

**Abandoned homestead gardens as a source of plant invasions in rural
South Africa**

By
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Declaration

I Moleseng Doreen Raseala declare that the thesis/dissertation, which I hereby submit for the degree M.Sc. Plant Science and Soil Sciences at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: 

DATE: 15/02/2022

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"Kodumela moepa thutse gago lehumo leo letswago kgauswi"

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Abstract

Alien invasions are a global concern, with impacts on native biodiversity. Invasive species may be introduced to new regions for many reasons, with ornamental horticulture being one of the major pathways for the entry of potentially invasive plant species. To prevent future alien invasions potentially invasive species should be detected early after their introduction. Newly introduced/naturalized alien plants can be identified during field surveys, and alien species with larger potential range sizes can be identified with the use of species distribution modelling techniques (SDMs). The aim of this study was to investigate if alien ornamental species were persisting and escaping from abandoned gardens in Limpopo and Mpumalanga provinces and to estimate their invasion potential. The first objective was to test which species have escaped cultivation from gardens since abandonment, and if these species' distance of spread was related to the taxonomic group, NEM: BA category, reproduction mode, or growth form. The second objective was to test if potential range size of species was correlated with their distance of spread, or if potential range size differed between NEM: BA listed and non-listed species, and between spreading and non-spreading species. Alien ornamental plant species were recorded from 13 abandoned gardens in north-eastern South Africa. The family Proteaceae had the highest average maximum distance of spread and the families with a high number of alien ornamental representatives recorded were Solanaceae, Rosaceae, Lauraceae, Euphorbiaceae, and Bignoniaceae. Species' maximum distance of spread from abandoned gardens was positively related to species' NEM: BA status, with species that are required to be controlled showing the greatest spread distances. Species' mode of reproduction and growth form were not related to spreading distances. Ensemble modelling of the potential distribution of the ornamental

plants recorded from the abandoned homesteads showed that the ability of a species to invade larger areas is not related to species NEM: BA status or whether species were spreading or not. No significant positive correlation was found between the species average maximum distance of spread and the predicted potential range size. Potential range size maps were overlaid to generate species richness maps per group (NEM: BA spreading, NEM: BA not spreading, non-listed spreading, and non-listed not spreading), and areas of high potential richness were similar between the four groups of species. These results are at least partly contingent on the data for this study having been collected from areas with relatively high rainfall, and therefore may not be representative of more arid areas in South Africa. In conclusion, several invasive alien ornamental plants were found escaping cultivation from abandoned gardens to surrounding natural vegetation. The species which are currently listed on NEM: BA were found to have spread considerable distances although non-listed species were also recorded to spread. As a result, further studies need to investigate abandoned gardens in other biomes and climatic zones to better understand which species can persist and spread from abandoned gardens.

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Chapter 1: Introduction

1.1 General Introduction

Alien species are introduced to new regions unintentionally, through contaminated goods, ballast water, and tourism, or intentionally as agricultural products, forestry, ornamental horticulture, and for medicinal use (Maurel et al., 2016, Chrobock et al., 2011, Pemberton and Liu, 2009). The invasion process starts when alien species are introduced to new regions by human aid (Figure 1). When alien species escape cultivation and sustain their population, they form naturalized populations. Invasions occur when the naturalized population starts to spread (Blackburn et al., 2011). Only a fraction of introduced species become invasive and often alien species remain confined to one location (Essl et al., 2012). Sometimes, invasions are observed decades after the initial introduction because alien species will first adapt to the new environment to be able to compete for resources and reproduce in competition with native species (Blackburn et al., 2011). This in turn gives rise to the initial lag phase which can be decades-long due to unfavourable environmental and climatic conditions in the invasion process (Guo et al., 2018, Kolar and Lodge, 2001, Geerts et al., 2013). Therefore, several recently introduced alien species that have not yet spread may emerge as invaders in the future (Rouget et al., 2016, Essl et al., 2012).

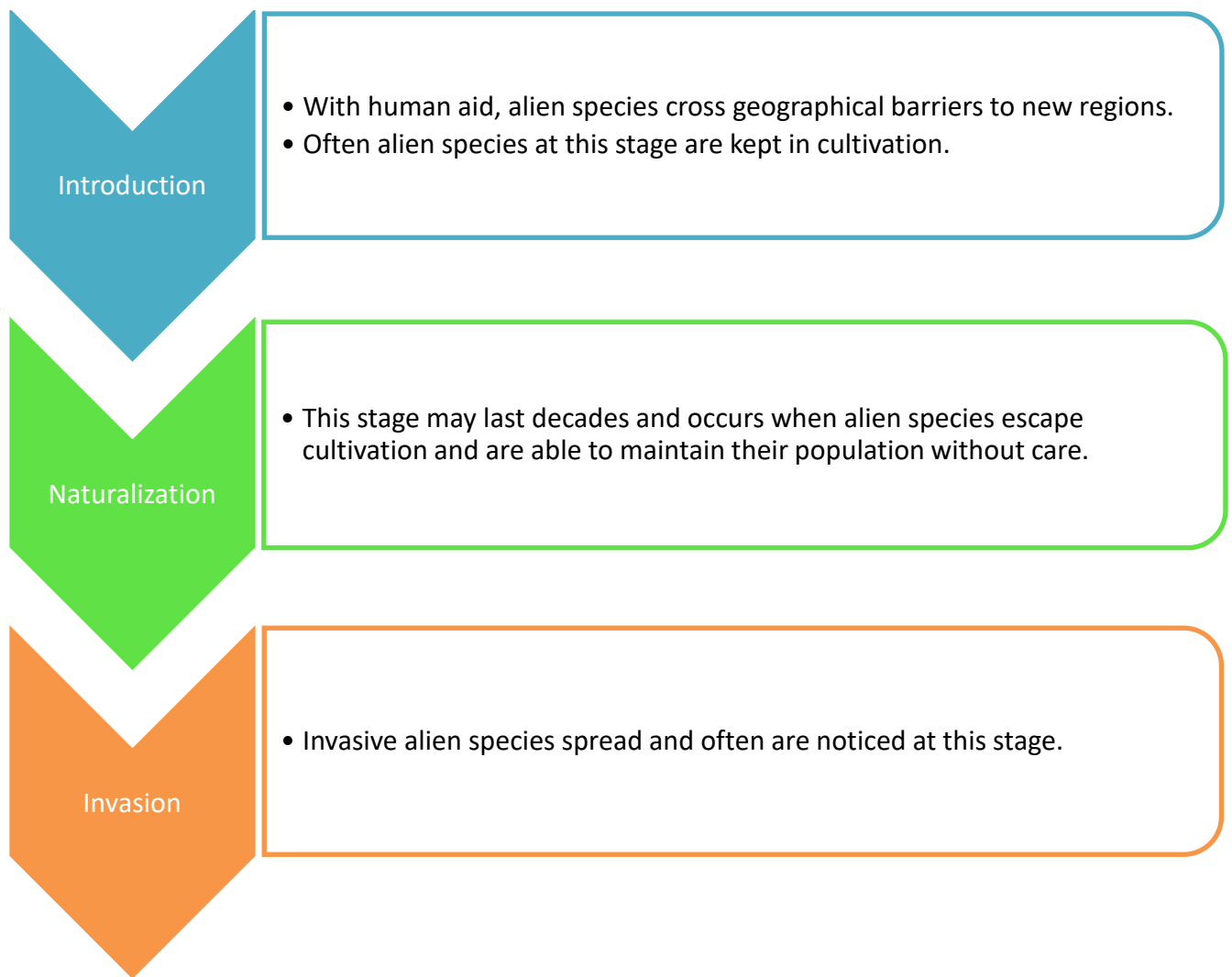


Figure 1: introduction occurs when alien species cross major geographical barriers to new environments. Naturalization occurs when alien species introduced and kept in cultivation escape and can sustain their population without human assistance. Invasion occurs only when alien naturalized species start to spread (Blackburn et al., 2011). The diagram refers specifically to ornamental plant species.

Irrespective of how alien species are introduced to new regions, their impacts have been observed globally (O'Connor and van Wilgen, 2020, Hulme, 2009, van Wilgen and Richardson, 1985). Studying alien plants is important because their impacts can be particularly detrimental to livelihoods (Terera et al., 2015, Gaertner et al., 2016, Hester and Hobbs, 1992). For example, pasture production is often reduced when native palatable plants are out-competed by unpalatable invasive plants (Mack et al., 2000, Nkambule et al., 2017, Turpie, 2004). Similarly, the production of native wild food and traditional herbs for

human consumption may also be reduced with heavy invasions (Richardson et al., 2007). Some alien invasive species consume larger amounts of water than natives, which can reduce river flow and underground water supplies (Terera et al., 2015, Gaertner et al., 2016, Hester and Hobbs, 1992). Alien invasions may also result in land degradation and denudation, which is often irreversible (Dehnen-Schmutz and Touza, 2008, Jardine and Sanchirico, 2018, Stafford et al., 2017). However, the impacts associated with invasions are often site and species-dependent, and cannot be generalized (Dassonville et al., 2008, Sardans et al., 2017, Le Maitre et al., 2011, Theoharides and Dukes, 2007).

In South Africa, the introduction of alien species dates back to pre-colonial years when the Cape coastal regions of South Africa were visited by trading ships from different continents (van Wilgen et al., 2020). From the 1650s, European settlers permanently settled in the Cape and introduced alien species both intentionally and unintentionally (Measey et al., 2020, O'Connor and van Wilgen, 2020). Intentional introductions included the introduction of *Acacia* and *Pinus* species for forestry, and for stabilizing soil dunes which were encouraged by the government (O'Connor and van Wilgen, 2020). The management of invasive species in South Africa began in the 1860s when an Act was passed for the control of *Xanthium spinosum*, this was followed by the biological control of the cacti *Opuntia monacantha* and *Opuntia ficus-indica* which began in 1913 (Moran et al., 2013). Currently, South Africa is managing alien invasions through the Department of Forestry, Fisheries, and the Environment, the Centre for Invasion Biology, the South African National Biodiversity Institute: Biological Invasion directorate, and Working for Water (van Wilgen et al., 2004, Department of Environmental Affairs, 2014). Even with the programmes available for alien invasion control, the most cost-effective way to manage alien invasions is to prevent introductions as clearing established species can be costly (Morokong et al., 2016, van Wilgen et al., 2001). Legal introductions of alien species are guided by conducting detailed species analysis reports to prevent potentially invasive species from entering the country (Kumschick et al., 2020). Alien species analysis reports can be time-consuming and not 100% effective for the species with no invasion history and poor pre-existing biological knowledge (Blackburn et al., 2014, Kumschick et al., 2020). The species with no biological information may be introduced to new environments and later on become invasive (Blackburn et al., 2014, Kumschick et al., 2020).

The second-best option will be to manage alien species during the lag-phase when species are still confined to smaller areas near their introduction sites (Coutts et al., 2018). The difficulty with controlling species during the lag-phase is the failure to differentiate between the species in the lag-phase and those with no invasion potential and also it is difficult to detect invasive species in the lag-phase because field surveys are required for detections (Crooks 2005). When there is no clarity of which species are in the lag-phase, eradication should be done as a precautionary manner.

Species distribution models (SDMs) are techniques that can be used to investigate the potential range size of species to determine habitat suitability (Witt et al., 2018, Barbet-Massin et al., 2018). Species distribution models make use of known occurrence records as well as environmental variables to make estimations of potential areas where species are likely to occur (Barbet-Massin et al., 2018, Elith and Leathwick, 2009, Gong et al., 2020). Species distribution models can be used to investigate the potential range size of alien species believed to be in a lag-phase or to estimate the invasive potential of species for which there is no a priori information about invasiveness (Crooks, 2005, Araújo and New, 2007). Thus, SDMs can provide a quick estimate of suitable areas and potential range sizes, and, thereby, assist managers to make informed decisions in regards to invasive species control and management (Barbet-Massin et al., 2018).

The limitations of SDMs are that the chosen environmental predictors should be extracted at the same time with occurrence localities for accurate species distribution models (Phillips et al., 2006). For example, environmental predictor variables such as current land cover are not to be used with old herbarium records (Anderson and Martínez-Meyer, 2004, Pearson et al., 2004). When interpreting the results from SDMs, it is important to keep in mind that the distribution of species is not only influenced by easily mapped environmental predictors, but also by factors such as disturbance, competition, and the organisms' traits and patterns; these are more difficult to be taken into consideration by SDMs (Dubuis et al., 2013, Buri et al., 2017). But it is possible to include other factors such as species traits to SDMs (Benito et al., 2019, Vesik et al., 2021). Also, species are not in equilibrium with the predicted potential range size (Sinclair et al., 2010). This is because SDMs predict potentially suitable areas where a species is likely to occur and not necessarily that the species are present in all the predicted areas (Sinclair et al., 2010). Another limitation of SDMs is that using presence-only data, which are often the only data available,

can overestimate the distribution of species (Barbet-Massin et al., 2018, Guisan and Thuiller, 2005). Even with these challenges, SDMs are cost and time effective tools when investigating potential invaders (Sinclair et al., 2010). SDMs may sometimes not reflect the invasive potential of species, it is important that the results produced by SDMs be used in conjunction with field survey reports.

It is important to study areas where alien species are typically introduced (Dehnen-Schmutz et al., 2007, Foxcroft et al., 2008, van Kleunen et al., 2018). When homesteads are abandoned, gardens are also left behind, and introduced ornamental plants might die, remain in the gardens, or even escape cultivation. Therefore, abandoned homestead gardens can act as important source of alien plant invasions, and they can be found across South Africa (Witt et al., 2018, Dehnen-Schmutz et al., 2007). This project investigated if alien ornamental species were persisting and escaping from abandoned gardens in Limpopo and Mpumalanga provinces, and estimated their invasion potential. In my second chapter, I set out to investigate which invasive species were escaping abandoned cultivation and which families had a higher number of species found persisting and escaping cultivation. For the alien ornamentals found naturalizing, I measured the maximum distance of spread from the source (a point of origin). I also investigated if NEM: BA status, mode of reproduction, growth-form, and taxonomy was correlated to species maximum distance of spread. In Chapter 3, I used ensemble modelling techniques to investigate the potential distribution of the ornamental escapees that were surveyed in Chapter 2. I specifically investigated if species' spread in the surveyed homesteads was correlated with species' potential range size modelled by ensemble modelling. Secondly, I investigated if the NEM: BA listed species had a higher potential range size than the non-listed species because NEM: BA species are declared invasive. The potential range size of the spreading species was also investigated if it was different from the potential range size of the non-spreading species. Finally, I investigated if the potential species richness patterns would differ between the NEM: BA listed spreading species, NEM: BA listed not spreading, non-listed spreading, and non-listed not spreading.

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Chapter 2: Abandoned homestead gardens as a source of plant invasions in rural South Africa

2.1 Introduction

The intentional introduction of alien plants has occurred through the importation of non-native species, for example, ornamental horticulture, plantations, food, and medicine (van Kleunen et al., 2015, Chen et al., 2017, Hulme, 2009). Of these introduction pathways, ornamental horticulture is one of the major routes through which alien species are introduced to new regions (van Kleunen et al., 2018, Mack and Erneberg, 2002, Reichard and White, 2001). With globalization, the movement of plants between countries by the horticulture industry has grown, mirroring the increase in the numbers of invasive plant species established globally (Dehnen-Schmutz et al., 2007, Humair et al., 2015, van Kleunen et al., 2015). In recent years, online plant trading has further increased the transportation of alien, and potentially invasive, ornamentals across national borders (Humair et al., 2015, Humair et al., 2014, Lenda et al., 2014). Indeed, the distance travelled by an alien ornamental species from their native country to the country where it is purchased has increased through online trading (Lenda et al., 2014, Humair et al., 2015, Ray, 2011).

In South Africa, the high sales of ornamental alien plants reflect an apparent preference amongst many gardeners for alien species over native plant species (Gaertner et al., 2016, Mayer et al., 2017, Foxcroft et al., 2008, McLean et al., 2018). In the past, most nurseries have been dominated by alien species (Cronin et al., 2017), likely reflecting gardeners wanting to recreate gardens from their homeland (e.g. European immigrant communities), known medicinal uses of some species, and a lack of awareness of the impacts associated with these species (Maema et al., 2016). Preferential planting of alien plants over natives has also been recorded in South Africa. For example, in the Kruger National Park, landscaping in gardens was historically mainly done with the use of alien plants, some of which were prohibited by invasion regulations (Foxcroft, 2001, Foxcroft et al., 2008, van Wilgen et al., 2017). The majority of these ornamentals produced fleshy fruits and the high availability of dispersers in the Park has resulted in several species spreading from the gardens (Foxcroft et al., 2008). Only more recently have native species been promoted for ornamental use in South Africa, in part to minimize or prevent further invasions (Foxcroft et al., 2008, Foxcroft, 2001).

Horticulturists tend to select plants with traits that may allow the species to survive in a broad range of new environments (Foxcroft et al., 2008, Alston and Richardson, 2006, Milton et al., 2007, Perrings et al., 2005). However, these traits tend to be positively related to a species' invasion potential. For example, plant species with a faster growth rate, vegetative reproduction, higher seed production, higher germination rate, and a higher fecundity are more likely to become invasive than species lacking these traits (Kolar and Lodge, 2001, Smith and Knapp, 2001, Gallagher et al., 2015, Maurel et al., 2016). Specifically, species that produce a higher number of seeds may increase their propagule pressure, and with long residency time, alien invasions may be promoted (Maurel et al., 2016). Reproductive traits may also influence species distance of spread, with seeds with lower mass typically having a greater chance of spreading further and invading larger areas than those species that only reproduce asexually (Moodley et al., 2013, Rejmanek and Richardson, 1996). Unique traits related to gardeners' preferences, such as colour and growth form, may also indirectly influence invasion as plants with these traits may be selected and distributed for horticulture more often, leading to an increase in their propagule pressure (Rojas-Sandoval and Ackerman, 2021).

Invasions can occur a long time after the initial introduction of a species and it is expected that more species may become invasive in the future after escaping gardens (Rouget et al., 2016, Essl et al., 2011). Without human maintenance and intervention, invasive species can spread outside of cultivation and are less likely to be subsequently recorded and managed than species that have not escaped (Ismail et al., 2016). Abandoned homesteads are of specific concern because they are located in remote rural areas and unlikely to be monitored; as a result, they can potentially act as a source of alien invasion to surrounding landscapes. The escape of cultivated alien plant species from urban areas has already been examined in several contexts and may be expected to be less likely to cause undetected invasions to surrounding areas (McLean et al., 2018, Baard et al., 2017, Foxcroft et al., 2003). Also, non-abandoned gardens are not expected to be that much of an issue because gardeners are more likely to monitor the spread of alien species from their gardens (Dehnen-Schmutz and Conroy, 2018). Therefore, the gardens of abandoned homesteads may provoke a risk to surrounding natural landscapes.

Abandoned farm homesteads can be found across South Africa, with abandonment occurring for several reasons, including land reform actions and farm consolidation

(O'Laughlin et al., 2013, Hall and Cousins, 2018). Under the apartheid regime in South Africa, racially discriminatory laws barred native South Africans from owning land (Maylam, 1990, Blair et al., 2018, Ramutsindela, 2002). As an act of addressing the past and imbalances of land ownership in South Africa, land reforms have been undertaken since 1994 (McCusker, 2004, Place, 2009, O'Laughlin et al., 2013), with the main goal of providing compensation for, or the return of land that was dispossessed as a result of racially discriminatory laws during the previous dispensation; however, this has resulted in the abandonment of some farm homesteads (Chikozho et al., 2019, Leyshon, 2009). Farm consolidation is another reason why some homesteads are abandoned. When farms are merged, because smaller farms are less profitable, some homesteads may become abandoned (Hall and Cousins, 2018, Andrew and Fox, 2004). Irrespective of the cause, where homesteads are without occupants and maintenance, abandoned gardens may potentially act as a source of alien invasion to surrounding natural vegetation (Cramer et al., 2008).

Several projects are attempting to eradicate or control invasive plant species in South Africa, including the Working for Water programme, and the Directorate of Biological Invasions within the South African National Biodiversity Institute. The National Environmental Management Biodiversity Act (NEM: BA) legislation regulates the use of invasive alien species in South Africa (Department of Environmental Affairs, 2014). This legislation indicates which species are to be eradicated nationally (NEM: BA category 1a), which are to be controlled and not allowed to spread (NEM: BA category 1b), which can be planted for commercial use but may not be allowed to spread outside cultivated area (NEM: BA category 2), and which can be kept without propagation and trading (NEM: BA category 3) (Department of Environmental Affairs, 2014). Plant species within the NEM: BA categories 1a, 1b, and 3 are prohibited (i.e. cannot be introduced into South Africa) and category 2 can only be introduced by permit holders (Department of Environmental Affairs, 2014). It is important to investigate if the species escaping cultivation are listed on NEM: BA for control and management purposes.

2.2 Aims, objectives, and hypothesis

Because plant species in gardens have the potential to spread beyond garden limits (Milton et al., 2007, Bigirimana et al., 2012, Mayer et al., 2017), I investigated the potential role of abandoned homesteads in South Africa as sources of alien ornamental escapees. I focused

on abandoned gardens because not much is known about their role as a source of alien invasion. This chapter quantifies the spread of invasive alien ornamentals from abandoned gardens into natural vegetation. The first objective was to assess what alien ornamental plant species are growing in the gardens of abandoned homesteads and to estimate their rate of spread into surrounding natural vegetation. The second objective of this study was to test if the rate of spread by species that have escaped cultivation is related to species taxonomic group, NEM: BA category, reproduction mode, and growth form.

2.3 Material and methods

Abandoned homesteads were sampled in two areas (Lekgalameetse Nature Reserve and Weltevreden), both located in north-eastern South Africa, locality coordinates and a map indicating study areas are in appendix (Table A1: Figure A1). The areas are both in a transition area from Savannah to Grassland biome that is characterized by summer rainfall and dry winters. Around the start of the 20th century, the area around the current Lekgalameetse Nature Reserve attracted the first white occupants who irrigated the land for commercial farming (Chapman, 2006). The Officers Colonial Land Company was then established in the 1920s and grazing activities of the local black communities were replaced by the white settler's intensive farming methods (Chapman, 2006, Liebrand et al., 2012). In the 1980s the apartheid government purchased the properties of the white farmers to expand Lebowa homelands but protected the upper catchment of the Selati River; Lekgalameetsee Nature Reserve was then founded in 1984 and the homesteads were abandoned (Liebrand et al., 2012, Chapman, 2006, Williams and Altenroxel, 2014). Lekgalameetsee Nature Reserve is situated in the Limpopo province, ± 80 km south-east of Tzaneen (24.1167° S 30.1167° E) (Liebrand et al., 2012).

The second study site is in the Weltevreden area, ± 40 km south-east of Mashishing (25.3156° S 30.4029° E). In this area, smaller farms were consolidated by a forestry company from 1957 or 1958, although some homesteads were abandoned more recently (Karl Reingruber, pers. comm.). Since consolidation, the abandoned homesteads have been surrounded by pine plantations. In all, 13 abandoned homesteads gardens were surveyed at Lekgalameetse Nature Reserve (N = 9) and in the Weltevreden area (N = 4).

2.3.1 Field methods

At each abandoned homestead, the geographic coordinates of the main house were taken. Abandoned homesteads (Figure 1) were systematically surveyed by walking away from the main house in a zigzag manner to cover all the area. All vascular plant species of alien ornamentals originating from the garden of the abandoned homestead were recorded (Figure 1). We only stopped surveying for alien species around the house when no alien ornamental plants species could still be seen. Where there was more than one building around the homestead, the main house was assumed to be the central point of the homestead.

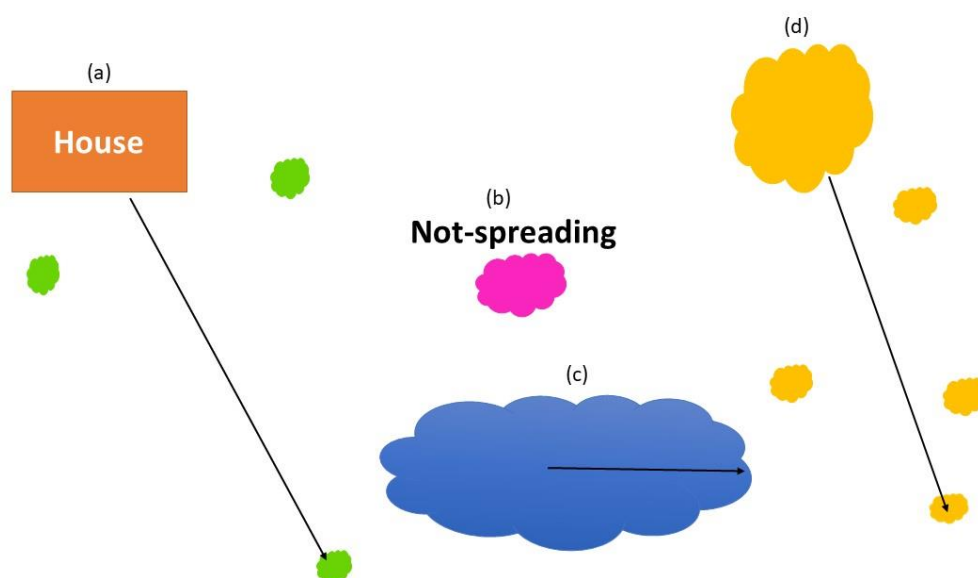


Figure 1: schematic diagram indicating how the distance of spread was determined for alien ornamental plant species. (a), if individuals of the same size were encountered with no clear parent plant, the maximum distance of spread was measured from the house to the furthest individual (green); (b), single plants of a species were recorded as not spreading (pink); (c), the maximum distance of spread for clump-forming species was measured from the centre of the clump to the edge of the clump (blue); and (d), if there was a clear parent plant, the maximum distance of spread was measured from the parent plant to the furthest young individual (orange).





Figure 2: (a-d) some of the abandoned homestead surveyed; (e-j) alien ornamental species found escaping cultivation. (e) *Wigandia urens*, (f) *Sphagneticola trilobata*, (g) *Aristolochia elegans*, (h) *Antigonon leptopus*, (i) *Hedychium gardnerianum*, and (j) *Stachytarpheta mutabilis*.

At each homestead, the maximum distance of spread was determined for individual species, and for each spreading species found, its maximum distance of spread was measured from the source (a point where a spreading species was assumed to have originated; Figure 1). When there were several individuals of the same species of the same approximate age (as assessed by, e.g., height or stem diameter), the source of invasion (i.e. the parent plant) could not be determined with certainty. Therefore, it was assumed that the species were spreading from the house. When several individuals of a species occurred and it was clear

that one individual was older than all others (e.g. one old tree and several younger trees of the same species), the maximum distance of spread was measured from the parent plant to the furthest young individual (i.e. the largest plant individual was recorded as the source). For all nucleating species (i.e. clump-forming species), a distance of spread was measured from the centre to the edge of the clump; it was assumed that the initial plant was planted at the centre and the plant spread evenly from the centre of the clump. When just a single individual of a species was encountered it was recorded as not spreading. When two or more individuals of the same species were encountered and it was clear that they had been planted separately, they were recorded as not spreading (e.g. trees found growing in a row at regular intervals). Alien invasive species which were found in the gardens, but were invasive in the wider landscape (e.g. widely distributed invasive species like *Lantana camara* or *Lilium formosanum*), were considered unlikely to have originated from the abandoned garden and were not surveyed. Native species and alien species growing away from the abandoned homestead with no clarity of origin (e.g. those growing in rivers) were not surveyed.

When the maximum distance of spread was ≤ 30 m, a measuring tape was used to measure the maximum distance of spread. If the maximum distance of spread extended beyond 30 m, a hand-held GPS unit was used to mark the waypoints, and the maximum distance of spread was calculated. In this research problematic species were defined as those which reached a maximum distance of spread above 100 meters irrespective of their reproduction mode (Richardson et al., 2000, Pyšek et al., 2004).

Species identification was done with the use of field guides, gardening books, and the H.G.W.J. Schweickerdt Herbarium (PRU) (Glen and van Wyk, 2016, van der Spuy, 1976a, van der Spuy, 1976b, Walters et al., 2011, Bromilow, 2018, Herbert et al., 1984, Godbold-Simpson and Pienaar, 1993). For each species, its growth form (succulent, tree, shrub, forb, creeper, fern, and grass) and mode of reproduction (sexual, both vegetative, and sexual) were recorded from field guides, the published literature (Foxcroft et al., 2003, Foxcroft et al., 2008, Henderson and Wilson, 2017), and an online database (<https://www.cabi.org/isc/citation>). Lastly, using the NEM: BA alien and invasive species list, I recorded each species' NEM: BA category if they were listed by this legislation (Department of Environmental Affairs, 2014).

