



Striking yet destructive: The potential expansion of pompom weed (*Campuloclinium macrocephalum* (Less.) DC.) in South Africa

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ABSTRACT

Pompom weed (*Campuloclinium macrocephalum* (Less.) DC.) is a serious invader of grasslands, savannas, and wetlands, where it decreases veld condition and biodiversity. This study aimed to create updated models to predict the spatial and environmental range suitable for the ever-expanding pompom weed invasion in South Africa. Two Ecological Niche Models (ENMs) were developed: calibrated 1) using invaded range data only (ENMinvaded) and 2) combining the native and invaded range data (ENMentire), of the weed. The two ENMs predicted similar environmentally suitable ranges for pompom weed, confined to the wetter and cooler eastern side of South Africa, with small pockets in the Western Cape near Cape Town and Stellenbosch and between George (Western Cape) and St Francis Bay (Eastern Cape). The two ENMs differed at the edges of the predicted distribution, with ENMinvaded projecting suitable areas further to the west. In contrast, ENMentire projected a greater suitable range in Mpumalanga and parts of Limpopo, the eastern Free State, KwaZulu-Natal, and the central Eastern Cape. ENMentire outperformed ENMinvaded, yielding an AUC¹ statistic of 0.923 vs 0.783, respectively. The most important environmental variables shown to influence the projected suitable range of pompom weed were elevation, the maximum temperature of the warmest month and rainfall-related variables, including annual precipitation, precipitation seasonality and precipitation of the coldest quarter. Pompom weed appears able to withstand the colder, frost-prone areas but is restricted by the warmer temperatures experienced in the savannas to the west of the highveld. The grassland biome, savanna, and lowveld along the east coast are at the greatest risk of new invasions by pompom weed. This insight contributes valuable information for targeted monitoring and management strategies in regions susceptible to the expansion of pompom weed.

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1. Introduction

Globally, natural ecosystems and native species are under threat from invasive alien plants (IAPs), which are one of the leading causes of biodiversity loss (Davis, 2003). IAPs pose one of the most crucial barriers to the restoration and conservation of native ecosystems (D'Antonio and Meyerson, 2002). IAPs alter species community structure and assembly (Gaertner et al., 2009; Vilà et al., 2011), soil properties (Aldorová et al., 2020), water systems (Gorgens and Van Wilgen, 2004; Richardson and Van Wilgen, 2004), nutrient cycling (Witkowski, 1991; Vilà et al., 2011) and fire regimes (Pejchar and Mooney, 2009; Van Wilgen, 2009). With increasing growth in the human population and advancements in technologies, new pathways are created for the movement of species far from their native ranges

(Wilson et al., 2009). As such, the expansion of many invasive species' geographical ranges is accelerating, occurring on larger scales and is primarily driven by anthropogenic activities (Walther et al., 2009). Mitigating the spread of IAPs is one of the current major conservation and management challenges globally (McNeely, 2001; Lazzaro et al., 2017).

Assessing the present and future distributions of such IAPs is essential for comprehensive management strategies (Eckert et al., 2020). Two primary approaches are employed to determine the potential area a species may invade: the examination of intrinsic characteristics, encompassing life history, morphology, and behaviour (Mowery et al., 2021), and the examination of extrinsic characteristics, specifically niche space (Curnutt, 2000). Inherent characteristics may include growth rates and size (Hamilton et al., 2005; Mowery et al., 2021), genetics (Lee, 2002; Lawson Handley et al., 2011), phenology (Gerlach and Rice, 2003), growth response to disturbances (Gerlach and Rice, 2003) and modes of reproduction such as high seed mass (Hamilton et al., 2005), dispersal rates

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¹ AUC- Area under the curve

(Brändle et al., 2003) and fecundity (Gibson et al., 2011; Mowery et al., 2021). Alternatively, extrinsic characteristics are environmental factors that create a specific niche (Curnutt, 2000), such as temperature, rainfall, elevation and soil type. With regards to many plants, there is often a notable resemblance between the climate in their native range and that of the environment where the species tends to invade (Thompson et al., 2011). Using this method, determining where a species may invade requires an understanding of the native range and knowledge of areas susceptible to current and further invasion (Suárez-Mota et al., 2016).

