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Insights into the invasion of the moth catcher vine, *Araujia sericifera* (Apocynaceae), in South Africa

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ABSTRACT

The moth catcher vine, *Araujia sericifera* Brotero (Apocynaceae), is a prevalent invader in many countries worldwide, where it has been reported to be a significant threat to biodiversity and agriculture. However, limited knowledge exists surrounding the ecology, invasion and impacts of *A. sericifera* in South Africa, challenging the implementation of management efforts. Therefore, this study sought to understand the vine's invasion within a South African context. To determine the density of *A. sericifera* in response to ecological and socio-economic predictors, its abundance along roads in 42 Johannesburg suburbs was measured. Additionally, *A. sericifera* abundance was recorded on foot within two nature reserves in Johannesburg, where density estimates were found to be 29 times higher than those obtained via roadside surveys. At a local scale, there was no evidence to indicate that vegetation, urban cover, and median household income influence *A. sericifera* density, suggesting that the vine establishes indiscriminately across Johannesburg. To determine whether this opportunistic behaviour was reflected in the vine's recruitment, its emergence rates in response to shaded and full-sun conditions were investigated. Seedling emergence was higher under shaded conditions (47.8%) than under full-sun (11%). Using MaxEnt models, environmental variables affecting the plant's distribution in South Africa were identified. Human disturbance had a permutation importance of 85.6%, indicating that *A. sericifera's* establishment is largely driven by disturbance. While *A. sericifera* appears to be in its lag phase of invasion and is unlikely to invade natural ecosystems in the short term, its abundance in the two nature reserves suggests that management should be prioritised during this lag phase, prior to its potential expansion into less-disturbed areas.

1. Introduction

Globalisation has led to unprecedented rates of alien species introduction, and it is estimated that over 37 000 alien species have established in non-native ranges throughout the earth's biomes, with an expected yearly increase in this estimate of 200 species (Faulkner et al., 2020; Roy et al., 2023). Nearly 10% of these species are regarded as invasive, as they present negative impacts to their recipient socio-ecological ecosystems, driving widespread biodiversity and economic losses (Bellard et al., 2016; Diagne et al., 2021; Roy et al., 2023). South Africa houses one of the highest numbers of invasive species worldwide (Pyšek et al., 2017), and is estimated to have over 10.1 million ha (~8.3% of the country) of invaded land (Le Maitre et al., 2000). Despite the extensive environmental and socio-economic consequences of invasive species, their management has frequently suffered insufficient financial allocation and substantial delays, with the onset of management often only occurring once an invasive species has already become widespread (van Wilgen and Wilson, 2018; Cuthbert et al., 2022; Zengeya and Wilson, 2023). Pre-invasion management costs are 25 times lower than post-invasion management costs, highlighting the importance of approaching the management of incipient invasive species proactively (Cuthbert et al., 2022). However, most studies pertaining to the management of invasive species focus on well-established invaders in natural ecosystems, and little attention is dedicated to urban invaders and well-known invaders that have not yet invaded new or larger areas (Mgidi et al., 2007; Potgieter et al., 2020). Potentially impactful invaders should therefore be assessed promptly to establish whether control or eradication is feasible, prior to the expansion of the problem (Wilson et al., 2013).

Araujia sericifera Brotero (Apocynaceae), native to much of neotropical humid South America, remains a problematic incipient invader in South Africa, and is invasive in Turkey, Australia, New Zealand, Italy, France, Spain, Greece, and Portugal, and citrus groves in the United States (Spellman and Gunn, 1976; Forster and Bruyns, 1992; Altinözlü and Dönmez, 2003; EPPO, 2008). Alien populations

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are present in at least 10 other countries worldwide (GBIF, 2023). In its invaded ranges, *A. sericifera* is common in tropical, subtropical, temperate, hot and cold semi-arid regions, as well as regions characterised by a hot-summer Mediterranean climate (Beck et al., 2018; GBIF, 2023). The introduction of *A. sericifera* into these non-native ranges was mainly for ornamental purposes, although anecdotal evidence suggests that it has also been cultivated for textile uses such as padding, cushions, and bedding (Winks and Fowler, 2000; Gaig et al., 2005). However, in South Africa, the exact date of and reason for the plant's introduction is unclear. It is thought to have been introduced into the country as an ornamental (Henderson, 2020) and the earliest herbarium record for *A. sericifera* is from 1918 (I. B. Pole-Evans, accession number PRE0341607-0, collected on 10/12/1918; SANBI, 2016).

Araujia sericifera tolerates a broad range of environments, which contributes to its encroachment and invasion of disturbed habitats, where indigenous species are rapidly outcompeted (Coulston, 2002). Due to its rapid climbing habit, *A. sericifera* can reach lengths of up to 10 m, often scrambling over trees, where it is capable of dominating and suppressing overstorey vegetation (Weber, 2003). The plant's persistence in tree canopies positions it favourably for the long-distance dispersal (over several hundred metres) of its tufted seeds, which are released upon dehiscence of the plant's pale green fruits (Winks and Fowler, 2000). Each fruit contains approximately 400 seeds that, following wind or (more seldomly) water dispersal, form a transient seed bank within the soil, which is quickly depleted by a high seedling emergence (Vivian-Smith and Panetta, 2005). The seeds are toxic, having been reported to cause the death of poultry and cattle upon ingestion, although incidences of ingestion are uncommon (Esler, 1988; Hill, 2019). While seeds are the primary mechanism for *A. sericifera* reproduction, it also reproduces vegetatively (USDA, 2012). Plant regrowth is common following chemical or mechanical clearing, which is often laborious and hazardous due to the plant's secretion of a toxic, milky latex via its stems, leaves, and fruits, which causes severe skin and eye irritation (Winks and Fowler, 2000; Gaig et al., 2005; EPPO, 2008; Kiwifruit Vine Health, 2016; Henderson, 2020). Infestations are thus difficult to eradicate without substantial costs (Winks and Fowler, 2000; Williams and Champion, 2008).

In New Zealand, *A. sericifera* germinates and establishes readily when exposed to full sunlight, despite a preference for partial shade, and persists well in deep, moist soils, but tolerates sandy soils or gravel (Williams and Champion, 2008). However, whether these broad ranges of environmental tolerances and high recruitment rates are evident in the seedling emergence of *A. sericifera* in South Africa is uncertain, although it is expected that similar preferences for shade will be observed. *Araujia sericifera* is abundant in New Zealand's urban reserves and natural forests but is also widespread in vulnerable habitats such as bush and forest margins, and coastal plains, where it adversely impacts indigenous vegetation (Winks and Fowler, 2000; Hill, 2018). In addition to its notoriety as a citrus grove invader in Spain and the United States, *A. sericifera* is a problematic invader in kiwi orchards in New Zealand (Kiwifruit Vine Health, 2016). However, in South Africa, *A. sericifera* has not yet been observed in agricultural plantations or closed forest habitats (Henderson, 2020). Rather, its opportunistic establishment in disturbed habitats renders it a prevalent urban invader, particularly in the metropolitan cities of Cape Town and Johannesburg (Henderson and Anderson, 1966; Henderson, 2007; Henderson, 2020). Given the prevalence of *A. sericifera* throughout a variety of habitats worldwide, an evaluation of the potential for the plant to invade vulnerable habitats in South Africa is valuable and necessary in determining whether it is likely to expand its range and threaten native biodiversity and agriculture.