2.3.2 Statistical analysis

Due to spread distance data being zero-inflated, I used zero-inflated hurdle mixed models to test whether species growth form, reproductive mode, and NEM: BA category are related to the maximum distance of spread (Zuur et al., 2009). To account for unmeasured homestead-specific environmental variables that may affect the spread of alien invasive ornamentals from abandoned gardens, species name and garden identity were included as random effects in the models. The average distance of spread per family was also calculated. First, for each species, I averaged the maximum distance of spread across all the homesteads in which the species spread; only species with a maximum distance of spread greater than zero were included. Thereafter, I averaged the distances of spread for all the species in a family. Statistical analyses were all run in R statistical software version 4.0.3 (Team, 2020) with the packages car, lmerTest, glmmTMB, reshape2, ggplot2, gridExtra (Baptiste, 2017, Kuznetsova et al., 2017, Brooks et al., 2017, Wickham, 2016, Wickham, 2007).

2.4 Results

From the 13 abandoned homestead gardens surveyed, 115 alien ornamental plant species were recorded (Table A2 in supplementary materials), of which 47 were NEM: BA listed and 68 were non-listed species. There were 65 spreading species, 52.3 % of which were NEM: BA listed, and 47.7% non-NEM: BA listed. There were 50 non-spreading species and 26% were NEM: BA listed.

The family with the highest average maximum distance of spread was Proteaceae with a single spreading species' *Hakea salicifolia*, followed by Simaroubaceae with 3 species, and Zingiberaceae with 4 species (Figure 3a). The families with the highest number of alien ornamental species recorded were Solanaceae, Rosaceae, Lauraceae, Euphorbiaceae, and Bignoniaceae (Figure 3b)

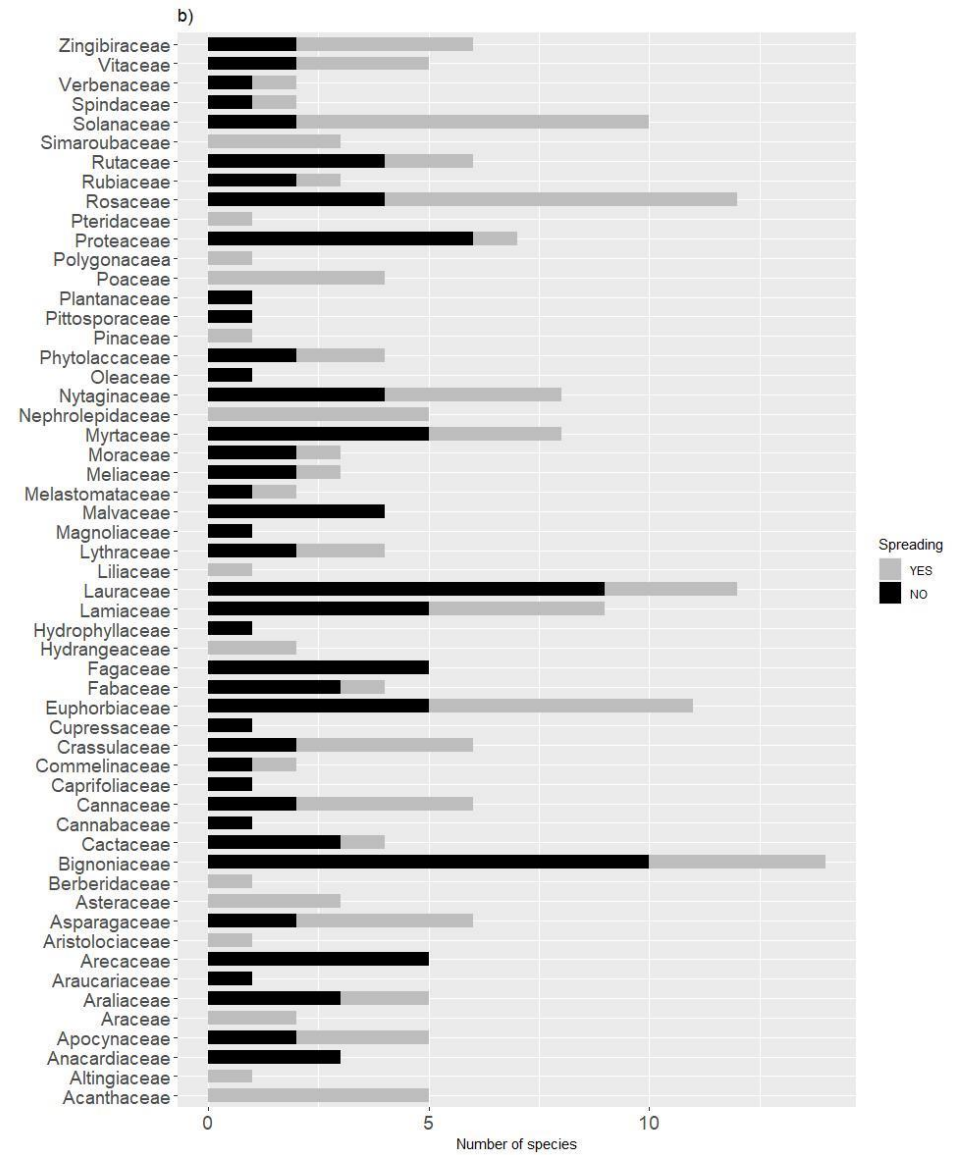
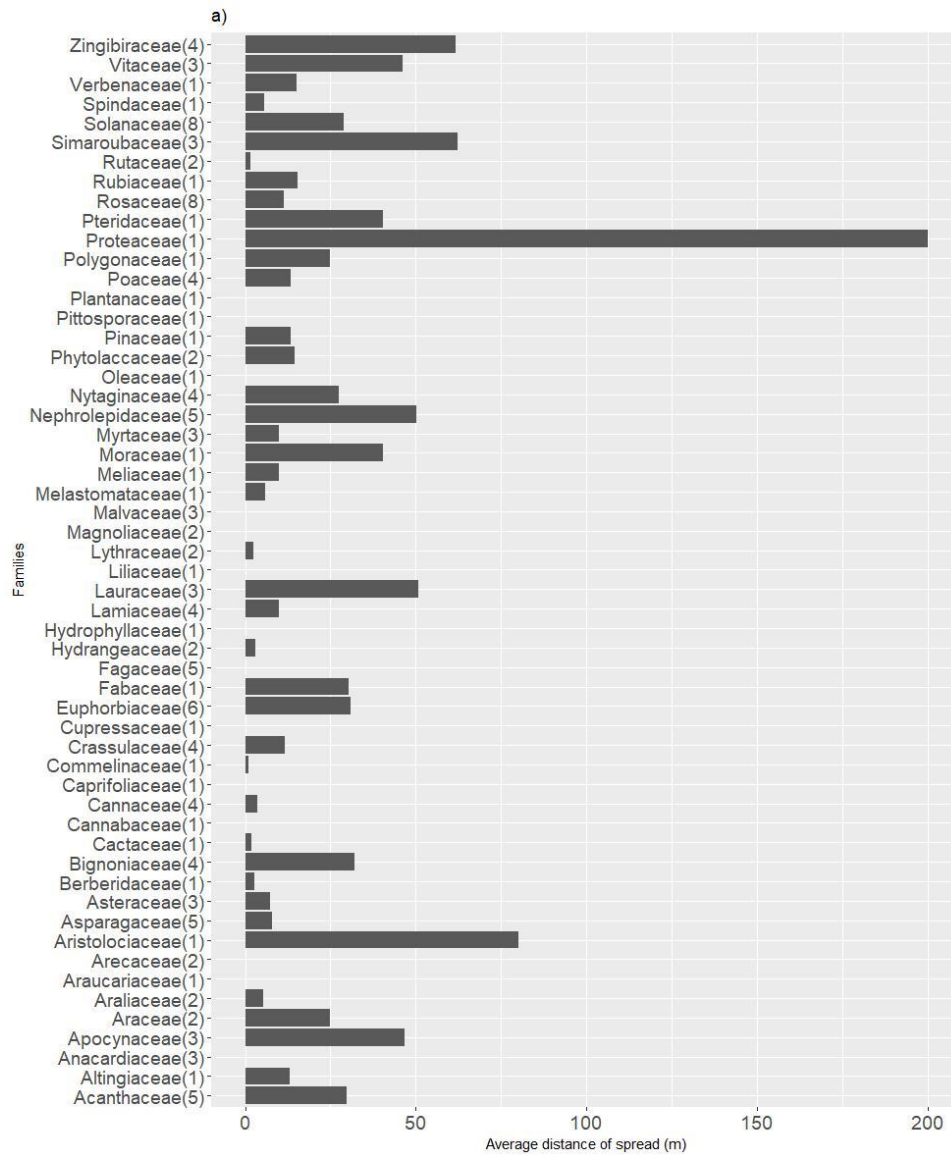


Figure 3: (a) the average maximum distance of spread per family. The number in brackets indicates the number of spreading species recorded per family. For each species, I averaged the maximum distance of spread across all the homesteads in which a species spread using only distances greater than zero. Thereafter, I averaged the distance of spread for all the species in a family; (b) a stacked bar graph showing the number of spreading and non-spreading species per family.

The maximum distance of spread was significantly higher for the NEM: BA listed species than for the non-listed species ($P = 0.003$; Figure 4a). There was no significant difference in the maximum distance of spread between the modes of reproduction ($P = 0.319$; Figure 4b). Species reproducing sexually spread to a maximum distance of 200 m, while those using both modes of reproduction reached 139 m ($P = 0.141$; Figure 4b). Growth form was not a significant predictor of the maximum distance of spread (Figure 4c). A higher number of shrubs were spreading followed by the herbs (Figure 5). The trees had the highest number of non-spreading species. The grasses ($n = 4$ species) and the ferns ($n = 6$ species) only had spreading species (Figure 5).

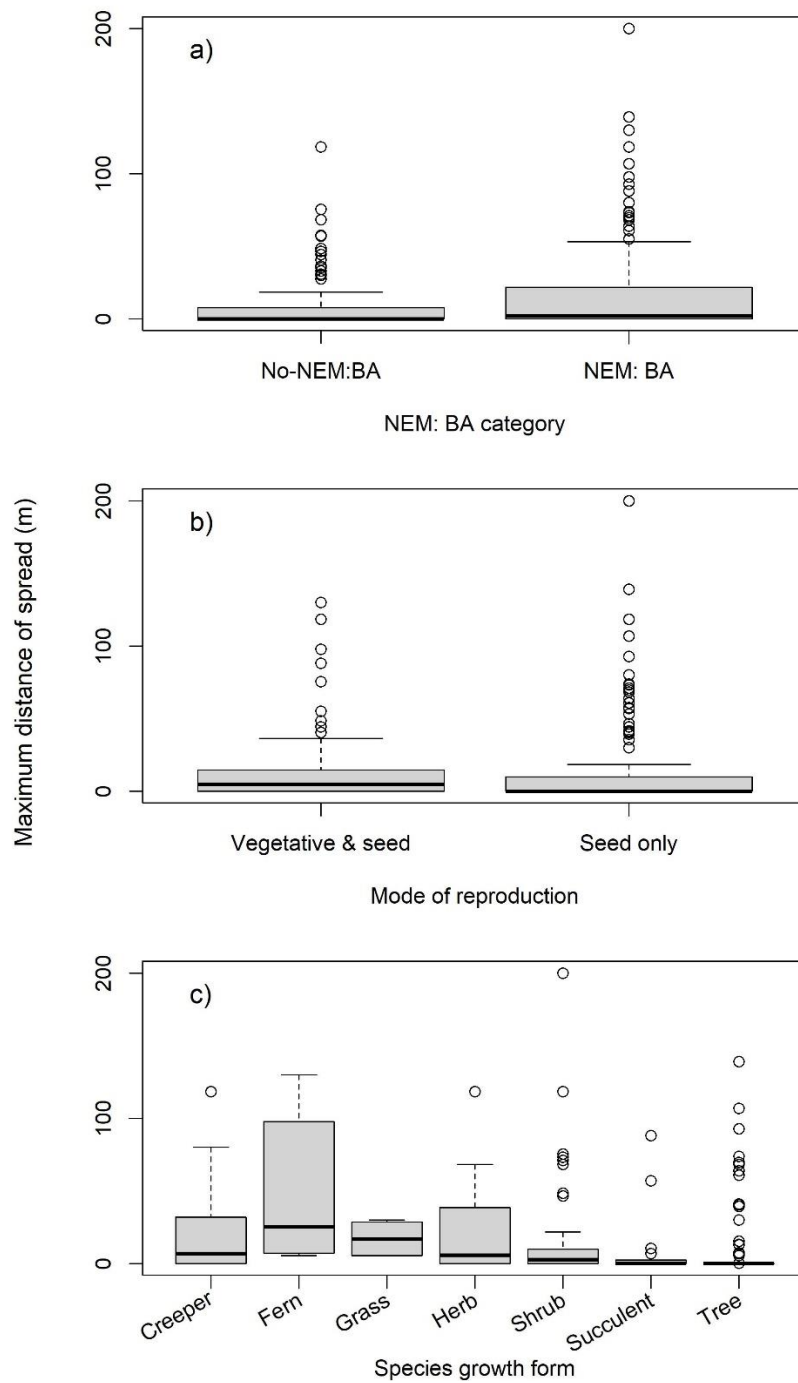


Figure 4: (a) NEM: BA listed species spread further than non-listed alien ornamentals ($P = 0.003$); (b) no significant difference found in the maximum distance of spread between different modes of reproduction ($P = 0.319$); (c) maximum distance of spread did not differ significantly between growth forms ($P = 0.141$). Boxes indicate the inter-quartile range and the black line indicates the median. The whiskers indicate the range of data and the circles indicate outliers.

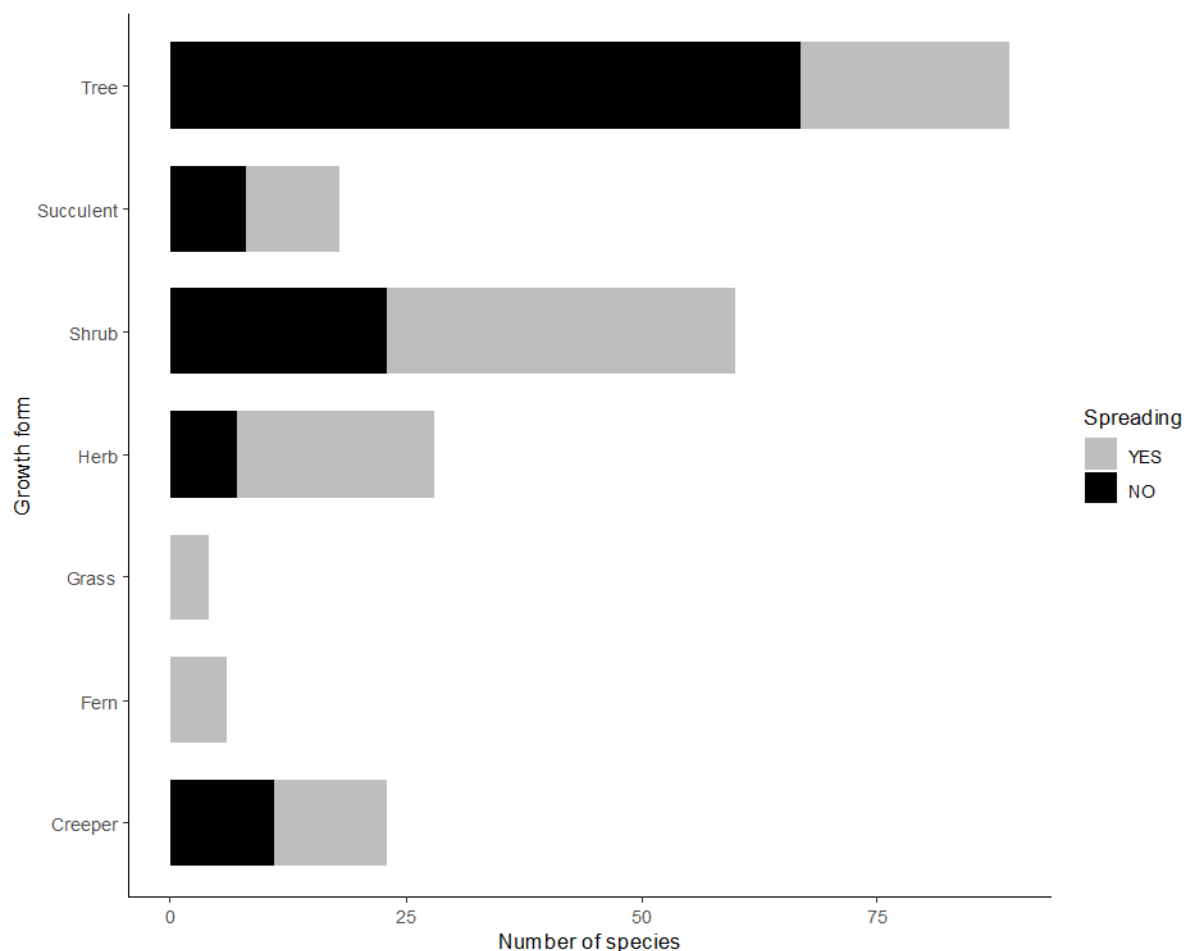


Figure 5: number of spreading and non-spreading species per growth form.

2.5 Discussion

Of the 115 alien ornamentals species that had remained in the 13 homesteads' gardens after several decades of abandonment, more than half were spreading into the surrounding natural vegetation. These ornamental escapees were spreading at different rates, although it was not possible to calculate the exact rate of spread at individual homesteads because the date of abandonment was not known. Some of the species which I found escaping cultivation were also recorded as cultivation escapees in east Africa, including *Antigonon leptopus*, *Bryophyllum delagoense*, *Chromolaena odorata*, *Cardiospermum grandiflorum*, and *Tecoma stans* (Witt et al., 2018), and in the Kruger National Park, including *Alpinia zerumbet*, *Aristolochia elegans*, *B. delagoense*, *Sphagneticola trilobata* and *T. stans* (Foxcroft et al., 2008).

The spreading species which were identified as problematic (here classified as those which spread >100 m) included *H. salicifolia*, *Cinnamomum camphora*, *Nephrolepis exaltata*,

Hedychium coronarium, and *Ailanthus altissima*. All these species are currently NEM: BA listed and have been recorded to be escaping cultivation elsewhere in southern Africa (Witt et al., 2018, Henderson and Wilson, 2017). Their records as cultivation escapees explain why they are already listed in the legislation, especially because NEM: BA is strongly influenced by the Southern Africa Plant Invader Atlas (SAPIA), which mainly records alien species escaping cultivation (Henderson and Wilson, 2017, McLean et al., 2017).

However, not all problematic species are currently listed on NEM: BA. For example, *Physalis peruviana* and *Vitis vinifera* are agricultural species that were also considered problematic and which are considered moderate invaders in South Africa (Nel et al., 2004, Henderson, 2007). The listing as moderate invaders does not adequately reflect the invasion potential posed by these species (since species that spread > 100 meters without human intervention in ≤ 50 years are considered invasive Pyšek et al., 2004). I suggest that *Physalis peruviana* and *Vitis vinifera* be listed on NEM: BA as category 2 which can be planted for commercial use and not allowed to spread outside of cultivation (Department of Environmental Affairs, 2014).

The number of invasive species varies among families, possibly reflecting how some families have been intentionally introduced more frequently than others. For example, the Fabaceae family dominate southern Africa in the number of alien species and the species escaping cultivation (Richardson et al., 2020), in part due to many species in this family having been intentionally introduced and distributed (Henderson and Wilson, 2017, Henderson, 2007, Silas Semanya and Maroyi, 2020). In contrast to what has been reported in other studies, I recorded a moderate number of Fabaceae species, most of which were not spreading. Indeed, only the ornamental Fabaceae species *Bauhinia variegata* was recorded spreading in this study, and the species is currently listed on NEM: BA. The discrepancy between my results and previous research may reflect how studies have typically found Fabaceae to dominate in a broad content whereas my work was specifically focused on alien ornamental plant species escaping abandoned gardens (de Castro et al., 2016, Richardson et al., 2020).

Families with > 2 species with an average maximum distance of spread > 25 m were Acanthaceae, Apocynaceae, Bignoniaceae, Euphorbiaceae, Lauraceae, Nephrolepidaceae, Nyctagynaceae, Simaroubaceae, Solanaceae, Vitaceae, and Zingibiraceae (Figure 3a). The 3 families with only spreading species and an average maximum distance of spread > 25 m

were Bignoniaceae, Nephrolepidaceae, and Simaroubaceae (Figure 3). This indicates a potential for these families to invade larger areas in the future since they were recorded to only having spreading species. Proteaceae showed the highest maximum distance of spread but was represented by a single species, *Hakea salicifolia*. Modelling for this species indicates that high summer rainfall areas are particularly suitable for its occurrence (Moodley et al., 2014). The Zingiberaceae family was recorded from many abandoned homesteads, possibly due to its medicinal and culinary uses. This family was also reported that it was cultivated in the Kruger National park (Foxcroft et al., 2008).

2.5.1 Factors related to the spread of alien ornamental plants

I expected to find NEM: BA status, growth form, and reproduction mode to influence the maximum distance of the spread, but observed that only NEM: BA status was related to the distance of spread (with listed species spreading further). No significant difference was found in the maximum distance of spread between growth form types. Growth form is not extensively explored in determining the maximum distance of spread of alien ornamental species (Beckman et al., 2018, Tamme et al., 2014). In general, most invasive species are trees and shrubs in South Africa, although this may just be a result of introducing more alien trees for timber and for stabilizing the soil than for ornamental purposes (Richardson et al., 2020, Le Maitre et al., 2002, Richardson, 1998), and likely not a result of disproportionate naturalization of these growth forms.

I expected to find species reproducing both sexually and asexually to spread further since dual reproductive modes could allow for multiple forms of dispersal (Albert et al., 2015). Species that reproduce asexually may be perceived to have a lower maximum distance of spread than those reproducing sexually because vegetative reproduction generally limits the distance of spread as offspring are typically growing adjacent to the parent plant. This, however, may be dependent on the environmental conditions because, for example, in an arid environment alluvial floods can spread vegetative propagules for considerable distances (Almirón et al., 2019, Guerrero-Campo et al., 2008, Barrett et al., 2008). Species only reproducing sexually may also face challenges in new environments (e.g. lack of specialist pollinators), and their adaptation to new environmental conditions may require longer residency time than for species reproducing asexually (eg. changing genetically in response to new environment, Gao et al., 2018, Barrett et al., 2008, Mazzolari

et al., 2017). My measurements of maximum distances of spread may be underestimates for some species because seeds could have reached greater distances than what was surveyed (Foxcroft et al., 2008). Therefore, the mode of reproduction may not be a good indicator of the maximum distance of spread for ornamental alien plant species. Indeed, species such as *Arundo donax* (recorded in this study) and *Bambusa* species, which mainly reproduce asexually, have invaded large areas globally despite lacking sexual reproduction (Visser et al., 2017, Milton, 2004, Canavan et al., 2019).

The maximum distance of spread of the NEM: BA listed species was significantly greater than that of the non-listed species. This agrees with research conducted at the national scale where NEM: BA listed species were recorded to have a larger range size than non-listed species (Henderson and Wilson, 2017). This pattern likely reflects that the NEM: BA-listed species have correctly been classified, and do represent a greater threat and require more attention than non-listed species. Nonetheless, it is important to continue monitoring the non-listed spreading species to prevent further invasions.

Some of the abandoned gardens had species confined to one area with naturalized populations. Some of these may have been in a lag phase (Crooks, 2005, Coutts et al., 2018), i.e. they will spread in future. This is of great concern particularly for the abandoned gardens found in Lekgalameetse Nature Reserve because with suitable conditions the species in lag phase may invade the area. This is an issue because when species are in lag phase often they may spread when suitable conditions rises. For example, in another study the invasive species *Bankia ericifolia* was in a lag-phase for a long time and only after wild fires the species became invasive (Geerts et al., 2013). In this study, the species *Wigandia urens* currently NEM: BA listed as category 3, was found not spreading, but is likely to spread in the future (Department of Environmental Affairs, 2014). Other species which were recorded as invasive but were not spreading, i.e. may currently be in a lag phase, include *Pereskia aculeate* and *Phytolacca dioica* (Department of Environmental Affairs, 2014). Other species were found to have just started to spread, some may just be exiting the lag phase (indicated by a short spreading distances from the source). These species could have been *Parthenocissus quinquefolia*, *Vincor minor*, and *Yucca filamentosa*. Of these *Vincor minor* was the only NEM: BA listed species in this case (Department of Environmental Affairs, 2014).

I show that some ornamental species from homesteads that have been abandoned for up to 63 years can maintain their populations and spread without human intervention. It is, therefore, important to investigate the role of abandoned homesteads gardens as a source of alien ornamental escapees that may invade surrounding natural landscapes, especially since abandoned rural homesteads are poorly explored in South Africa and little is known about the species growing around them. Not only are abandoned gardens a problem but also abandoned cultivated lands may act as a source of alien invasion. It was found that, in the Eastern Cape province of South Africa, abandoned farmlands promoted the spread of invasive plant species to surrounding natural environments (Scorer et al., 2019). Species from abandoned cultivation show a potential to compete with native species and if not controlled their population sizes can be increased and may dominate native plant communities (Foxcroft et al., 2019, Sheppard et al., 2010). My results specifically suggest that Solanaceae, Rosaceae, Lauraceae, Euphorbiaceae, and Bignoniaceae should be monitored and cleared as they comprised a large number of spreading species. Information on potential threats by specific families can be made available in the form of posters and be distributed to different stakeholders (including specifically farmers). Farmers should also be encouraged to plant native species in their gardens instead of alien ornamental species now that their impacts are known.

My observations during data collection suggest that further work is required to examine the spread of alien plant species along riparian corridors. While this study focused on alien ornamental species escaping cultivation, some observations were also made in adjacent riparian habitats that species were spreading along streams with naturalized populations (including *Alpinia zerumbet*, *Hedychium coronarium*, and *Hedychium gardnerianum*). These species that formed the naturalized populations were not surveyed because they were not of interest to this study but still remain a concern.

2.5.2 Management

Abandoned homesteads' gardens can be a source of alien invasion to surrounding landscapes as some alien ornamental plant species have been shown in this study to survive and spread (see also: Foxcroft et al., 2008, van Wilgen et al., 2020). This is despite the fact that many of the species that may previously have occurred in the gardens have died off. To prevent or minimise the risk from abandoned homesteads it will be best to remove all alien

plants from cultivation following abandonment. I further recommend that five ornamental escapees, *Adiantum raddianum*, *Hypoestes phyllostachya*, *Monstera deliciosa*, *Parthenocissus quinquefolia*, and *Solanum dulcamara* be additionally listed on NEM: BA because they were found spreading > 30 m without human care (Kumschick et al., 2020, Blackburn et al., 2014). Furthermore, *Physalis peruviana*, *Prunus persica*, and *Vitis vinifera* should be listed on NEM: BA as category 2, only be grown in cultivation, and should not be allowed to spread. The rationale for listing these species as category 2 is because the species are commercially important and edible. The farmers should be informed that the species are not allowed to spread from cultivation to adjacent natural landscapes.

