

Assessing success in attempts to eradicate an emerging invader plant: *Tephrocactus articulatus* (Pfeiff.) Backeb in arid areas of South Africa

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ABSTRACT

Tephrocactus articulatus (Pfeiff.) Backeb (family: Cactaceae) is an emerging invader plant that is native to Argentina and was introduced as an ornamental plant in South Africa. The South African national regulations and legislation for controlling biological invasions dictate that emerging alien species must be eradicated. We evaluated the effectiveness of foliar spray in clearing the populations of *T. articulatus*, and determined the management challenges in 16 representative sites. We also applied bioclimatic models to forecast how *T. articulatus* invasion might respond to climate change. The exposure to climate change forecasts for *T. articulatus* was quantified using the Intergovernmental Panel on Climate Change - IPCC (2014) two representative concentration pathways – RCP scenarios (4.5 and 8.5) for the 2061–2080 period. Overall, the foliar spray method significantly suppressed *T. articulatus* populations in all sites (i.e., 75–99%) except in four sites that did not display the population suppression threshold of $X \geq 75\%$. The clearing success (i.e., % of dead plants), was significantly and negatively correlated to the size of the site (ha) wherein the bigger sites had relatively low success. Climate suitability projections under the RCP4.5 and RCP8.5 scenarios for *T. articulatus* produced excellent data fits (i.e., training AUC = 0.939 and test AUC = 0.914). Noteworthy, both future scenarios model projections have shown an expansion of suitable habitat for *T. articulatus*: 49.9% and 60.4% respectively, of the current estimated total spatial coverage of 219102 km², and with possible expansion into neighbouring countries, Namibia and Botswana. The significant variation in the projections was contributed by precipitation in the wettest (47.5%) and warmest quarters (48.9%). Our results advance the importance of predictive models in planning optimisation in the management of emerging alien plant species in South Africa: if the ongoing eradication of *T. articulatus* in the core invasion areas fails, and climate change prevails, a switch from foliar spray to biological control method will be essential.

1. Introduction

Alien and invasive plant species are considered a major factor driving biodiversity loss and causing economic loss, which threatens human livelihoods (Pimentel et al., 2001; Senator and Rozenberg, 2017; Mussa et al., 2018; Archer et al., 2018; Reynolds et al., 2020). Among others, cacti invasion is representing a continuous problem in South Africa (Novoa et al., 2017; Kaplan et al., 2017; Masocha and Dube, 2018; Wilson et al., 2016). It has been shown that cacti are among the most widespread species and, globally, South Africa is reviewed as the second most invaded of all countries, with 35 taxa recorded (Novoa et al., 2014). Historically, more than 200 cacti species have been introduced into South Africa for various socio-economic purposes (Novoa et al.,

2014; van Wilgen and Wilson, 2018). Thus, partly, the multiple introductions through important activities such as the horticulture trade, commercial and subsistence agriculture could have increased the propagule pressure and invasion success (Lockwood et al., 2009; Kaplan et al., 2017). In addition, cacti species generally have high tolerance to extreme conditions and prolific reproduction rates (Walters et al., 2011). Consequently, this, in combination with the high diversity of local environmental conditions (Richardson and Thuiller, 2007), has led to most cacti species forming large, dense infestations that reduce the quality of grazing land in South Africa (Du Toit, 1942; Dean and Milton, 2000; Walters et al., 2011). Evidently, more than 900 000 ha in South Africa were abandoned by landowners in the 1940s owing to the invasion of Sweet prickly pear *Opuntia ficus-indica* (Du Toit, 1942; Dean and

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Milton, 2000).

Since 1995, the management of biological invasions including cacti species has been prioritised for reduction of their negative impacts in South Africa and this led establishment of clearing programmes such as Working for Water (Cheek and Crouch, 2015; Novoa et al., 2015; Henderson and Wilson, 2017; van Wilgen and Wilson, 2018). Because of the severity of the negative impacts of biological invasions, for effective management, South Africa has also developed and enacted legislation and policy – the National Environmental Management: Biodiversity Act (NEM:BA, Act 10 of 2004) and the Alien and Invasive Species Regulations (hereafter called NEM:BA-A&IS Regulations; Department of Environmental Affairs, 2014; revised in 2020). According to the NEM:BA-A&IS Regulations 2020, ten cacti species are listed under category 1a of alien species including *Tephrocactus articulatus* (Pfeiff.) Backeb, and the national regulations earmarked them as targets for national eradication (van Wilgen and Wilson, 2018; DFFE, 2020). The early detection and rapid response division housed in the South African National Biodiversity Institute (SANBI) was established to eradicate emerging alien species populations and provide policy guidelines for effective management of biological invasions (Wilson et al., 2013).

Eradication is described as the application of control measures aiming to extirpate the entire population of a targeted emerging alien species from an area (Parkes and Panetta, 2009; Pyšek and Richardson, 2010). Effective clearing efforts can limit the spread of the emerging alien species (Wilson et al., 2013, 2017), and clearing is cheaper since it deals with species having restricted range (Mokotjomela et al., 2022). Nevertheless, reports have shown that successful eradication is difficult to achieve especially when the infested site is huge (Parkes and Panetta, 2009; Pluess et al., 2012; Wilson et al., 2013). Another factor accounting for limited success in the eradication of emerging alien species is patchy scientific knowledge of the target species (Pluess et al., 2012), and an absence or limited species' detection data beyond standard surveys by managers (Wilson et al., 2016) of which retards effective planning of management actions. According to Wilson et al. (2013), South Africa has documented only one example of a successful eradication programme for the emerging Mediterranean snail *Otala punctata* in Cape Town. Thus, alternatively, the biological control method represents the most effective and cheap approach for the management of the species that have expanded distributional range in South Africa (Moran et al., 2013; Zachariades et al., 2017). For example, biological control agents have been successfully released to control 34 of the 59 alien plant species including the cacti species in South Africa (Zachariades et al., 2017).