Despite its classification as a common, Category 1b invader (removal and destruction of individuals is mandated due to potentially high invasiveness) in South Africa (Nel et al., 2004; Department of Environment, Forestry and Fisheries, 2020), baseline data regarding the plant's impacts, ecology, and invasion history are scant. Nevertheless, evidence of the plant's impacts on New Zealand's socio-ecological systems and the implementation of a successful biocontrol programme against *A. sericifera* with the release of a leaf-feeding beetle, *Freudeita cf. cupripennis* Lefèvre (Coleoptera: Chrysomelidae), has bolstered the candidacy of *A. sericifera* for biocontrol in South Africa (Canavan et al., 2021). South African biocontrol programmes have benefitted greatly from the expertise developed by other countries, and this practice has proven to be largely successful and pragmatic (Byrne et al., 2021). The transferability of New Zealand knowledge and the absence of indigenous plants closely related to *A. sericifera* in South Africa indicate promising prospects for successful biocontrol.

Understanding the plant's invasion dynamics in a South African context is necessary for determining the extent of the threat that *A. sericifera* poses, as well as in identifying potential factors that promote its invasiveness, as the invasion biology of *A. sericifera* worldwide remains largely underexplored. A search for "*Araujia sericifera*" or "*Araujia hortorum*", the accepted name in New Zealand (Champion et al., 2010), combined with keywords related to the invasion, ecology, biology, and management of the plant in ISI Web of Science (Supplementary Box S1) returned only 27 publications. Of these, 37% pertain to the biochemistry of the plant, and only 7% focus on its invasion biology, highlighting the need for a better understanding of the plant in this context. Evaluating the invasion dynamics of *A. sericifera* will contribute to optimising any potential biocontrol programme such that management can be directed towards sites that are most severely impacted or most vulnerable to invasion. Particularly, assessing the biology, abundance, distribution, and climatic requirements of an invasive species within the introduced range is important in tailoring management efforts (Mgidi et al., 2007). The abundance and distribution of an invader are two of the three parameters (the last one being the environmental effect of the invader) used to determine its potential impact (Parker et al., 1999). While these parameters do not encompass all the complexities associated with understanding biological invasions, they provide important proxies for assessing the magnitude of the threat that invasive species pose. These measures, along with a baseline assessment of the biology and ecology of *A. sericifera* are thus important to evaluate in the absence of quantitative impact data.

Araujia sericifera has expanded its range in South Africa over the last two decades (O'Connor and van Wilgen, 2020), and is an opportunistic urban invader, demonstrating the potential for its invasion to worsen and accrue management costs (Coombs and Peter, 2010; Henderson, 2020). To evaluate the invasion dynamics of *A. sericifera* in South Africa, this study sought to determine (1) the density of *A. sericifera* in urban Johannesburg, (2) the ecological and socio-economic drivers of *A. sericifera* density in Johannesburg, (3) seedling emergence rates of *A. sericifera* seeds collected in Johannesburg in response to full-sun and shaded environments, and (4) the environmental drivers of *A. sericifera* habitat suitability (or species distribution) in South Africa. This will contribute to understanding the invasiveness of *A. sericifera* and the potential extent of its invasion throughout South Africa, ensuring that effective management decisions can be made.

2. Methods and materials

2.1. Study species

Araujia sericifera is a perennial climber, marked by its rapidly-growing twining stems that typically reach a diameter of 40 mm, and opposite leaves (of an estimated 3 – 12 cm long and 2 – 6 cm wide) that are characterised by a glabrous and dark upper surface and a pale green lower surface (Fig. 1a; Winks and Fowler, 2000; EPPO, 2008). The leaves and stems may undergo senescence towards the

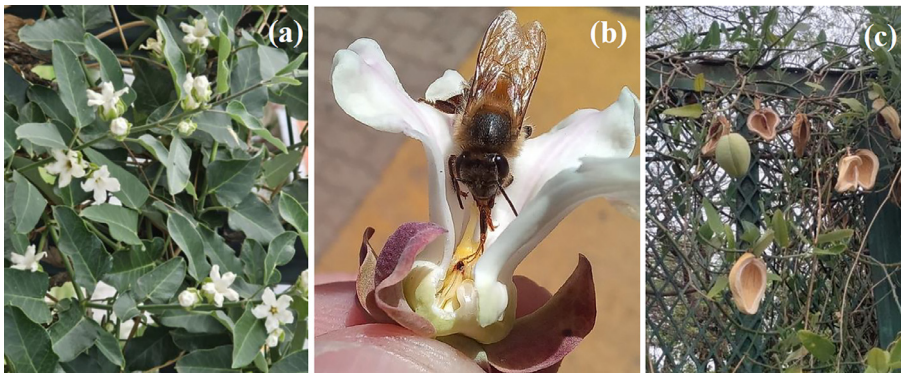

Fig. 1. (a) Tubular flowers and glabrous, opposite leaves of *Araujia sericifera*, (b) *Apis mellifera* subsp. *scutellata* trapped within a flower of *A. sericifera*, and (c) fruiting *A. sericifera* individual established on a fence (Photos: B. W. Cowie, N. Venter, and S. Maharaj).

end of summer or beginning of autumn, although the plant is mostly evergreen (EPPO, 2008). The plant has tough, flexible stems that become woody near the base, and a shallow, fibrous tap-root system. In South Africa, white, tubular inflorescences (sometimes marked with pink or maroon) appear in profusion on *A. sericifera* between November and April (Henderson, 2020; Fig. 1a). The vine's common names, "moth catcher", "moth plant", and "cruel vine" originate from its reputation for killing lepidopterans and bees within the flowers through accidental entrapment (Stearns, 1887; Coombs and Peter, 2010; Fig. 1b).

Anecdotal evidence suggests that the time to reproduction of *A. sericifera* is 12 – 18 months, and following seed dispersal and establishment of a transient seed bank, seed viability is lost for seeds that fail to germinate (Vivian-Smith and Panetta, 2005). Once mature, *A. sericifera* usually produces several spongy green fruits (~12 cm long and 6 cm wide) per plant, that remain on the vine following dehiscence (Winks and Fowler, 2000; Waipara et al., 2006; EPPO, 2008; Fig. 1c). The small seeds, which measure 7 – 8 mm, are initially cream-coloured but darken as the fruit matures (EPPO, 2008).

The reproductive success of *A. sericifera* in South Africa is attributed to its ability to self-pollinate (via geitonogamy), as well as its co-option of native pollinators, particularly honeybees (*Apis mellifera* subsp. *scutellata*) (Coombs and Peter, 2010). Despite their ability to access the nectar within *A. sericifera* flowers, honeybees are occasionally trapped on the flowers, although most individuals are able to free themselves (Coombs and Peter, 2010).

The presence of *A. sericifera* has been recorded in all provinces in South Africa, excluding the arid Northern Cape, and it has also established populations in Lesotho (GBIF, 2023) (Fig. 2; Supplementary Table S1). The vine is a common invader of abandoned fields, watercourses, and urban open spaces (Henderson, 2020) throughout the country. *Araujia sericifera* is widespread throughout the Western Cape and Eastern Cape, but is most abundant within the Gauteng Province, where it is common in the City of Johannesburg (Fig. 2; Supplementary Table S1).

