averaged 60 km/h but ranged from 20 km/h in densely populated areas (e.g., suburbs) to 100 km/h in sparsely populated areas (e.g., national roads) (Geerts et al. 2013; Henderson 1998). Roads between coastal towns were surveyed if they occurred close to the coast. One driver and one passenger were in the vehicle, and each scanned their side of the road (Baard and Kraaij 2019; Shuster et al. 2005; Starr et al. 2005). For each sighting of *M. excelsa*, the location (coordinates, and city suburb or town name), land use (garden, roadside, urban park, or natural), plant attributes (invasion status, number of individuals, presence of reproductive structures, and whether single-or multi-stemmed; Table S1) and habitat attributes (altitude, slope, soil type, soil moisture, sun exposure, major vegetation type and landform; Table S1) were collected. Plants were considered 'cultivated' (or planted, sensu Brundu et al. 2011) if they occurred inside a fenced or clearly demarcated property, occurred in clear rows or hedges, or were visibly pruned. Plants were considered 'naturalised' if they occurred in natural or semi-natural vegetation outside the confinement of parks or gardens and appeared to have established there without human assistance (Blackburn et al. 2011).

All populations were surveyed on foot and individual plants recorded by walking parallel transects, 5 m apart and searching > 100 m in all directions beyond the last plant encountered. For large dense infestations, the population density was estimated by counting plants within plots of known size and then extrapolated (Afonso et al. 2020, 2022). Distribution data from the roadside surveys were collated in GIS (QGIS Development Team 2018).

A beta regression model was created, using the package *betareg* due to a proportional dependent variable for naturalised populations, to test whether habitat attributes (e.g., altitude, slope, soil type, major vegetation type, and landform) influenced the incidence of naturalised populations (Cribari-Neto and Zeileis 2010). All naturalised populations occurred in wet areas and this attribute was therefore not included in the model (and sample size for permanently wet was too small at $n = 7$). The best fit model was determined using the log likelihood ratio test from the package *lmtest* (Zeileis and Hothorn 2002) as well as the Akaike Information Criterion (AIC) score (where an absolute change of more than two in the AIC meant the factor significantly contributed). An AIC score is a metric for selecting the best statistical model among multiple candidate models. The main effects for the analysis of variance were calculated using the package *car* (Fox and Weisberg 2019). The post hoc analysis for the within group differences were calculated using the package *emmeans* (Lenth 2024).

2.3 | Species Distribution Modelling

Detailed methods for species distribution modelling are provided in Data S1. A total of 4490 occurrences of *M. excelsa* from across the globe were sourced from online biodiversity portals, and from the roadside surveys conducted in this study. After removing problematic and cultivated records, we were left with 1131 cleaned occurrences. We analysed occurrence data for *M. excelsa* within a point process model framework (Renner et al. 2015) and fitted species distribution models in R (version 4.3.0) (R Core Team 2025) using the *maxent* package (Phillips et al. 2017).

We used non-cultivated (records not flagged as being cultivated) and naturalised occurrences (records flagged as such, or field verified as naturalised in the current study) to conduct SDMs. We ran three model ensembles using occurrences from: (1) across the globe, (2) the native range, and (3) South Africa (hereafter referred to as the global, native range and South African ensembles, respectively). This was done because the predicted distributions of invasive species can be influenced by range status (native vs. introduced) (Beaumont et al. 2009), as alien species sometime undergo niche shifts in their introduced ranges (Atwater et al. 2017). For each ensemble, we created 100 models with parameter specifications determined through a Sobol sampling process using the *parameterSets* function from the R package *sensitivity* (Convertino et al. 2014; Araújo et al. 2019; Zurell et al. 2020). Model specifications included the background extent buffer distance, the number of background points, the MaxEnt regularisation parameter, and the types of MaxEnt features used. As predictors for the occurrence of *M. excelsa*, we initially selected 30 candidate variables based on their hypothesised causal relevance to the species' distribution (Araújo et al. 2019). These included

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24 climate variables from the 10-arcmin (~20 km^2) CHELSA-BIOCLIM+ dataset (Brun et al. 2022), namely the 19 Bioclim variables as well as potential net primary productivity, growing season length, soil water balance, mean near-surface relative humidity, and mean near-surface wind speed. From the 250 m SoilGrids dataset (Hengl et al. 2017), we chose three candidate soil predictor variables: gravimetric clay, sand, and silt content (kg.kg^{-1}), which we calculated for the top 15 cm of the soil profile and aggregated to match the resolution of the climate data.

Metrosideros excelsa is typically found near the coast (Bylsma et al. 2014). We created a distance-to-coast variable and included a layer representing mean elevation above sea level as to incorporate habitat preference (Fick and Hijmans 2017). We included a global accessibility index (Weiss et al. 2018), representing travel time to the nearest city (> 50 000 population) in the year 2000. We selected 13 uncorrelated ($r < |0.8|$) variables that are potentially ecologically relevant for predicting the occurrence of this species: annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, temperature of the wettest quarter, temperature of the driest quarter, precipitation of the wettest month, precipitation seasonality, precipitation of the coldest quarter, mean near-surface wind speed, soil clay and silt content, distance to the ocean and accessibility to the nearest city. We also used an alternative set of predictors—the first eight principal components of a principal components analysis on all 30 potential predictors—as a comparison of possible effects of predictor collinearity or choice (Low et al. 2021).