Ecological niche models (ENMs) are effective computational tools that predict the potential geographic areas where a species could exist based on a combination of environmental and species occurrence data (Elith and Leathwick, 2009). ENMs are employed across space and time for various purposes, including the modelling of data deficient species such as endangered (Peterson and Robins, 2003; Bartel and Sexton, 2009; Blank and Blaustein, 2012; Wilkening et al., 2019), or newly introduced invasive species (Jiménez-Valverde et al., 2011). ENMs are also used to assess areas or ecosystems at risk, into which established invasive species could spread. Studies using ENMs to forecast potential invasions of specific species include the Pink Spotted Hawkmoth (*Agrius cingulata*) across Africa (Ballesteros-Mejia et al., 2011); the neurotoxic sea-slug (*Pleurobranchaea maculata*) in the southwestern Atlantic (Battini et al., 2019); triffid weed (*Chromolaena odorata* (Asteraceae)) in South Africa (Suárez-Mota et al., 2016), and *Campuloclinium macrocephalum* (pompom weed) in South Africa (Trethowan et al., 2011). ENMs may incorporate species data from the invaded range, native range or a combination of the two (Trethowan et al., 2011). The data used to train the models largely depends on data available for both the native and invaded ranges. Nonetheless, incorporating a combination of invaded and native data provides a more comprehensive understanding of the potential areas where the species might spread (Trethowan et al., 2011). ENMs may also be used to determine the range of potential biocontrol agents in comparison to the distribution of target IAPs. This approach has been applied, for instance, in studies involving the leaf beetle *Gratiana boliviana* Spaeth (Coleoptera: Chrysomelidae) and its target the invasive tropical soda apple (*Solanum viarum* Dunal (Solanaceae)) in the USA (Mukherjee et al., 2012); the Australian gall-forming wasp *Trichilogaster acaciaelongifoliae*, and its target *Acacia longifolia* in Portugal (Dinis et al., 2020); and the leaf-deforming thrips *Liothrips tractabilis* and the flower feeding moth *Cochylis campuloclinium* and their target weed *Campuloclinium macrocephalum* (pompom weed) in South Africa (Trethowan et al., 2011).

pompom weed, *Campuloclinium macrocephalum* (Less.) DC. (Asteraceae), is a severe herbaceous invader of South African grasslands and savannas. This unpalatable weed reduces range condition, leading to decreased grazing capacity, species diversity and species richness (Goodall et al., 2010). Pompom weed capitalises on areas with elevated levels of disturbance and human activity as these provide the ideal conditions for establishment of the copious numbers of wind-dispersed seeds. These include road verges, abandoned fields (McConnachie et al., 2011) and poorly managed or degraded rangelands (Goodall and Witkowski, 2014). However, from such bridgeheads, the weed subsequently expands into natural grasslands, savannas and wetlands (McConnachie et al., 2011). The grassland biome of South Africa is the country's second largest biome, covering 28 % of the terrestrial surface (Mucina and Rutherford, 2006). The landscape of the grassland biome ranges topographically from flat and undulating hills with small valleys to rocky mountain escarpments. The grassland biome is one of the most threatened biomes of South Africa, with only 2 % formally conserved and 40–60 % irreversibly transformed (Muller et al., 2021; Carbutt and Kirkman, 2022). The main threat to grasslands is loss due to anthropogenic transformation, including agriculture and livestock farming as well as flooding for dams and mining for coal or gold (Carbutt et al., 2011).

Pristine grasslands and savannas are less likely to be invaded by the weed as its density is restricted by higher grass basal cover (Goodall et al., 2011). Pompom weed originates from South and Central America, and the first records of pompom weed come from the Fountains Valley, Pretoria, in the 1960s and Westville, near Durban, in 1972. It is thought to have been introduced in the early 1960s and has since naturalised (Goodall et al., 2011). Roughly sixty years later, pompom weed has become one of the worst IAPs in South Africa, with occurrences in eight of the nine provinces (Henderson, 2020).