Tephrocactus articulatus (Pfeiff.) Backeb, was introduced in South Africa in 1953 through the horticultural trade as an ornamental plant species (Walters et al., 2011). *Tephrocactus articulatus* commonly known as pine-cone cactus, is an emerging cacti species native to Argentina (Garralla and Cuadrado, 2007; Novoa et al., 2017). It is a succulent and has thickened and fleshy parts that are adapted for water storage (Henderson, 2020). *Tephrocactus articulatus* grows up to more than 30 cm tall with the stems being 2–4 cm broad and 5–10 cm long (Henderson, 2020; Mokotjomela et al., 2022). The segments are oval for elongation and grow like sausage links, one springing forth from the next (Akulova-Barlow, 2007). The flowers are bell-shaped, 3–4 cm broad and 4–5 cm long, and (Walters et al., 2011). The fruits are white to pale pink in colour and about 15 mm large (Akulova-Barlow, 2007). The seeds are 1 cm long with a yellowish to tan colour and they are released when fruit walls are dry (Henderson, 2020). *Tephrocactus articulatus* reproduces by seeds (winged and corky seeds; Walters et al., 2011) and vegetative reproduction such as dislocated cladodes that develop roots and grow into new plants (Walters et al., 2011; Gorelick and Mahr, 2013). Walters et al. (2011) indicated that the dislocated cladodes of this species are easily dispersed by the wind for shorter distances and by water for long distances. A recent study suggested that humans are also key dispersers because of home garden refuse – *T. articulatus* has been recorded in the dumping sites in South Africa (Mokotjomela et al., 2022).

Negative impacts of *T. articulatus* invasions include eliminating native biodiversity, threatening human livelihoods, and increasing socio-economic loss (Paterson et al., 2011, 2021) as it grows vigorously forming a dense thicket and outcompeting the native species (Henderson and Wilson, 2017; Van Wilgen and Wilson, 2018; Guerrero et al., 2019). The ribbed stem expands and contract easily for quick water absorption after rain (Guerrero et al., 2019) whilst it is also well-adapted to arid conditions (Walters et al., 2011). In the absence of typical leaves, photosynthesis takes place in the stem (Guerrero et al., 2019). In South Africa, *T. articulatus* has been recorded in many small towns and farming areas of the Northern Cape, Free State, Eastern Cape, and Western Cape provinces (Van Wilgen and Wilson, 2018; Mokotjomela et al., 2022). *Tephrocactus articulatus* is also invading Western Australia where it disrupts the rangelands' capacity and quality with its dense and highly competitive infestations (Biosecurity Southern Australia, 2009; Government of Western Australia). Partly, because of climate change, the number of invasive alien species and their negative impacts are increasing (Pyšek et al., 2020; Venter et al., 2022).

Many alien species perform well under elevated atmospheric carbon dioxide (Rodgers et al., 2008; Venter et al., 2022). The elevated carbon dioxide reportedly stimulates photosynthesis and resource-use efficiency (Rodgers et al., 2008; Venter et al., 2022), and increases ambient global temperatures through ozone depletion (Anderson et al., 2016). Consequently, the application of the predictive models has been recommended since they can allow the development and implementation of proactive management strategies that match the booming problem of biological invasions (Rejmánek et al., 2005; Pyšek et al., 2012; Capinha et al., 2023), and their alien plant population dynamics in the face of changing climate (Barbet-Massin et al., 2018; Hui, 2023), including cacti species (Larios et al., 2020). The species habitat projection models correlate the known occurrences of species with environmental variables to predict potential climatically suitable habitats for a species to survive (Araújo et al., 2019; Srivastava et al., 2019; Hui, 2023). However, recent studies have presented mixed projections for suitable climate areas for different cactus species (Butler et al., 2012; Benavides et al., 2021; Pillet et al., 2022). For contrasting examples, Barbet-Massin et al. (2018) found better accuracy results when species data from native range was excluded in the habitat projections while Briscoe Runquist et al. (2019) argue that the use of early records of invasions without native range records resulted in poor future invasion predictions. Thus, the application of species habitat projections must follow a set of best-practice standards proposed (Araújo et al., 2019) and with specific reference to invasion biology as reported by Hui (2023). In this study, we assume the effective species distribution projections from early invasion (i.e., emerging species), can allow the preparation of implementation of alternative methods such as biological control where eradication attempts with foliar spray have failed in the core invasion areas.

For containment of cacti invasion, the foliar spray method is common in South Africa. Historically, the chemical method was introduced after limited success in the application of mechanical methods to clear the invasion of *Opuntia ficus-indica* and *Opuntia aurantiaca* jointed cactus in South Africa (Walters et al., 2011). The use of Garlon 430 EC with a spray oil at a concentration of 2% has been 100% effective in eradicating Hudson pear *Cylindropuntia pallida* infestations in Spain (Deltoro et al., 2013; Bromilow, 2018). However, the chemical method also displayed limited success in controlling large infestations of *Opuntia stricta* in Kruger National Park, South Africa (Hoffmann et al., 1998), and even became too expensive (Zimmermann, 2017). Despite this, the detected emerging populations of *T. articulatus* are treated with the foliar spray method using Garlon 430 EC (i.e., approved for minor and limited use for clearing the emerging alien plants) in South Africa (<https://invasives.org.za/herbicides/>), and to this end, no study has evaluated the effectiveness of the implemented management plan for *T. articulatus*.

In view of these arguments, we aimed: 1) to assess the effectiveness of the foliar spray method in clearing populations of *T. articulatus* by

comparing population size before and after clearing, and to determine the challenges of the current methods; and 2) to use bioclimatic models to determine the current and future potential distribution of *T. articulatus*. It is envisaged that the results of this study will guide decision-making in optimising the clearing of *T. articulatus* as an emerging species targeted for eradication using the foliar spray method in South Africa while the results from the species habitat projection models will assist in preparing the relevant biological control agent in cases where the foliar spray method failed to contain the emerging invasion.