Model performance was assessed using two commonly applied threshold-independent metrics: the area under the receiver operating characteristic curve (AUC; Hanley and McNeil 1982) and the continuous Boyce Index (Hirzel et al. 2006). The AUC quantifies the ability of the model to discriminate between presence and background locations, with values ranging from 0.5 (no better than random) to 1 (perfect discrimination). However, the AUC can be influenced by the spatial extent of the study area and the number of background points (Lobo et al. 2008). The Boyce Index assesses model reliability by measuring how closely the predicted suitability values correspond with the frequency of observed presences, with values close to 1 indicating a high degree of agreement between predicted suitability and observed presences, values near 0 indicating random performance, and negative values indicating counter-predictive models. Models were evaluated using fivefold spatial cross-validation implemented in the R package *blockCV* (Valavi et al. 2019). In each fold, 80% of the data were used for model training and 20% for testing, ensuring all folds were used for testing at least once. We used the cloglog output of MaxEnt to represent relative environmental suitability (Soley-Guardia et al. 2024). For each of the three models, we calculated a mean weighted predicted distribution across the 100 model runs and used this to map predicted suitability within South Africa, as well as at a global scale. To assess model extrapolation into novel environmental conditions, we calculated Multivariate Environmental Similarity Surfaces (MESS; Elith et al. 2011) using the R package *dismo*.

As an additional test of the SDM outputs, we examined predicted suitability values for *M. excelsa* occurrences in South Africa in relation to whether they were cultivated, naturalised, or non-cultivated (detailed description of methods in Data S1). We used the *ggbetweenstats* function from the *ggstatsplot* package to visualise and statistically compare mean suitability values among these categories via a one-way ANOVA.

2.4 | Risk Analysis

A detailed risk analysis, based on the literature and data collected in this study, was conducted to assess the risk posed by *M. excelsa* (Kumschick et al. 2020). The RAAT framework is specifically designed for the purpose of listing alien species under the regulatory framework of the South African Alien and Invasive Species Regulations promulgated under the NEM:BA (Act 10 of 2004). RAAT is structured to evaluate whether a species is likely to become invasive, to recognise current or possible impacts and benefits, to identify management possibilities, and to provide a suggested regulatory category (Wilson and Kumschick 2024).

3 | Results

3.1 | History and Current Distribution of Metrosideros Excelsa in South Africa

Metrosideros excelsa has invaded predominantly wet, fynbos soils in coastal areas in which it forms dense monospecific stands. By the 1990s there were two areas in which *M. excelsa* naturalised: the Overstrand and the Cape Peninsula. By 2014, *M. excelsa* was also recorded as naturalised in the coastal areas of the Garden Route National Park, approximately 300 km east of the first invasion (Table 1). Since the 1990s, local communities have helped control *M. excelsa* (via “hack groups”), but no formal management plan has been formulated.

During roadside surveys, *M. excelsa* was recorded at 1541 locations (Figure 1; roads surveyed are shown in Figure S1). *Metrosideros excelsa* was still present at 27 of the 44 historically known locations in South Africa (Appendix S1). Most populations were small, but a few had more than a thousand individuals (Figure 1). *Metrosideros excelsa* only occurred in the Fynbos and Forest biomes of the southwest and south coast (Figure 1A,B,D) and the Thicket biome of the southeast coast (Figure 1C). Naturalised populations frequented seepage or seasonal wet areas (Figure 1D). A total of 79 towns had *M. excelsa* present, with the highest number of occurrences recorded in Cape Town (394), East London (110) and Gqeberha (77), while the most individual trees were observed in Betty's Bay (2898), Cape Town (1975) and Gqeberha (335). In total, at 47 of the 1541 *M. excelsa* locations, the populations were naturalising. The cultivated plants were taller and more commonly (67% of plants) possessed reproductive structures than naturalised plants (44%). Multi-stemmed individuals were more prevalent in both naturalised (77% of observations) and cultivated (64%) populations than single-stemmed. Cultivated individuals were on average five metres in height, with some over 10 m tall, while naturalised plants were rarely over five metres in height (Figure S2).

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TABLE 1 | History of *Metrosideros excelsa* occurrence, legislation and management in South Africa.