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2.7 Appendix

Table A1: coordinates of all the abandoned homesteads surveyed

Site	Location point
Mpumalanga: Weltevreden Sappi plantations	
House 1	S 25.33520°, E 30.55092
House 2	S 25.33738°, E 30.53455
House 3	S 25.31226°, E 30.53011
House 4	S 25.33794°, E 30.56130
Limpopo: Lekgalameetse Nature Reserve	
House 5	S 24.09126°, E 30.18319
House 6	S 24.14271°, E 30.19798
House 7	S 24.13521°, E 30.17993
House 8	S 24.13579°, E 30.18299
House 9	S 24.10068°, E 30.14096
House 10	S 24.10803°, E 30.21214
House 11	S 24.10068°, E 30.14096
House 12	S 24.13855°, E 30.17958
House 13	S 24.12384°, E 30.17959

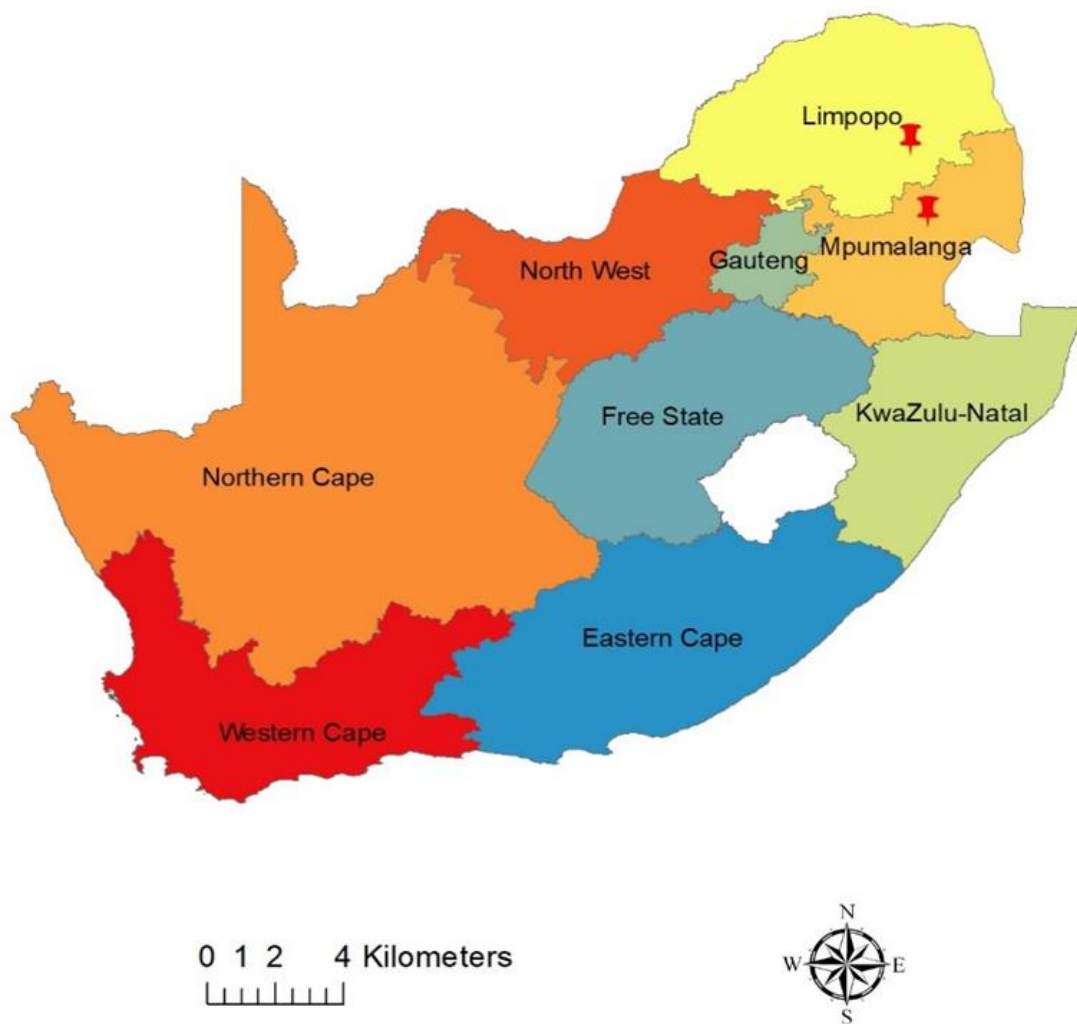


Figure A1: the location pin indicates the study areas in Limpopo and Mpumalanga provinces

Table A2: alien ornamental species recorded in field, family, NEM: BA status, growth form and mode of reproduction

Species name	Family	NEMBA	Growth form	Reproduction mode
<i>Acalypha wilkesiana</i> Müll Arg.	Euphorbiaceae	Not listed	Shrub	Sexual
<i>Acer buergerianum</i> Miq.	Spindaceae	3	Tree	Sexual
<i>Adiantum raddianum</i> C.Presl.	Pteridaceae	Not listed	Fern	Sexual and vegetative
<i>Aesculus hippocastanum</i> L.	Spindaceae	Not listed	Tree	Sexual

<i>Agave sisalana</i> Perrine.	Asparagaceae	2	Succulent	Sexual and vegetative
<i>Ailanthus altissima</i> (Milli.) Swingle.	Simaroubaceae	1b	Tree	Sexual
<i>Alpinia zerumbet</i> (Pers.) B.L.Burt & Perrine.	Zingiberaceae	3	Shrub	Sexual and vegetative
<i>Antigonon leptopus</i> Hook. & Arn.	Polygonaceae	1b	Creeper	Sexual and vegetative
<i>Araucaria heterophylla</i> (Salisb.) Franco.	Araucariaceae	Not listed	Tree	Sexual and vegetative
<i>Archontophoenix alexandrae</i> (F.Muell.) H.Wendl & Drude.	Arecaceae	Not listed	Tree	Sexual
<i>Aristolochia elegans</i> Mast.	Aristolochiaceae	1b	Creeper	Sexual
<i>Arundo donax</i> L.	Poaceae	1b	Grass	Sexual and vegetative
<i>Bambusa balcooa</i> Roxb.	Poaceae	Not listed	Grass	Sexual and vegetative
<i>Bambusa oldhamii</i> Munro.	Poaceae	Not listed	Grass	Sexual and vegetative
<i>Bauhinia variegata</i> L.	Fabaceae	1b	Tree	Sexual
<i>Berberis thunbergii</i> DC.	Berberidaceae	Not listed	Shrub	Sexual
<i>Bougainvillea glabra</i> Choisy.	Nyctaginaceae	Not listed	Shrub	Sexual and vegetative
<i>Bougainvillea spectabilis</i> Willd.	Nyctaginaceae	Not listed	Shrub	Sexual and vegetative
<i>Brachychiton populneus</i> (Schott & Endl.) R.Br.	Malvaceae	Not listed	Tree	Sexual
<i>Bryophyllum delagoense</i> (Eckl & Zeyh) Schinz.	Crassulaceae	1b	Succulent	Sexual and vegetative
<i>Butia capitata</i> (Mart.) Becc.	Aracaceae	Not listed	Tree	Sexual

<i>Caesalpinia pulcherrima</i> (L.) Sw.	Fabaceae	Not listed	Tree	Sexual
<i>Callistemon citrinus</i> (Curtis) Skeels.	Myrtaceae	3	Tree	Sexual
<i>Callistemon rigidus</i> R.Br.	Myrtaceae	3	Shrub	Sexual
<i>Campsis radicans</i> (L.) Seem.	Bignoniaceae	Not listed	Creeper	Sexual and vegetative
<i>Canna indica</i> L.	Cannaceae	1b	Shrub	Sexual and vegetative
<i>Casimiroa edulis</i> La Llave & Lex.	Rutaceae	Not listed	Tree	Sexual
<i>Catharanthus roseus</i> (L.) G.Don.	Apocynaceae	1b	Herb	Sexual
<i>Cedrus deodara</i> (Lamb) G.Don.	Pinaceae	Not listed	Tree	Sexual
<i>Ceiba speciosa</i> (A.st. -Hil., A.juss. & Cambess) Ravenna.	Malvaceae	Not listed	Tree	Sexual
<i>Celtis sinensis</i> Pers.	Cannabaceae	3	Tree	Sexual
<i>Cestrum aurantiacum</i> Lindl.	Solanaceae	1b	Shrub	Sexual and vegetative
<i>Cinnamomum camphora</i> (L.) J.Presl.	Lauraceae	1b	Tree	Sexual
<i>Citrus limon</i> (L.) Burm.fil.	Rutaceae	Not listed	Tree	Sexual
<i>Coffea arabica</i> L.	Rubiaceae	Not listed	Shrub	Sexual
<i>Cotoneaster franchetii</i> Boiss.	Rosaceae	1b	Shrub	Sexual
<i>Dahlia pinnata</i> Cav.	Asteraceae	Not listed	Shrub	Sexual and vegetative
<i>Dolichandra unguis-cati</i> (L.) L.G.Lohmann.	Bignoniaceae	1b	Creeper	Sexual and vegetative
<i>Duranta erecta</i> L.	Verbenaceae	3	Shrub	Sexual
<i>Echinopsis chamaecereus</i> H.Friedrich & Glaetzle.	Cactaceae	Not listed	Succulent	Sexual and vegetative

<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Rosaceae	3	Tree	Sexual
<i>Euphorbia milii</i> Des Moul.	Euphorbiaceae	Not listed	Succulent	Sexual and vegetative
<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch.	Euphorbiaceae	Not listed	Shrub	Sexual
<i>Fagus sylvatica</i> L.	Fagaceae	Not listed	Tree	Sexual
<i>Ficus rubiginosa</i> Desf.	Moraceae	Not listed	Tree	Sexual
<i>Grevillea robusta</i> A.Cunn. ex R.Br.	Proteaceae	3	Tree	Sexual and vegetative
<i>Hakea salicifolia</i> (Vent.) B.L.Burt.	Proteaceae	1b	Shrub	Sexual
<i>Hedera helix</i> L.	Araliaceae	3	Creeper	Sexual and vegetative
<i>Hedychium coronarium</i> J.Koenig.	Zingiberaceae	1b	Herb	Sexual and vegetative
<i>Hedychium gardnerianum</i> Sheppard ex Ker Gawl.	Zingiberaceae	1b	Herb	Sexual and vegetative
<i>Hibiscus rosa-sinensis</i> L.	Malvaceae	Not listed	Tree	Sexual
<i>Hydrangea macrophylla</i> (Thunb.) Ser.	Hydrangeaceae	Not listed	Herb	Sexual
<i>Hypoestes phyllostachya</i> Baker.	Acanthaceae	Not listed	Herb	Sexual and vegetative
<i>Jacaranda mimosifolia</i> D.Don.	Bignoniaceae	1b	Tree	Sexual
<i>Jatropha gossypifolia</i> L.	Euphorbiaceae	1b	Shrub	Sexual
<i>Kalanchoe baharensis</i> Drake.	Crassulaceae	Not listed	Succulent	Sexual and vegetative
<i>Lagerstroemia indica</i> L.	Lythraceae	Not listed	Tree	Sexual
<i>Ligustrum ovalifolium</i> Hassk.	Oleaceae	1b	Tree	Sexual
<i>Liquidambar styraciflua</i> L.	Altingiaceae	Not listed	Tree	Sexual
<i>Liriodendron tulipifera</i> L.	Magnoliaceae	Not listed	Tree	Sexual

<i>Lonicera japonica</i> Thunb.	Caprifoliaceae	3	Creeper	Sexual and vegetative
<i>Macadamia intergrifolia</i> Maiden & Betch.	Proteaceae	Not listed	Tree	Sexual
<i>Magnolia grandiflora</i> L.	Proteaceae	Not listed	Tree	Sexual
<i>Mangifera indica</i> L.	Anacardiaceae	Not listed	Tree	Sexual
<i>Melia azedarach</i> L.	Meliaceae	1b	Tree	Sexual
<i>Mirabilis jalapa</i> L.	Nyctaginaceae	1b	Herb	Sexual
<i>Monstera deliciosa</i> Liebm.	Araceae	Not listed	Creeper	Sexual and vegetative
<i>Morus alba</i> L.	Moraceae	3	Tree	Sexual
<i>Nephrolepis exaltata</i> (L.) Schott.	Nephrolepidaceae	1b	Fern	Sexual and vegetative
<i>Opuntia monacantha</i> (Willd) Haw.	Cactaceae	1b	Succulent	Sexual and vegetative
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Vitaceae	Not listed	Creeper	Sexual and vegetative
<i>Pedilanthus tithymaloides</i> (L.) Poit.	Euphorbiaceae	Not listed	Succulent	Sexual
<i>Pereskia aculeate</i> Mill.	Cactaceae	1b	Creeper	Sexual
<i>Persea Americana</i> Mill.	Lauraceae	Not listed	Tree	Sexual
<i>Phoenix roebelenii</i> O'Brien.	Arecaceae	Not listed	Tree	Sexual
<i>Physalis angulate</i> L.	Solanaceae	Not listed	Herb	Sexual
<i>Physalis peruviana</i> L.	Solanaceae	Not listed	Shrub	Sexual
<i>Phytolacca dioica</i> L.	Phytolaccaceae	3	Tree	Sexual
<i>Phytolacca octandra</i> L.	Phytolaccaceae	1b	Herb	Sexual
<i>Pittosporum undulatum</i> Vent.	Pittosporaceae	1b	Shrub	Sexual
<i>Platanus acerifolia</i> (Aiton) Willd.	Plantanaceae	Not listed	Tree	Sexual
<i>Platycladus orientalis</i> (L.) Franco.	Cupressaceae	Not listed	Tree	Sexual

<i>Plectranthus amboinicus</i> (Lour.) Spreng.	Lamiaceae	Not listed	Shrub	Sexual and vegetative
<i>Plectranthus argentatus</i> (S.T.Blake).	Lamiaceae	Not listed	Herb	Sexual
<i>Plectranthus comosus</i> Sims.	Lamiaceae	1b	Herb	Sexual
<i>Plumeria alba</i> L.	Apocynaceae	Not listed	Tree	Sexual
<i>Prunus persica</i> (L.) Stokes.	Rosaceae	Not listed	Tree	Sexual
<i>Psidium guajava</i> L.	Myrtaceae	2	Shrub	Sexual
<i>Punica granatum</i> L.	Lythraceae	Not listed	Shrub	Sexual
<i>Pyracantha angustifolia</i> (Franch.) C.K.Schneid.	Rosaceae	Not listed	Shrub	Sexual
<i>Quercus acutissima</i> Carruth.	Fagaceae	Not listed	Tree	Sexual
<i>Quercus palustris</i> Münchh.	Fagaceae	Not listed	Tree	Sexual
<i>Quercus robur</i> L.	Fagaceae	Not listed	Tree	Sexual
<i>Quercus suber</i> L.	Fagaceae	Not listed	Tree	Sexual
<i>Salvia coccinea</i> Buc'hoz ex Etl.	Lamiaceae	Not listed	Herb	Sexual
<i>Sansevieria trifasciata</i> Prain.	Aparagaceae	Not listed	Succulent	Sexual and vegetative
<i>Solanum dulcamara</i> L.	Solanaceae	Not listed	Creeper	Sexual and vegetative
<i>Spathodea campanulate</i> Beauv.	Bignoniaceae	3	Tree	Sexual
<i>Sphagneticola trilobata</i> (L.) Pruski.	Asteraceae	1b	Herb	Sexual and vegetative
<i>Spiraea cantoniensis</i> Lour.	Rosaceae	Not listed	Shrub	Sexual
<i>Stachytarpheta mutabilis</i> (Jacq.) Vahl.	Verbenaceae	3	Herb	Sexual
<i>Syagrus romanzoffiana</i> (Cham.) Glassman.	Arecaceae	Not listed	Tree	Sexual
<i>Synadenium grantii</i> Hook.f.	Euphorbiaceae	Not listed	Succulent	Sexual

<i>Syngonium podophyllum</i> Schott.	Areceae	1b	Creeper	Sexual and vegetative
<i>Syzygium jambos</i> (L.) Alston.	Myrtaceae	3	Tree	Sexual
<i>Tecoma stans</i> Juss. ex Kunth.	Bignoniaceae	1b	Tree	Sexual
<i>Tibouchina granulosa</i> (Desr.) Cogn.	Melastomataceae	Not listed	Shrub	Sexual
<i>Tibouchina urvilleana</i> (DC.) Cogn.	Melastomataceae	Not listed	Shrub	Sexual
<i>Tipuana tipu</i> (Benth.) Kuntze.	Fabaceae	3	Tree	Sexual
<i>Tradescantia pallida</i> (Rose) D.R.Hunt.	Commelinaceae	1b	Herb	Sexual and vegetative
<i>Vinca minor</i> L.	Apocynaceae	1b	Herb	Sexual and vegetative
<i>Vitis vinifera</i> L.	Vitaceae	Not listed	Creeper	Sexual and vegetative
<i>Wigandia urens</i> (Ruiz & Pav.) Kunth.	Hydrophyllaceae	3	Shrub	Sexual
<i>Yucca filamentosa</i> L.	Aparagaceae	Not listed	Shrub	Sexual and vegetative

Chapter 3: The potential distribution and richness of alien ornamental plants escaping abandoned gardens

3.1 Introduction

Alien invasions are a major problem globally (Picker and Griffiths, 2017, Vilà et al., 2011, Richardson and van Wilgen, 2004), with detrimental impacts on the environment, biodiversity, the economy, and human health (van Wilgen et al., 2004, Pimentel et al., 2005, de Lange and van Wilgen, 2010, van Wilgen et al., 2012). The problematic nature of invasive alien plants can partially be attributed to the fact that their invasiveness is often only detected at later stages (i.e. once already naturalized and starting to spread) (Bergmans and Blom, 2001, Wilson et al., 2013). Late detection can be due to the species being inconspicuous (Panetta and Timmins, 2004, Harris et al., 2001), remaining undetected, or growing in areas infrequently accessed or difficult to access (Allen, 2003, Balas and Momsen, 2014).

To mitigate the impacts of alien species, control methods are often implemented (Department of Environmental Affairs, 2014). This requires cooperation from different stakeholders and can be challenging and costly (Bergmans and Blom, 2001, Simberloff et al., 2005). Several methods can be used to control alien invasions, with mechanical and chemical control methods often used in conjunction, though this may lead to soil erosion, leaching, and chemical pollution (Bromilow, 2018, Geerts et al., 2017). Biological control is considered the most environmental-friendly method, but often the introduction of alien biological control agents such as insects and pathogens require extensive testing which is time-consuming and costly; additionally, effective biocontrol agent for number of species are not available (de Lange and van Wilgen, 2010, van Wilgen et al., 2004). Even when extirpation of invasive populations occurs, it is not guaranteed that native vegetation will re-colonize cleared areas (Hobbs and Humphries, 1995, Witkowski et al., 2011) as secondary invasions often follow (O'Loughlin and Green, 2017, Yelenik et al., 2004, Nsikani et al., 2020). Therefore, it is important to detect alien species with invasive potential early for management purposes (Wilson et al., 2013). Early detection of invasive alien plants should be a priority since this could prevent future invasions, and reduce the impacts of invasions on the environment and the resources required for invasion management (Richardson and van Wilgen, 2004, Pimentel et al., 2005, Wilson et al., 2013). At the early stages of invasion,

the potential range size (in terms of climate) of invaders is unknown, but with species distribution models (SDMs) potential range sizes can be predicted. Species distribution models are widely used to estimate the size and location of suitable environments for invasive species (Santamarina et al., 2019, Zhang et al., 2017, Elith and Leathwick, 2009). Species distribution models have gained in popularity since the increase in the digitization of biological collections (such as herbaria) and the growth of open access online resources, such as the Global Biodiversity Information Facility (GBIF) and the Invasive Species Compendium (CABI) (Miller, 2010, Martinez-Minaya et al., 2018). Species distribution models make use of known species occurrence records along with environmental predictor variables (e.g. climate) to make predictions of potential (i.e. suitable) sites where species could occur based mostly on the set of climatic and environmental conditions under which the species currently occurs (Fick et al., 2017, Elith and Leathwick, 2009). (Although in some cases other factors could still be included when modelling species potential distribution, for example biotic interactions and traits (Benito et al., 2019, Veski et al., 2021, Pollock et al., 2018)). SDMs use either presence-only data or both absence and present data (Elith et al., 2006, Elith and Leathwick, 2009, Brotons et al., 2004), with a range of techniques available to analyse both types of occurrence data. SDMs which make use of presence-only data are specifically valuable for modelling the distributions of alien species because these types of data are readily available from herbarium records, published literature, and online databases; in contrast, absence data are typically not readily available and may thus be expensive to collect (Henderson, 2007, Merow et al., 2013).

Several SDM algorithms exist, each with advantages and disadvantages (Benito et al., 2013). A combination of models can be used to overcome this uncertainty (Araújo and New, 2007), with, for example, ensemble modelling techniques using several distribution models that are calibrated using the same data, with the best performing models being given the predictive power (Thuiller, 2003, Ng et al., 2018). Several studies have used ensemble modelling techniques to predict invasive alien species' distribution and found the technique to produce accurate results (Ng et al., 2018, Walker et al., 2017, Fernandes et al., 2019). For example, the distribution of the invasive species *Vespa mandarinia* was modelled using ensemble modelling techniques (Barbet-Massin et al., 2018), with results showing that the species was not yet in equilibrium with the environment, but also that its range size had

increased from the initial occurrence records (Barbet-Massin et al., 2018). Similarly, in Turkana County, Kenya the distribution of *Prosopis* species was calibrated using ensemble modelling technique, which also suggested that these species were not yet in equilibrium with the environment (Ng et al., 2018). Ensemble models have been employed for the distribution of several other invasive species and have been found to produce valuable results, including guiding where to implement monitoring (Ncube et al., 2020, Walker et al., 2017, Gong et al., 2020).

South Africa has been invaded by a large number of alien species, with invasions of new species continuing (van Wilgen et al., 2020). The use and management of invasive species in South Africa are regulated by the National Environmental Management Biodiversity Act (NEM: BA) legislation (Department of Environmental Affairs, 2014). This legislation indicates which species are to be eradicated nationally (NEM: BA category 1a), which are to be controlled and not allowed to spread (NEM: BA category 1b), which can be planted for commercial use and not allowed to spread beyond cultivated areas (NEM: BA category 2), and which can be kept without propagation and trading (NEM: BA category 3). Plant species with the NEM: BA category 1a, 1b, and 3 are prohibited (i.e. cannot be introduced into the country) and category 2 can only be introduced by permit holders (Department of Environmental Affairs, 2014). The legislation does not predict which of the already introduced species are likely to be invasive in the future and not all emerging invasive species are listed. Currently, almost 9000 alien species are known to occur in South Africa (Henderson and Wilson, 2017). For this reason, it is important to model the potential distribution of the NEM: BA listed and the non-listed alien species to further assess their potential threats for management purposes. The produced distribution maps can be used in conjunction with the legislation.

3.2 Aim, objectives and hypotheses

This chapter aimed to assess the potential distribution (i.e. distribution modelled by SDMs) of alien ornamental plant species that persist in, and are escaping cultivation from, abandoned homesteads in South Africa.

The specific objectives were to test:

- a) if there was a correlation between species' distance of spread from abandoned homestead (locally) and their predicted potential distribution range sizes (nationally);
- b) if the species listed on NEM: BA have a higher potential range size than the non-listed species;
- c) if the species which were escaping cultivation had a higher potential range size than the non-spreading species;
- d) if the potential species richness of NEM: BA listed spreading species, NEM: BA listed non-spreading species, non-listed spreading species and non-listed not spreading species differed between regions.

3.3 Methods

Two study sites situated in the north-eastern parts of South Africa were visited and thirteen abandoned gardens were surveyed (Chapter 2). The species modelled in this chapter were recorded in these abandoned homesteads gardens in Limpopo (Lekgalameetse Nature Reserve) and Mpumalanga (Weltevreden area Sappi plantations). The two sites surveyed are located within high rainfall areas of the two provinces (mean annual precipitation of 800 to 1 200 mm p.a.) (Adeola et al., 2019, Dippenaar et al., 2005). All the alien ornamental plant species found with a clear sign of cultivation were recorded (Chapter 2). Each species (from the surveyed gardens) was classified according to the following criteria: NEM: BA listed and escaping cultivation, NEM: BA listed and not escaping cultivation, non-NEM: BA and escaping cultivation, and non-NEM: BA and not escaping cultivation.

The potential distribution of 114 alien ornamental species (Table 1) recorded from abandoned gardens was modelled for South Africa, Lesotho, and Swaziland with an ensemble modelling approach. A *Dahlia* species recorded in Chapter 2 was excluded from the models because it was not identified to species level. The ensemble modelling approach was chosen because the technique makes use of several distribution models which are calibrated using the same data, and the best performing models (in this case with a TSS score > 0.7) are given predictive power (Allouche et al., 2006). This method eliminates uncertainties in choosing the best-performing model (Araújo and New, 2007, Hao et al., 2019, Stohlgren et al., 2010). I used six different SDMs which were calibrated in R statistical

software (version 4.0.2) using the R package biomod2 for ensemble modelling (Thuiller et al., 2016). My ensemble modelling incorporated the following SDM algorithms: generalised additive model (GAM), generalised linear model (GLM), random forests (RF), artificial neural network (ANN), boosted regression trees (GBM), and maximum entropy (Maxent) (Thuiller et al., 2009, Stohlgren et al., 2010, Elith et al., 2006).

Table 1: alien ornamentals recorded from 13 abandoned gardens in the Mpumalanga and Limpopo provinces. NEM: BA = National Environmental Management: Biodiversity Act.