2. Methods and material

2.1. Study area

The choice of the study sites was solely determined by the occurrence of *T. articulatus* and by the presence of sites in which the species had been treated with foliar spray by SANBI-DBE contractors (see images captured by field scientists, Fig. 1). Overall, there were 172 sites that occurred in arid areas of South Africa, following the description by Mucina and Rutherford (2006), and were considered for predicting potential species distribution. This was above the minimum threshold of 100 for successfully running species distribution models (Hui, 2023). Out of the 172 sites, 16 sites were used to evaluate the effectiveness of the foliar spray method and the sites were located in Free State, Eastern Cape, Western Cape, and Northern Cape provinces of South Africa (Table 1; Fig. 2). In addition, the arid area focus was instigated by the predominance of cacti species in a recent study sampling both the urban and peri-urban dumpsites (Mokotjomela et al., 2022). The terrestrial biomes that include the arid areas of South Africa have been reported to be highly vulnerable to invasions by various cactus species (Walters et al., 2011; Masocha and Dube, 2018; Mokotjomela et al., 2022).

At present, *T. articulatus* has mostly been recorded in the Nama-Karoo biome and the Savanna biome, but is expanding to Grassland, Succulent Karoo, and Fynbos biomes. Fig. 2 shows the current occurrence records including the cleared sites in different biomes in South Africa. Overall, 65 populations were treated but we identified 16 populations that were comparable based on their sizes with each having more than 200 plants (Tables 1 and 2).

Just as a note that this new novel alien species is put into these biomes by humans spreading this species, and there are not samples taken to prove it does not exist in the other biomes. This species can thrive and spread in all the biomes and ecosystems, wherever humans choose to

spread them. So, at biome level, biomes and vegetation type may not be a constraint at all, since it can potentially or may already exist in other biomes not shown on the map. Even though the Masocha and Dube (2018) have raised the alarm about the cacti invasion in the terrestrial arid habitats, there is not enough research done.

2.2. Data collection

2.2.1. Site verification: Recording *Tephrocactus articulatus* before and after site treatment

Following the detection of emerging alien species in South Africa, the management implementing authority plans eradication. Partly, this entails the estimation of the spatial extent of the targeted species' population and determining the resources required to clear the species to determine the feasibility of eradication (i.e., complete removal of the species from the habitat) of the species (Parkes and Panetta, 2009; Pluess et al., 2012).

During pre-clearing site verifications of *T. articulatus*, different populations were mapped (using the Garmin Oregon 750 model) in the invaded area marked with a polygon. The individual plants consisted of multiple cladodes, and any individual cladode that was found away from the main plant and having roots since cacti reproduce vegetatively (Walters et al., 2011; Fig. 1c). The GPS coordinates of all plants sighted were documented for comparison with the post-clearing surveys at each site, which were conducted in the same way but looked for living plants on each site after treatment. The post-clearing monitoring in each site was conducted after at least one to two growing seasons to allow sighting of either the new or missed plants or recovering plants. The location of each *T. articulatus* plant was coded by allocation of number "1" to classify the data (number of plants) recorded before and number "2" after clearing in each site. All GPS coordinates for plants recorded before were coded as "B" and those sighted after clearing as "A". It was assumed that clearing (i.e., application of herbicide to all sighted plants) would be successful and effective if the population suppression was greater than 75% of the total number of plants sighted during verification in each site, in line with national standards.

2.2.2. Bioclimatic modelling of *Tephrocactus articulatus* occurrence: Current and future

In this study, we used the Max Planck Institute Earth System Model (MPI-ESM) to predict the geographical range and habitat suitability for *T. articulatus* for the 2061–2080 period. The MPI-ESM is a comprehensive earth system model that combines model components of ocean,



Fig. 1. *Tephrocactus articulatus* images taken in different sites in South Africa: adult plants in the wild before treatment with herbicides (a1&2), after treatment with herbicide the plant disintegrates into cladodes (b1), and the treated plants occasionally resist and regenerate into plants after rainy season (b2&3), and some cladodes that could have dispersed during treatment are found on sites developing roots to become new plants (c).

Table 1

Site descriptions: Provinces and names of the 16 towns where different sampling sites were located, their GPS locations, their South African biome, their vegetation types, and the protection status of the local vegetation following the National [Biosecurity Southern Australia, 2009](#) Red List Status: LC = Least Concern, NT = Not Threatened.

Province	Town	GPS location	SA Biome	Vegetation type (NBA, 2018)	NBA 2018 Red List Status
Free State	Gelukspruit	−28.106846, 20.959089	Grassland	Central Free State Grassland	LC
Northern Cape	Prieska	−29.677719, 22.741524	Nama-Karoo Biome	Northern Upper Karoo	LC
Free State	Jacobsdal	−29.128235, 24.768655	Nama-Karoo Biome	Northern Upper Karoo	LC
Western Cape	Williston	−31.342405, 20.924461	Nama-Karoo Biome	Western Upper Karoo	LC
Northern Cape	Hope town	−29.6422, 24.0845	Azonal Vegetation	Southern Karoo Riviere	LC
Northern Cape	De Aar	−30.65662, 23.998232	Nama-Karoo Biome	Northern Upper Karoo	LC
Free State	Luckhoff	−29.75043, 24.78764	Nama-Karoo Biome	Northern Upper Karoo	LC
Northern Cape	Victoria West	−31.395817, 23.135279	Nama-Karoo Biome	Eastern Upper Karoo	LC
Northern Cape	Keimoes	−28.718432, 20.986517	Nama-Karoo Biome	Bushmanland Arid Grassland	LC
Western Cape	Prince Albert	−33.000152, 21.997616	Nama-Karoo Biome	Gamka Karoo	LC
Western Cape	Leeu-Gamka	−32.366859, 22.601174	Azonal Vegetation	Southern Karoo Riviere	LC
Western Cape	Merweville	−32.679217, 21.518329	Nama-Karoo Biome	Gamka Karoo	LC
Eastern Cape	Aberdeen	−32.481285, 24.066506	Azonal Vegetation	Southern Karoo Riviere	LC
Eastern Cape	Graaff-Reinet	−32.288239, 24.545045	Albany Thicket Biome	Escarpment Valley Thicket	NT
Western Cape	Beaufort West	−32.366859, 22.601174	Azonal Vegetation	Southern Karoo Riviere	LC
Western Cape	Bloukrans	−32.808367, 24.643934	Azonal Vegetation	Southern Karoo Riviere	LC