Year	Narrative	Source
1940s	The first *Metrosideros excelsa* plants were planted in coastal areas of the fynbos biome	Allen and Lee (2006); Richardson and Rejmánek (1999)
1960s	Horticulturalists recommended *M. excelsa* as a safe replacement hedge plant for the invasive *Leptospermum laevigatum*	Richardson and Rejmánek (1999); van Wilgen et al. (2020)
1980s	Spread into native fynbos vegetation in the coastal areas around the Overstand area. Control of *M. excelsa* started. No formal management plans	Allen and Lee (2006); Henderson (1998); Richardson and Rejmánek (1999)
1990s	Residents use *ad hoc* methods to control *M. excelsa*	Harris (2002); Richardson and Rejmánek (1999)
1992	The Southern African Plant Invaders Atlas recorded two additional localities on the Cape Peninsula with self- sown populations	Richardson and Rejmánek (1999)
2001	Listed in the Conservation of Agricultural Resources Act as a Category 3 invader	Government Gazette (1983)
2004	Determined that coastal seepage and wetland areas were most likely to be invaded	Allen and Lee (2006); Rejmánek et al. (2005)
2009	Proposed as a Category 1 plant under National Environmental Management Biodiversity Act (Act 10 of 2004) in the Overstrand District	South African Plant Invaders Atlas (2009)
2014	Recorded as naturalised in parts of the Garden Route National Park. Listed as a Category 1a invader under National Environmental Management Biodiversity Act (Act 10 of 2004): Alien and Invasive Species Regulations	Baard and Kraaij (2014); Government Gazette (2004)
2015	The South African National Biodiversity Institute holds a stakeholder meeting with the Overstrand community to gauge perceptions and importance of *M. excelsa* as a barrier plant	van Wyk pers. com
2015–2024	No formal management strategy has been implemented by government agencies	Jubase., N, pers. comm., 2019

3.2 | Habitat Preferences of *M. excelsa* in South Africa

Cultivated trees occurred in a variety of habitats (Figure 2 and Table S2). Cultivated individuals of *M. excelsa* occurred in 47 vegetation types (i.e., vegetation type of the area before urbanisation) whereas naturalised populations occurred in only five vegetation types, mostly sand fynbos (Table S3). The best fit model for the incidence of naturalised populations included altitude, slope, soil type and landform (Figure 2B,C,E). These variables explained 50% of the variation in the model. The Chi squared main effects identified by the beta regression model showed that lower altitudes ($\chi^2 = 14.72$, df $= 2$, $p = 0.001$), flat slopes ($\chi^2 = 11.61$, df $= 2$, $p = 0.003$) and certain landforms ($\chi^2 = 11.45$, df $= 3$, $p = 0.010$) are significantly associated with higher proportions of naturalised populations recorded, but soil type is not (Figure 2; $\chi^2 = 0.0005$, df $= 1$, $p = 0.995$). All naturalised populations occurred in wet areas (Figure 2D).

3.3 | Species Distribution Modelling

The South African model using the 13 selected predictors performed the best of the three ensembles and had high evaluation metrics (mean AUC $= 0.97 \pm 0.001$ 95% CI; mean Boyce $= 0.93 \pm 0.01$; Table S4). The global model had moderate predictive ability (mean AUC $= 0.93 \pm 0.01$ 95% CI; mean Boyce $= 0.65 \pm 0.02$; Table S4), but the native range model performed relatively poorly (mean AUC $= 0.97 \pm 0.002$ 95% CI; mean Boyce $= 0.56 \pm 0.01$; Table S4). Differences between ensembles using the 13 selected predictors or eight principal components as predictors were very similar in terms of evaluation metrics (Table S4) and spatial predictions, particularly for South Africa (Figures S3 and S4; Table S5). Therefore, we focus on the results of the South African ensemble using the 13 selected predictors, but we provide the results for all models (Figures S3–S8 and Table S4). High suitability was predicted for *M. excelsa* in the extreme southwest of South Africa where this species was first recorded as having naturalised

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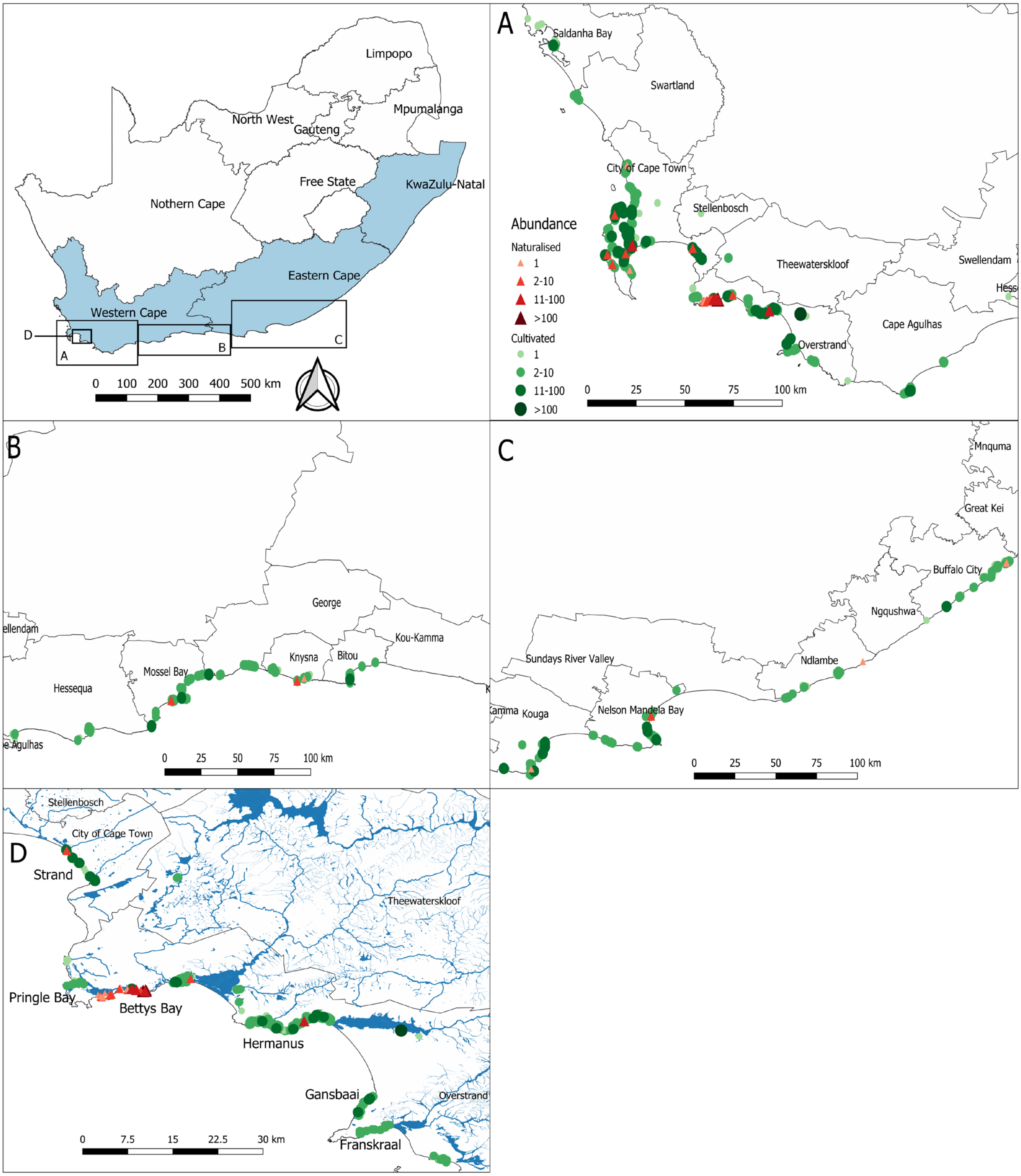