Species	NEM: BA classification	Status as cultivation escapees or not
<i>Acalypha wilkesiana</i> Müll Arg.	Not listed	Not escaping cultivation
<i>Acer buergerianum</i> Miq.	3	Not escaping cultivation
<i>Adiantum raddianum</i> C.Presl.	Not listed	Escaping cultivation
<i>Aesculus hippocastanum</i> L.	Not listed	Escaping cultivation
<i>Agave sisalana</i> Perrine.	2	Escaping cultivation
<i>Ailanthus altissima</i> (Milli.) Swingle.	1b	Escaping cultivation
<i>Alpinia zerumbet</i> (Pers.) B.L.Burt & Perrine.	3	Escaping cultivation
<i>Antigonon leptopus</i> Hook. & Arn.	1b	Escaping cultivation
<i>Araucaria heterophylla</i> (Salisb.) Franco.	Not listed	Not escaping cultivation
<i>Archontophoenix alexandrae</i> (F.Muell.) H.Wendl & Drude.	Not listed	Not escaping cultivation
<i>Aristolochia elegans</i> Mast.	1b	Escaping cultivation
<i>Arundo donax</i> L.	1b	Escaping cultivation
<i>Bambusa balcooa</i> Roxb.	Not listed	Escaping cultivation
<i>Bambusa oldhamii</i> Munro.	Not listed	Escaping cultivation
<i>Bauhinia variegata</i> L.	3	Escaping cultivation
<i>Berberis thunbergii</i> DC.	3	Escaping cultivation
<i>Bougainvillea glabra</i> Choisy.	Not listed	Escaping cultivation
<i>Bougainvillea spectabilis</i> Willd.	Not listed	Escaping cultivation

<i>Brachychiton populneus</i> (Schott & Endl.) R.Br.	Not listed	Not escaping cultivation
<i>Bryophyllum delagoense</i> (Eckl & Zeyh) Schinz.	1b	Escaping cultivation
<i>Butia capitata</i> (Mart.) Becc.	Not listed	Not escaping cultivation
<i>Caesalpinia pulcherrima</i> (L.) Sw.	Not listed	Not escaping cultivation
<i>Callistemon citrinus</i> (Curtis) Skeels.	3	Not escaping cultivation
<i>Callistemon rigidus</i> R.Br.	3	Escaping cultivation
<i>Campsis radicans</i> (L.) Seem.	Not listed	Escaping cultivation
<i>Canna indica</i> L.	1b	Escaping cultivation
<i>Casimiroa edulis</i> La Llave & Lex.	Not listed	Not escaping cultivation
<i>Catharanthus roseus</i> (L.) G.Don.	1b	Escaping cultivation
<i>Cedrus deodara</i> (Lamb) G.Don.	Not listed	Escaping cultivation
<i>Ceiba speciosa</i> (A.st. -Hil., A.juss. & Cambess) Ravenna.	Not listed	Not escaping cultivation
<i>Celtis sinensis</i> Pers.	Not listed	Not escaping cultivation
<i>Cestrum aurantiacum</i> Lindl.	1b	Escaping cultivation
<i>Cinnamomum camphora</i> (L.) J.Presl.	1b	Escaping cultivation
<i>Citrus limon</i> (L.) Burm. fil.	Not listed	Escaping cultivation
<i>Coffea arabica</i> L.	Not listed	Not escaping cultivation
<i>Cotoneaster franchetii</i> Boiss.	1b	Escaping cultivation
<i>Dahlia pinnata</i> Cav.	Not listed	Escaping cultivation
<i>Dolichandra unguis-cati</i> (L.) L.G.Lohmann.	1b	Escaping cultivation
<i>Duranta erecta</i> L.	3	Not escaping cultivation
<i>Echinopsis chamaecereus</i> H.Friedrich & Glaetzle.	Not listed	Not escaping cultivation
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	1b	Escaping cultivation
<i>Euphorbia milii</i> Des Moul.	Not listed	Not escaping cultivation
<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch.	Not listed	Escaping cultivation

<i>Fagus sylvatica</i> L.	Not listed	Not escaping cultivation
<i>Ficus rubiginosa</i> Desf.	Not listed	Not escaping cultivation
<i>Grevillea robusta</i> A.Cunn. ex R.Br.	3	Not escaping cultivation
<i>Hakea salicifolia</i> (Vent.) B.L.Burt.	1b	Escaping cultivation
<i>Hedera helix</i> L.	3	Escaping cultivation
<i>Hedychium coronarium</i> J.Koenig.	1b	Escaping cultivation
<i>Hedychium gardnerianum</i> Sheppard ex Ker Gawl.	1b	Not escaping cultivation
<i>Hibiscus rosa-sinensis</i> L.	Not listed	Not escaping cultivation
<i>Hydrangea macrophylla</i> (Thunb.) Ser.	Not listed	Escaping cultivation
<i>Hypoestes phyllostachya</i> Baker.	Not listed	Escaping cultivation
<i>Jacaranda mimosifolia</i> D.Don.	1b	Not escaping cultivation
<i>Jatropha gossypifolia</i> L.	2	Escaping cultivation
<i>Kalanchoe baharensis</i> Drake.	Not listed	Escaping cultivation
<i>Lagerstroemia indica</i> L.	Not listed	Escaping cultivation
<i>Ligustrum ovalifolium</i> Hassk.	1b	Not escaping cultivation
<i>Liquidambar styraciflua</i> L.	Not listed	Not escaping cultivation
<i>Liriodendron tulipifera</i> L.	Not listed	Not escaping cultivation
<i>Lonicera japonica</i> Thunb.	3	Not escaping cultivation
<i>Macadamia intergrifolia</i> Maiden & Betch.	Not listed	Not escaping cultivation
<i>Magnolia grandiflora</i> L.	Not listed	Not escaping cultivation
<i>Mangifera indica</i> L.	Not listed	Not escaping cultivation
<i>Melia azedarach</i> L.	1b	Escaping cultivation
<i>Mirabilis jalapa</i> L.	1b	Escaping cultivation
<i>Monstera deliciosa</i> Liebm.	Not listed	Escaping cultivation
<i>Morus alba</i> L.	3	Escaping cultivation
<i>Nephrolepis exaltata</i> (L.) Schott.	1b	Escaping cultivation
<i>Opuntia monacantha</i> (Willd) Haw.	1b	Escaping cultivation
<i>Parthenocissus quinquefolia</i> (L.) Planch.	Not listed	Escaping cultivation

<i>Pedilanthus tithymaloides</i> (L.) Poit.	Not listed	Not escaping cultivation
<i>Pereskia aculeate</i> Mill.	1b	Not escaping cultivation
<i>Persea americana</i> Mill.	Not listed	Not escaping cultivation
<i>Phoenix roebelenii</i> O'Brien.	Not listed	Not escaping cultivation
<i>Physalis angulata</i> L.	Not listed	Escaping cultivation
<i>Physalis peruviana</i> L.	Not listed	Escaping cultivation
<i>Phytolacca dioica</i> L.	3	Escaping cultivation
<i>Phytolacca octandra</i> L.	1b	Escaping cultivation
<i>Pittosporum undulatum</i> Vent.	1b	Not escaping cultivation
<i>Platanus acerifolia</i> (Aiton) Willd.	Not listed	Not escaping cultivation
<i>Platycladus orientalis</i> (L.) Franco.	Not listed	Not escaping cultivation
<i>Plectranthus amboinicus</i> (Lour.) Spreng.	Not listed	Not escaping cultivation
<i>Plectranthus argentatus</i> (S.T.Blake).	Not listed	Not escaping cultivation
<i>Plectranthus comosus</i> Sims.	Not listed	Escaping cultivation
<i>Plumeria alba</i> L.	Not listed	Not escaping cultivation
<i>Prunus persica</i> (L.) Stokes.	Not listed	Not escaping cultivation
<i>Psidium guajava</i> L.	2	Escaping cultivation
<i>Punica granatum</i> L.	Not listed	Not escaping cultivation
<i>Pyracantha angustifolia</i> (Franch.) C.K.Schneid.	1b	Escaping cultivation
<i>Quercus acutissima</i> Carruth.	Not listed	Not escaping cultivation
<i>Quercus palustris</i> Münchh.	Not listed	Not escaping cultivation
<i>Quercus robur</i> L.	Not listed	Not escaping cultivation
<i>Quercus suber</i> L.	Not listed	Not escaping cultivation
<i>Salvia coccinea</i> Buc'hoz ex Etl.	Not listed	Not escaping cultivation
<i>Sansevieria trifasciata</i> Prain.	Not listed	Escaping cultivation
<i>Solanum dulcamara</i> L.	Not listed	Escaping cultivation
<i>Spathodea campanulate</i> Beauv.	3	Escaping cultivation
<i>Sphagneticola trilobata</i> (L.) Pruski.	1b	Escaping cultivation
<i>Spiraea cantoniensis</i> Lour.	Not listed	Escaping cultivation

<i>Stachytarpheta mutabilis</i> (Jacq.) Vahl.	3	Escaping cultivation
<i>Syagrus romanzoffiana</i> (Cham.) Glassman.	Not listed	Not escaping cultivation
<i>Synadenium grantii</i> Hook.f.	Not listed	Escaping cultivation
<i>Syngonium podophyllum</i> Schott.	1b	Escaping cultivation
<i>Syzygium jambos</i> (L.) Alston.	3	Not escaping cultivation
<i>Tecoma stans</i> Juss. ex Kunth.	1b	Escaping cultivation
<i>Tibouchina granulosa</i> (Desr.) Cogn.	Not listed	Not escaping cultivation
<i>Tibouchina urvilleana</i> (DC.) Cogn.	Not listed	Escaping cultivation
<i>Tipuana tipu</i> (Benth.) Kuntze.	3	Not escaping cultivation
<i>Tradescantia pallida</i> (Rose) D.R.Hunt.	Not listed	Escaping cultivation
<i>Vinca minor</i> L.	1b	Escaping cultivation
<i>Vitis vinifera</i> L.	Not listed	Escaping cultivation
<i>Wigandia urens</i> (Ruiz & Pav.) Kunth.	3	Not escaping cultivation
<i>Yucca filamentosa</i> L.	Not listed	Escaping cultivation

Climatic predictor variables were extracted from WorldClim version 2.0 (Fick et al., 2017), at a spatial resolution of 2.5 minutes ($\pm 5 \text{ km}^2$). The variables extracted were BIO₁ = annual mean temperature, BIO₄ = temperature seasonality, BIO₅ = maximum temperature of the warmest month, BIO₆ = minimum temperature of the coldest month, BIO₁₂ = annual precipitation, BIO₁₅ = precipitation seasonality, BIO₁₆ = precipitation of wettest quarter, and BIO₁₈ = precipitation of warmest quarter (Fick et al., 2017). The above-mentioned variables were selected because they can directly influence plant growth and survival and are considered to be important determinants of plant distribution in the area of interest (Dale, 1981, McConnachie et al., 2011, Wilson et al., 2020). Global locality records for each species were extracted from the Global Biodiversity Information Facility. Data were extracted on 12 December 2020 and restricted to 800 occurrence records per species. Up to 800 records were selected before cleaning was so that, after cleaning, enough records for SDMs would be available. Number of locality records after cleaning ranged from 800 to 28 per species. Data cleaning was done to remove erroneous or incomplete occurrence records, testing coordinate validity, equal latitude/longitude, zero coordinates, country capitals, country

centroids, GBIF headquarters (flagging records around Copenhagen and biodiversity institutions), and occurrence records that contained blank fields (Zizka et al., 2019).

3.3.1 Model calibration, evaluation, and projection

Pseudo-absence locations were chosen randomly and were double the number of cleaned presence records for each species (Barbet-Massin et al., 2012, Fourcade et al., 2014, Thuiller et al., 2009). The models were calibrated using data from across the whole world; 80% of the cleaned data and pseudo-absences were used for model calibration and the remaining 20% for model validation. The entire five-fold cross-validation was repeated three times.

True skill statistic (TSS) and area under the ROC curve (AUC) were used for model evaluation, and ensemble projection was predicted with TSS (Fielding et al., 1997). All models with a TSS value > 0.7 were automatically included in model projection (Allouche et al., 2006).

The models were projected under the current climatic conditions for South Africa, Lesotho, and Swaziland. Ensemble modelling was run twice, and this generated two presence vs absence maps for each species and the two binary maps were produced using TSS as a threshold (Liu et al., 2005). I then overlaid the produced binary maps per species to determine to which grid cells presences vs absences had been predicted. When overlaying two binary maps, a presence point in the consolidated map was only calculated if both the original maps predicted a presence on the same grid cell, reflecting a conservative approach. These maps were thus consolidated into a single presence-absence map per species from which potential range size in km² was calculated by multiplying the number of cells with presences by the area of the raster cells.

To test for correlation between the species' average maximum distance of spread (the furthest distance a species has spread across all gardens, see Chapter 2) and the predicted potential range size, Pearson's correlation coefficient test was applied.

To investigate the differences in alien ornamental species' range sizes between the spreading and non-spreading species and between the NEM: BA and non-NEM: BA species, the potential distribution range size (as modelled by SDMs) of all the 114 species was calculated. A general linear model was run to test if there were significant differences in species' range sizes between the spreading and non-spreading species and also between the NEM: BA listed and non-NEM: BA species.

To create a potential species richness map, the binary distribution maps of all species were overlaid and summed per group (NEM: BA spreading, NEM: BA not spreading, non-listed spreading, and non-listed not spreading). Therefore, the map showed the richness of species of each group predicted for each grid cell across the modelled area.

R version 4.3.2 was used to run the analyses (Team, 2020), with packages biomod2, car, countrycode, CoordinateCleaner, ggplot2, maps, raster, rgbif, and rgdal (Roger et al., 2020, Wilfried et al., 2020, Arel-Bundock et al., 2018, Zizka et al., 2019, Wickham, 2016, Richard et al., 2018, Robert J. Hijmans, 2020, Chamberlain et al., 2021, Weisberg, 2019).

3.4 Results

SDMs performed well, with averaged model evaluation scores for the species in each group ranging from 0.917 to 0.995 for both TSS and AUC scores (Table 2). Of the 114 species modelled, 7 % had a predicted potential range size of zero. Of these, five were spreading from the abandoned gardens (*Berberis thunbergii*, *Campsis radicans*, *Synadenium grantii*, *Vinca minor*, and *Yucca filamentosa*). *Vinca minor* and *Berberis thunbergii* are both NEM:BA listed (Table 1). The species *Liriodendron tulipifera*, *Magnolia grandiflora*, and *Quercus acutissima* had a zero predicted potential range size, but were not escaping cultivation, and are not listed on NEM: BA (Table A1).

The four species with the highest predicted potential range size were *Canna indica*, *Bauhinia variegata*, *Mirabilis jalapa*, and *Echinopsis chamaecereus*. *Echinopsis chamaecereus* specifically was predicted to have a potential range size of 929'049 km² (c. 73% of the area of South Africa, Lesotho and Eswatini). The species is currently not NEM:BA listed and was not escaping cultivation (Table A1).

Table 2: model evaluation scores for the four different groups of species. True skill statistic (TSS), under the ROC curve (AUC), and their standard deviation (SD).

Potential species richness	TSS: mean $\pm$ SD	AUC: mean $\pm$ SD
NEM: BA listed and spreading	0.917 $\pm$ 0.039	0.992 $\pm$ 0.006
NEM: BA listed and not spreading	0.942 $\pm$ 0.03	0.995 $\pm$ 0.004
Non-listed and spreading	0.925 $\pm$ 0.041	0.992 $\pm$ 0.006

Non-listed and not spreading	0.937 ± 0.044	0.994 ± 0.006
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There was no significant correlation between species' average maximum distance of spread and their predicted potential range size (Figure 1).

No significant difference was found in species potential range size between the NEM: BA listed species and non-listed species (Figure 2a), and no differences were found in potential range size between the spreading species and the non-spreading species (Figure 2b).

The areas of highest potential species richness of the alien ornamental plant species were along the South African eastern and southern coastline and the escarpment. All four sets of species showed similar patterns of highest potential species richness (Figure 3). The biomes potentially at risk of invasion by the alien ornamental escapees modelled here include Savannahs, Grasslands, Forests, Albany Thicket, Fynbos, and the Indian Ocean Coastal Belt (Figure 3). A very low richness was predicted to occur in the Succulent Karoo, the Nama Karoo, or the Desert biome (Figure 3). Minor differences were observed along the Garden Route, with both the NEM: BA listed and non-listed spreading species showing high potential species richness compared to both the NEM: BA listed not spreading species and non-listed not spreading species (Figure 3).

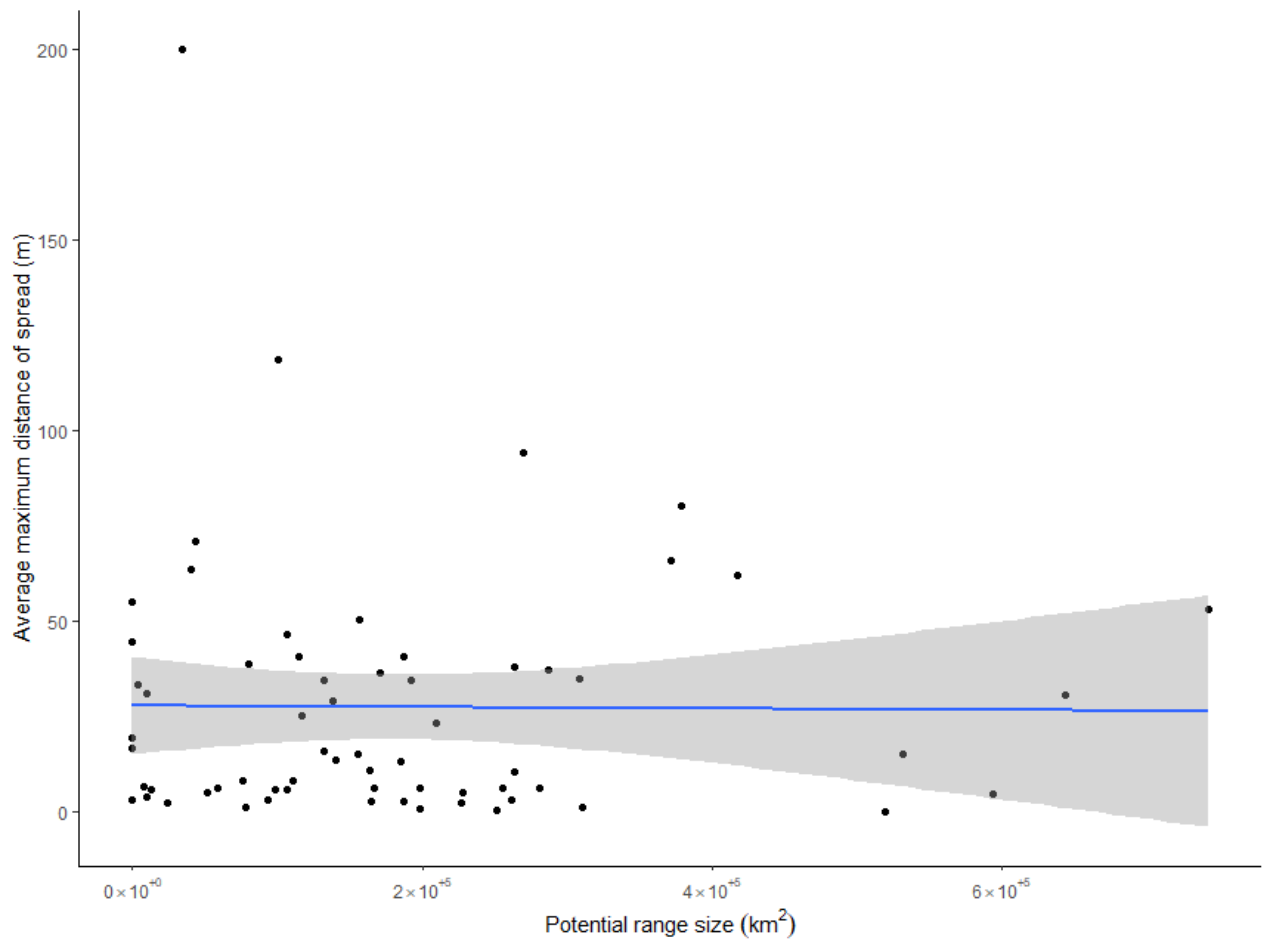


Figure 1: the relationship between species average maximum distance of spread and the predicted potential range size. Average maximum distance of spread for the ornamental escapee species does not influence potential range size ($P = 0.942$, coefficient = -0.010 , $T = -0.0723$; $df = 62$).

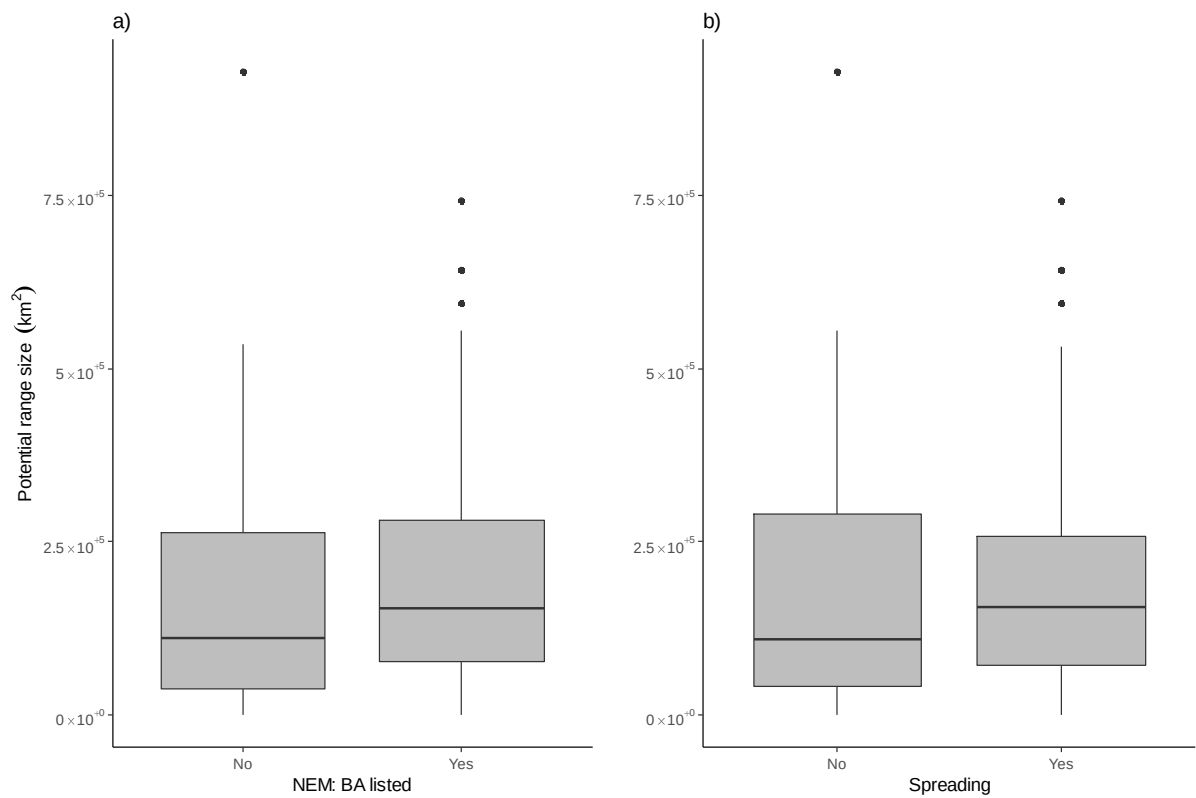


Figure 2: potential species range sizes, predicted from species distribution modelling, of (a) non-NEM: BA listed species and NEM: BA listed species (P-value = 0.184) and (b) non-spreading species and spreading species (P-value = 0.776). Model P-value = 0.409, F-statistic = 0.902, adjusted R-squared = 0%, df = 2 and 111. Boxes indicate the inter-quartile range and the black line indicates the median. The whiskers indicate the range of data and the circles indicate outliers.

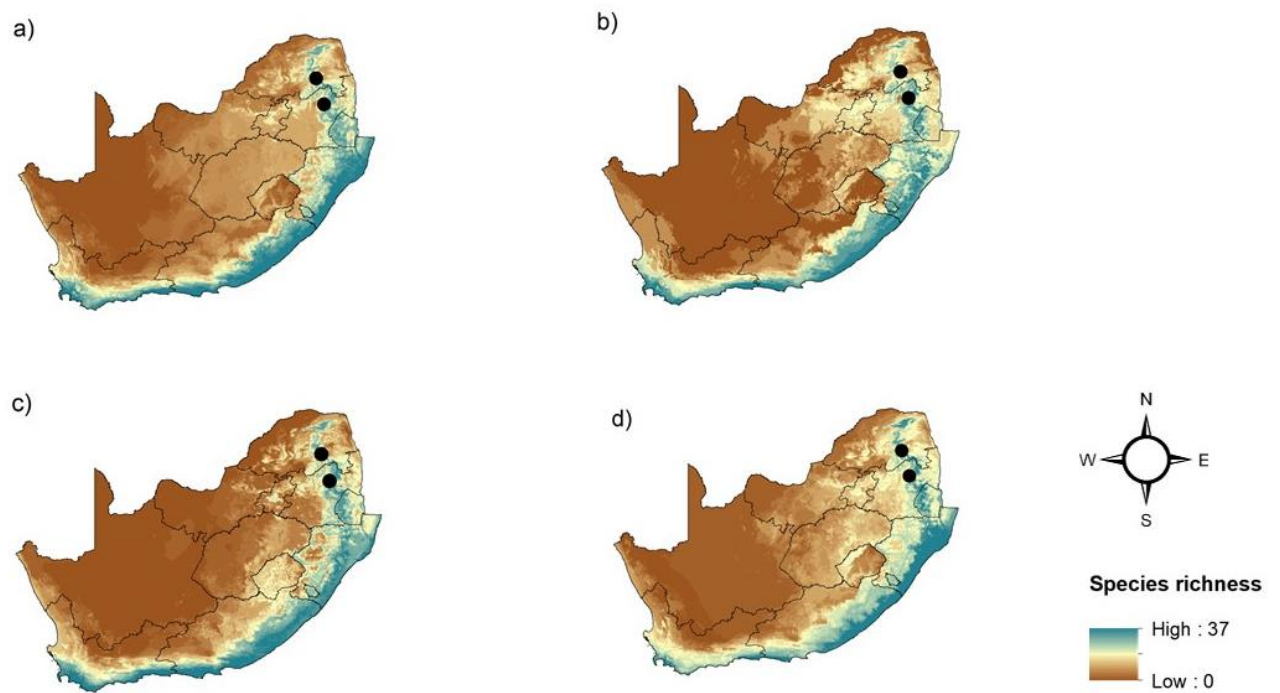


Figure 3: the potential species richness of (a) NEM: BA listed spreading species; (b) NEM: BA listed non-spreading species; (c) non-listed spreading species; (d) non-listed not spreading species. The locations of the abandoned gardens that were surveyed in Limpopo and Mpumalanga are represented by the two black dots.

3.5 Discussion

Overall model performance was good with both TSS and AUC scores ranging from 0.8 to 1 (Table A1). SDM modelling of the 114 alien ornamental plant species suggests that many ornamental species, including those not currently spreading from abandoned gardens and those not listed by NEM: BA legislation, have the potential to spread and invade large areas in southern Africa.

The lack of a relationship between species' average maximum distance of spread and their predicted potential range size indicates that no generalizations should be made that alien ornamentals escaping cultivation have a larger potential range size than the species not currently escaping cultivation (Figure 1). For example, *Echinopsis chamaecereus* was not escaping cultivation, is currently not listed on NEM: BA, and has no invasive records in the literature for South Africa, but the species had the largest potential distribution of all the alien ornamental escapees modelled (Table A1). On the other hand, *Yucca filamentosa* was

escaping cultivation, has no invasive records for South Africa but the species was predicted to have a zero potential range size in South Africa. *E. chamaecereus* was not spreading even with suitable climatic conditions; this could be the results of the species lacking biotic interactions to enable the spread or it could be that environmental variables important for the species were not included in the SDMs. I have not found records of the species being invasive in southern Africa but this does not mean that the species may not be able to spread in the future (Henderson and Wilson, 2017).

This indicates that it is difficult to predict which alien ornamental species from abandoned homesteads' gardens have the potential to spread and invade larger areas from SDMs only. It is difficult to know which species are likely to spread using SDMs results only. Since invasion success is influenced by a combination of factors such as suitable climate and traits it may be difficult to know with certainty what influences a successful invasion. However, I speculate that species reproducing sexually may spread far and invade large areas. Shrubs and trees reached a high maximum distance of spread indicating that they can spread further and invade large areas (Chapter 2: Figure 4c).

The potential range size did not differ between the non-listed and NEM: BA listed species and between the spreading and the non-spreading species (Figure 2). The results indicate that the probability of a species to invade larger areas in South Africa is not influenced by NEM: BA status and the status as a garden escapee; therefore, management selection criteria of emerging invasive species should not only be influenced by species NEM: BA status but by how well invasive species are adapted to a specific area. Invasive species' adaptation can be determined by how far the species have spread since introduction, for example, species reproducing sexually and spreading distances of > 100 m in 50 years, and species spreading > 6 m in 3 years for asexually reproducing species can be considered invasive and should be eradicated (Richardson et al., 2000, Pyšek et al., 2004). I recommend that if species are found persisting and escaping cultivation, they should be considered potential invaders regardless of the number of years they have been spreading. I give this recommendation because with some abandoned gardens the exact time of abandonment may not be known and also because alien invasion is a global concern. The non-significant results also indicate that species found invading one province or area may not be problematic elsewhere in South Africa, but equally species not invading one area may be problematic elsewhere, and therefore this cannot be generalised. This is further

explained by the NEM: BA legislation where for example the species *Hakea salicifolia* is only listed 1b for the Western Cape indicating that the species is not problematic in all the South African provinces (Department of Environmental Affairs, 2014). Similar results were recorded in the Garden Route National Park of South Africa where 35 alien plant species which are not listed on NEM: BA were spreading; five of the 35 species had invaded larger areas than the other emerging invasive species recorded (Baard and Kraaij, 2019). Non-listed alien plants with invasive potential (as inferred from their modelled potential distribution) should be monitored, and preferably eradicated early on, to prevent the species from invading larger areas because some species may be able to increase their potential range in the future due to climate change (Trethowan et al., 2011, Walker et al., 2017, Geerts et al., 2017). Species distribution models by themselves should not dictate which species are potentially invasive, since many other factors influence invasiveness.

The potential species richness of NEM: BA listed spreading species peaks in similar areas as the potential species richness of NEM: BA listed non-spreading species (Figure 3a and b). The expectation was to find the potential species richness hotspots in different areas because the NEM: BA listed spreading species would peak in similar climatic conditions as those of the abandoned gardens and the NEM: BA listed non-spreading species would peak in different climatic condition from those of abandoned gardens. The comparison between the potential species richness of NEM: BA listed spreading species and the non-listed spreading species also showed no differences (Figure 3a and c). NEM: BA listed species are declared problematic in South Africa and their ability to escape abandoned gardens without human care gave an impression that their hotspots may be different from those of the non-listed spreading species. The potential species richness of the non-listed spreading and non-listed not spreading also peaked in similar areas. All the species richness predictions are similar, and this was unexpected. A possible explanation why the species richness peaked in similar areas could be that the species found in the abandoned gardens were introduced into the study area because they are well adapted to the climate of the area. Additionally, species that were unable to survive the climate of the region without human intervention would have quickly died out after abandonment.

My findings are in line with what several other studies have reported that invasions are likely to occur in wetter areas of the country (Richardson et al., 2020, O'Connor and van Wilgen, 2020, Bezeng et al., 2020). Similar results were found for the potential distribution

of the NEM: BA listed invasive ornamental escapee species *Centranthus ruber* which was modelled for southern Africa and the results indicated that the southern coastline and the eastern inland parts of South Africa are at a higher risk of invasion (Geerts et al., 2017). Also, the potential distribution of *Alnus glutinosa* and *Schinus terebinthifolia* indicated similar areas to be at risk (Keet et al., 2020, Martin et al., 2020).

My results may, however, be contingent on the fact that the data for this study were collected from two areas that receive relatively high rainfall, and the dry areas of the country may be under-estimated as areas likely to be invaded. This is because SDMs results are influenced by the species of interest, data used, and the predictor variables. Different species richness hotspots could have been generated if data were collected from the more arid western inland areas of South Africa where drought-tolerant alien species dominate (Masubelele et al., 2009, Petersen et al., 2020). For example, a number of Cactaceae species, which were not observed in this study, are escaping cultivation in the North West and Northern Cape provinces, and different potential hotspots may be produced than what was observed in this Chapter (Chapter 4: Table 1). For the species which were not predicted to occur in South Africa even though the models were calibrated with global data, it could be because of sampling bias (e.g. some species did not have enough GBIF records for regions with similar climate as South Africa). Modelling methods depend also on species having adequate occurrence records, and poorly sampled species may therefore not always have accurately predicted potential range sizes (Syfert et al., 2013).