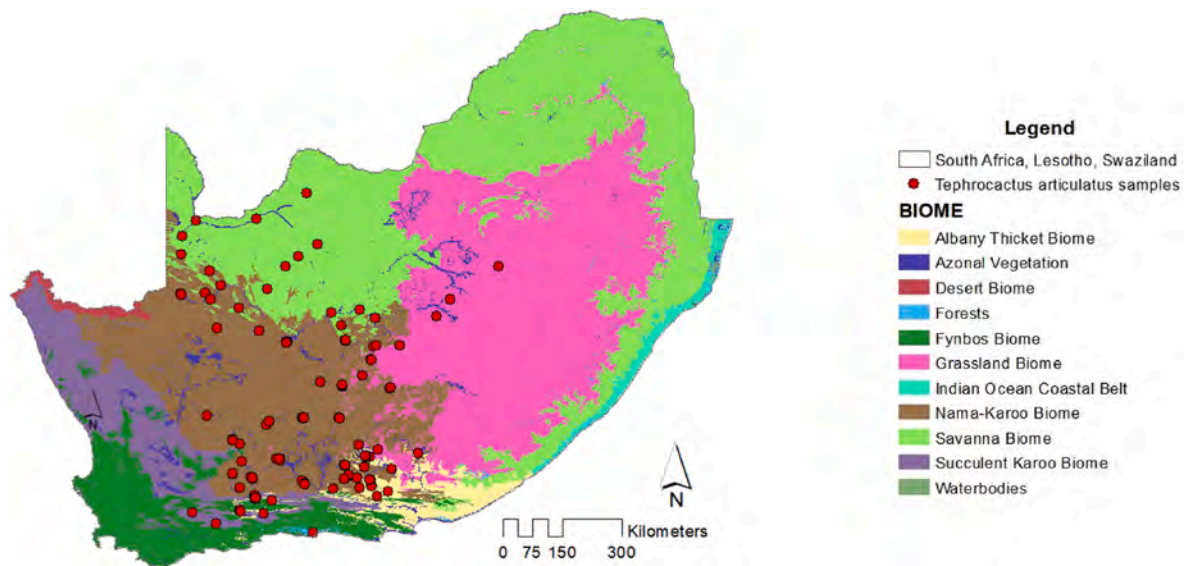


Fig. 2. Locations of different 172 sites that have the occurrence of *T. articulatus*, including the 16 sampled sites that were treated with the foliar spray in different biomes in South Africa.

atmosphere, and land surface through exchanges of energy, momentum, water, and carbon dioxide (Muller et al., 2018). It is fairly conservative and is well-suited for predictions about Southern Africa's climate (Connolly and Bracegirdle, 2007). The current climate used was that for 1950–2000 (Hijmans et al., 2005; Fick and Hijmans, 2017), using the Representative Concentration Pathway RCP4.5 and RCP8.5 as the future scenarios for the projected future period of 2061–2080. Representative concentration pathways (RCPs) are greenhouse gas concentration trajectories used by the Intergovernmental Panel on Climate Change for its fifth Assessment Report in 2014. The RCP4.5 is described as an intermediate scenario in which carbon dioxide emissions peak around the year 2040, and then decline due to mitigative actions of the society, while RCP8.5 assumes that carbon dioxide emissions continue to increase throughout the 21st century (IPCC, 2014). The distribution model was used to estimate the relationship between the sample records (Booth et al., 2014) and the environmental and spatial characteristics of those sample sites (Phillips et al., 2004, 2006, 2017).

In order to predict the potential distribution of the *T. articulatus* species and its relationship with the environmental and climatic variables, the species distribution models were performed to show the climatic niche of *T. articulatus* using the MaxEnt (version 3.4.4). MaxEnt

applies Bayesian methods to estimate the potential geographic distribution of species, by finding the probability distribution of maximum entropy (Phillips et al., 2004, 2006, 2017). Gibbs sampling is a statistical algorithm that Bayesian inference uses in the MaxEnt program (Phillips et al., 2017). The Gibbs family is described as $\{q_\lambda(x), \lambda \in L\}$, where:

$$q_\lambda(x) = \frac{1}{Z_\lambda(x)} \exp \left(\sum_{i=1}^m \lambda_i f_i(x) \right) \quad (1)$$

and $\lambda_i = (\lambda_1, \lambda_2, \dots, \lambda_m)$ is the weight vector, λ_i is the weight parameters, and L is the m -dimensional space, with $f_i(x)$ representing species i is a probability distribution, and $Z_\lambda(x)$ is the normalised constant, and also each element x is a pixel of the investigated area (Guo et al., 2016). The probabilities $f_i(x)$ represent the relative suitability of the environmental and climatic conditions in each pixel (Phillips et al., 2004, 2006, 2017).

The climate variables used in the study were 19 bioclimatic variables of BIOCLIM (Booth et al., 2014), which is a bioclimatic prediction system that uses the bioclimatic parameters derived from mean monthly climate estimates to estimate the energy and water balances at a given location (Nix, 1986; Fenner School, 2016). After test runs, six climate variables were selected from the 19 variables to use for future

Table 2

Generalised linear model results testing significant differences between the number of individual *T. articulatus* plants recorded before and after foliar spray treatment in different sites. The site locations, initial population size, clearing success (i.e., i.e., the % number of dead *T. articulatus* plants) and statistical comparisons before and after clearing population sizes. ** Denotes the significant differences based on herbicide manufacturer specifications (i.e., $X > 75\%$ of the population).