FIGURE 1 | Occurrence and abundance of cultivated and naturalised individuals of *Metrosideros excelsa* along the (A) southwest coast, (B) south coast, (C) southeast coast, and (D) Overberg region overlain with the National Ecosystem Freshwater Priority Area waterbodies (roads surveyed presented in Figure S1).

(Figure 3 and Figure S3). Additional areas of high suitability were scattered up the east coast of the country, but these areas generally did not have high consensus among model runs that these areas were suitable (Figure 3A,B and Figure S3). At a global scale, according to the South African ensemble, the predicted potential distribution for *M. excelsa* outside of its native range in New Zealand was limited to the south coast of mainland Australia and some coastal regions of Tasmania, some coastal regions of southern Brazil, Uruguay and Argentina, a few small, scattered areas in the mountains of northern South America, and a few small areas spread along the coast of the Mediterranean, Portugal, Morocco and the Canary Islands

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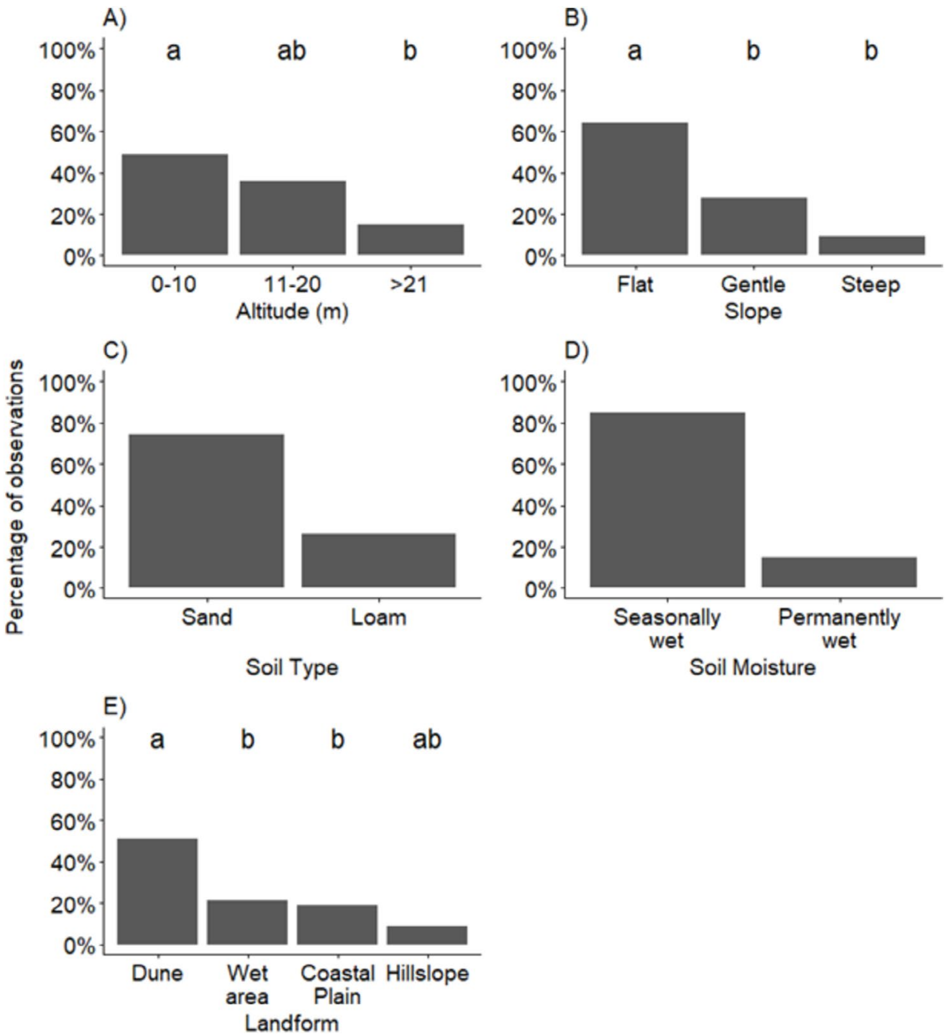