NEM: BA legislation is a good indicator for alien invasion management but my results indicate that the legislation should not be the only tool used to predict potentially invasive species as it only lists naturalized and invasive species. Species distribution modelling techniques provide an objective method for estimating areas at risk and potential invaders, and from this information, biomes and species can be prioritized on the proposed management plans (van Wilgen et al., 2012).

3.5 1 Management

The potential species distributions modelled in this study indicate areas that are most likely to be invaded by the alien ornamental species observed in abandoned gardens in Mpumalanga and Limpopo should they be successful in spreading (Figure A1). While the SDMs showed high overall accuracy, some species that are spreading were predicted to not

occur within South Africa. I recommend that SDMs results be used in combination with field survey reports for invasive species management (Chapter 2). This will ensure that potentially invasive species are not missed when using one method because SDMs results and field observations estimate different results (Figure A1: Chapter 2). For example, *Echinopsis chamaecereus* (not listed) had the largest potential distribution but is not spreading, while *Yucca fillamentosa* was predicted to a zero potential range size and was found escaping cultivation (Table A1: Chapter 2).

This chapter highlighted that non-listed spreading species are potentially emerging invaders and that SDMs are not always good predictors of the ability of alien species to spread. Further investigations are required to know which species are harmful and which are not, and this can be achieved when field observations and SDMs are used in combination to get more accurate results to which individual alien ornamental species are likely to invade larger areas.

3.6 References

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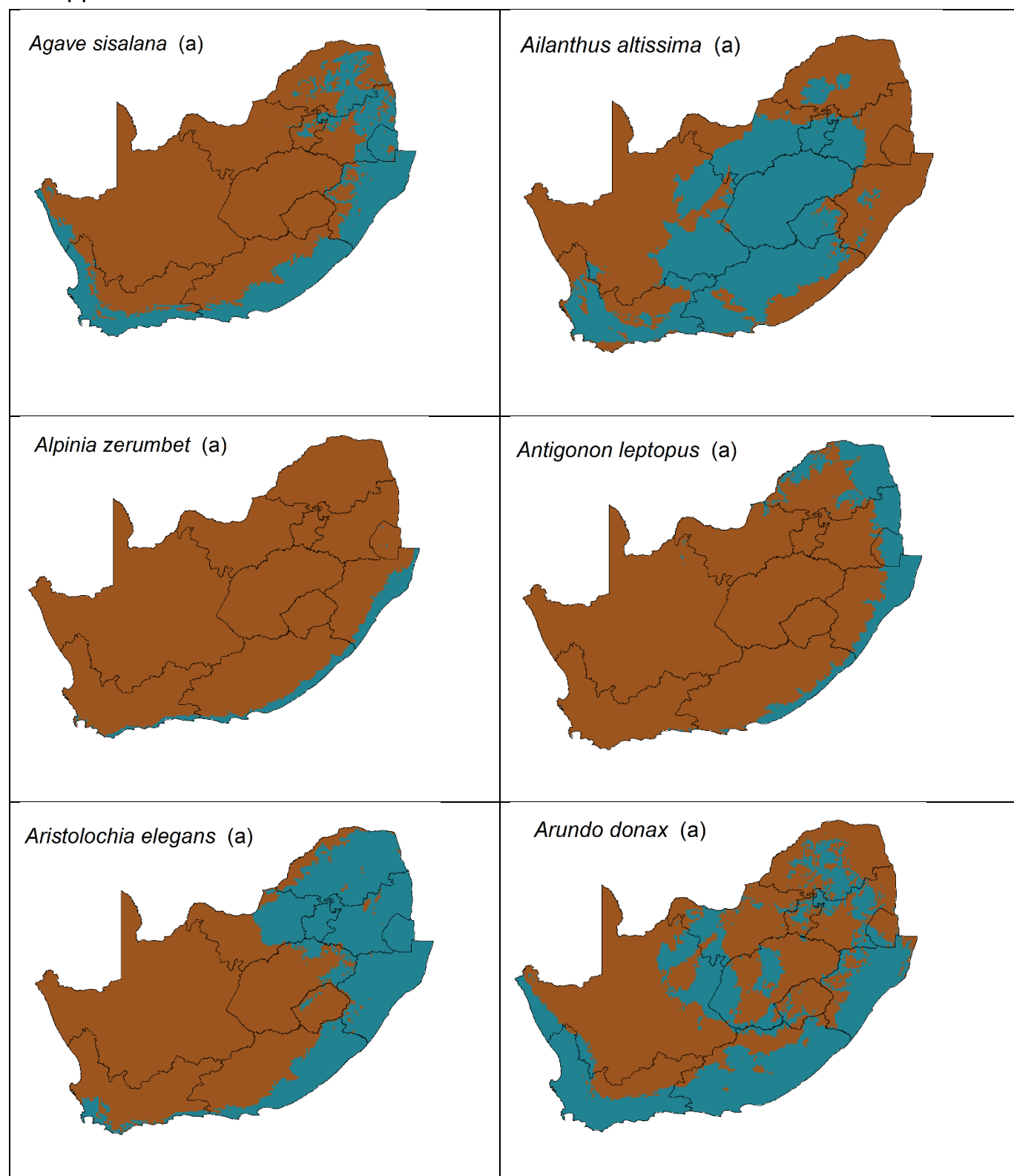
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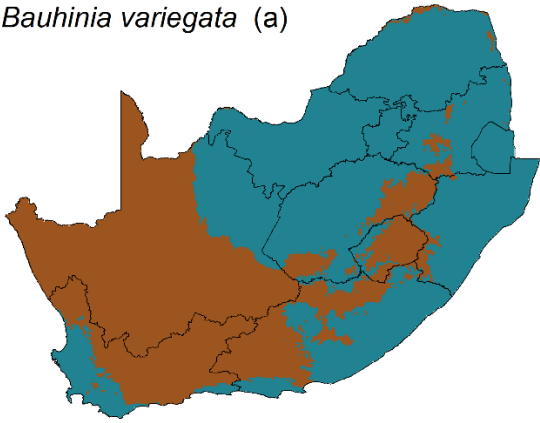
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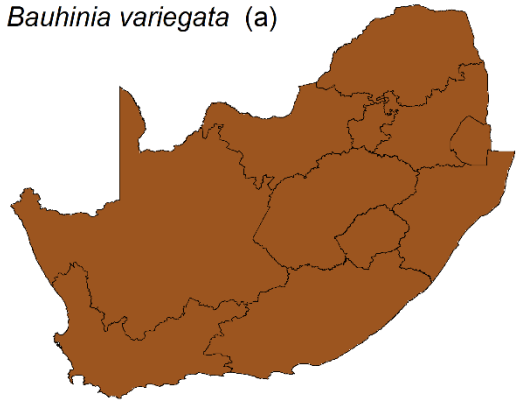
3.9 Appendix



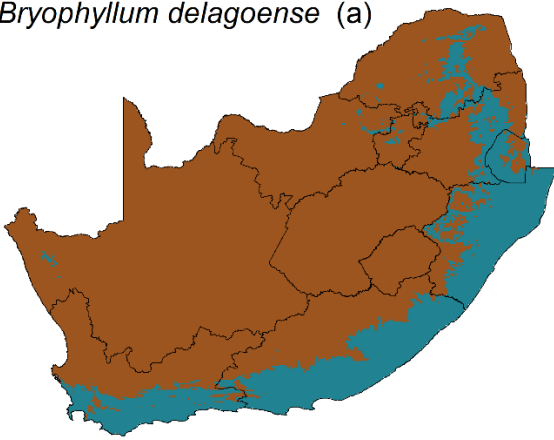
Bauhinia variegata (a)



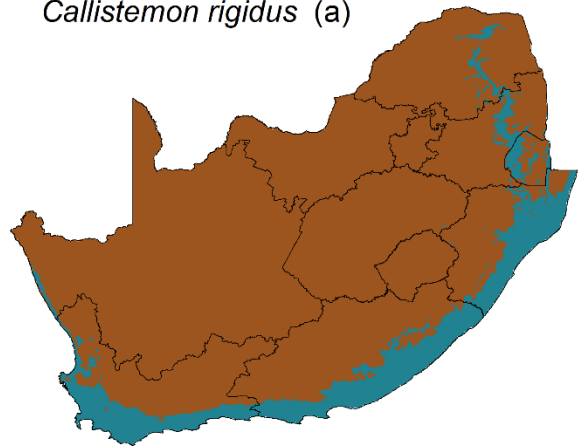
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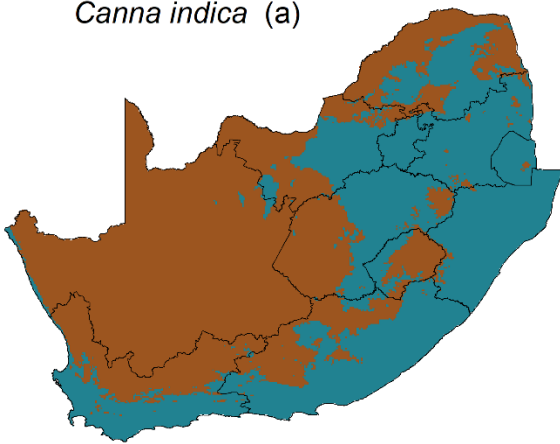
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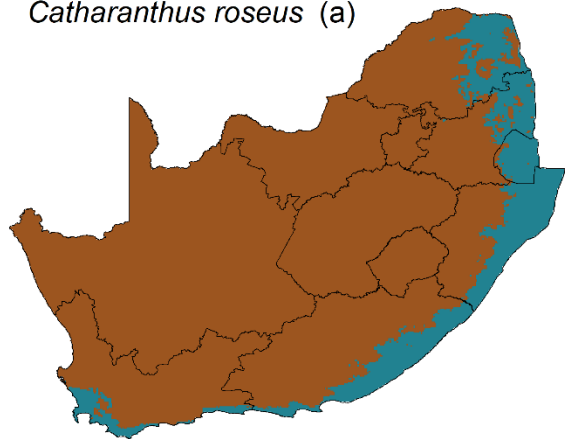
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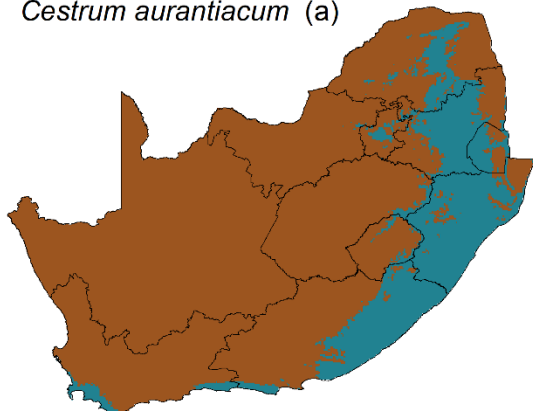
Canna indica (a)



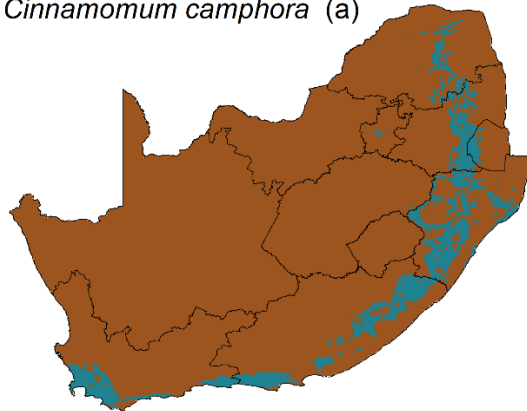
Catharanthus roseus (a)



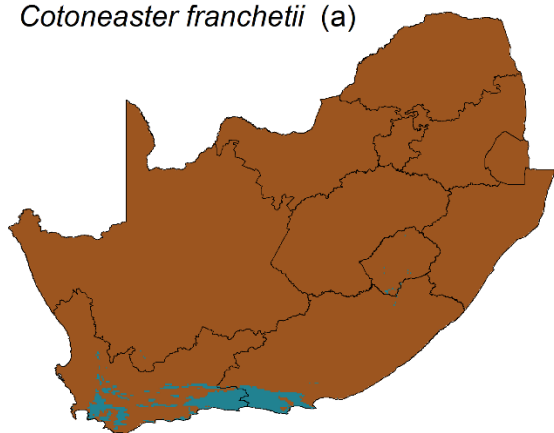
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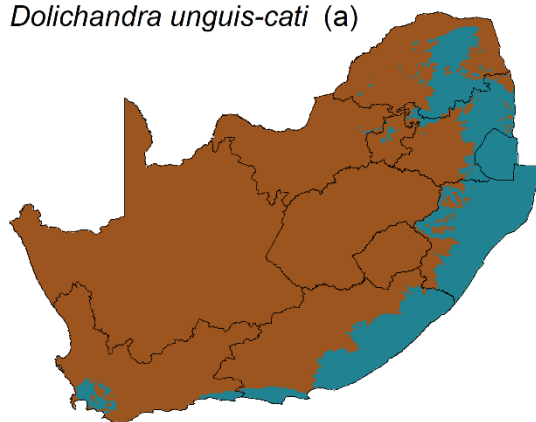
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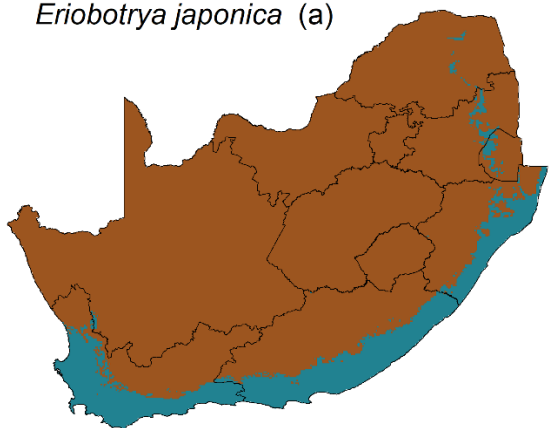
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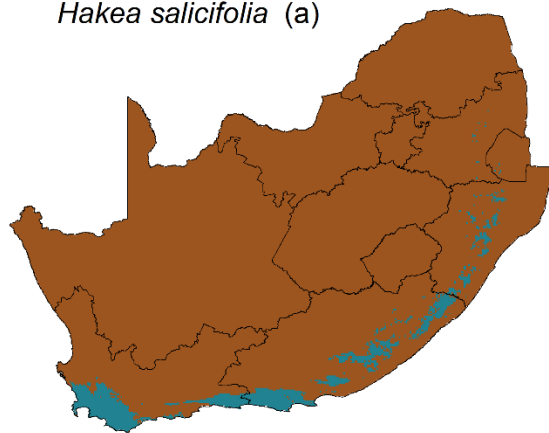
Dolichandra unguis-cati (a)

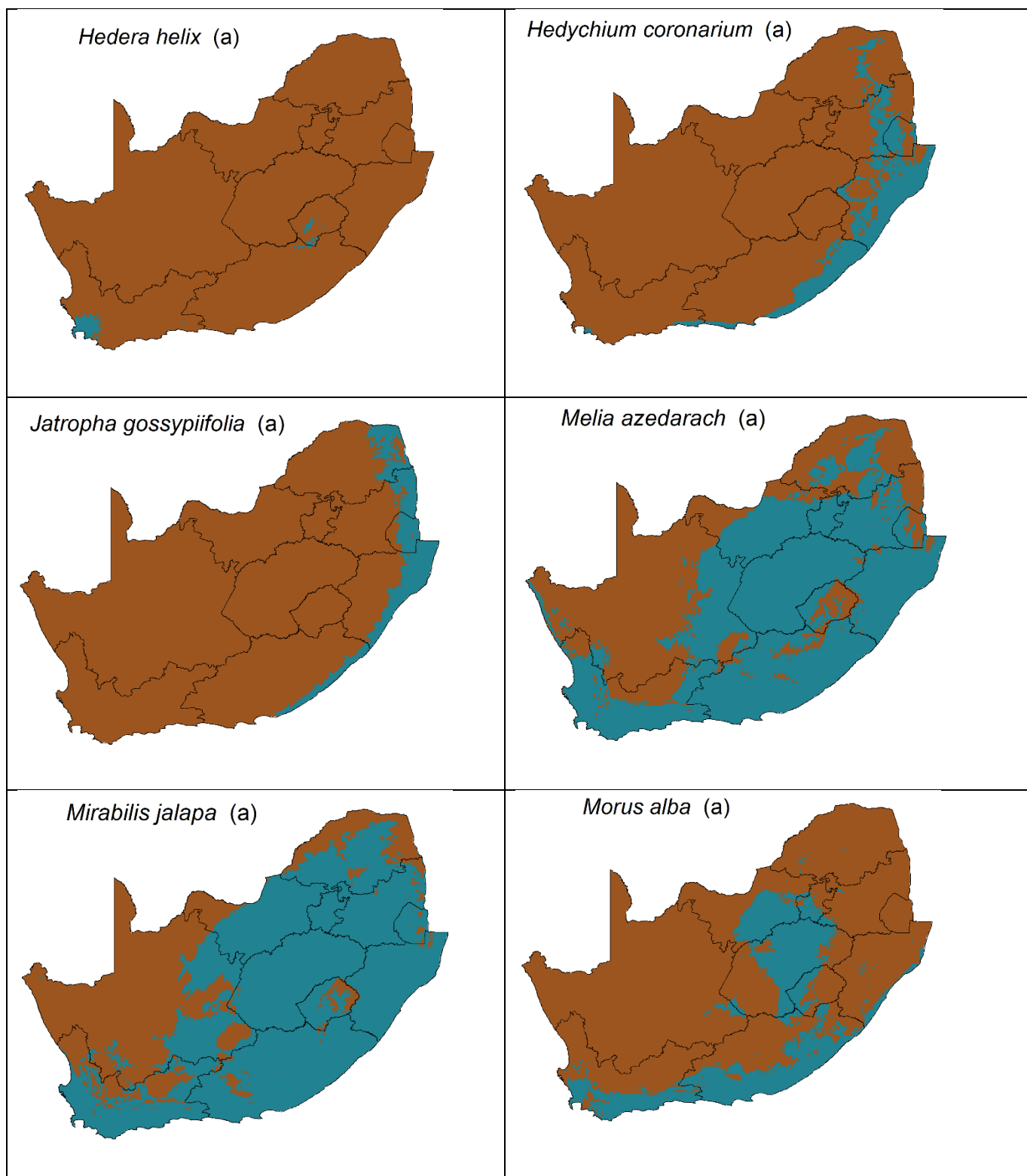


Eriobotrya japonica (a)

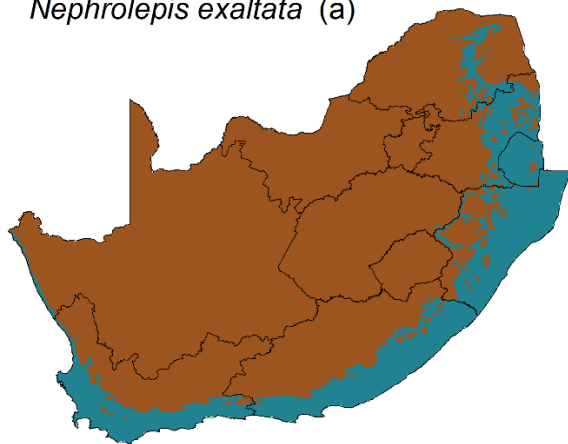


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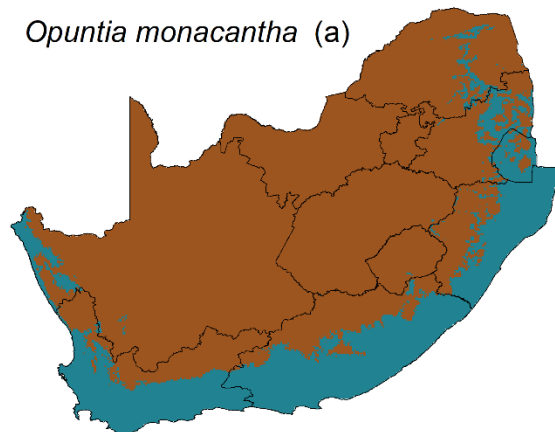




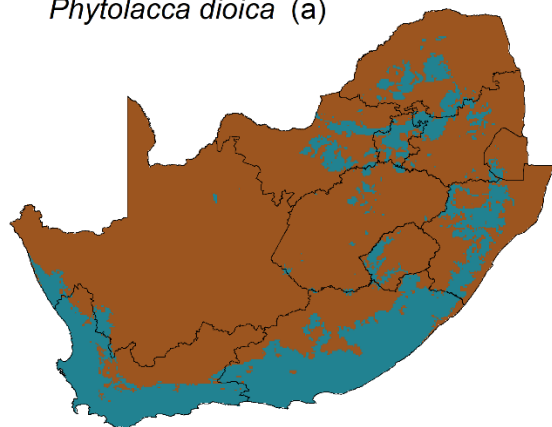
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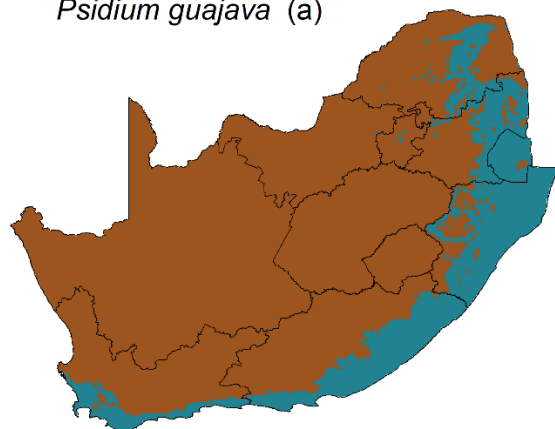
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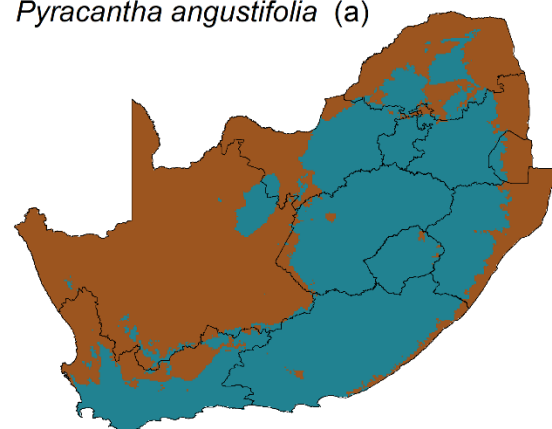
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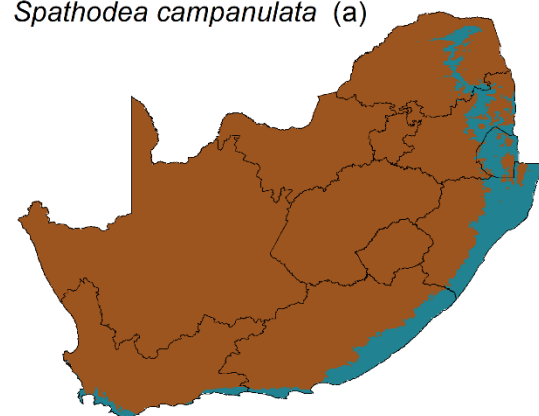
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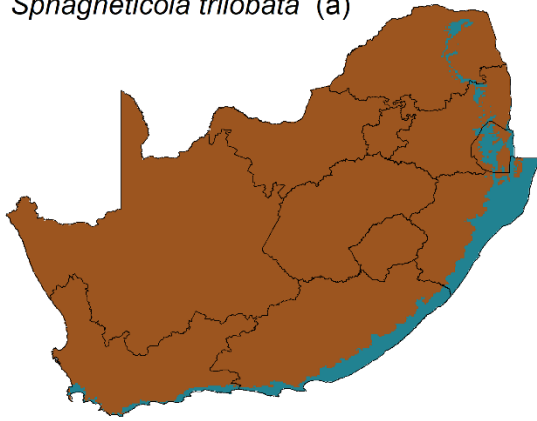
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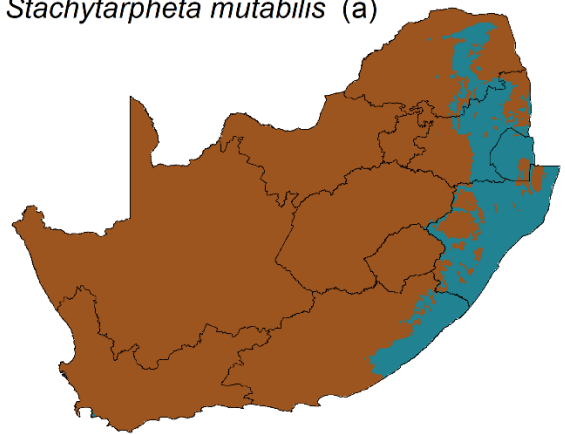
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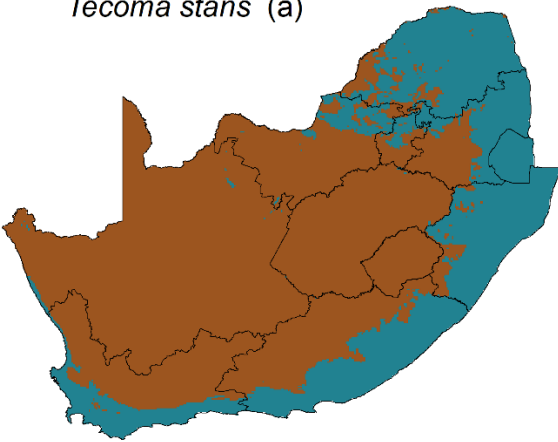
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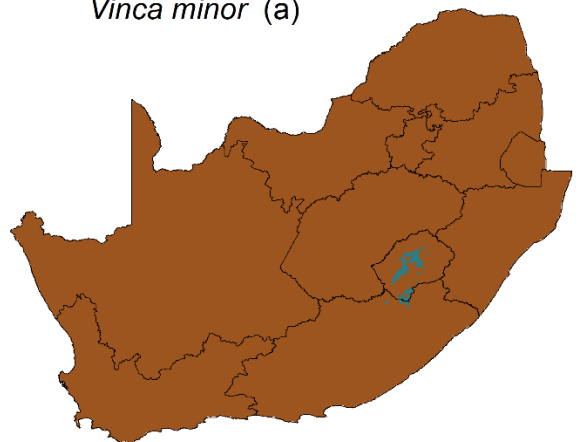
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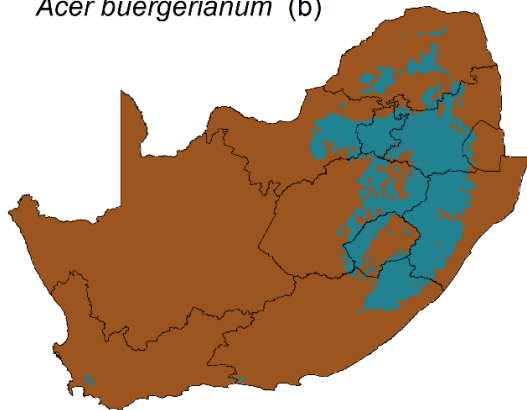
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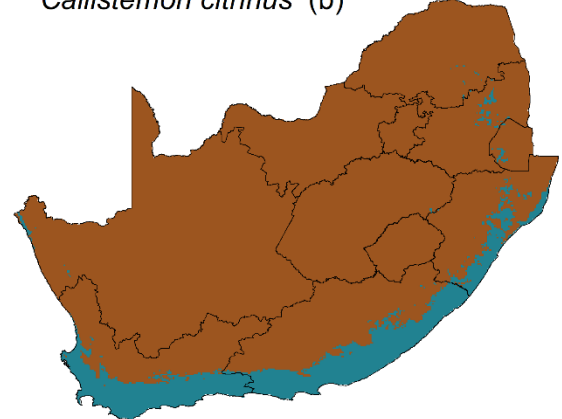
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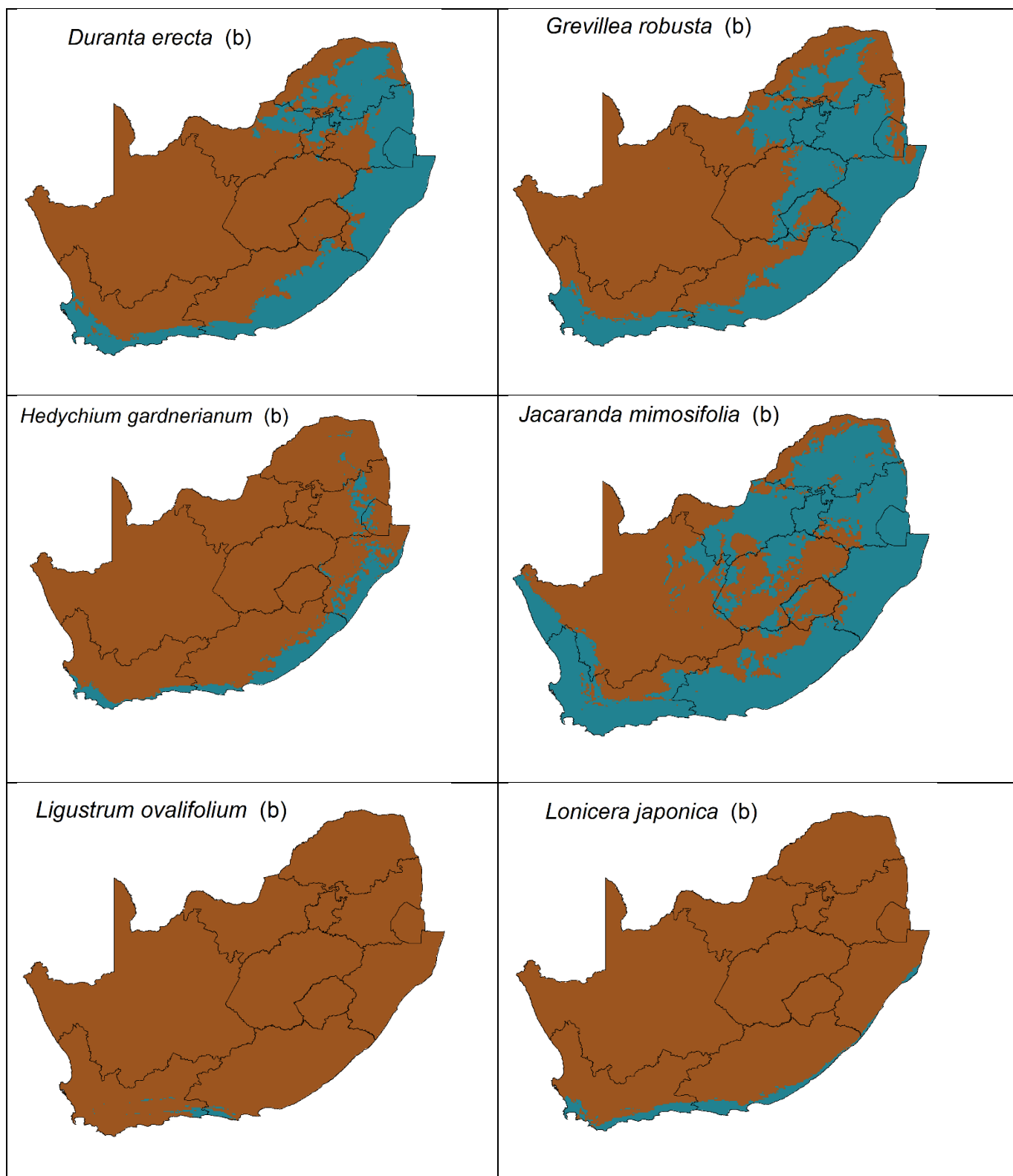