Site			Statistics		
Town (Site locations)	Population size (N)	Clearing success (%)	Pearson - χ^2	df	Significance (P value)
Gelukspruit	1348	88.4**	1741.6	1	0.0001
Prieska	773	72.0	136.6	1	0.0001
Jacobsdal	838	69.8	131.5	1	0.0001
Williston	596	82.4**	250.0	1	0.0001
Hope town	581	95.9**	489.0	1	0.0001
De Aar	535	96.3**	457.0	1	0.0001
Luckhoff	770	91.2**	558.6	1	0.0001
Victoria West	998	89.1**	149.6	1	0.0001
Keimoes	1124	97.0**	658.1	1	0.0001
Prince Albert	470	91.2**	1028.6	1	0.0001
Leeu-Gamka	305	99.0**	558.9	1	0.001
Merweville	2026	68.5	239.0	1	0.0001
Aberdeen	440	77.4**	159	1	0.0001
Graaff-Reinet	273	72.0	156.0	1	0.0001
Beaufort West	238	96.8**	131.5	1	0.0001
Bloukrans	1145	68.4	443.2	1	0.0001

projections, based on variable importance and contributions to the model. Biome for the future projections is excluded, as biome will mostly likely change/contract/expand in the future, and so only climate variables are selected for projections. The selected six variables are ecologically relevant for cacti species in South Africa (Masocha and Dube, 2018; Araújo et al., 2019; Hui, 2022). The selected six variables are ecologically relevant for cacti species in South Africa (Masocha and Dube, 2018; Araújo et al., 2019; Hui, 2023), and the biome to account for the role of vegetation in the invasion risk predictions. An additional variable biome is added as a constraint (Mucina and Rutherford, 2006), to assist in examining which current variables are important to the species. The species projections were modelled in the alien range (i.e., South Africa), and *T. articulatus* is currently considered an emerging invader without much knowledge about factors driving its ecological performance in South Africa (Parkes and Panetta, 2009; Hui, 2023).

3. Data analysis

Data on the GPS locations of individual plants provided the distribution of plants observed. The same locations of sighted plants were coded to generate a count of plants, and this allowed a comparison of the number of plants before and after treatment. We used two different codes for each site's pre- and post-clearing counts of plants. The counts of plants were specified as ordinal response variables, while different sites were specified as predictor variables. We defined the clearing success at each site as the percentage of the number of plants that died from herbicide treatment out of the total number of plants that were recorded during site verification. Following the Working for Water standards on the effectiveness of clearing methods, we considered the sites that displayed greater than 75% population suppression as significant results, despite the significant statistical differences observed between the numbers of plants recorded before and after clearing.

A generalised linear model (GLM) fitted Poisson errors was used to test the statistical differences between the number of plants that were recorded and treated, and the number of plants that were found alive on-site during the post-treatment surveys; this was done in SPSS software, version 28. We specified the counts of plants at each site as response variables and different sites and treatments as predictor variables.

To determine whether the size of each treated site influenced

population clearing success, we correlated the clearing success (i.e., the % difference between the number of plants before and after clearing) with the patch size measured in hectares for 65 sites that were cleared.

4. Results

4.1. Population suppression

Overall, the foliar spray method significantly suppressed *T. articulatus* populations in all 16 sites (i.e., 75–99%; see Table 2). However, four sites did not display the desired relative significance in the population suppression threshold of $X > 75\%$, as stipulated herbicide efficiency for cactus (Table 2).

4.2. Species' clearing success and size of the patch

There was a significant and negative correlation between the size of the site cleared (ha) and the relative number of plants effectively killed (Pearson correlation: $r = -0.45$; $N = 65$; $P = 0.002$; Fig. 3), with the bigger sites having relatively low success.

4.3. Projected species distribution: Current and future

Overall, the fitting of the data was very good with Training AUC = 0.939 and Test AUC = 0.914 (Table 3; Fig. S5). Fig. 4 A & B show climate change impact on *T. articulatus* species only, without considering humans as the main instigators of the fast spread of the alien species. The maps show areas of expansion as well as areas of shrinkage. In both scenarios, the variables most affecting this species are precipitation of the wettest quarter and precipitation of the warmest quarter. The RCP4.5 climate scenario as an intermediate scenario is only possible if carbon emissions peak around 2040, and then decline afterwards. In this scenario, with active reduction of carbon emission, *T. articulatus* has some current habitat range shrinking although it has the potential to spread into an additional 49.9% of new areas covering its current estimated total spatial coverage of 219102 km² (Fig. 4A). Under the RCP8.5 climate scenario, where carbon emissions are left unchecked, *T. articulatus* can spread faster into more ecosystems (60.4%, Fig. 4B). The most important variable that contributed to the model predictions was the precipitation in the wettest and warmest quarters for both RCP4.5 and RCP8.5 (Table 3).

Of note here, in Fig. 4 A&B, these show climate change impact on *T. articulatus* species only, without taking account humans are main instigators of the fast spread of the alien species. The maps show areas of expansion as well as areas shrinking. Contrary to popular thinking, cactus species can decline due to future climate adverse impacts (Pillet et al., 2022). In both scenarios, the variables most affecting this species are precipitation of wettest quarter and precipitation of warmest quarter. The RCP4.5 climate scenario as an intermediate scenario is only possible if carbon emissions peak around 2040, then decline afterwards. In this scenario, with active reduction of carbon emission, *T. articulatus* has some current habitat range shrinking, and does spread into new areas. Under RCP8.5 climate scenario, where carbon emissions are left unchecked, the *T. articulatus* species can spread faster into more ecosystems, as it will survive, also with some loss of suitable habitat and distribution. Therefore, this alien species, even without human spreading it further (i.e., the realistic likely scenario) in this model, it will survive and spread across the ecosystem. Both future scenario model projections have shown an expansion of the species, and with possible expansion into neighbouring countries, Namibia and Botswana. While RCP8.5 climate scenario shows more possible habitat loss, but it also comes with much higher habitat expansion.