FIGURE 2 | The incidence of naturalised populations ($n = 47$) of *Metrosideros excelsa* across categories of (A) altitude, (B) slope, (C) soil type, (D) soil moisture and (E) landform. Bars with different letters are significantly different. For bars without letters (C, D) sample sizes were too low for analyses.

(Figure 3C and Figure S4). The native range ensemble was extrapolating into novel environmental space across much of the globe (Figure S4). The predictions of the global and South African ensembles were largely concurrent in the southern hemisphere, except that the global model predicted many more areas to be suitable. The global ensemble, furthermore, predicted considerable areas in the tropics and subtropics and many oceanic islands to be suitable for *M. excelsa*. In South Africa, naturalised plants often had higher predicted mean suitability values than cultivated plants although the difference in mean values across categories was not statistically significant (Figure 4 and Figure S5).

The most important environmental correlate was the minimum temperature of the coldest month (41.6%), which exhibited low suitability below freezing (0°C) and a rapid increase in suitability above about 8°C (Figure S6). Maximum temperature of the warmest month was the only other variable of relatively high importance (16.6%), with high suitability up until 22°C, after which it rapidly decreased (Figure S6). Minimum temperature of the coldest month was also the most important correlate according to the native range model, while the global model showed precipitation variables to be the most important (Figures S7 and S8). Accessibility to the nearest city was also important (34.2%), potentially suggestive of higher propagule pressure closer to cities (Figure S6).

3.4 | Risk Analysis

The risk analysis for *M. excelsa* in South Africa suggests that the species poses a high risk, has potential moderate environmental impacts and minor socio-economic impacts (Appendix S2). The recommended listing is category 1b which implies the taxon should be controlled as part of a national management programme. Regulation at a national scale is recommended since *M. excelsa* is not planted in inland areas (and thus no conflict of interest), and most of the coastline is suitable and these are also the areas in which it is planted. In coastal areas, *M. excelsa* is used as a wind break tree on some residential properties (representing a continuous source of propagules which lead to invasion of sensitive wetland habitats) and could likely result in conflicts for management efforts.

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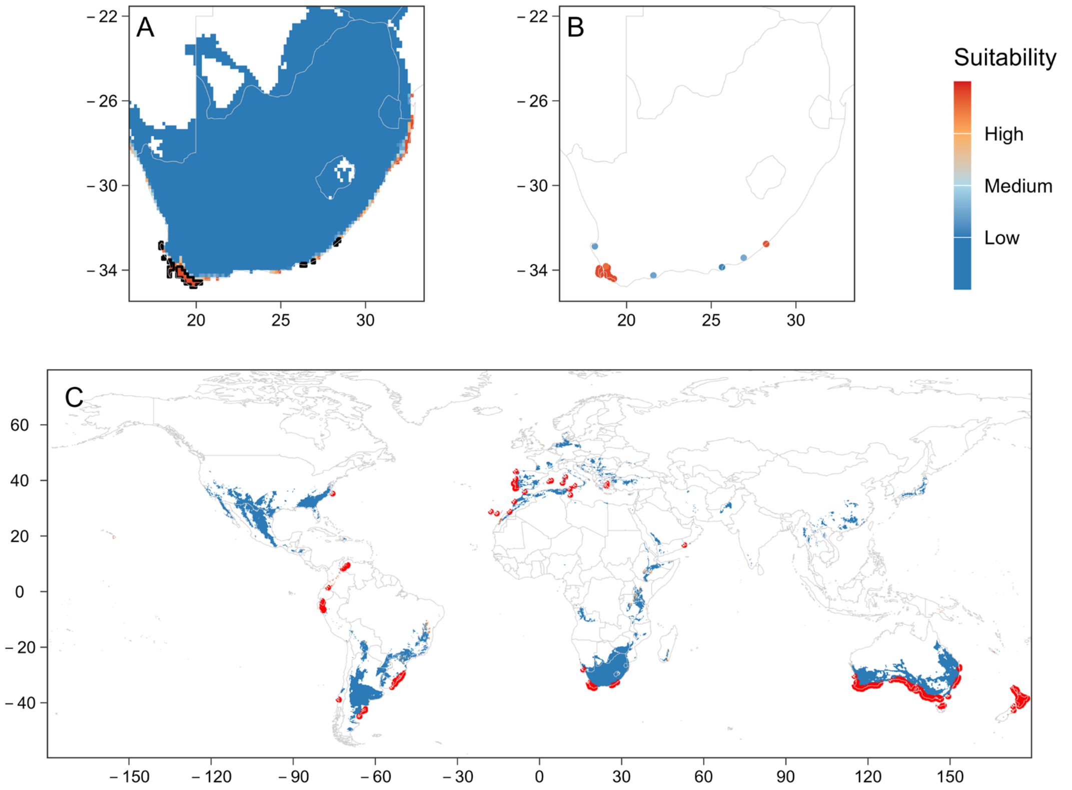