Acer buergerianum (b)

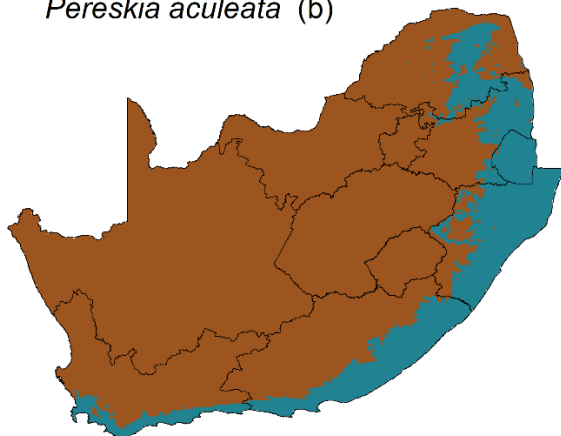


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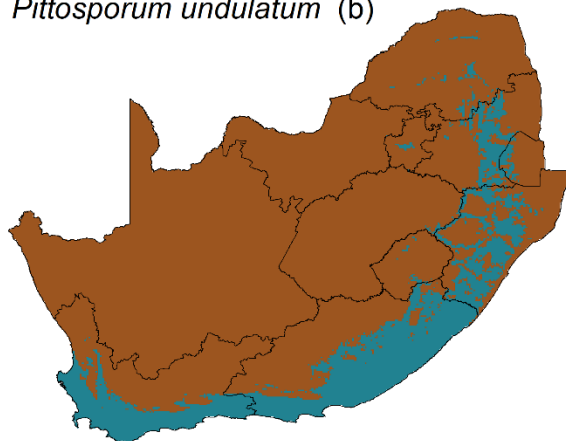




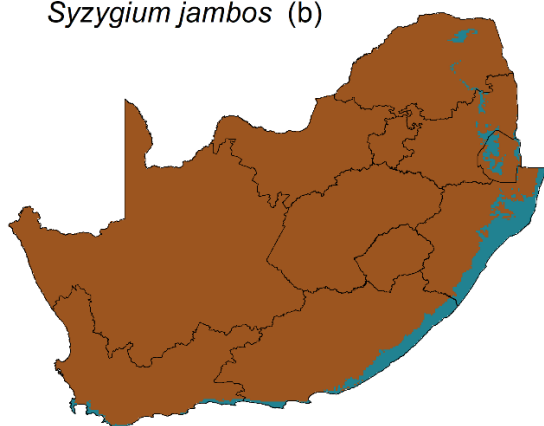
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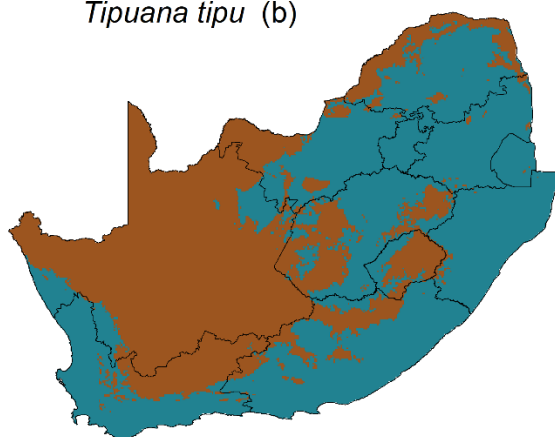
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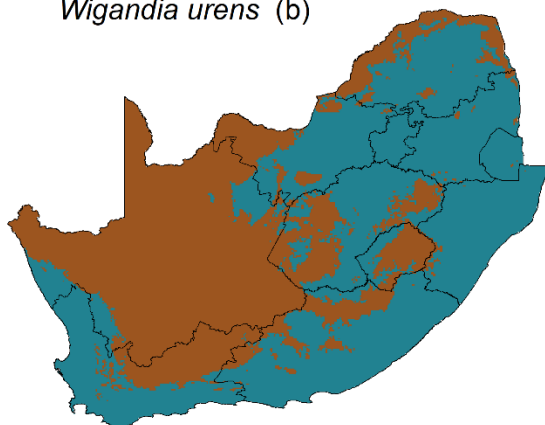
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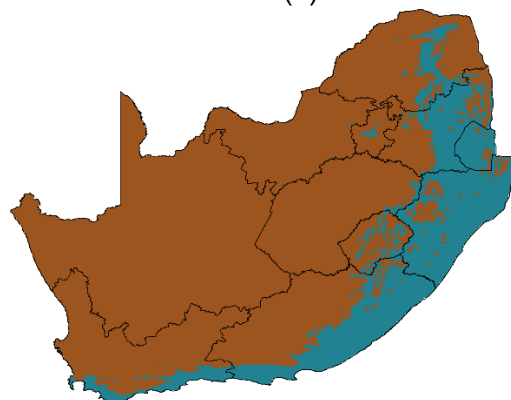
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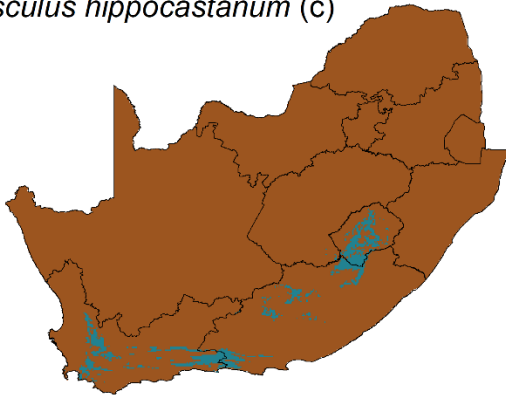
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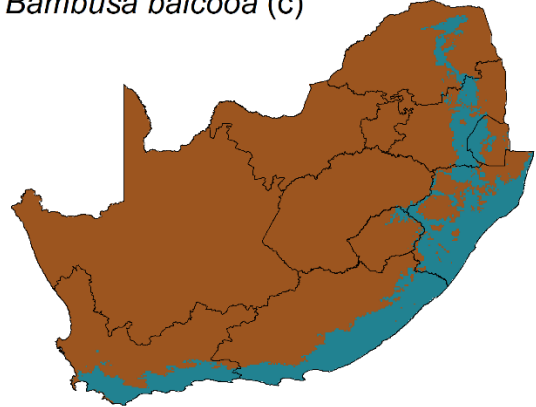
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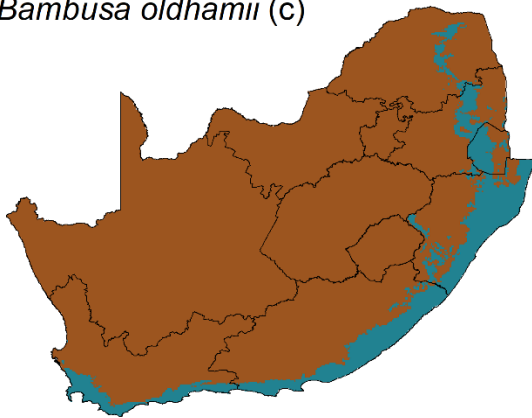
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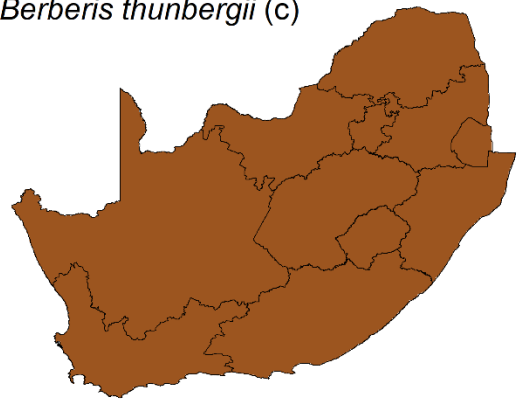
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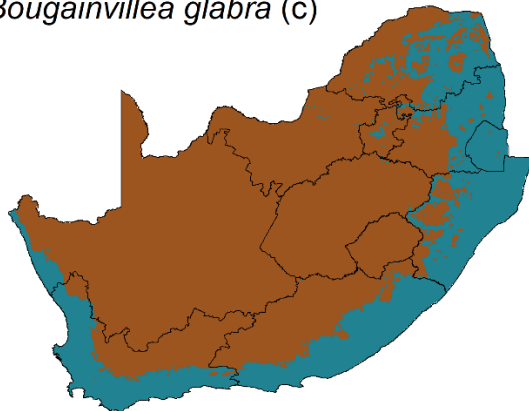
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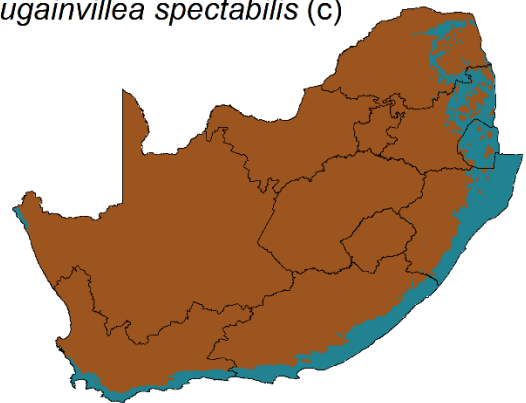
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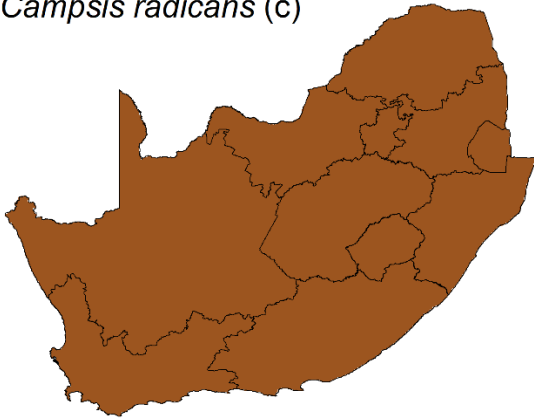
Bougainvillea glabra (c)



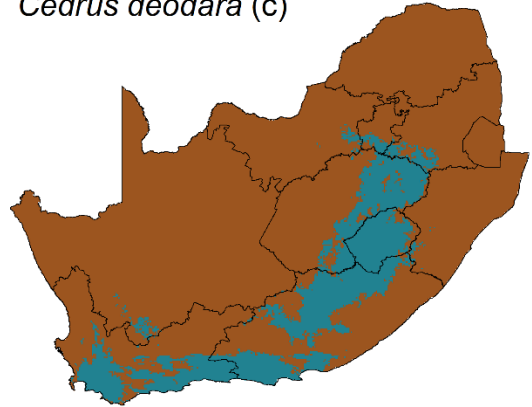
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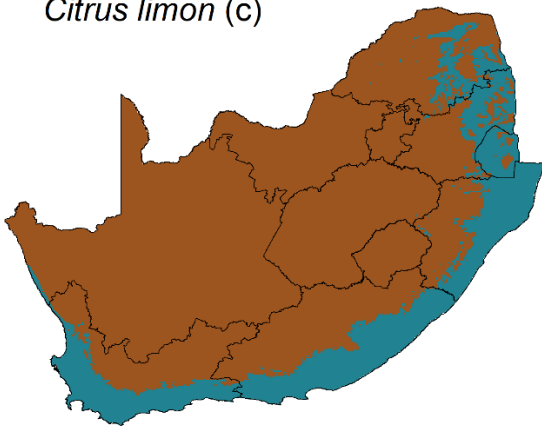
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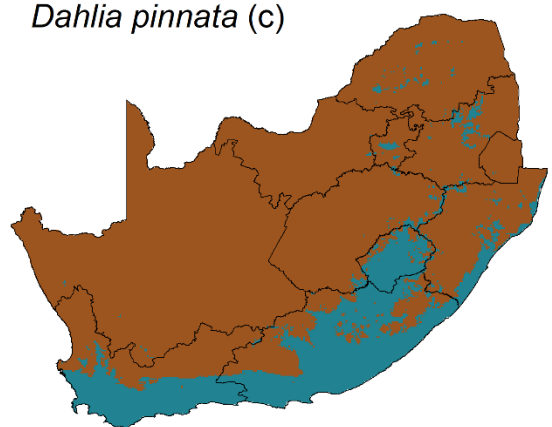
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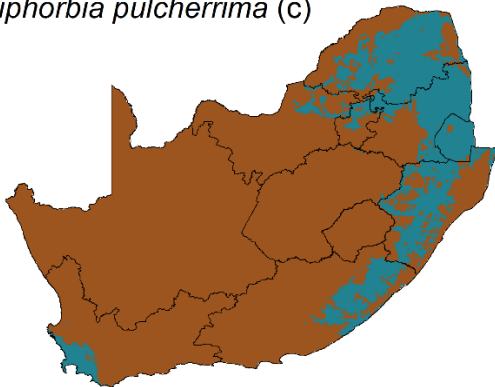
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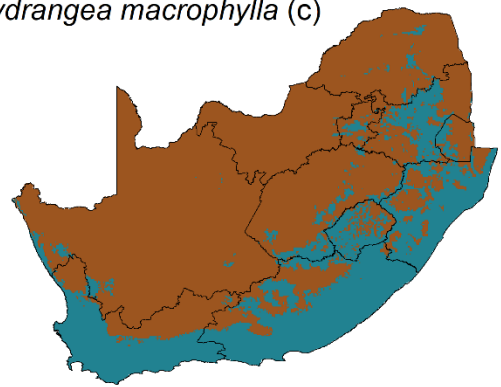
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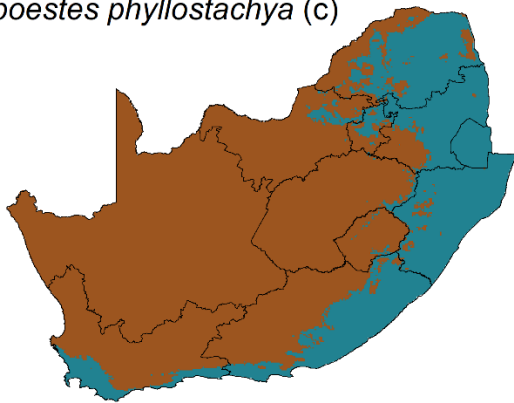
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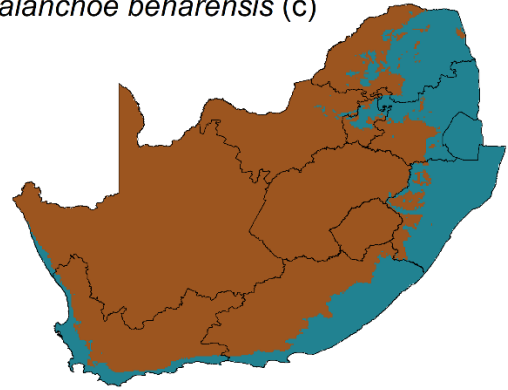
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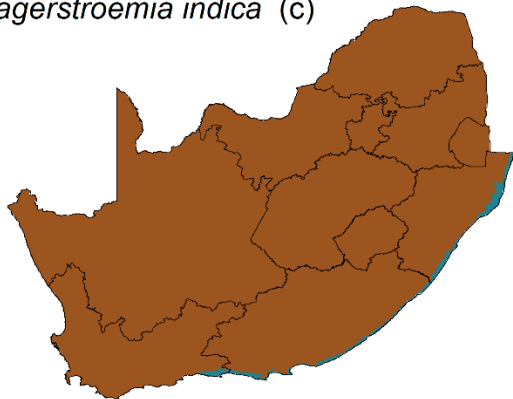
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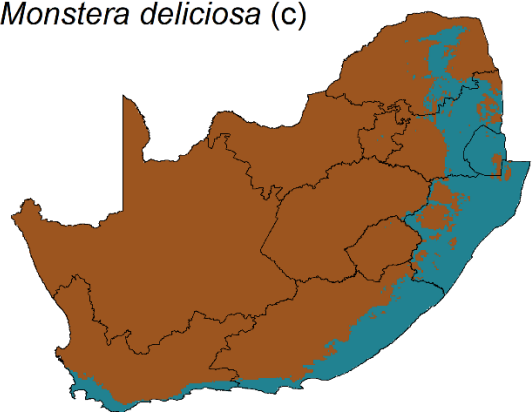
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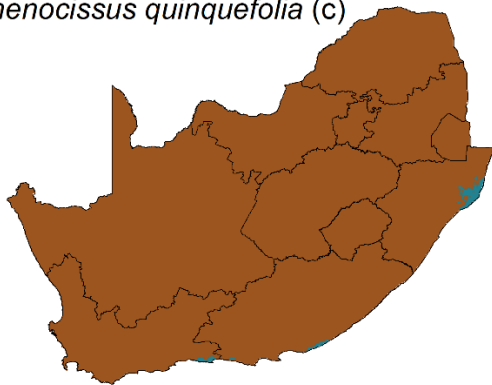
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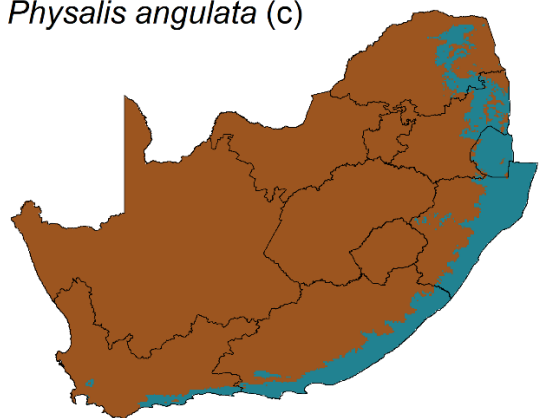
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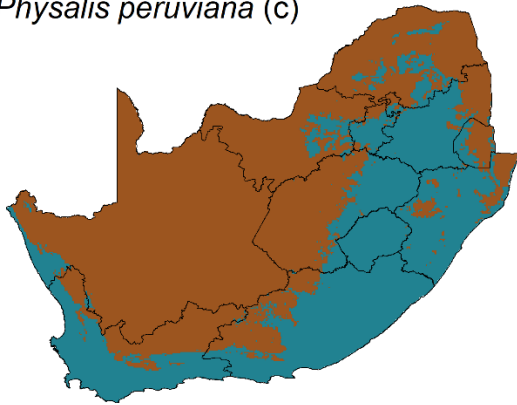
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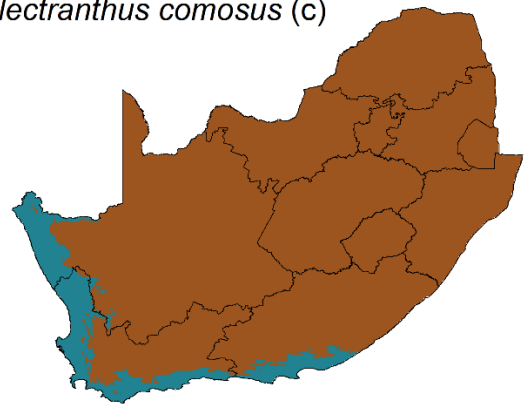
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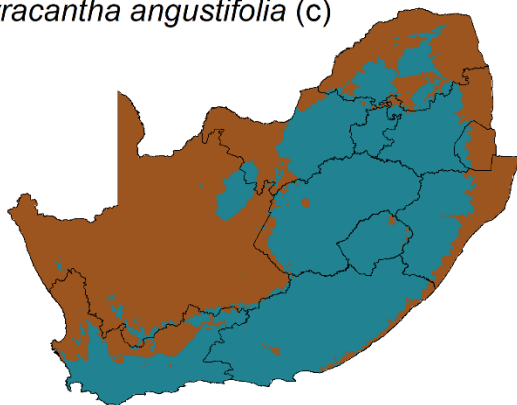
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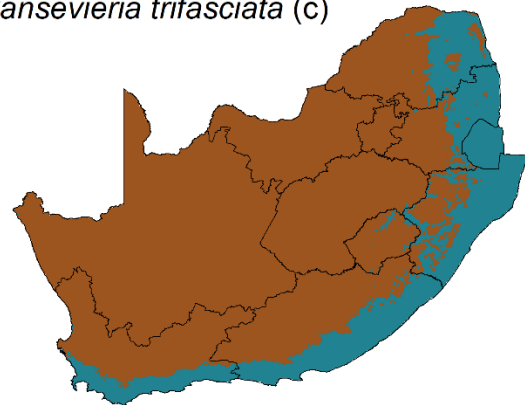
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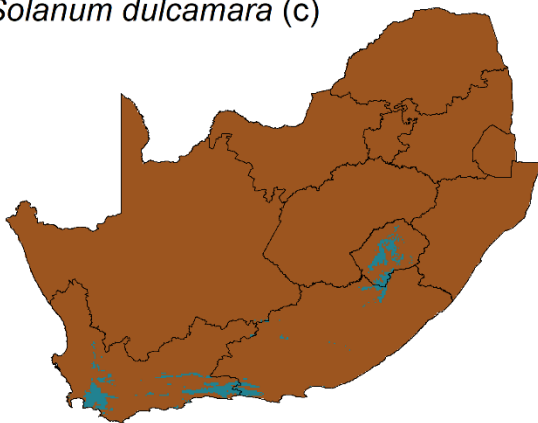
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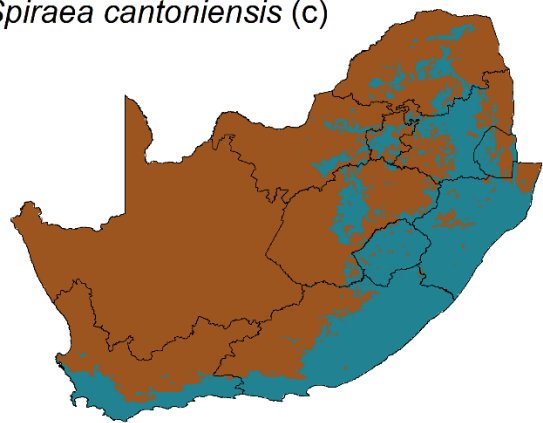
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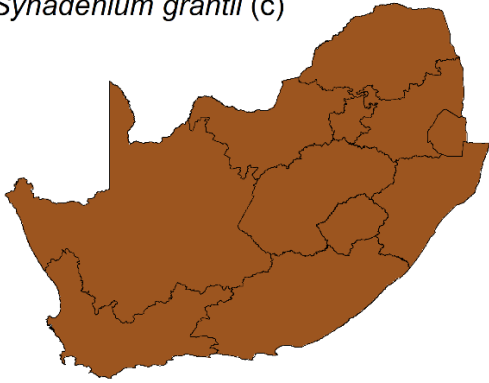
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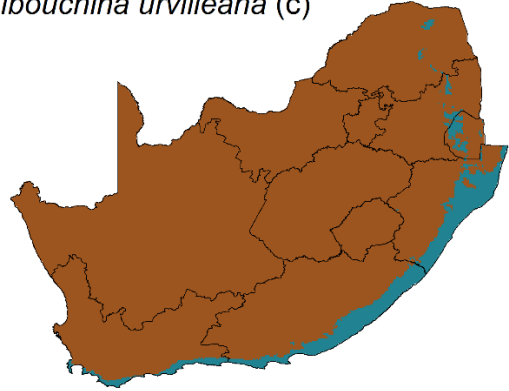
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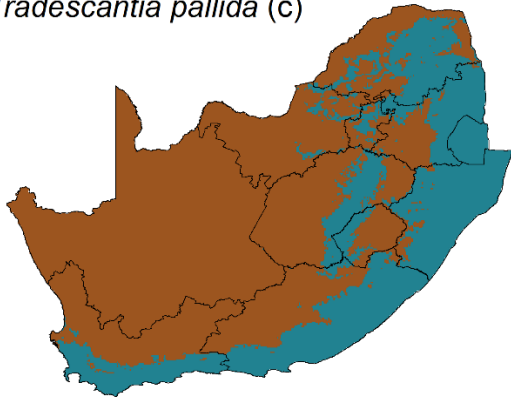
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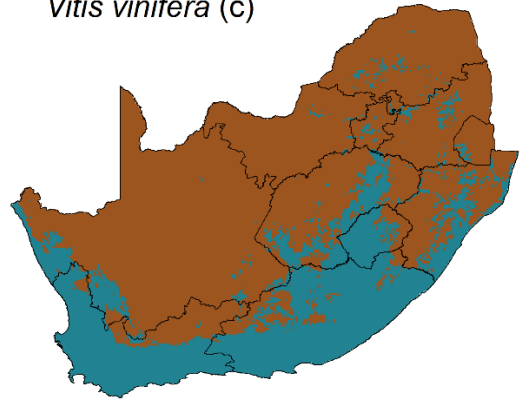
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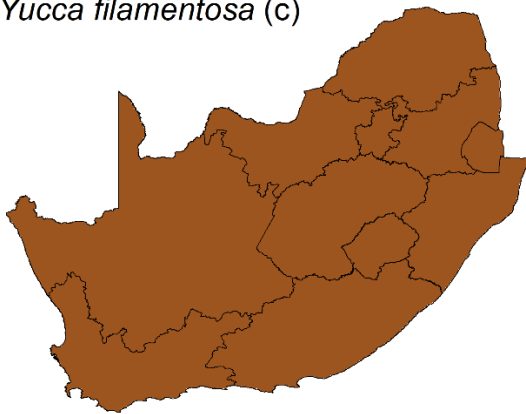
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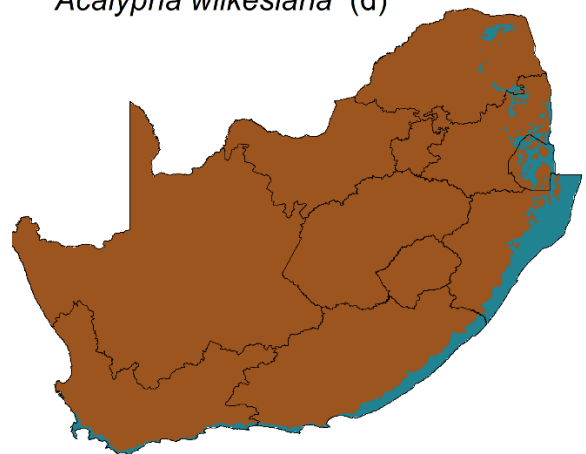
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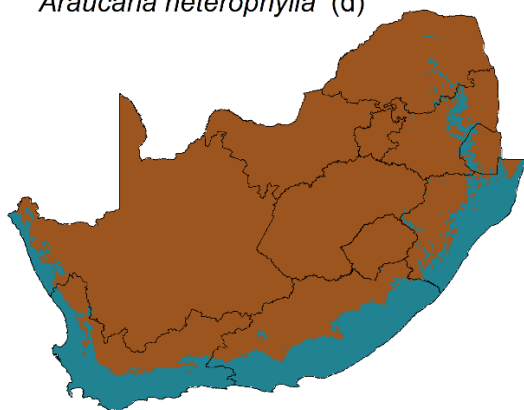
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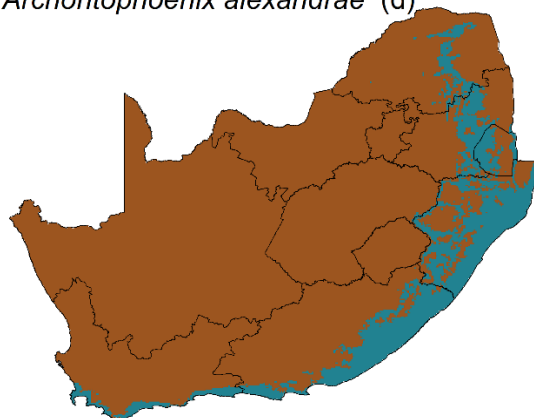
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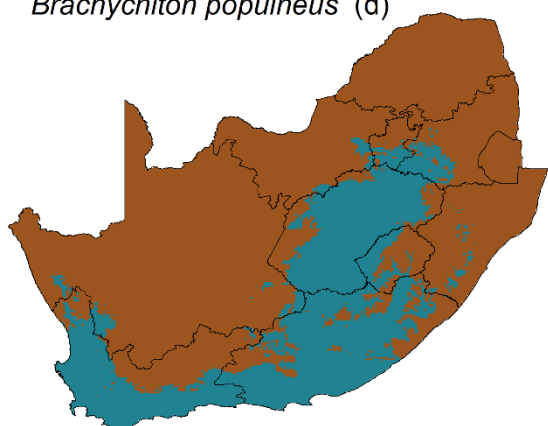
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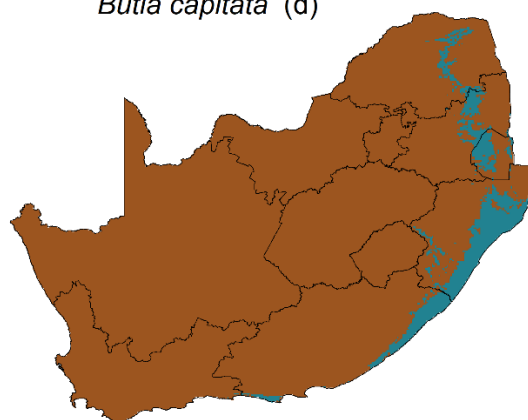
Archontophoenix alexandrae (d)