Trethowan et al. (2011) predicted the potential suitable habitat for both pompom weed and potential biocontrol agents in South Africa. They calibrated pompom weed ENMs using invasive range data from SAPIA 2010 data, native range data using GBIF, Tropicos, field data, and the invasive range and native range data combined. They found the sole use of native range data to be insufficient in predicting areas suitable for pompom weed in South Africa, with the model generating an Area Under the Curve (AUC) statistic of 0.764. The AUC statistic is a performance metric for classification models, where it measures the model's ability to differentiate between classes, reflecting the area beneath the Receiver Operating Characteristic (ROC) curve. In terms of training data for pompom weed, Trethowan et al. (2011) used one occurrence record per 10 min grid cell (roughly 200–350 km²), resulting in 187 points for the native range (South America) and 130 points for the invaded range (Southern Africa). Between 2000 and 2016, pompom weed spread at an alarming rate, increasing from 14 QDS (8750 km²) in 2000 to 108 QDS (67500 km²) in 2016 (Henderson and Wilson, 2017). Locality records prior to 2016 were provided by SAPIA at a coarse QDS scale (roughly 625 km²), although some records include GPS coordinates with moderate precision (5-minute grid or 1-minute grid, roughly 2–10 km²) (Robertson et al., 2010). Post-2016 occurrence records are from iNaturalist and GBIF, which provide higher-resolution GPS coordinates. The increase in the number of potential training points, along with their more accurate location information, allows for more precise environmental data to be incorporated into an ENM to predict suitable areas for pompom weed compared to the prior models, and to better define its environmental niche. It is valuable to produce updated ENM models for pompom weed in South Africa, building on the Trethowan et al. (2011) study by refining distribution estimates with more recent data while also identifying the key environmental drivers of the species' spread—an essential aspect not addressed in their work. As such, this study aimed to generate improved ecological niche models based on an updated and more accurate 1) invaded area data (ENMinvaded), 2) using both native and invasive area data combined (ENMentire), and 3) going further to determine the main environmental drivers for the potential distribution of pompom weed in South Africa.

2. Methods

The process of accessing geospatial and environmental datasets, model construction and analyses was conducted exclusively using the cloud-based Google Earth Engine (GEE) platform.

2.1. Study area

Pompom weed originates from Brazil, Bolivia, Paraguay, Uruguay, and Argentina in South America (Trethowan et al., 2011) (Fig. 1). This range falls into the tropical and subtropical grassland, savanna and broadleaf forest biomes (Eva et al., 2002). In South Africa, pompom weed is predominantly found across the country's eastern half, with the worst of the invasion in and around Gauteng Province (Henderson, 2020) (Fig. 2). Genetic evidence suggests that the South African population likely originated from Argentina, as both regions exhibit similar ploidy diversity, indicating multiple introductions or a genetically diverse source population (Gitonga et al., 2015).



Fig. 1. The native range of *Campuloclinium macrocephalum* (pompom weed) in South America, based on occurrence records from iNaturalist and GBIF.