FIGURE 3 | (A) Predicted environmental suitability for *Metrosideros excelsa* in South Africa, (B) observed occurrences of *M. excelsa* in South Africa colour coded by predicted environmental suitability, and (C) the predicted global distribution of *M. excelsa* based on the South African ensemble (which was the most accurate of the three ensembles, but the predictions for the global and native range ensembles are provided in Figures S3 and S4). The predicted distribution is the weighted mean suitability determined from the South African ensemble of 100 model runs. Environmental suitability is represented by a blue (low) to red (high) colour scale. Suitability maps were masked to areas in which Multivariate Environmental Similarity Surface values were above zero, i.e., where models were not predicting into novel environmental space. Pixels for which at least 90% of the models in the South African ensemble predicted *M. excelsa* to be present are surrounded by black polygons in (A) and red polygons in (C).

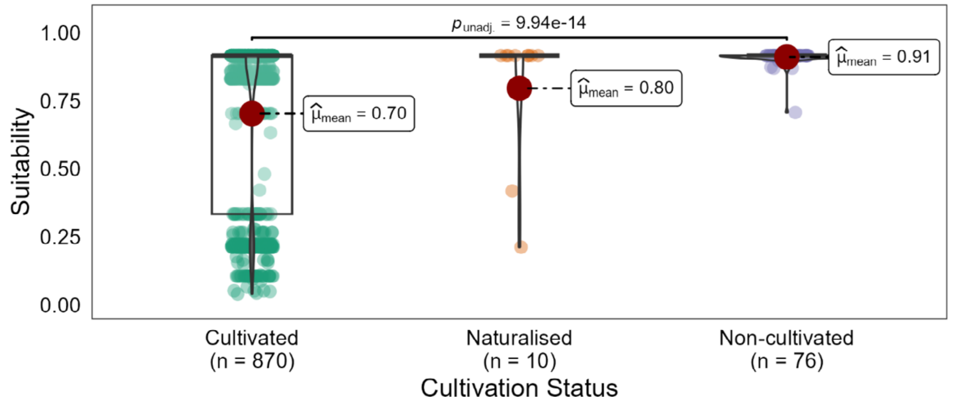

FIGURE 4 | Predicted environmental suitability values for cleaned *Metrosideros excelsa* occurrences in South Africa (from the South African ensemble of 100 model runs) that were either cultivated, naturalised or non-cultivated (see Data S1 for details). Many cultivated occurrences are predicted to have much lower suitability values than most naturalised occurrences. The red point represents the mean suitability value. Box or violin plots illustrate the distribution of suitability values, with the median indicated by the solid horizontal black bar. Opaque points represent individual suitability values. Note that the number of cleaned occurrences was substantially reduced if multiple occurrences occurred together in raster pixels of the predictor environmental variables (which was often the case with naturalised occurrences and, therefore, the sample size of naturalised is so small).

4 | Discussion

Metrosideros excelsa was introduced to South Africa during the 1940s as a windbreak for residential areas in coastal treeless fynbos areas. By the 1990s there were two areas in which *M. excelsa* naturalised: the Overstrand and the Cape Peninsula. Here we found that *M. excelsa* populations were present in more than 1500 locations, of which 47 populations were naturalising, often in close proximity (<1 km) to planted hedges. Forty-one of these naturalised populations occur along the southwest and

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south coast and six along the southeast coast, which may be attributed to a shorter residence time or to lower environmental suitability in the latter. The cultivated populations of *M. excelsa* in South Africa largely comprised adults, indicating that it was historically popular as an ornamental species. Only a few new plantings were recorded, potentially indicating a decline in popularity and more recently, the result of being legislated. However, the many naturalising populations suggest that *M. excelsa* is spreading and has invasive potential in environmentally suitable areas of South Africa.

The current distribution of *M. excelsa* in South Africa suggests the species already occupies a substantial part of the potential environmentally suitable areas, principally along the temperate southwest, south, and southeast coast (Figure 3). Globally, we found relatively small areas that are potentially suitable (Figure 3C and Figure S3). In South America, parts of the coast in southern Brazil into Uruguay were predicted to be environmentally suitable for *M. excelsa*, but we did not find any records of occurrences of this species in the databases we searched. The differences in predicted suitable area among the model ensembles—particularly the inability of the native-range ensemble to make reliable predictions across much of the globe due to the species' relatively narrow and unique environmental conditions in New Zealand—underscore how strongly model outcomes depend on differences between the environmental space of the training region and that of the areas into which projections are made, and the uncertainty this mismatch introduces (Feng et al. 2019; Low et al. 2021). Nevertheless, our study highlighted areas globally that are possibly climatically suitable, and where planting should be discouraged, and if already present, where action should be taken to prevent invasion of *M. excelsa*. These results underline the value of SDMs for species with narrow climatic requirements such as *M. excelsa* (Barbet-Massin et al. 2018). SDMs are particularly relevant if combined with extensive field sampling and microhabitat quantification, as was done here, while acknowledging that factors such as seed-dispersal distance and mutualistic interactions could further enhance the accuracy (Geerts and le Roux 2025; Srivastava et al. 2019).