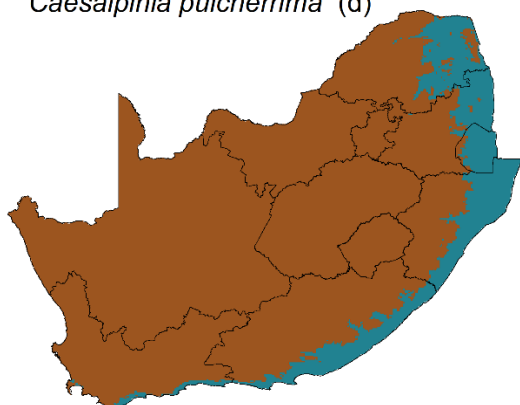
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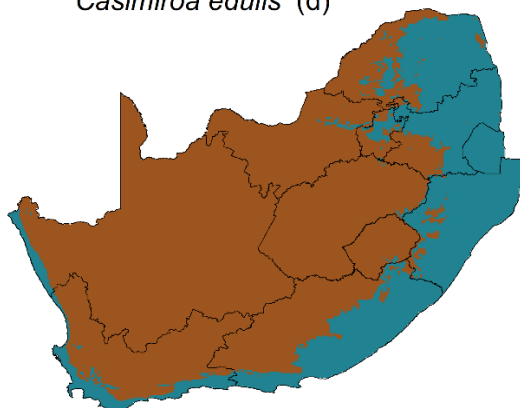
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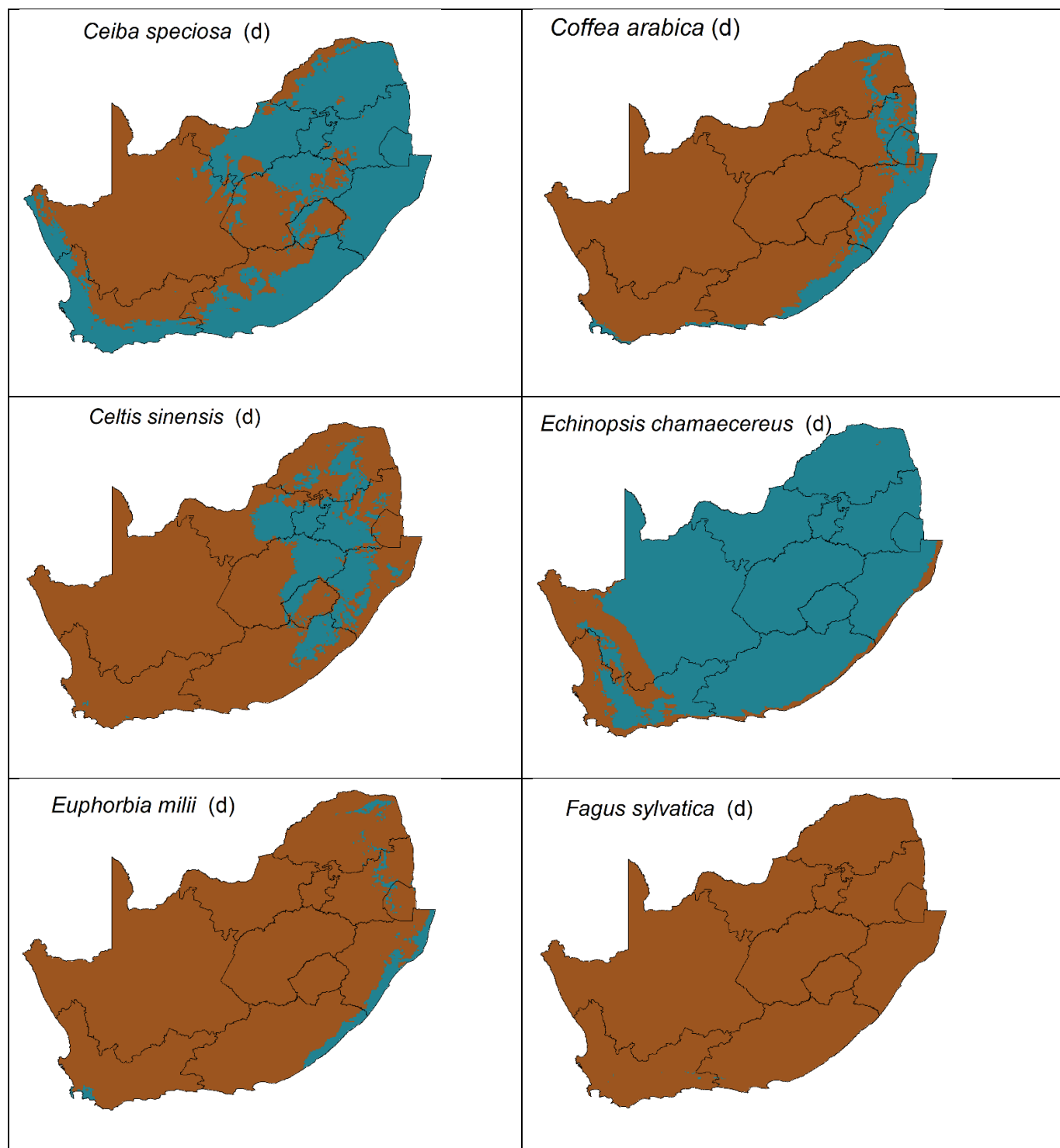


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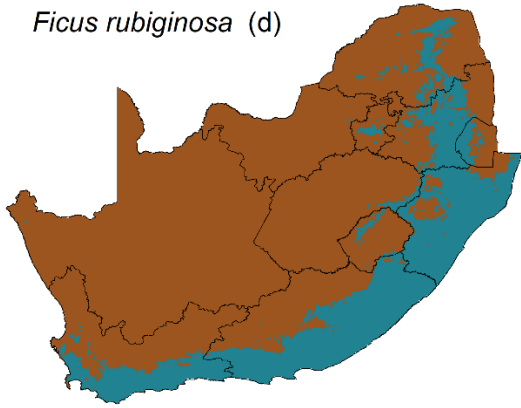


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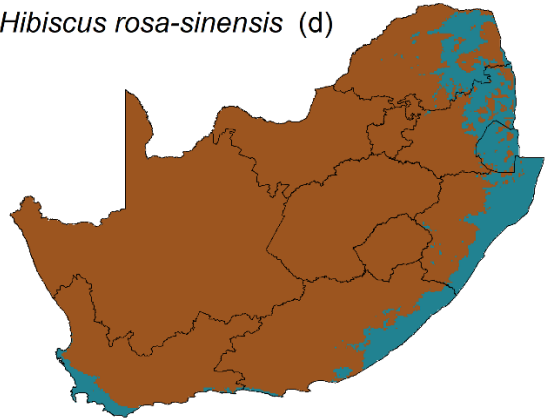




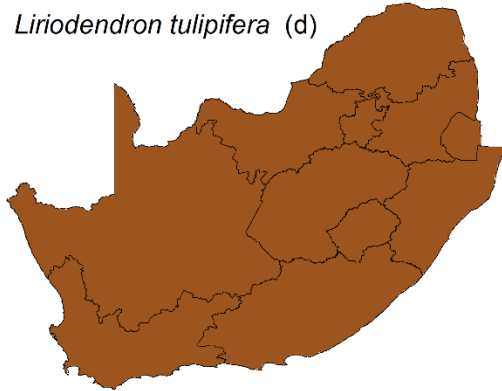
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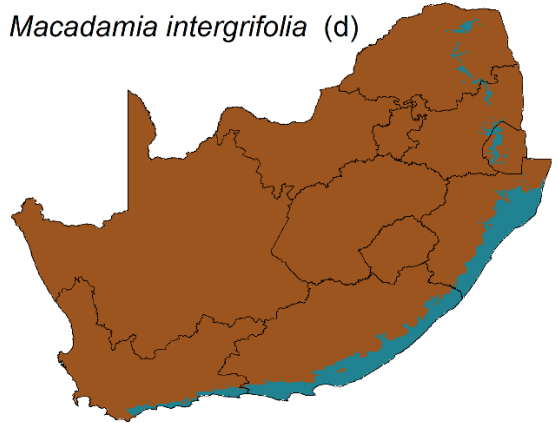
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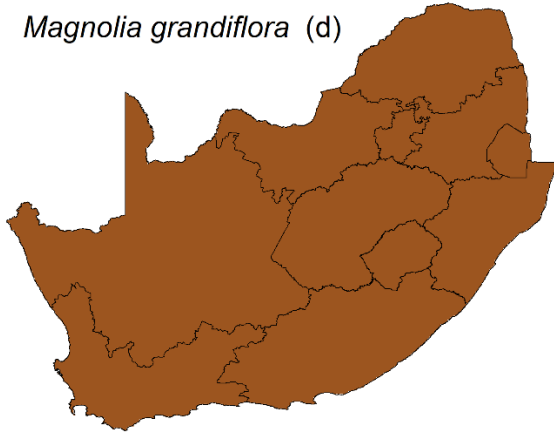
Liriodendron tulipifera (d)



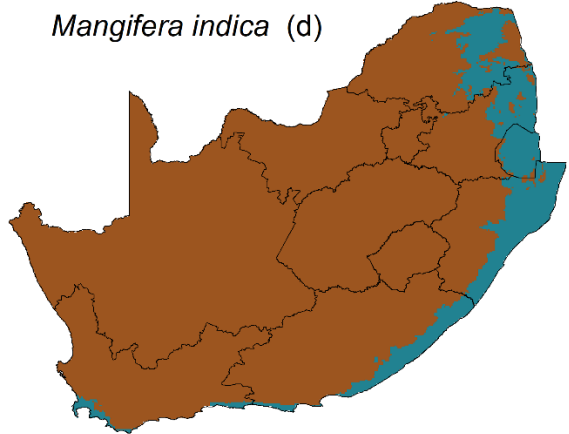
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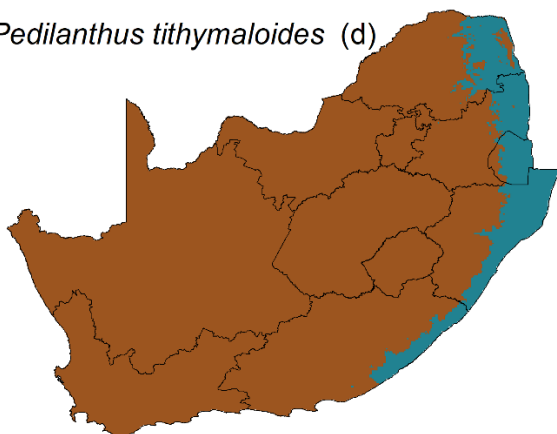
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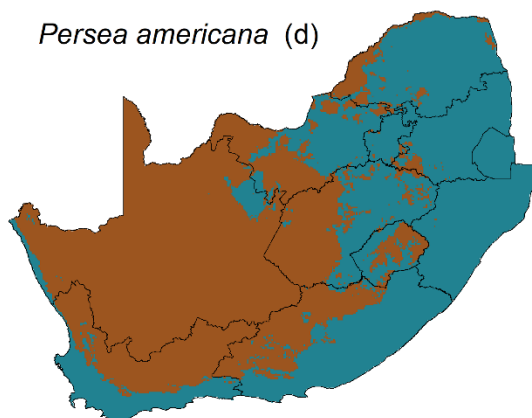
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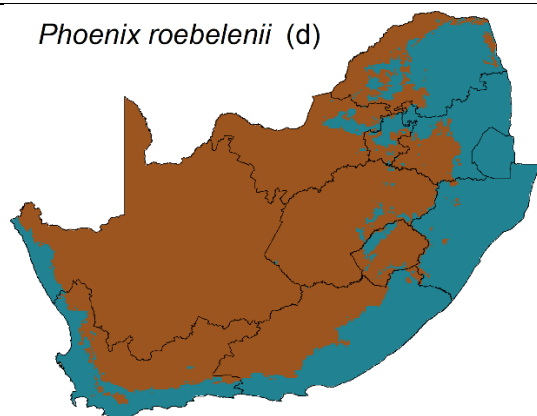
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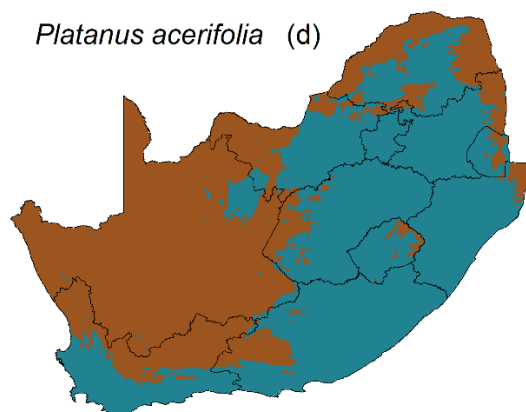
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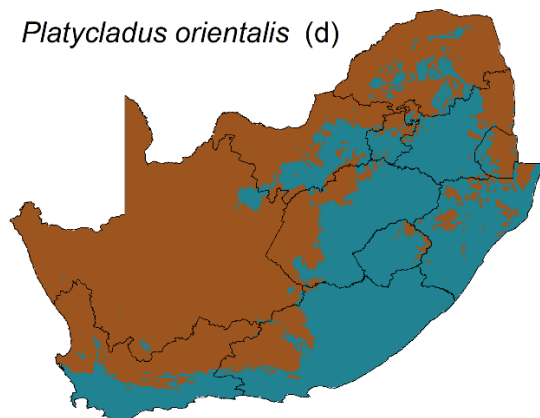
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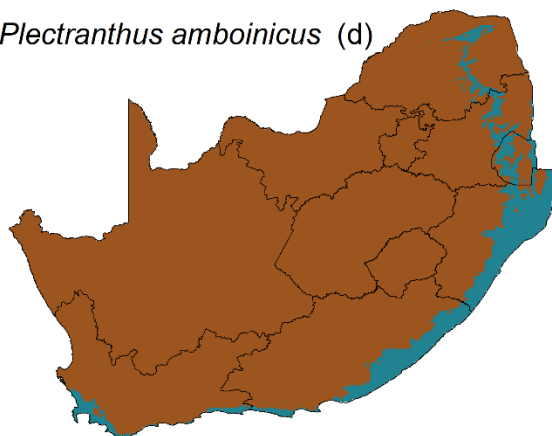
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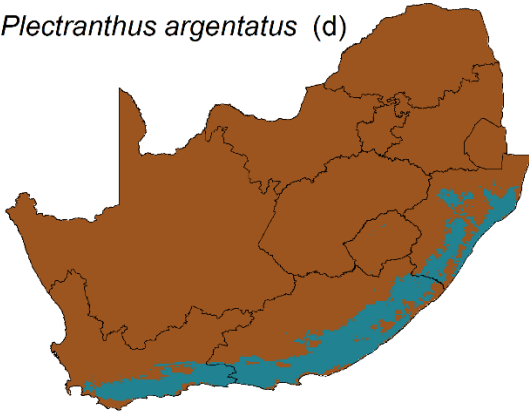
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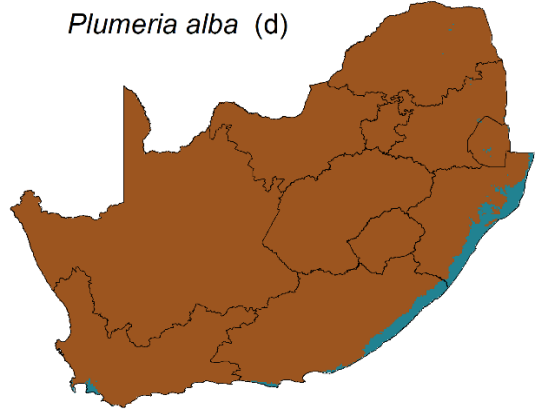
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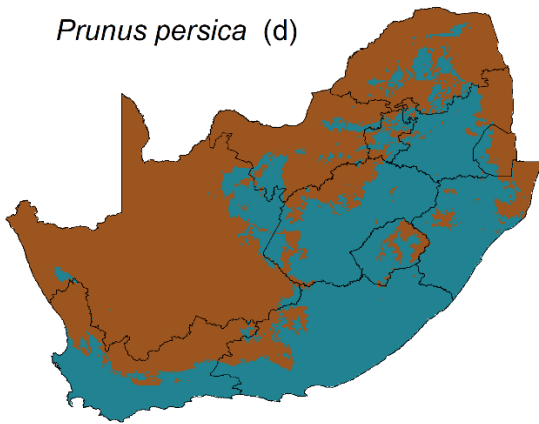
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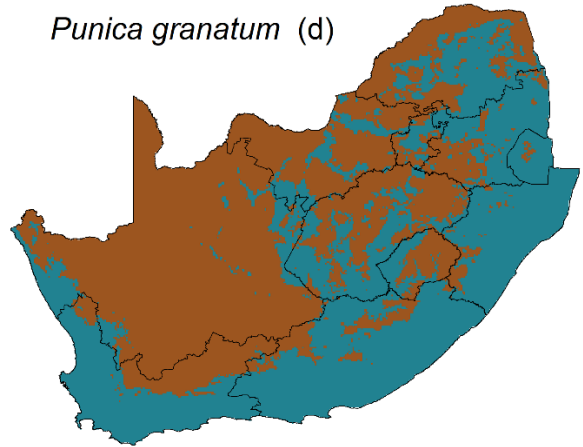
Plumeria alba (d)



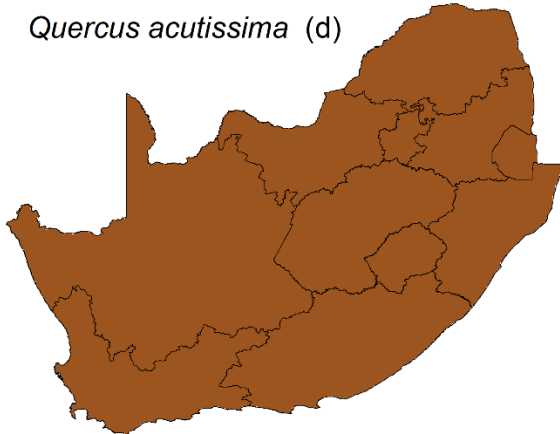
Prunus persica (d)



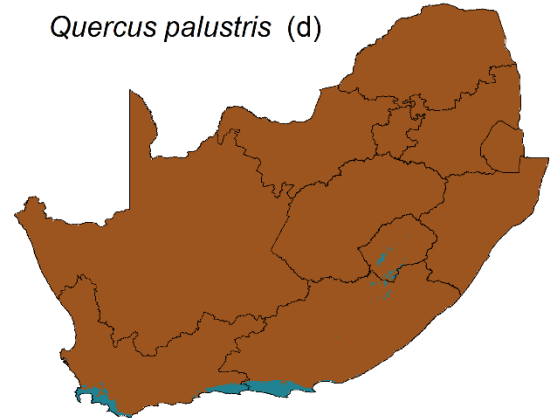
Punica granatum (d)



Quercus acutissima (d)



Quercus palustris (d)



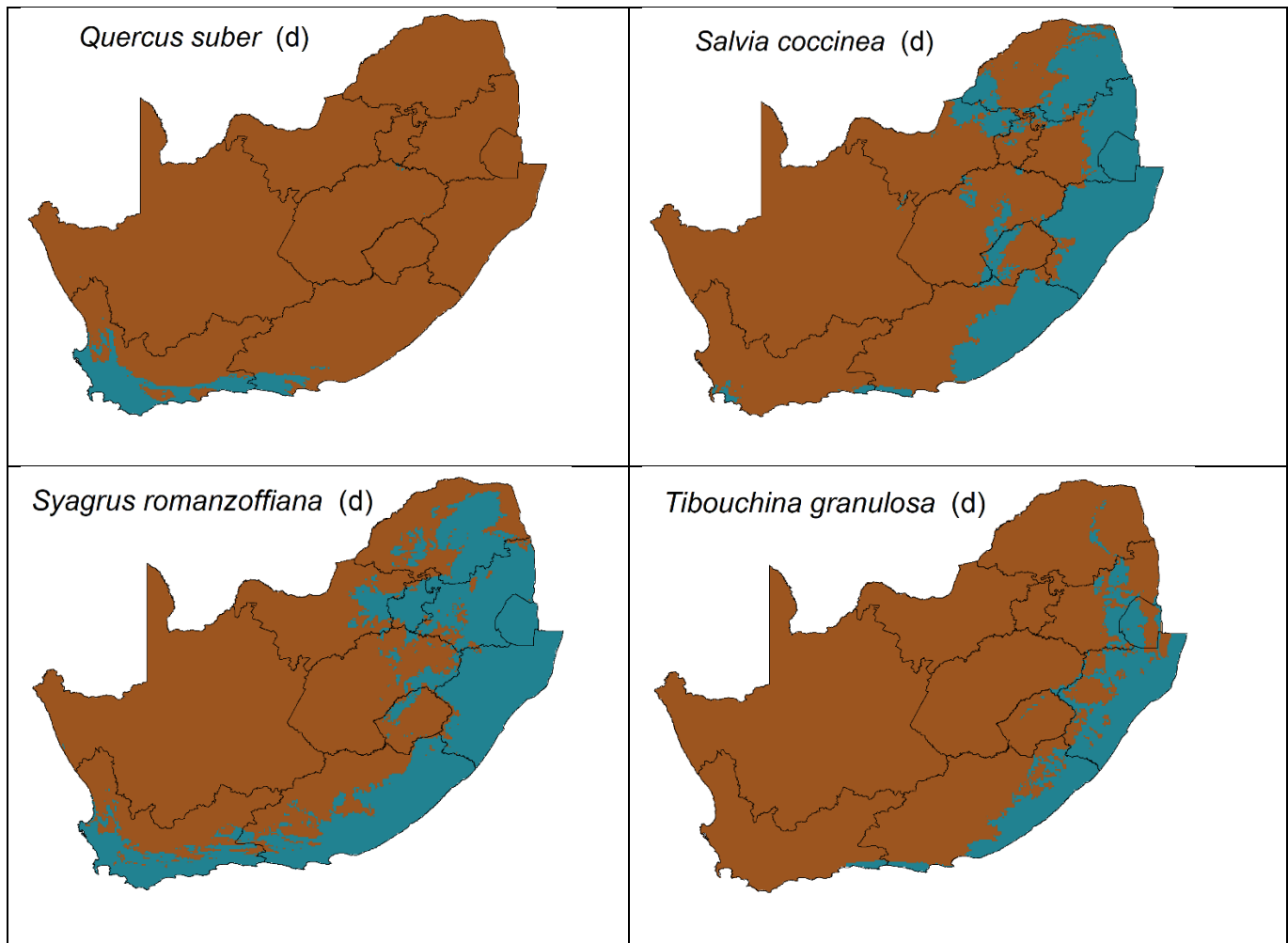


Figure A1: potential distribution of all alien ornamentals under current climatic conditions.

Blue on the maps indicates modelled presences and brown absences. a = NEM: BA listed spreading species; b = NEM: BA listed non-spreading species; c = non-listed spreading species; d = non-listed not spreading species.

Table A1: model evaluation of species distribution models (based on an ensemble technique comprising generalised additive model, generalised linear model, random forests, artificial neural network, boosted regression trees, and maximum entropy approaches). Models were calibrated using 80% of the dataset for each species, and the results were calculated for the withheld 20% of the data, with this model evaluation run twice for each species.