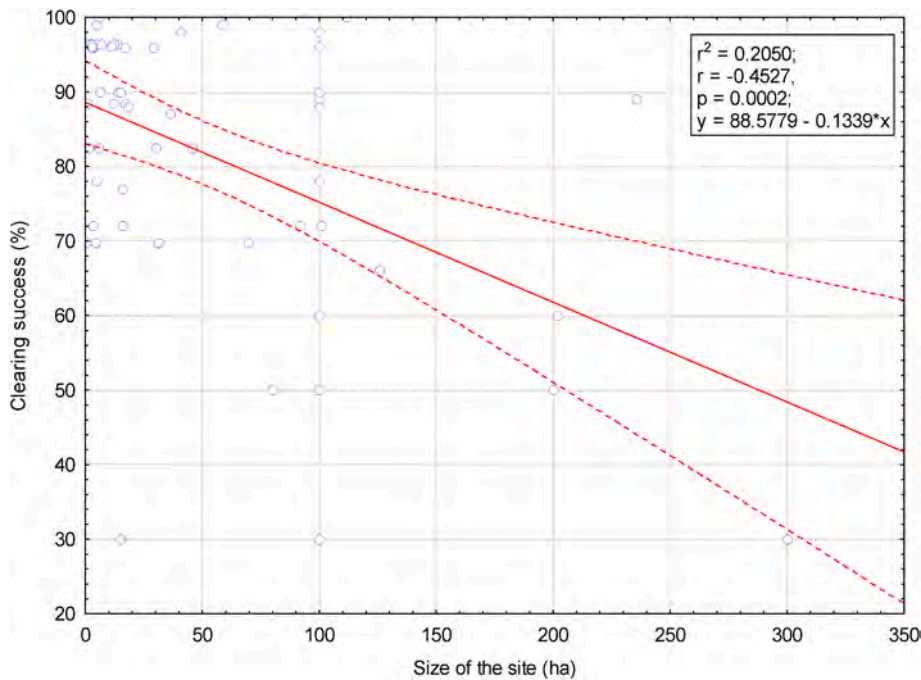


Fig. 3. Correlation between the clearing success (%) for *T. articulatus* using the foliar spray method and the size of the site (ha). Regression bands represent the $\pm 95\%$ confidence intervals.

Table 3
Different climatic predictor variables (6) and their contribution in influencing the observed variation during the development of the bioclimatic model for *T. articulatus* distribution in South Africa. Green bolded text shows variables that contributed significantly to the variation in the habitat predictions under the RCP4.5 and RCP8.5 scenarios.

Maxent model variable contributions			RCP4.5		RCP8.5	
Training data AUC			0.939		0.902	
Test data AUC			0.914		0.906	
Testing all variables			Projected variable importance RCP4.5		Projected variable importance RCP8.5	
variables	variable contributions	permutation importance	variable contributions (RCP4.5)	permutation importance (RCP4.5)	variable contributions (RCP8.5)	permutation importance (RCP8.5)
1 BIO5 = Max Temperature of Warmest Month	9.0543	15.4067	11.6438	22.1397	12.9722	30.5363
2 BIO7 = Temperature Annual Range	4.8634	12.9168	5.0214	6.4628	2.8633	9.0578
3 BIO9 = Mean Temperature of Driest Quarter	7.9091	0.9731	6.4806	7.3497	9.4465	8.8922
4 BIO12 = Annual Precipitation	9.5515	18.0701	10.3924	4.1357	9.4316	4.2027
5 BIO16 = Precipitation of Wettest Quarter	10.7473	0	47.5018	11.0489	50.2819	8.885
6 BIO18 = Precipitation of Warmest Quarter	7.1929	25.1256	18.96	48.8633	15.0044	38.426
7 Biome	37.5975	8.5213				

5. Discussion

5.1. Population clearing success

Our finding that the foliar spray method significantly suppressed populations of *T. articulatus* in most of the sites is a positive step towards

the management of emerging biological invasions in South Africa. This finding complements the previous reports that herbicides are known to be more effective than mechanical methods (Walters et al., 2011; Martens et al., 2021). The observed success could also be attributed to substantial and positive developments in manufacturing herbicides that comply with environmental, health, and safety standards such that there

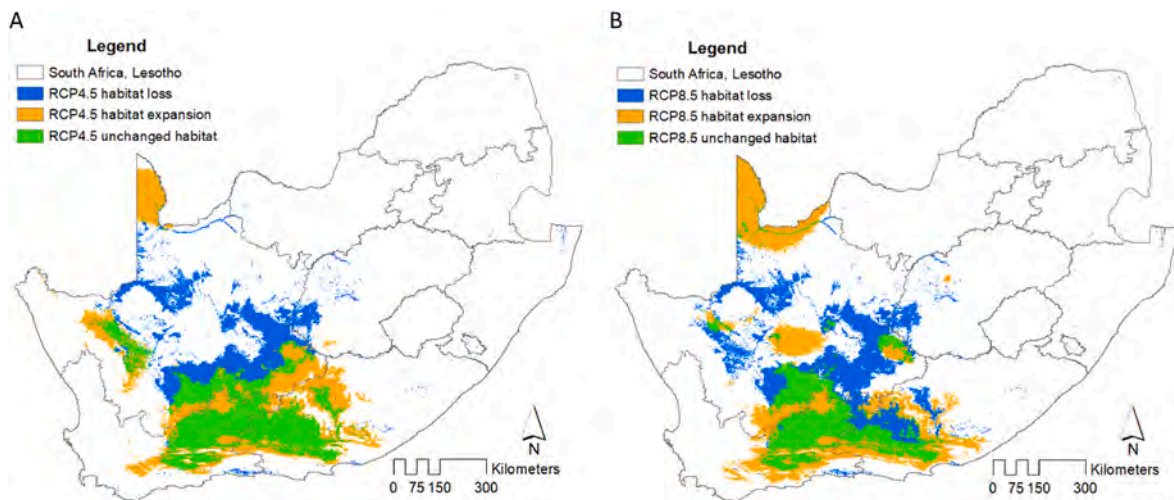


Fig. 4. Different carbon emissions scenarios in projecting future (2061–2080) *T. articulatus* species distribution in South Africa. Two different RCP models were used: (a) Future RCP4.5 projection of *T. articulatus* habitat change map; and (b) Future RCP8.5 projection of *T. articulatus* habitat change map.