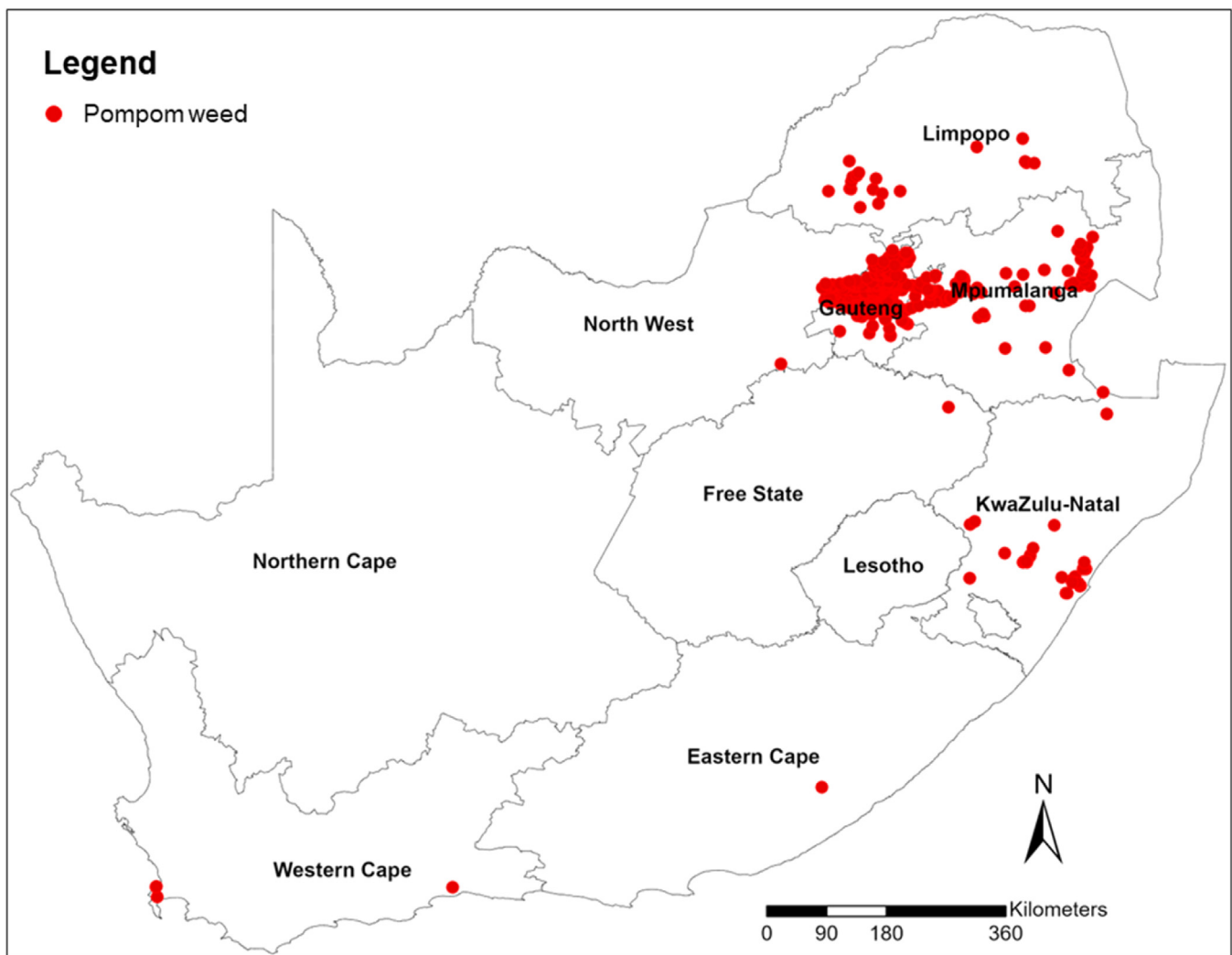


Fig. 2. The current invaded range of *Campuloclinium macrocephalum* (pompom weed) across South Africa, based on occurrence records from field surveys, citizen science, iNaturalist and GBIF.

2.2. Occurrence data

The presence data from the native range was collected from iNaturalist (iNaturalist Community, 2023) and GBIF (Global Biodiversity Information Facility) (GBIF, 2023) (Fig. 1). Presence data for pompom weed in South Africa (Fig. 2) was sourced from field surveys, iNaturalist, GBIF and citizen science data received in response to an informational flyer distributed across social media platforms. The accuracy of all the citizen science data was assessed by validating the GPS points and accompanying pictures by cross-referencing them with Google Earth and Google Street Views. A total of 702 points were obtained from the native range (Fig. 1) and 3802 points for the invaded range in South Africa (Fig. 2). Absence points of pompom weed were located near both invaded areas and areas completely without pompom weed. These included large expanses of pompom-free grassy areas, along with a variety of other vegetation and land cover types, such as shrubs, trees, and monoculture crops. The presence and absence reference points were used to create training and validation points for the models, where the occurrence data was randomly divided into 70 % for training and 30 % for validation.