In South Africa, *M. excelsa* largely mimics the habitat preferences from its native range in New Zealand, i.e., growing in coastal areas at low altitudes (Bylsma et al. 2014), and in well-drained soils that remain moist for part of the year (Bergin and Hosking 2006; Yamamoto et al. 1989). *Metrosideros excelsa* was introduced to the country for human use like species in other major invasive tree genera, e.g., *Acacia*, *Hakea* and *Pinus* (van Wilgen et al. 2020). However, *M. excelsa* appears less invasive than many of these widespread tree invaders. This is possibly because *M. excelsa* had a lower propagule pressure than many widespread tree invaders as it was introduced exclusively for ornamental purposes, and only to a few coastal towns in South Africa. Furthermore, unlike *Acacias* that have a large geographical native range encompassing various habitats and climatic zones (Castro-Díez et al. 2011), *M. excelsa* is very climate and habitat specific which limits its potential distribution (Figure 3).

The limited current range of *M. excelsa* in South Africa may be due to several factors, such as that the seeds do not disperse as well as previously surmised (Harper 1977), that large parts of the fynbos are not suitable for germination and persistence (Hobbs and Huenneke 1992), or that the released seeds are of poor quality (Anderson 2003; Kraaij et al. 2024). This study identified the habitat types in which *M. excelsa* establishes, but it did not indicate the conditions suitable for germination, an aspect that requires further study since this might, for instance, differ in the summer rainfall areas of South Africa (Britton-Simmons and Abbott 2008). This is similar to other emerging invaders, such as the hedge plant *Hakea salicifolia* which is reliant on disturbance and water availability for establishment in drier areas (Moodley et al. 2014). Potential microsite factors and landscape context impacting invasiveness and the distribution warrant further attention (Thomas and Moloney 2013). Currently, the threat of *M. excelsa* invasion adds pressure to coastal areas in South Africa that are already under threat from habitat fragmentation, development, and agricultural activities, but contain high plant biodiversity (Mucina and Rutherford 2006).