are selective herbicides as reported by Martens et al. (2021). Furthermore, the existence of a regulatory policy for using herbicides has prompted a stringent choice of products based on their efficiency and on the risks as a way of optimising their function (Gandhi et al., 2021; Martens et al., 2021). Beyond being a legal requirement, the eradication of *T. articulatus* in South Africa is critical because the favourable interior environmental conditions make it a global hotspot for invasion by cacti (Kaplan et al., 2017), and thus new populations must be cleared to prevent the species' density-based negative impacts (Pluess et al., 2012). That we did not find 100% eradication of the populations of *T. articulatus* in any site is a likely result of missing small plants concealed by native local vegetation during clearing operations. A similar observation was reported during the control of *Opuntia stricta* in Kruger National Park, South Africa (Lotter and Hoffmann, 1998); and this might point to the risk of site re-infestation although this situation can be averted through regular follow-up actions (Parkes and Panetta, 2009; Pluess et al., 2012). Nevertheless, studies have shown that the number of emerging and invasive species is increasing (Pyšek et al., 2012), and the resources for managing them could be the main limiting factor (Zengeya and Wilson, 2020) thereby suggesting the need for more innovative approaches.

We suggest that the varying levels of significance among the sampled sites could be explained by context-specific factors ranging from the abundance of the species relative to the size of the site and the age of the plants that are being treated with the foliar spray method. Subsequently, a significant and negative correlation between clearing success and the size of the site is likely a result of the small teams (e.g., fewer than 15 people; Lotter and Hoffmann, 1998) that are allocated on the basis of the notion that the emerging alien species have a limited distribution (Pluess et al., 2012; Wilson et al., 2013). Indeed, a review showed that the spatial extent of the infestation was significantly related to the eradication success, with localised campaigns being better than regional ones (Pluess et al., 2012), and that plant eradications generally take longer to achieve (Rejmánek and Pitcairn, 2002; Parkes and Panetta, 2009). This finding concurs with a previous report that suggested that limited human capacity and financial resources are a common cause of slow progress in the management of biological invasions in South Africa (Wilson et al., 2016). Consequently, we recommend further social awareness programmes about the *T. articulatus* and its potential impacts. Furthermore, the use of drones to survey prospective sites for clearing could increase spatial coverage and thus increase efficiency in clearing the local populations.

The age and/or size of the alien plant being treated can influence the success of clearing since smaller plants are generally more susceptible than adult ones (Malan, 1989; Lotter and Hoffmann, 1998; Larios et al.,

2020). As an evolutionary adaptation to arid environments and other extreme conditions, adult cacti have a waxy layer that covers most of the plant's surface to prevent excessive evaporation while also keeping adequate water in the tissues (Mauseth, 2006a,b; Musengi, 2018; Larios et al., 2020; Pillet et al., 2022). It is possible that the waxy skin is resistant to herbicide application, and water in the tissues helps them to regenerate (Henderson, 2020). Moreover, *T. articulatus* has stomata that are found deep in the tissue rather than on the surface; and these open at night – Crassulacean acid metabolism (Leegood, 2013; Pillet et al., 2022) – leading to the proposal that herbicide application be done during either early mornings or late afternoons. Another challenge is the continued spread of *T. articulatus*, which increases invasion success through increased propagule pressure (Lockwood et al., 2009; Kaplan et al., 2017). *T. articulatus* is still used as an ornamental plant in South Africa and has been successfully established in the wild partly by being spread through garden waste in dumpsites (Mokotjomela et al., 2022). Invasion can also be worsened by the ability of cacti species to reproduce prolifically (Walters et al., 2011) because of a possible increase in cacti species seed germination rates under changing climate (Seal et al., 2017); and this is coupled with observed effective long-distance dispersal mechanisms by birds in South Africa (Mokotjomela et al., 2021).

5.2. Projected species distribution: Current and future

Our finding of the potential gain of suitable habitat although there is also accompanied by some habitat loss for *T. articulatus* under RCP4.5 highlights the existence of strong interactive effects between temperature changes and water availability in supporting plant life. Since the biological invasions are also fuelled by other environmental factors operating in synergy (Hulme, 2017), climate alone cannot adequately describe and thus, where climate suitability has changed, other factors can still drive *T. articulatus* invasion. For example, global climate change has been predicted to accelerate dryland expansion (Huang et al., 2016), including in South Africa, the cacti's special physiological tolerances and high water-use efficiencies (Pillet et al., 2022) might result in a competitive advantage for invasion regardless of contained carbon emissions. Whereas the positive interactions have been reported by Venter et al. (2022), our results highlight the importance of carbon dioxide over water in cacti metabolism. Indeed, the current land use patterns are also implicated in high greenhouse emissions, with precipitation being the key driver of high photosynthesis process rates in plants – a physiological dynamic that is favourable to making alien plants superior to native plants. We therefore propose considerations for

the integrated management of the cacti invasion in which the role of climate change's role is factored into the species' management plan. The observed habitat gains and loss suggest that there is a possible niche shift for the *T. articulatus* in the alien range (Guisan et al., 2014; Pili et al., 2020) and may need to be considered to determine vulnerable areas in future management.