Species name	TSS	ROC	Potential range size (km ²)	Average distance of spread (m)
<i>Acalypha wilkesiana</i> Müll Arg.	0.880	0.988	51293	0
<i>Acer buergerianum</i> Miq.	0.941	0.997	153536	0
<i>Adiantum raddianum</i> C.Presl.	0.954	0.997	186948	40.5
<i>Aesculus hippocastanum</i> L.	0.960	0.997	13142	5.5
<i>Agave sisalana</i> Perrine.	0.900	0.994	198288	0.8
<i>Ailanthus altissima</i> (Milli.) Swingle.	0.900	0.994	417616	62
<i>Alpinia zerumbet</i> (Pers.) B.L.Burt & Perrine.	0.900	0.997	51921	5
<i>Antigonon leptopus</i> Hook. & Arn.	0.900	0.989	116559	25
<i>Araucaria heterophylla</i> (Salisb.) Franco.	0.941	0.996	175446	0

<i>Archontophoenix alexandrae</i> (F.Muell.) H.Wendl & Drude.	0.970	0.999	106637	0
<i>Aristolochia elegans</i> Mast.	0.892	0.989	378716	80.2
<i>Arundo donax</i> L.	0.904	0.993	281394	6
<i>Bambusa balcooa</i> Roxb.	0.980	0.999	138065	28.8
<i>Bambusa oldhamii</i> Munro.	0.994	0.999	98537	5.5
<i>Bauhinia variegata</i> L.	0.881	0.985	643586	30.4
<i>Berberis thunbergii</i> DC.	0.969	0.998	0	2.8
<i>Bougainvillea glabra</i> Choisy.	0.875	0.984	263939	37.8
<i>Bougainvillea spectabilis</i> Willd.	0.880	0.986	106819	5.7
<i>Brachychiton populneus</i> (Schott & Endl.) R.Br.	0.973	0.999	272930	0
<i>Bryophyllum delagoense</i> (Eckl & Zeyh) Schinz.	0.963	0.999	209406	23.2
<i>Butia capitata</i> (Mart.) Becc.	0.985	0.999	42707	0
<i>Caesalpinia pulcherrima</i> (L.) Sw.	0.841	0.981	126178	0

<i>Callistemon citrinus</i> (Curtis) Skeels.	0.966	0.999	101716	0
<i>Callistemon rigidus</i> R.Br.	0.986	0.999	93211	3
<i>Campsis radicans</i> (L.) Seem.	0.969	0.999	0	44.5
<i>Canna indica</i> L.	0.861	0.981	594176	4.4
<i>Casimiroa edulis</i> La Llave & Lex.	0.943	0.996	288502	0
<i>Catharanthus roseus</i> (L.) G.Don.	0.868	0.983	79765	38.5
<i>Cedrus deodara</i> (Lamb) G.Don.	0.942	0.995	140434	13.4
<i>Ceiba speciosa</i> (A.st. -Hil., A.juss. & Cambess) Ravenna.	0.910	0.991	516638	0
<i>Celtis sinensis</i> Pers.	0.966	0.999	165341	0
<i>Cestrum aurantiacum</i> Lindl.	0.938	0.997	163924	10.9
<i>Cinnamomum camphora</i> (L.) J.Presl.	0.971	0.999	39933	63.5
<i>Citrus limon</i> (L.) Burm. fil.	0.849	0.979	187556	2.5
<i>Coffea arabica</i> L.	0.909	0.992	90882	23.3

<i>Cotoneaster franchetii</i> Boiss.	0.978	0.999	23895	2.1
<i>Dahlia pinnata</i> Cav.	0.897	0.988	166860	6
<i>Dolichandra unguis-cati</i> (L.) L.G.Lohmann.	0.910	0.992	228218	5
<i>Duranta erecta</i> L.	0.888	0.986	290669	0
<i>Echinopsis chamaecereus</i> H.Friedrich & Glaetzle.	0.975	0.999	929050	0
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	0.940	0.996	132212	15.7
<i>Euphorbia milii</i> Des Moul.	0.936	0.994	28168	0
<i>Euphorbia pulcherrima</i> Willd. ex Klotzsch.	0.909	0.991	165119	2.4
<i>Fagus sylvatica</i> L.	0.976	0.999	20	0
<i>Ficus rubiginosa</i> Desf.	0.984	1	220502	0
<i>Grevillea robusta</i> A.Cunn. ex R.Br.	0.910	0.990	366383	0
<i>Hakea salicifolia</i> (Vent.) B.L.Burt.	0.990	1	34445	200
<i>Hedera helix</i> L.	0.947	0.996	7857	6.5
<i>Hedychium coronarium</i> J.Koenig.	0.902	0.990	100035	118.6

<i>Hedychium gardnerianum</i> Sheppard ex Ker Gawl.	0.984	1	71908	0
<i>Hibiscus rosa-sinensis</i> L.	0.903	0.989	110201	0
<i>Hydrangea macrophylla</i> (Thunb.) Ser.	0.906	0.990	261812	3
<i>Hypoestes phyllostachya</i> Baker.	0.893	0.987	286922	37.2
<i>Jacaranda mimosifolia</i> D.Don.	0.912	0.992	517347	0
<i>Jatropha gossypifolia</i> L.	0.890	0.985	43436	71
<i>Kalanchoe baharensis</i> Drake.	0.968	0.998	251343	0.3
<i>Lagerstroemia indica</i> L.	0.896	0.989	9578	3.7
<i>Ligustrum ovalifolium</i> Hassk.	0.985	1	3382	0
<i>Liquidambar styraciflua</i> L.	0.972	0.999	1357	13
<i>Liriodendron tulipifera</i> L.	0.978	0.999	0	0
<i>Lonicera japonica</i> Thunb.	0.956	0.997	27722	0
<i>Macadamia intergrifolia</i> Maiden & Betcher.	0.979	0.999	57794	0

<i>Magnolia grandiflora</i> L.	0.985	1	0	0
<i>Mangifera indica</i> L.	0.863	0.983	109310	0
<i>Melia azedarach</i> L.	0.912	0.992	531259	15
<i>Mirabilis jalapa</i> L.	0.871	0.985	742507	53.1
<i>Monstera deliciosa</i> Liebm.	0.931	0.993	170951	36.4
<i>Morus alba</i> L.	0.882	0.989	114392	40.5
<i>Nephrolepis exaltata</i> (L.) Schott.	0.857	0.985	156107	50.2
<i>Opuntia monacantha</i> (Willd) Haw.	0.917	0.992	226395	2
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0.961	0.999	3827	33.2
<i>Pedilanthus tithymaloides</i> (L.) Poit.	0.937	0.996	93575	0
<i>Pereskia aculeata</i> Mill.	0.930	0.995	178342	0
<i>Persea americana</i> Mill.	0.859	0.979	479297	0
<i>Phoenix roebelenii</i> O'Brien.	0.946	0.997	321246	0
<i>Physalis angulata</i> L.	0.852	0.982	110201	8.1

<i>Physalis peruviana</i> L.	0.903	0.989	371750	65.6
<i>Phytolacca dioica</i> L.	0.963	0.998	132476	34.2
<i>Phytolacca octandra</i> L.	0.973	0.999	255494	6
<i>Pittosporum undulatum</i> Vent.	0.986	1	139745	0
<i>Platanus acerifolia</i> (Aiton) Willd.	0.939	0.997	535106	0
<i>Platycladus orientalis</i> (L.) Franco.	0.842	0.98	385884	0
<i>Plectranthus amboinicus</i> (Lour.) Spreng.	0.866	0.987	69903	1.8
<i>Plectranthus argentatus</i> (S.T.Blake).	0.975	1	85860	28.8
<i>Plectranthus comosus</i> Sims.	1	1	75998	8
<i>Plumeria alba</i> L.	0.927	0.996	24037	15.4
<i>Prunus persica</i> (L.) Stokes.	0.931	0.995	416117	0
<i>Psidium guajava</i> L.	0.871	0.983	191889	34.2
<i>Punica granatum</i> L.	0.851	0.981	437927	28.2
<i>Pyracantha angustifolia</i> (Franch.) C.K.Schneid.	0.945	0.996	519878	0

<i>Quercus acutissima</i> Carruth.	0.957	0.998	0	11
<i>Quercus palustris</i> Münchh.	0.965	0.998	11563	0
<i>Quercus robur</i> L.	0.956	0.997	30638	0
<i>Quercus suber</i> L.	0.980	0.999	38232	0
<i>Salvia coccinea</i> Buc'hoz ex Etl.	0.952	0.997	249197	0
<i>Sansevieria trifasciata</i> Prain.	0.88	0.984	198653	5.9
<i>Solanum dulcamara</i> L.	0.918	0.992	9740	31
<i>Spathodea campanulata</i> Beauv.	0.892	0.989	106414	46.4
<i>Sphagneticola trilobata</i> (L.) Pruski.	0.911	0.991	77679	1
<i>Spiraea cantoniensis</i> Lour.	0.897	0.989	263918	10.4
<i>Stachytarpheta mutabilis</i> (Jacq.) Vahl.	0.921	0.994	155095	15
<i>Syagrus romanzoffiana</i> (Cham.) Glassman.	0.962	0.998	322016	0
<i>Synadenium grantii</i> Hook.f.	0.944	0.993	0	19.2
<i>Syngonium podophyllum</i> Schott.	0.884	0.988	184741	13

<i>Syzygium jambos</i> (L.) Alston.	0.925	0.992	39771	0
<i>Tecoma stans</i> Juss. ex Kunth.	0.866	0.983	308914	34.9
<i>Tibouchina granulosa</i> (Desr.) Cogn.	0.963	0.998	106029	0
<i>Tibouchina urvilleana</i> (DC.) Cogn.	0.960	0.998	58968	6
<i>Tipuana tipu</i> (Benth.) Kuntze.	0.930	0.994	555134	0
<i>Tradescantia pallida</i> (Rose) D.R.Hunt.	0.896	0.989	310007	1
<i>Vinca minor</i> L.	0.954	0.997	0	55.1
<i>Vitis vinifera</i> L.	0.913	0.992	270196	94.3
<i>Wigandia urens</i> (Ruiz & Pav.) Kunth.	0.937	0.996	123039	0
<i>Yucca filamentosa</i> L.	0.961	0.997	0	16.7

Chapter 4: General Conclusion

The role of abandoned gardens as potential sources of alien invasions, and the severity of the impacts caused by abandoned gardens in rural areas, are not well researched. My research investigated whether alien ornamental species can escape cultivation from abandoned homesteads' gardens. My findings demonstrate that alien plant species do spread from, and invade into, the landscapes surrounding abandoned gardens (Chapter 2). My work only covers abandoned gardens from two locations; in reality, this problem is bigger. Therefore, to fully understand what influences alien ornamental species to spread, more abandoned homesteads should be sampled. This project showed that spread distances and the richness of spreading species differed strongly between families. The traits, growth form and mode of reproduction, were not significant predictors of the maximum distance of spread. Additionally, I found that NEM: BA listed species were spreading further than non-listed species.

In Chapter 3, I assessed which areas in South Africa are at risk of invasion by the species recorded in Chapter 2. Additionally, I tested if there was a correlation between the species' average maximum distance of spread and the predicted potential range size if NEM: BA listed species and the species found escaping cultivation had a higher potential range size than the non-listed and the not spreading species. Lastly, I compared the potential species richness of the NEM: BA listed spreading species with the NEM: BA listed non-spreading species and with the non-listed spreading species. I also compared the richness of the non-listed spreading with the non-listed, not spreading species. No relationship was found between species averaged maximum distance of spread and their potential range sizes, suggesting the probability of a species to invade larger areas in South Africa is not influenced by species being garden escapees. The potential range size of species that are currently listed on NEM: BA and those found escaping cultivation did not significantly differ from that of the non-listed and the non-spreading species. Also, the potential species richness peaked at similar areas for the four different groups, NEM: BA listed spreading species, NEM: BA listed non-spreading species, non-listed spreading species, and the non-listed not spreading species.

4.1 Recommendations

The maximum distance of spread for the NEM: BA listed species was higher though other factors influencing the spread of alien ornamentals from the abandoned gardens are currently not known (Richardson et al., 2000, Mayer et al., 2017). Invasion success can be driven by site-dependent factors (e.g. environmental conditions), or by species-dependent factors (e.g. dispersal mechanisms) that may give some alien invasive species a greater advantage than others (Ehrenfeld, 2003, Davis et al., 2000, Lonsdale, 1999). An understanding of the types of mechanisms that drive variation in invasion success is key in predicting, managing, and controlling future invasions (Daehler, 2003). Because the species from the abandoned homesteads gardens were introduced years ago, I recommend that more abandoned gardens should be investigated to keep a record of what is persisting to guide alien management. A concern is that the species were in a lag phase and can become invasive in the future. This will be a problem especially for the abandoned gardens in nature reserves to manage invasive ornamental plants if in the future.

Since invasive alien ornamental plant species are likely to continue escaping cultivation, a more direct approach in controlling the matter could be to first identify abandoned homesteads in all the biomes of South Africa. This can be done through word of mouth and by contacting the Department of Agriculture for inquiries. Awareness campaigns can also be made in a way that information can be entered by people who have encountered abandoned homesteads through social platforms or citizen science projects. Alien invasion management and control plan should only be implemented when abandoned homesteads have been located and pre-visited with a record of what is persisting, escaping cultivation, and to what extent. Such a survey will give the required information of how much time, funds, and labour will be required to clear sites.

In addition to the homesteads, I sampled for this dissertation, I also visited previously abandoned homesteads that were re-occupied in the North West and Northern Cape provinces. The localities were Biesjesdal, Heuningvlei Pan, Lykso, Stella, and Vostershoop in the North West Province (Figure 1). The areas visited are in a Savannah biome characterized by summer rainfall and dry winters. Ornamental plants had also spread from these gardens, though by the time I visited new occupants of the homesteads were in a process of clearing some of the species. The species recorded were different from those collected in Mpumalanga and Limpopo, and only *Melia azedarach* (Meliaceae) was in

common with those I recorded in Limpopo and Mpumalanga. Of the 17 species recorded from the North West province, 82 % were Cactaceae species and 64.7% are NEM: BA listed (Table 1). I modelled the potential distribution of the alien species detected in the North West and Northern Cape gardens using the same methods as in Chapter 3. I found that these species are more likely to spread inland to the drier parts of the country (Figure 1, Figure A1) compared to the distributions of the species that had been detected from the wetter Limpopo and Mpumalanga provinces (Chapter 3). The potential species richness peaked between the North West and Northern Cape provinces (Savannah biome) towards Nama Karoo. For the species collected in the higher rainfall areas, these regions showed low potential richness (Figure 1 and Chapter 3: Figure 3). These observations and models highlight the potential for different alien species to occur in, and escape from, gardens in other parts of the country, and suggests that different climatic regions may face risks of invasion from different species. From the high rainfall homesteads surveyed in Chapter 2, only nine of out of 115 succulent species were recorded from 13 abandoned gardens indicating that fewer succulents invade high rainfall areas than the drier parts of the country where 14 out of 17 species were succulents (Table 1).

Table 1: species recorded in the North West and Northern Cape Provinces and NEM: BA category numbers. The two species in bold were excluded from modelling (see Figure A1) due to few GBIF occurrence records.

Family	Species name	NEM: BA
Asparagaceae	<i>Agave sisalana</i> Perrine.	2
Cactaceae	<i>Austrocylindropuntia subulata</i> (Engelm.) Backeb.	1b
Cactaceae	<i>Cereus jamacaru</i> DC.	1b
Cactaceae	<i>Cylindropuntia fulgida</i> (Engelm.) F.M.Knuth.	1b
Cactaceae	<i>Cylindropuntia imbricata</i> (Haw.) F.M.Knuth.	1b
Cactaceae	<i>Echinocactus grusonii</i> Hildm.	Not listed
Cactaceae	<i>Echinocactus schickendantzii</i> F.A.C.Weber.	Not listed
Cactaceae	<i>Echinopsis peruviana</i> (Britton&Rose) Friedrich & CD. Rowley.	Not listed
Meliaceae	<i>Melia azedarach</i> L.	1b
Cactaceae	<i>Opuntia elata</i> Link & Otto ex Salm-Dyck.	1b

Cactaceae	<i>Opuntia ficus-indica</i> (L.) Mill.	1b
Cactaceae	<i>Opuntia humifusa</i> Raf.	1b
Cactaceae	<i>Opuntia lindheimeri</i> Engelm.	1b
Cactaceae	<i>Opuntia stricta</i> Haw.	1b
Cactaceae	<i>Pachycereus marginatus</i> (DC.) Britton & Rose	Not listed
Fabaceae	<i>Prosopis juliflora</i> (Sw.) DC.	Not listed
Cactaceae	<i>Tephrocactus articulatus</i> (Pfeiff. ex Otto) Backeb.	Not listed

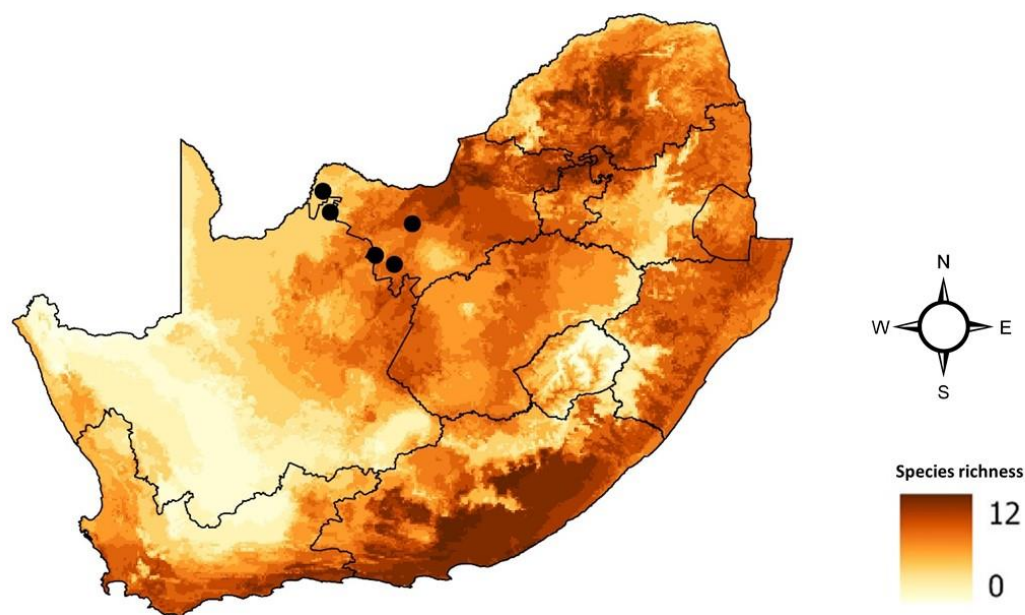


Figure 1: potential species richness of the species recorded in North West and Northern Cape Provinces, the dots indicate areas visited. The areas with low species richness are the dry central regions of South Africa and the Great Escarpment.

4.2 Alien ornamentals escapees as a global problem

Alien ornamental species do escape cultivation internationally as observed in different countries (Dehnen-Schmutz et al., 2007, Witt et al., 2018). The main factors influencing species to escape cultivation have been linked to an increased propagule pressure (Dehnen-Schmutz et al., 2007) and the availability of dispersers in Africa (Foxcroft et al., 2008). This indicates that for a species to successfully escape cultivation, a combination of factors

including suitable climate, dispersers, and species traits act together to ensure success (Richardson and Pyšek, 2012).

To understand which species can persist and therefore escape abandoned cultivation, a comparison can be made between the species currently in cared-for gardens and those found in abandoned gardens. Also, comparisons can be made with species sold in nurseries to investigate which potential invaders are still on the market. Riverine areas adjacent to abandoned homestead gardens should also receive special attention. Some of the gardens I visited which were adjacent to streams showed species spreading from the gardens downstream. This will however be determined by the availability of study sites.

4.3 A way forward

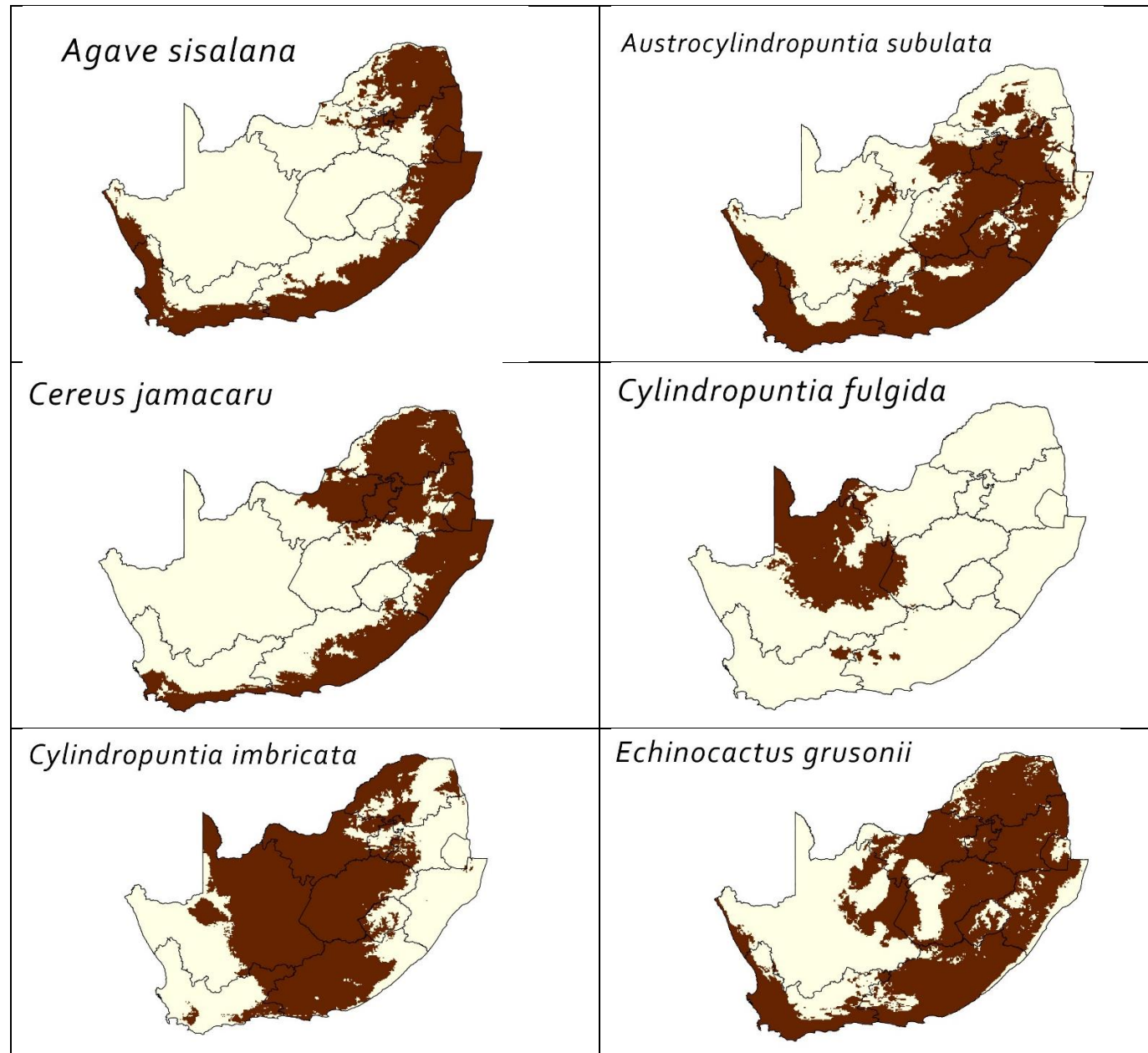
Rural areas are not well researched in invasion ecology and this project indicated that rural areas can also be a source of alien invasion, just like urban areas. This is because invasive ornamentals can escape from abandoned gardens into adjacent natural or disturbed vegetation (Chapter 2). My study indicates that rural areas have the same if not equal potential to spread invasive plant species as cities. This is a concern particularly for abandoned homesteads gardens because species can spread long distances invading natural habitats unnoticed. Ornamental plant species escaping cultivation can include both NEM: BA listed species and non-listed species. The project indicated that abandoned homestead gardens could be sources of emerging invaders. To list all the potential and emerging invaders in South Africa more abandoned gardens will need to be sampled.

4.4 References

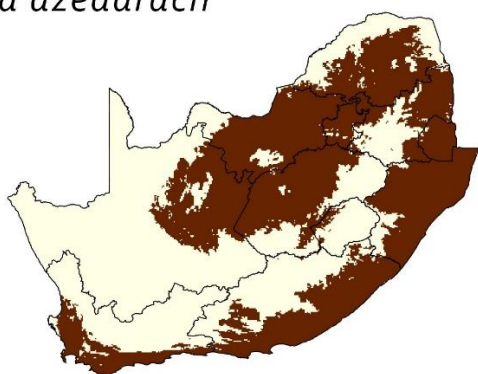
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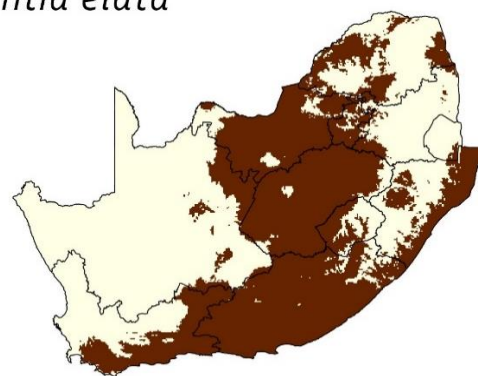
4.5 Appendix



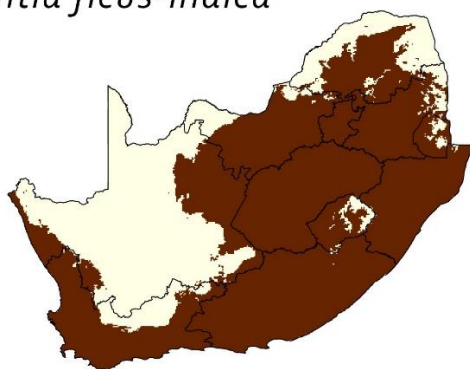
Melia azedarach



Opuntia elata



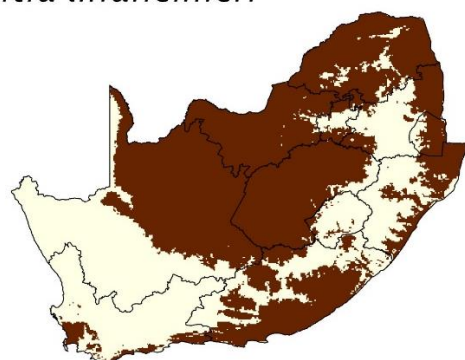
Opuntia ficus-indica



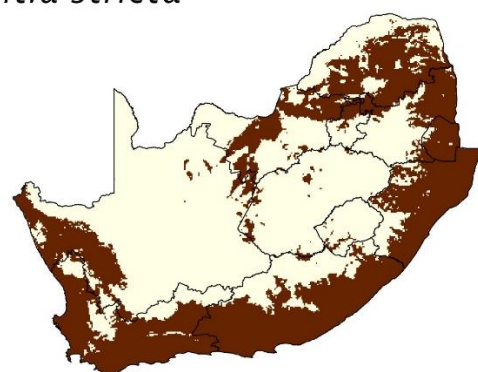
Opuntia humifusa



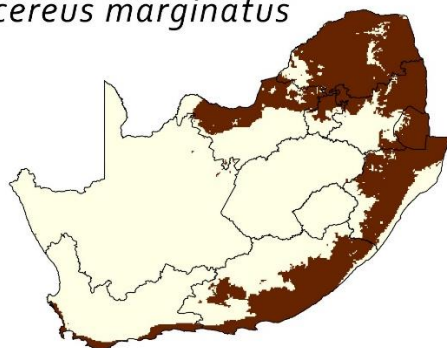
Opuntia lindheimeri



Opuntia stricta



Pachycereus marginatus



Prosopis juliflora



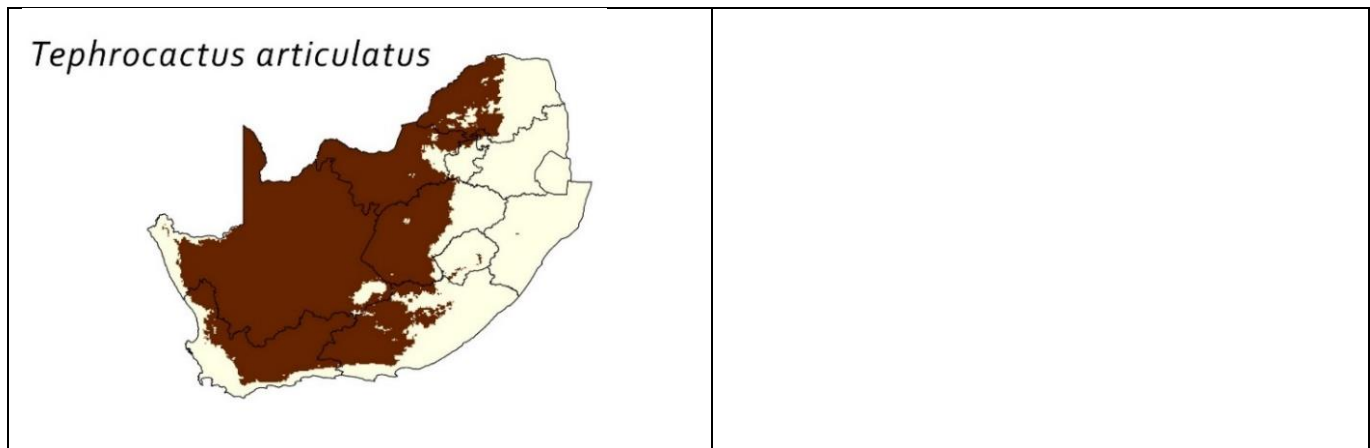


Figure A1: potential distribution of alien ornamentals under current climatic conditions. Brown on the maps indicates modelled presences, and cream white indicates absences.