2.2. Density and demographics surveys

The density study was conducted along main and secondary roads in 42 suburbs throughout Johannesburg (26.2041° S, 28.0473° E) between June and August 2023 (winter). Johannesburg is South Africa's largest metropolitan municipality (spanning 164 458 ha) and exhibits a diverse topography, situated at an average altitude of ~1750 m above sea level on the Highveld plateau. The city is characterised by a mild climate, as it falls within the subtropical highland Köppen–Geiger climate zone (Beck et al., 2018). The mean daily summer temperature is just below 22°C, while mean daily winter temperatures lie between 10°C and 12°C (South African Weather Service, 2021). The city receives a mean annual rainfall of between 700 mm and 800 mm, with most of the precipitation occurring during summer (South African Weather Service, 2021).

Surveys were conducted along 296 km of roads to detect the presence of *A. sericifera* adult plants (woody, fruiting individuals) and juveniles (herbaceous, non-fruiting individuals). Target roads were selected based on the presence of at least one iNaturalist observation within or adjacent to the suburb in which the observation was made. Speeds of 60 to 80 kmh^{-1} were maintained on main roads, while speeds of 40 to 60 kmh^{-1} were sustained on secondary roads. A driver and a passenger recorded the presence of *A. sericifera* visible on or immediately adjacent to the road, as well as the substrate (both artificial, such as fencing, and natural, such as other vegetation) that the plant was found on. Where possible, *A. sericifera* abundance obtained during roadside surveys was confirmed on foot. Additionally, the east section of the Melville Koppies Nature Reserve (26.1675° S, 28.0042° E), and the Beaulieu Bird Sanctuary (25.9804° S, 28.0697° E) were surveyed on foot (by which method individuals are more detectable) for *A. sericifera* along and adjacent to the walking trails along the perimeters of the reserves on 6 June 2023 and 27 August 2023, respectively. Plant density per kilometre surveyed was calculated by dividing the total number of plants observed by the sampling effort distances (Baard and Kraaij, 2019). The number of adults was compared to the number of juveniles, and the number of individuals per substrate was compared using Kruskal-Wallis tests to examine the population age structure. A Chi-squared test was used to determine whether the two life stages were associated with any particular substrates. Conover-Iman *post-hoc* tests were performed where differences were statistically significant using R version 4.3.1 (R Core Team, 2023) and the package 'conover.test' (Dinno, 2017).

2.3. Local invasion drivers

Johannesburg has a history of rapid urbanisation, which has resulted in the transformation of large areas of grassland to urban woodland. Approximately 16.1% of Johannesburg is occupied by non-native trees such as *Jacaranda mimosifolia* and *Plantanus* × *acerifolia*, along with indigenous trees such as *Celtis africana*, forming a mosaic of afforested areas and open grasslands throughout the city's green spaces (Schäffler and Swilling, 2013; Symes et al., 2017). The remainder of the city's land cover is allocated to formal and informal housing, farmland, and commercial and industrial areas (Katumba and Everatt, 2021). Despite being one of the centres of economic activity in South Africa, income inequality is highly prevalent in Johannesburg (Ballard and Hamann, 2021), with median annual household income of the surveyed suburbs ranging from R14 600 to R921 400 (Statistics South Africa, 2023). This income disparity is echoed by a disparity in urban vegetation, with greater access to green spaces in more affluent suburbs, such as those located in northern Johannesburg (Schäffler and Swilling, 2013; Souverijns et al., 2022). However,

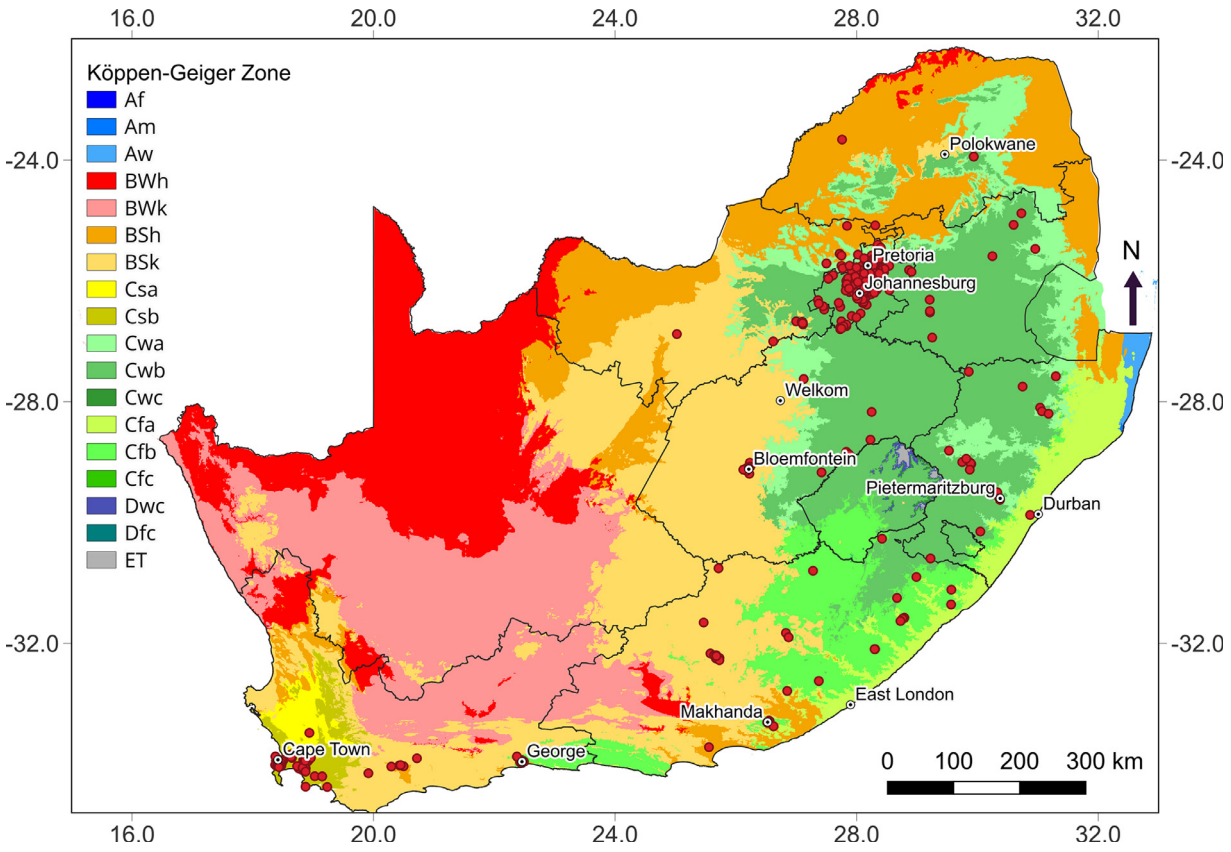

Fig. 2. Distribution of *Araujia sericifera* in South Africa's Köppen-Geiger zones based on occurrences from the South African Plant Invaders Atlas (SAPIA) and the Global Biodiversity Information Facility (GBIF, 2023). Full legend for Köppen-Geiger zones is shown in Supplementary Table S1.

the Normalized Difference Vegetation Index (NDVI), used as an indicator of the quality of vegetation greenness, has not been shown to vary greatly along a socio-economic gradient in Johannesburg (Abutaleb et al., 2021).