Our finding that the uncontrolled carbon emissions under the RCP8.5 scenario had a positive influence through increasing suitable habitat for *T. articulatus* corroborates the previous studies that have reported that a rise in atmospheric carbon dioxide concentrations presents favourable conditions to alien and invasive plants (Masocha and Dube, 2018). For example, the elevated carbon dioxide experiments showed increased growth rates and biomass accumulation in *Pereskia aculeata* (Cactaceae) in South Africa (Venter et al., 2022). Other studies reported rising efficiency in some alien plant species' water use (Rodgers et al., 2008), which might complicate the predicted drought problems (IPCC et al., 2014). This observation contradicts the popular notion that many cacti species could decline because of adverse future climate impacts in their native range – the Americas (Larios et al., 2020; Pillet et al., 2022) although Larios et al. (2020) found that the populations of the threatened and declining acuña cactus would remain stable under 2080 climate projections. It is possible that the myriad of environmental conditions and the associated biomes in South Africa create refugia for many alien and invasive species, including the cacti species as previously demonstrated (Richardson and Thuiller, 2007). Our findings complement the report by Masocha and Dube (2018), who showed that global terrestrial habitats, including southern Africa, are susceptible to cacti invasions under climate change. We also noted that *T. articulatus* has neither natural enemies nor barriers to its spreading to the rest of South Africa (Le Roux et al., 2020). This, together with human cultivation of *T. articulatus* for ornamental purposes might play a big role in its further spread in South Africa (Mokotjomela et al., 2022). Noteworthy is that the invasion risk assessment of *T. articulatus* is still in progress focusing on the current state of knowledge of species' impacts on the environment, economy, and society (*sensu* Kumschick et al., 2020), and will guide the listing and proposal of its management prescriptions in the South African National Regulations for Alien and Invasive Species.

5.3. Conclusions

We have shown that foliar sprays are effective in clearing the populations of the emerging cactus species *T. articulatus* in South Africa, and that knowledge of its future population dynamics might bolster investment decisions about its management under climate change (Hui, 2023). Based on the apparent resistance of the *T. articulatus* (i.e., cladodes from treated plant regenerating into plants), and the predicted increase in habitat suitability for both scenarios of RCP4.5 and RCP 8.5, we suggest that future invasions of the *T. articulatus* is possible although habitat gain has some offsets wherein other areas become unsuitable. Thus, future research may also need to do fine-scale investigations into the physiology of *T. articulatus* in the invasive range to effectively revise the implemented management plan. In cases where eradication efforts using foliar spray have failed to contain invasion in the core invasion areas,

immediate preparation of the biological control method as a cheaper option for species with expansive home range can be considered. Because the spread of the alien species *T. articulatus* in South Africa is mainly caused by the human factor (Mokotjomela et al., 2022), our models showed that climate alone cannot explain its spread. Nevertheless, with respect to future invasion modelling, we recommend that additional random points over South Africa and Lesotho are added to show the possible spread of *T. articulatus* with a human factor included, in the cases where the *T. articulatus* is uncontrolled, and without government policies to curb the fast-spreading alien species. We suggest that the use of predictive models also needs to be matched by increased management resources and the rapid implementation of action to yield positive eradication results. Finally, it is recommended that prior to full uptake and implementation of this combination of approaches, further experimental trials with other emerging species be done.

CRedit authorship contribution statement

Thabiso M. Mokotjomela: Conceptualised the MS, collected and analysed data, wrote MS. **Loyd R. Vukeya:** Analysed data, drew maps, wrote MS. **Danni Guo:** Applied the SDMs, analysed data, drew maps, wrote MS. **Thembelihle J. Mbele:** Collected and analysed data, wrote MS. **Travor Xivuri:** Collected data and wrote MS. **Anesu G. Kuhudzai:** Analysed data, wrote MS.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Thabiso MOKOTJOMELA reports financial support was provided by the South African National Biodiversity Institute. Thabiso MOKOTJOMELA reports financial support was provided by the Republic of South Africa Department of Forestry Fisheries and the Environment. Data c.

Data availability

Data will be made available on request.

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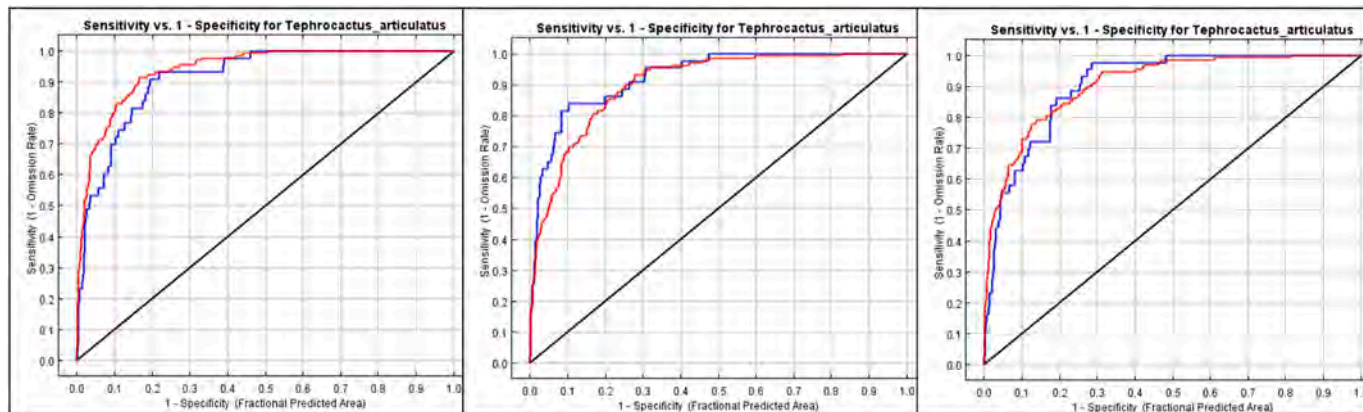
Annexure.1. Receiver operating characteristic (ROC) curve for the model, current species projections (left), with future RCP4.5 projections (middle), and future RCP8.5 projections (right)

The six selected bioclimatic variables for projections are: BIO5 = Max Temperature of Warmest Month.

BIO7 = Temperature Annual Range (P5–P6)
 BIO9 = Mean Temperature of Driest Quarter
 BIO12 = Annual Precipitation
 BIO16 = Precipitation of Wettest Quarter

BIO18 = Precipitation of Warmest Quarter

The fit of the data is very good for the model performance under current conditions, with Training AUC (area under curve) = 0.939 and Test AUC = 0.914. For the future RCP4.5 climate projections, the model performance is good as well, with Training AUC = 0.902 and Test AUC = 0.926. For the future RCP8.5 climate projections, the model performance is equally good, with Training AUC = 0.907 and Test AUC = 0.906.



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