Eradication of *M. excelsa* is not feasible given the many naturalised populations and large number of cultivated individuals scattered along the Cape coast. Furthermore, *M. excelsa* is a 'conflict of interest' species among stakeholders as it is an important hedge plant in some windy coastal towns. Even though a relatively small percentage of invasive species are conflict of interest species, these pose unique management challenges (Novoa et al. 2018; Nsikani and Geerts 2024). In the case of *M. excelsa*, which prefers moist habitats in coastal areas, legislating these areas only is impractical since seeds are small and can potentially disperse inland from planted garden hedges. Moreover, coastal seepage areas and seasonal wetlands are not accurately mapped in South Africa. Also, if clearing is conducted, the concern of secondary invaders should be considered in these seepage areas (Geerts et al. 2022). Other than being a hedge plant, *M. excelsa* poses little to no economic value, and therefore potential biological control agents should be explored (Davies et al. 2018; Rawnsley 2006). The implementation of early detection systems in areas predicted to be suitable for *M. excelsa*, but where it is not yet present, e.g., along the southeast and east coast of South Africa, is important to prevent establishment and foci of invasion. Globally, countries with conditions that favour *M. excelsa* need to implement early detection approaches, especially in those countries where *M. excelsa* is already a favoured horticultural species and the climate and habitat conditions are favourable for invasion.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Plant and habitat attributes surveyed during the roadside survey. **Table S2:** Post hoc emmean results for each of the significant factors namely altitude, slope and landform. The level of significance is given by *The main effect ANOVA showed that altitude ($F = 7.36$, df = 2, $\mathrm{df}_{\mathrm{residual}} = 12$, $p = 0.008$), slope ($F = 5.80$, df = 2, $\mathrm{df}_{\mathrm{residual}} = 12$, $p = 0.017$) and landform ($F = 3.82$, df = 3, $\mathrm{df}_{\mathrm{residual}} = 12$, $p = 0.039$) had significant differences in the proportion, where soil type did not ($F = 0.00005$, df = 1, $\mathrm{df}_{\mathrm{residual}} = 12$, $p = 0.995$). **Table S3:** South African vegetation types (Mucina and Rutherford 2006) where *Metrosideros excelsa* occurs that have a conservation status of 'Threatened' or higher under the International Union for the Conservation of Nature (Bland et al. 2017). The asterisk indicates vegetation types where *M. excelsa* has naturalised. **Table S4:** Species distribution model evaluation metrics for the three model ensembles—global, native range, and South Africa, and using either the 13 selected predictor variables (selected predictors) or eight principal components from a principal components analysis on all 30 candidate predictor variables (PCA approach). Models were evaluated for their ability to accurately discriminate presence from background points using the Area Under the receiver operating characteristic Curve (AUC), and for transferability and predictive accuracy using the continuous Boyce Index. Values represent mean suitability values and 95% confidence intervals. **Table S5:** Number of cleaned occurrences per model region and per plant status as naturalised, cultivated (not used to test the model) or non-cultivated. **Figure S1:** Roads driven along the (A) southwest coast, (B) south coast, and (C) southeast coast during the roadside survey to verify *Metrosideros excelsa* occurrences in South Africa. **Figure S2:** Plant height frequency (number of plants) distribution of *Metrosideros excelsa* compared between cultivated and naturalised stands. **Figure S3:** (A–F) Predicted environmental suitability for *Metrosideros excelsa* in South Africa using 13 selected environmental predictors (A–C) or the first eight principal components of a principal components all 30 potential environmental predictors (D–F). Suitability maps were masked to areas with Multivariate Environmental Similarity Surface values above zero, i.e., where models were not predicting into novel environmental space. (G–L) Non-cultivated and naturalised occurrences of *M. excelsa* used to train species distribution models colour coded by predicted environmental suitability (G–L). Maps in the first column used occurrences and background points from across the globe, those in the middle column from the species' native range in New Zealand, and those in the right column from South Africa. The global ensemble (A, D) predicted almost no suitable areas in South Africa compared to the South African ensemble (C, F). The native range ensemble (B, E) was extrapolating into novel environmental space for the whole of South Africa. Environmental suitability is represented by a blue (low) to red (high) colour scale (grey circles for occurrences in map E indicate the predictions were extrapolating into novel environmental space). Pixels for which at least 90% of the models predicted *M. excelsa* to be present based on the maximum of the sum of specificity and sensitivity threshold are surrounded by black polygons (only visible in C). **Figure S4:** (A–F) Environmental suitability for *Metrosideros excelsa* predicted across the world from the (A) global ensemble using the 13 selected predictor variables (selected variables), (B) global ensemble using the first eight principal components of a principal components analysis (PCA) on all 30 possible predictor variables (PCA approach), (C) native range ensemble using selected variables, (D) native range ensemble using a PCA approach, (E) South African ensemble using selected variables, and (F) South African ensemble using a PCA approach. The predicted distribution is the weighted mean suitability across the 100 model runs of each ensemble. Environmental suitability is represented by a blue (low) to red (high) colour scale. Suitability maps were masked to areas with Multivariate Environmental Similarity Surface values above zero, i.e., where models were not predicting into novel environmental space. (G, H) Non-cultivated and naturalised occurrences of *M. excelsa* used for species distribution modelling colour coded by weighted mean suitability from the South African ensemble using (G) selected predictors or (H) a PCA approach. **Figure S5:** Predicted environmental suitability values for *Metrosideros excelsa* occurrences in South Africa across different cultivation statuses (cultivated, naturalised, or non-cultivated), based on (A) the global ensemble, and (B) the South African ensemble. For the native range ensemble, all occurrences had predictions that were in environmental space novel to the native range and, therefore, are not shown here. Red points represent mean suitability values. Box or violin plots illustrate the distribution of suitability values, with the median indicated by the solid horizontal black bar. Opaque points represent individual suitability values. Significant differences in mean suitability values between cultivation statuses are denoted by solid black bars with associated *p*-values. Despite the global (A) ensemble having generally lower suitability values across all cultivation statuses, the results are in agreement with the South African ensemble (C) that cultivated plants often had lower environmental suitability values than naturalised plants, and that non-cultivated plants had mean suitability

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values that were similar to naturalised plants. **Figure S6:** Response curves for the South African ensemble showing the relationship between individual predictors used to train species distribution models and the predicted environmental suitability. The grey lines represent individual models from the 100 runs comprising the South African ensemble. These are marginal response curves, i.e., each variable is predicted across the full continuum of values sampled while holding all other predictors constant at their mean values. Values in parentheses are the permutation-based importance values for each variable. Blue lines represent the model with the highest Boyce index value and green lines the model with the highest AUC (Area Under the receiver operating characteristic Curve). **Figure S7:** Response curves for the global ensemble showing the relationship between individual predictors used to train species distribution models and the predicted environmental suitability. The grey lines represent individual models from the 100 runs comprising the global ensemble. These are marginal response curves, i.e., each variable is predicted across the full continuum of values sampled while holding all other predictors constant at their mean values. Values in parentheses are the permutation-based importance values for each variable. Blue lines represent the model with the highest Boyce index value and green lines the model with the highest AUC (Area Under the receiver operating characteristic Curve). **Figure S8:** Response curves for the native range ensemble showing the relationship between individual predictors used to train species distribution models and the predicted environmental suitability. The grey lines represent individual models from the 100 runs comprising the native range ensemble. These are marginal response curves, i.e., each variable is predicted across the full continuum of values sampled while holding all other predictors constant at their mean values. Values in parentheses are the permutation-based importance values for each variable. Blue lines represent the model with the highest Boyce index value and green lines the model with the highest AUC (Area Under the receiver operating characteristic Curve). **Appendix S1:** aec70189-sup-0002-Data S2.docx.

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