Two socio-economic predictors, urban cover percentage and median annual household income, and two ecological predictors, urban vegetation cover percentage and NDVI, were extracted within 500 m, 1 km, 2.5 km, and 5 km buffers around each sampled suburb. There was significant overlap between the buffer zones surrounding each suburb due to sampling in adjacent suburbs. To calculate the percentage of urban land cover and urban vegetation cover within each buffer zone, five classes were derived from the South African National Land Cover (SANLC) 2020 dataset (Department of Forestry, Fisheries, and the Environment, 2021), denoting natural vegetation cover, water sources, urban vegetation cover, urban structures, and miscellaneous cover. Median annual household income was obtained from the 2011 South African National Population Census (Statistics South Africa, 2023). Median income in South Africa is strongly linked to various socio-economic indicators and can serve as an effective surrogate measure for overall socio-economic status (Chamberlain et al., 2019). Lastly, NDVI, which is a surrogate measure for primary productivity (Pettorelli et al., 2005), was obtained at 500 m resolution for Johannesburg from Moderate Resolution Imaging Spectroradiometer (MODIS) 16-day composite satellite imagery (Didan, 2021).

Fifteen generalised linear mixed-effects models (reduced and full) with a Poisson link were compared against the null model at each of the four buffer resolutions (and without a buffer) to investigate the effects of the ecological and socio-economic predictors on *A. sericifera* density for the suburbs that remained (after excluding suburbs for which no predictor data were available). Suburb was included as a nested random effect in the models and was the only predictor used for the null model. The 'glmer' function from the package 'lme4' (Bates et al., 2015) was used to run all models in R. Prior to analysis, all predictor variables were scaled to facilitate effective model comparison. For all the models, variance inflation factors (VIFs) were less than 3.00 units, indicating low multicollinearity between predictor variables.

The fit of each model was compared using Akaike's information criterion with a second-order correction for small sample sizes (AICc) and Akaike weights (w_i), and the residuals of each model were assessed for normality and goodness of fit. All models were compared relative to a top model with ΔAICc = 0, and models with AICc values within 2.00 units of the null model were regarded as having comparable predictive capability to that of the null model.

2.4. Seedling emergence rates

Mature fruits were collected from 20 individuals from five representative populations in each cardinal region (n = 4 for central, west, and south, n = 5 for north, and n = 3 for east) of Johannesburg between August and September 2023. Sampled individuals were a minimum distance of 3 km apart. Thirty seeds from each fruit were sown at a depth of ~1 cm in trays measuring 15 cm × 23 cm × 6 cm and covered lightly with a sandy loam soil (60% sand: 35% silt: 5% clay). Seeds were sown on 19 September 2023, with two replicate trays per fruit for both the full-sun and shaded treatments (n = 40 per full-sun treatment and n = 40 per shaded treatment). Photosynthetically active radiation (PAR), measured as photosynthetic photon flux density (PPFD) (McCree, 1972) and soil temperature were measured at noon each day, and trays subsequently received ~300 ml of tap water per day. Hygrochron iButton temperature and humidity loggers (Maxim Integrated, California, USA) were placed in close proximity to both treatments to best record ambient temperature and humidity every two hours from midday. Emerging seedlings were

recorded in order to quantify emergence percentage (EP), calculated as $EP = \frac{\sum E_i}{N} \times 100$, where "$E_i$" is the number of seedlings that emerged each day, and "N" is the total number of seeds sown (Bewley and Black, 1994). Mean emergence time (MET), which was calculated as $MET = \frac{\sum(n \times d)}{N}$, where "n" represents the count of seeds that emerged each day, "d" denotes the number of days elapsed from the start of the experiment, and "N" signifies the total number of seeds that had emerged by the end of the experiment (Ellis and Roberts, 1981). Emergence scoring was done once a day for 31 days or until no further emergence was observed.

Emergence percentage, mean emergence time, and the environmental predictors (PAR, ambient temperature and humidity, and midday soil temperature) were compared between the full-sun and shaded treatments using a Wilcoxon Rank-Sum Test. Emergence percentage and mean emergence time were also compared between the Johannesburg north, east, central, west, and south populations of *A. sericifera* using a Kruskal-Wallis test. A principal component analysis (PCA) was used to determine the relative importance of the environmental variables affecting emergence for both treatments.

2.5. Habitat suitability modelling

Presence data, recording 533 occurrences of *A. sericifera* in South Africa obtained from the Global Biodiversity Information Facility (GBIF, 2023) and 10 000 pseudoabsence data points were used to develop habitat suitability models using the maximum entropy modelling software, MaxEnt 3.4.3, implemented in the 'dismo' package in R (Hijmans et al., 2021). MaxEnt can make predictions of suitability based on small datasets (Pearson et al., 2007; Phillips et al., 2017), and uses the theory of maximum entropy to predict species distributions that are closest to uniform, with due consideration of the constraints imposed by the predictor variables incorporated in the model (Phillips et al., 2004). To account for spatial autocorrelation in the occurrences which may affect the quality of model outputs (Veloz, 2009), the data were filtered based on a nearest neighbour distance of 10 km using the 'spThin' package in R (Aiello-Lammens et al., 2015).

A set of 19 climatic variables, which incorporate annual and quarterly temperature and precipitation metrics and their variability, averaged over the period from 1970 to 2000 (representing the current climate), were obtained from the WorldClim 2.1 database (www.worldclim.org) at a 30-arcsecond resolution (~1 km^2) (Fick and Hijmans, 2017). Additionally, due to the prevalence of *A. sericifera* in disturbed environments, a variable combining anthropogenic disturbance (broadly classed as human settlements, agriculture, transportation, mining and energy production, and electrical infrastructure) was used (Kennedy et al., 2019). Given that little is known about the ecophysiology of *A. sericifera*, models were initially run with all 20 predictor variables, and a subset of uncorrelated variables (VIF < 4.00) was selected based on permutation importance, which is a reliable indicator of the variables that best define a species' niche, while percentage contribution can be subject to bias when variables are multicollinear (Searcy and Shaffer, 2016). The reduced set of environmental predictors included four variables: bio2 – mean diurnal temperature range (mean of monthly [maximum temperature – minimum temperature]), bio11 – mean temperature of coldest quarter, bio15 – precipitation seasonality (coefficient of variation), and human disturbance. A model without disturbance was run similarly for comparison, including bio12 – mean annual precipitation, bio8 – mean temperature of wettest quarter, bio14 – precipitation of driest month, bio19 – precipitation of coldest quarter, bio1 – annual mean temperature, and bio15, as predictors.

Model performance was evaluated using the 'SDMtune' package (Vignali et al., 2020) using two metrics: the area under the receiver operating characteristic (ROC) curve (AUC; Fielding and Bell, 1997) and the true skill statistic (TSS; Allouche et al., 2006). Higher AUC values indicate a better capacity to differentiate between points from testing and background datasets, with poor models having AUC values < 0.8, fair models having AUC values between 0.8 and 0.9, and good models, > 0.9 (Fielding and Bell, 1997). For TSS, which ranges between -1 and 1, larger values indicate a high predictive accuracy, as the model is able to distinguish between false negatives and false positives for species pseudoabsence (background) and presence data points.

3. Results

3.1. Density and demographics surveys

Araujia sericifera juveniles and adults were found to be abundant throughout suburban roads of Johannesburg (Table 1) as well as within the two nature reserves (Table 2), establishing primarily on woody vegetation and fencing along roadsides. The number of juveniles detected did not differ significantly from the number of adults detected (Kruskal-Wallis: $\chi^2_{(2)} = 0.82$, p = 0.36).

The number of *A. sericifera* individuals detected via roadside surveys differed between substrates (Kruskal-Wallis: $\chi^2_{(2)} = 7.66$, p = 0.02). The number of individuals detected on fencing was greater than the number of individuals present on woody vegetation (Conover-Iman: t = -2.34, p = 0.01), and the number of individuals detected on the ground (Conover-Iman: t = -2.06, p = 0.02). Additionally, there was a strong association between the life stage of the plant and the substrate on which it was detected, with juveniles most prevalent on fencing, and adults, on woody vegetation (Chi-Square: $\chi^2_{(2)} = 218.36$, p < 0.001).

Within both nature reserves, *A. sericifera* was found primarily on woody vegetation. While the proportions of juveniles detected via surveys within the reserves were much larger than those detected via roadside surveys (68.6% of total individuals detected within the reserve, n = 388 compared to 47.3% detected via roadside surveys, n = 1257), there was no evidence of a statistical difference between the number of adults and juveniles within the two reserves (Kruskal-Wallis: $\chi^2_{(1)} = 1.88$, p = 0.17). In addition, the number of individuals per substrate differed non-significantly (Kruskal-Wallis: $\chi^2_{(4)} = 7.93$, p = 0.09).

3.2. Local invasion drivers

Without a buffer around the 42 suburbs, the top model included urban vegetation cover (AICc = 215.8, p = 0.09), however, this model

Table 1
Number and density of *Araujia sericifera* along main and secondary roads in 42 suburbs throughout Johannesburg.

Region	Number of Juveniles	Number of Adults	Total Individuals	Sampling Effort (km)	Density (plants/km)
North	83	135	218	81.76	3
East	98	134	232	62.08	4
Central	176	45	221	18.65	12
West	150	53	203	62.38	3
South	87	296	383	70.97	5
Total/Mean	594	663	1257	295.84	4 (mean)

Table 2
Number and density of *Araujia sericifera* within two nature reserves located in the suburbs of Johannesburg.

Nature Reserve	Number of Juveniles	Number of Adults	Total Individuals	Sampling Effort (km)	Density (plants/km)
Melville Koppies (East)	186	68	254	2.15	118
Beaulieu Bird Sanctuary	80	54	134	1.2	112
Total/Mean	266	122	388	3.35	116 (mean)

had similar predictive power to the null model (AICc = 216.5; Table 3). Using 500 m and 1 km buffers around each suburb, there were four competing models (Table 3). However, none of these models performed significantly better than the null model (< 2.00 AICc), suggesting no significant influence of median income, NDVI, urban cover or urban vegetation cover on *A. sericifera* density. While there were two competing models at 2.5 km and 5 km buffer resolutions, similarly, these models did not show an increase of < 2.00 AICc units over the null models (Table 3). At these resolutions, many of the buffer zones extended beyond the city of Johannesburg, for which median income, land cover, and NDVI data were not available, resulting in the inclusion of only 27 suburbs in the models using 2.5 km buffers, and only 13 suburbs at a 5 km buffer resolution (Supplementary Table S2).

3.3. Emergence rates

Araujia sericifera emergence was observed 13 days following sowing for the shaded and full-sun treatments (Fig. 3). For shaded seeds, an average of 31 seedlings emerged per day, while for sun-exposed seeds, the average rate was 7 seedlings per day. Seven days during the study were overcast, and 33 mm of rain fell on 30 September 2023. Hot, humid conditions prevailed throughout the remainder of the study (Table 4).

All environmental parameters differed significantly between emergence treatments, with higher midday photosynthetic photon flux density (W = 78, $p < 0.001$), daily ambient temperature (W = 57542, $p < 0.01$), ambient relative humidity (W = 73 316, $p < 0.01$), and midday soil temperature (W = 47, $p < 0.001$) in the full-sun treatment.

The emergence percentage of *A. sericifera* was significantly higher for shaded trays (47.8% compared to 11% in trays exposed to full sun;

Table 3
The best-fitting linear mixed-effects models for *Araujia sericifera* density in the suburbs of Johannesburg without a buffer, and with buffer diameters of 500 m, 1 km, 2.5 km, and 5 km. Full model set results are shown in Supplementary Table S3.

Model	K	ΔAICc	Res. LogLikelihood	Weight
No Buffer				
Urban Vegetation Cover	3	0	-104.6	0.2429
Null	2	0.6	-106.1	0.1773
500 m Buffer Zones				
Null	2	0	-91	0.2615
NDVI	3	1.4	-90.6	0.1268
Urban Cover	3	1.6	-90.7	0.1159
Urban Vegetation Cover	3	1.8	-90.8	0.1054
1 km Buffer Zones				
Null	2	0	-91	0.25
Urban Cover	3	1.3	-90.5	0.1282
NDVI	3	1.4	-90.6	0.1225
Urban Vegetation Cover	3	1.9	-90.8	0.0963
2.5 km Buffer Zones				
Null	2	0	-66.2	0.2456
Urban Vegetation Cover	3	0.2	-65	0.2173
5 km Buffer Zones				
Income	3	0	-30.8	0.3614
Null	2	0.5	-32.8	0.2764

W = 1511.5, $p < 0.001$; Fig. 4). Mean emergence time for seeds exposed to full sun was 17.7 days, while shaded seeds took significantly longer to emerge (W = 735.5, p = 0.01; Fig. 4), with a mean emergence time of 19.5 days. Emergence percentage did not differ significantly between populations of *A. sericifera* (Kruskal-Wallis: $\chi^2_{(4)} = 2.15$, p = 0.7), but mean emergence time was significantly shorter for north (Conover-Iman: t = -2.68, $p < 0.01$) and central (Conover-Iman: t = -3.66, $p < 0.001$) populations compared to south populations, and for central populations compared to east populations (Conover Iman: t = -2.49, $p < 0.01$).

3.4. Habitat suitability

Based on the model that included human disturbance, approximately 0.55% of South Africa (672 650 ha) was found to be suitable for the establishment of *A. sericifera*, mainly in Gauteng and the Western Cape as well as in Gqeberha in the Eastern Cape (Climatic Suitability > 0.7, $AUC_{test} = 0.921$, TSS = 0.76; Fig. 5). Disturbance was found to be the most important predictor of *A. sericifera* distribution, with a permutation importance of 85.6% (Table 5). Excluding disturbance, the model overfitted the distribution of *A. sericifera*, with

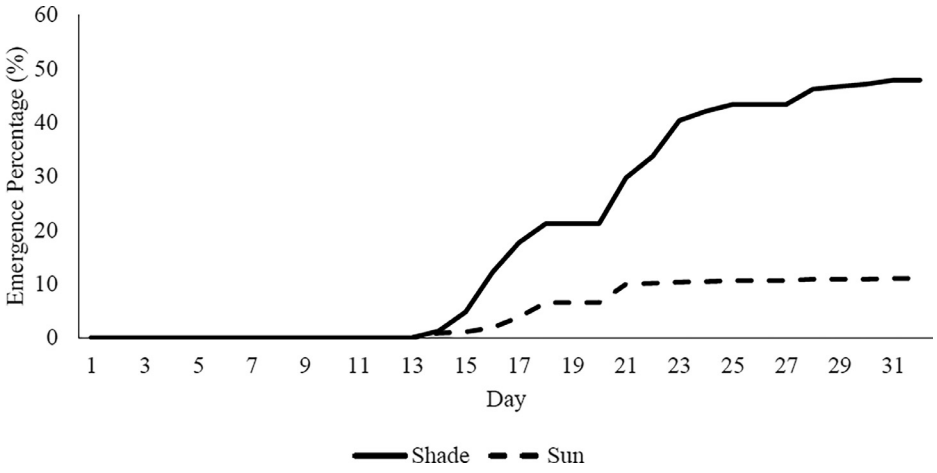

Fig. 3. Cumulative emergence percentage (%) of *Araujia sericifera* seeds sown in trays under shaded and full-sun treatments over a 31-day period (n = 30 seeds per tray; n = 40 trays per light treatment). Seeds were sown during spring (September).

Table 4
Mean (± S.E.) environmental conditions of the shaded and full-sun treatments of *Araujia sericifera* emergence trial. Superscripted lowercase letters indicate significant differences between treatments in the same row.

Environmental conditions	Treatment	
	Shade	Full Sun
Midday Photosynthetic Photon Flux Density (μmol m^{-2} s^{-1})	441 (± 29) ^{b}	1560 (± 135) ^{a}
Daily Ambient Temperature (°C)	18.9 (± 0.3) ^{b}	19.7 (± 0.3) ^{a}
Daily Ambient Relative Humidity (%)	52.4 (± 1.4) ^{b}	46.9 (± 1.3) ^{a}
Midday Soil Temperature (°C)	21.9 (± 0.1) ^{b}	38 (± 0.4) ^{a}

1.07% of the country found to be climatically suitable (Climatic Suitability > 0.7, AUC_{test} = 0.864, TSS = 0.61; Fig. 6).

4. Discussion

Most evaluations pertaining to biological invasions, particularly invasive alien plants, have focused largely on natural ecosystems, however, cities are now being recognised as hotspots for the establishment and proliferation of invasive species (Kowarik, 2011; Scalera and Genovesi, 2013; Gaertner et al., 2017). Disturbance often serves as a mediator for this process, making previously occupied landscapes available for invasion and facilitating the development of dispersal corridors, such as roads and waterways, which provide pathways for propagule spread and establishment (Parendes and

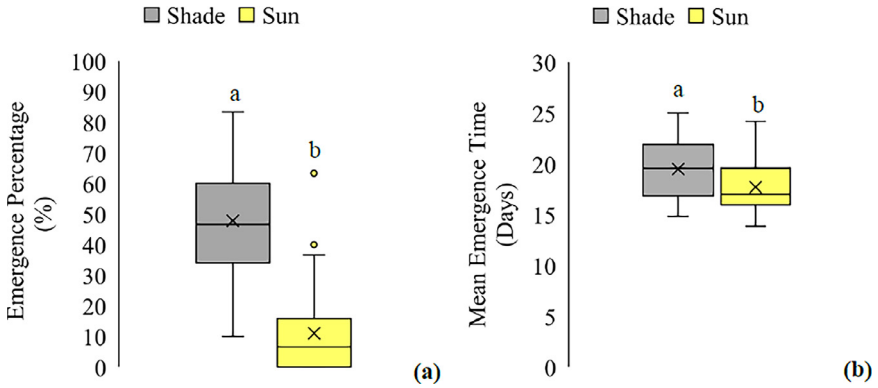

Fig. 4. (a) Emergence percentage and (b) mean emergence time of *Araujia sericifera* seeds under shaded and full-sun conditions showing the 25th percentile, the median, the 75th percentile, and the mean, denoted by a cross. Circles indicate outliers, and superscripted small case letters indicate significant differences between treatments.

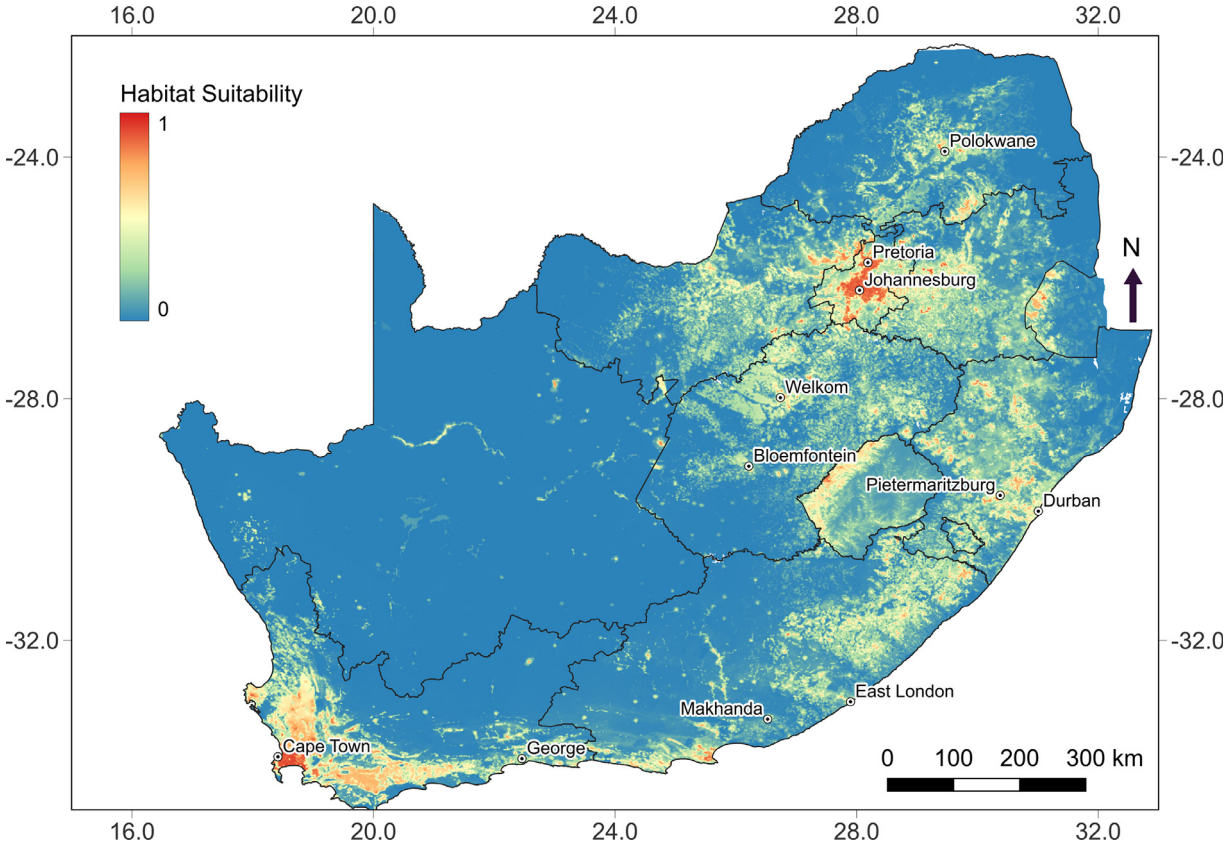

Fig. 5. Predicted MaxEnt habitat suitability for *Araujia sericifera* in South Africa using climatic variables and human disturbance as environmental predictors. Decimal degrees are denoted on the x and y axes.

Table 5
Environmental variables, obtained from the WorldClim 2.1 database (www.worldclim.org) for the period 1970–2000 at a 30-arcsecond resolution (~1 km^2), included in the MaxEnt models for predicted habitat suitability of *Araujia sericifera* in South Africa.

Code	Environmental Variable	Unit	Permutation Importance
South Africa (including disturbance)			
DIST	Human Disturbance	%	85.6
BIO11	Mean Temperature of Coldest Quarter	°C × 10	10.6
BIO2	Mean Diurnal Range	°C × 10	3.3
BIO15	Precipitation Seasonality	%	0.4
South Africa (excluding disturbance)			
BIO12	Mean Annual Precipitation	mm	48.3
BIO8	Mean Temperature of Wettest Quarter	°C × 10	35.5
BIO1	Mean Annual Temperature	°C × 10	9.3
BIO14	Precipitation of Driest Month	mm	6.9

Jones, 2000; Faulkner et al., 2020). The prevalence of *A. sericifera* throughout Johannesburg and the plant's strong association with human disturbance throughout the country corroborate this. While roadside surveys through the city enabled the detection of an average of four individuals per kilometre, the density estimates obtained on foot for the Melville Koppies Nature Reserve and the Beaulieu Bird Sanctuary are, on average, 29 times greater than the roadside estimates. In addition, *A. sericifera* densities are likely to be higher during summer when the plant is flowering and emergence conditions are favourable, and the winter density estimates obtained during this study may not reflect peak rates. To date, the abundance of *A. sericifera* has been considered high in only one quarter-degree grid square throughout South Africa, based primarily on roadside surveys as part of the Southern African Plant Invaders Atlas (SAPIA) mapping project (Henderson, 2007), but the density difference between roadside surveys and surveys of the two reserves highlights that *A. sericifera* is far more abundant than current SAPIA and community science records may suggest. iNaturalist (https://inaturalist.org), a leading global community science platform, shows less than 200 records of the plant in the city of Johannesburg, and less than 900 records across South Africa. While iNaturalist is a useful tool for understanding *A. sericifera* distribution at a broad scale, its ability to capture the abundance of the plant at local scales is limited. Density estimates obtained from the roadside surveys are likely to be conservative, as juveniles of *A. sericifera* are particularly inconspicuous and difficult to detect when employing this sampling method. Surveys on foot suggest that *A. sericifera* juvenile abundance throughout Johannesburg is likely to be much higher than roadside estimates might indicate.

In contrast, adults, identifiable by their large and abundant fruits, were easily detectable both via roadside surveys and throughout the two urban nature reserves. Adults were especially common on tall woody vegetation, which act as centres of seed dispersal as individuals climb high into branches and tree canopies. While the woody vegetation of Johannesburg represents a combination of native and alien species, the invasion of *A. sericifera* in New Zealand, Spain, and the United States demonstrates the vine's potential to threaten commercial agricultural (usually citrus and kiwi plants) and native woody plant survival (Winks and Fowler, 2000; USDA, 2012; Kiwifruit Vine Health, 2016; Bellache et al., 2022). However, the precise native species under threat and quantitative accounts of the damage caused by the plant are yet to be fully described in the literature. Nonetheless, in New Zealand, *A. sericifera* is recognised as high risk to peri-urban reserves and forests, where the vine smothers and causes the collapse of shrubs, trees, and regenerating seedlings (Hill, 2018). The prevalence of *A. sericifera* in two nature reserves in Johannesburg suggests its potential to invade protected habitats in South Africa and establish dense populations, especially at the interface between urban and natural areas. These regions are particularly susceptible to invasion as they are often subject to human disturbance (Alston and Richardson, 2006).

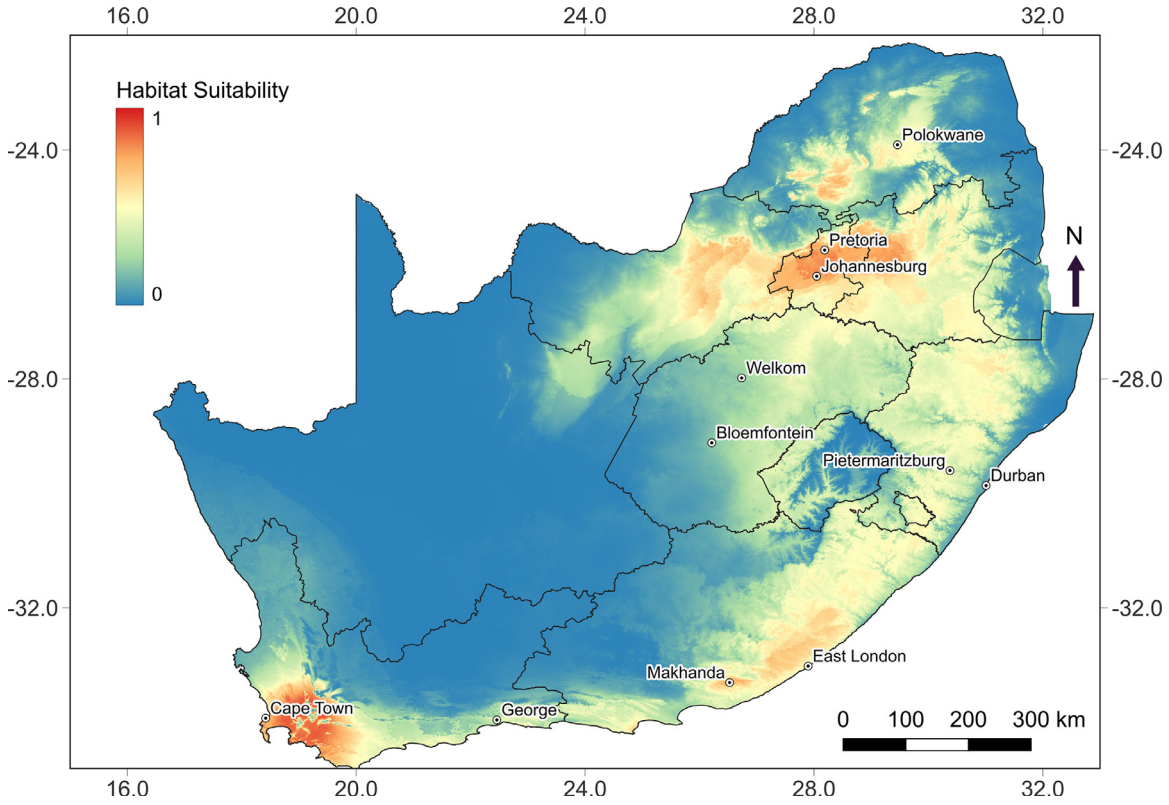

Fig. 6. Predicted MaxEnt habitat suitability for *Araujia sericifera* in South Africa including only climatic predictors. Decimal degrees are denoted on the x and y axes.

Additionally, the broad-scale establishment of *A. sericifera* irrespective of urban cover percentage, median income, urban vegetation cover percentage and NDVI reinforces its status as an opportunistic invader of urban habitats that can persist under a variety of microhabitat conditions. Its persistence on several substrates along roadsides and within reserves demonstrates its impartiality towards these variables, provided that the landscape is subject to some form of human disturbance. Urban areas are more homogenised systems compared to natural areas (McKinney, 2006), which offer a higher degree of biotic resistance against invasion due to a greater diversity of competitors and predators (Levine and D'Antonio, 1999). Resources provisioned through human activity, a lack of competitors, and extensive transport networks associated with urban systems are therefore considered favourable for the rapid establishment and spread of invasive species (Gaertner et al., 2017; Faulkner et al., 2020). An abundance of pollinators is also common within urban systems, and *A. sericifera* is known to exploit native honeybees for pollination, contributing to its proliferation in South Africa (Coombs and Peter, 2010). Urban Johannesburg, therefore, provides several opportunities for the persistence and spread of *A. sericifera*. Comparable densities of *A. sericifera* in Cape Town are also likely to be supported by these factors.

While the establishment of *A. sericifera* appears independent of the socio-economic and ecological variables that were measured, the plant's emergence is better under shaded conditions, consistent with the plant's growth form that lends itself to establishment on support structures that provide shade. Nevertheless, seedlings of *A. sericifera* can establish in full sun and, on average, in less time than when shaded. Emergence of seeds in full-sun reached saturation (maximum emergence percentage) much earlier than in shaded seeds, and midday soil temperatures frequently exceeded 50°C, resulting in potential losses in seed viability (Roberts, 1988). With rapid growth rates, several fruits per plant, and several hundred seeds per fruit, the potential for *A. sericifera* to establish abundantly under both sun and shaded conditions is high. Under similar shaded conditions and with an absence of supplementary watering, Vivian-Smith and Panetta (2005) obtained a mean emergence percentage for surface-sown *A. sericifera* seeds of 30.7%, further highlighting the plant's ability to establish under field conditions.

At a broader scale, however, the association between *A. sericifera* and human disturbance could restrict the plant to cities like Johannesburg, Cape Town, Bloemfontein and Gqeberha, despite climatically suitable habitats available elsewhere in the country outside of urban areas. This may provide a unique opportunity for its management, as *A. sericifera* populations appear largely accessible and localised predominantly to urban and peri-urban areas throughout the country. Nonetheless, 672 650 ha is a large area of suitable habitat, and urban areas do have the potential to promote invasion and spread into natural areas (Byrne et al., 2017; McLean et al., 2017; Faulkner et al., 2020; Le Roux et al., 2020) as observed for the sampled nature reserves. Self-sustaining, long-term management within these centres is essential prior to exacerbation of the problem. However, the efficacy of biocontrol against invasive plants, and particularly, invasive climbers, in urban areas remains understudied (Francis and Chadwick, 2015).

Climbers allocate most of their resources towards the rapid production of photosynthetic biomass, stem and root elongation, and reproduction (Angyalossy et al., 2015). Their resilience to breaking and cutting makes climbers difficult to control chemically (and there are no registered herbicides available for *A. sericifera* in South Africa) or mechanically, and their potential to compromise the growth, survival, reproduction, and recruitment of their supporting vegetation via physical damage and competition for resources renders climbers particularly problematic as invaders (Estrada-Villegas et al., 2021; Becknell et al., 2022). Many invasive climbing plants are widespread throughout South Africa, posing a risk to native biodiversity and plant community structure (King et al., 2021). Conventional control methods for these species have largely been ineffective, while biocontrol has had varied degrees of success (King et al., 2021).

Insights from the biocontrol of functionally similar climbers, such as Cat's claw creeper, *Dolichandra unguis-cati* (L.) L.G. Lohmann (Bignoniaceae) (see King et al., 2021) and Balloon vine, *Cardiospermum grandiflorum* Sw. (Sapindaceae) (Simelane et al. 2011; Simelane and Mawela, 2019) in South Africa, offer important lessons for efforts towards managing *A. sericifera*. Firstly, ensuring that potential biocontrol agents are climatically suitable for establishment in South Africa is crucial, particularly within the *A. sericifera* invaded Highveld region, where cold winter temperatures have constrained other weed biocontrol programmes (Byrne et al., 2002; Cowie et al., 2016). Secondly, matching the biocontrol agent to the appropriate plant biotype is of particular importance when the target plant has a broad native distribution, encompassing a variety of climate zones (Robertson et al., 2008), as is the case with *A. sericifera.* Habitat suitability models, or climatic matching approaches, such as CLIMEX, are useful in generally assessing the suitability of biocontrol candidates for specific regions (Robertson et al., 2008; Cowie et al., 2023). Given the broad-scale climatic differences between South Africa and South America (Beck et al., 2018; Supplementary Fig. S1), selecting biocontrol agents from a range that is most climatically similar to the target regions in South Africa is imperative.

Identifying the appropriate candidate agents is a resource-intensive and laborious process, and in recent years, transfer projects have offered a pragmatic approach to managing biological invasions via the exchange of knowledge and expertise (Byrne et al., 2021). Therefore, recent biocontrol efforts undertaken in New Zealand against *A. sericifera* offer an ideal collaborative opportunity to establish and fast-track a biocontrol programme in South Africa (Canavan et al., 2021). Since the release of the leaf-feeding beetle, *Freudeita cf. cupripennis* Lefèvre (Coleoptera: Chrysomelidae) in New Zealand in December 2019 — following collection from humid, subtropical Montevideo in Uruguay (Beck et al., 2018; McGrath et al., unpubl.; Supplementary Fig. S1) — the beetle has shown promise in reducing populations of *A. sericifera*, however, large-scale post-release evaluations are yet to be conducted (Manaaki Whenua-Landcare Research, 2020). Information regarding the agent's success in managing *A. sericifera* in urban and natural infestations is also not yet available. For *D. unguis-cati*, smaller infestations within urban areas were deemed unsuitable for biocontrol agent establishment. Smaller infestations, such as those observed in these roadside surveys and on private property, are unlikely to support abundant agent populations, and insect dispersal within urban areas may often be challenged by urban infrastructure, which acts as a dispersal barrier (Corcos et al., 2019). The presence of generalist and highly mobile insects is therefore favoured, whereas specialist insects, such as biocontrol agents, are usually rare in urban environments (Corcos et al., 2019). Additionally, human interference (usually chemical or mechanical) with target populations may challenge agent survival and success (Francis and Chadwick, 2015).

Collaboration between South African and New Zealand researchers regarding the prospects for using *F. cf. cupripennis* as a biocontrol agent will be essential in determining the feasibility of *A. sericifera* biocontrol for South Africa (Canavan et al., 2021). In addition to the transferability of New Zealand biocontrol knowledge, the absence of indigenous plants closely related to *A. sericifera* in South Africa further the prospects for successful biocontrol, but additional research regarding the impacts, ecology, and biocontrol of *A. sericifera* in South Africa is warranted. Nonetheless, the abundance and persistence of *A. sericifera* in a variety of cities throughout the country qualify it as a threatening invader, for which control measures should be investigated before further expansion of the invasion. Given that the management of invasive species is a resource-intensive process, management strategies should be tailored to the circumstances in

the invaded range, and future studies on *A. sericifera* should focus on quantifying its impacts and exploring the potential agent establishment and overall feasibility for *A. sericifera* biocontrol in South Africa.

Declaration of competing interest

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

CRediT authorship contribution statement

Shréyan Maharaj: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Blair W. Cowie:** Writing – review & editing, Methodology, Investigation. **Marcus J. Byrne:** Writing – review & editing, Supervision, Methodology, Funding acquisition. **Nic Venter:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2024.06.034.

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