2.3. Predictor variables

The WorldClimBio temperature and rainfall variables (1961–1990) (Hijmans et al., 2005) are commonly used for ENMs to establish

environmental drivers for potential species distribution. For example, Trethowan et al. (2011) used a subset of these variables from the WorldClim database, including mean diurnal temperature range, maximum temperature of the warmest month, mean temperature of the coldest quarter, annual precipitation, precipitation of the driest month, and precipitation seasonality. However, to create an up-to-date dataset covering 2001–2022, MODIS land surface temperature data (MOD21A1D/N.061 Terra Land Surface Temperature and 3-Band Emissivity Daily Global 1 km) and CHIRPS daily rainfall data (CHIRPS Daily: Climate Hazards Group InfraRed Precipitation with Station Data) (Funk et al., 2015), were used to derive similar environmental variables as the WorldClimBio. Due to the limited knowledge of what environmental variables determine pompom weed distribution, all the derived variables were retained to allow the model to identify the potential drivers. The NASA Digital Elevation 30 m dataset was also incorporated to account for elevation, aspect, hillshade, and slope.

2.4. Ecological niche models

Two ENMs were generated using a random forest model, which were calibrated with 1) the invasive data only (ENMinvaded) and 2) both invasive and native data (ENMentire). The ENMs were derived from the average presence probability across ten iterations of a random forest classifier using various combinations of the presence-absence data (Crego et al., 2022). A correlation matrix was used to

analyse the predictor variables using RStudio to develop the most effective models. When a strong correlation ($r > \pm 0.95$) was found between two variables, the variable with the lower importance score was systematically eliminated. This approach addressed multicollinearity and enhanced the model's performance by retaining only the most informative and independent variables. The random forest classifier in Google Earth Engine then evaluated predictor importance of the environmental variables by determining variable significance through the mean decrease in accuracy when predictor values are randomly permuted (Breiman, 2001).

The Dynamic World V1 landcover dataset (Brown et al., 2022), derived from Sentinel-2 L1C collection, was incorporated into the ENMs to provide detailed landcover information. This dataset classifies nine terrestrial landcover types—water, trees, grass, flooded vegetation, crops, shrub and scrub, built, bare, and ice and snow—at a 10 m resolution.

2.5. Accuracy assessment

The Area Under Curve (AUC) statistic was calculated to assess the model performance. The AUC metric is derived from the area under the Receiver Operating Characteristic (ROC) curve. The ROC curve is a graphical representation of the trade-off between the true positive rate and the false positive rate for different threshold values of a classification model (Vujović, 2021). As such, the AUC statistic summarises the model's performance across various threshold values. The AUC is a metric commonly used to assess the performance of binary classification models. AUC values range from 0.5 to 1, with 0.5 signifying a model that performs no better than random chance and values closer to 1 reflecting better model discrimination. Values between 0.9 and 0.95 are considered to indicate a very good model, while values greater than 0.95 an excellent model (Fawcett, 2006; Crego et al., 2022).

3. Results

3.1. Pompom weed ecological niche models

The two ENMs developed in this study predicted similar suitable ranges for pompom weed, however, the AUC statistics varied substantially. ENMinvaded produced an AUC statistic of 0.783, indicating a good model, while ENMentire yielded a very good model with an AUC statistic of 0.923 (Fig. 3A and B). The environmentally suitable areas predicted for pompom weed are confined to the wetter and cooler eastern side of South Africa, with small pockets in the Western Cape near Cape Town and Stellenbosch, as well as between George in the Western Cape and St Francis Bay in the Eastern Cape. (Fig. 3A and B). The two ENMs differ most where the edges of the suitable habitats are predicted, with ENMinvaded projecting pompom suitable areas further west into these provinces and in the pockets of the Eastern and Western Cape provinces (Fig. 3C). In comparison, ENMentire projected suitable pompom areas to the east of the North West, Free State and Eastern Cape provinces (Fig. 3C).

The ENMentire suitability range was overlaid with six sensitive South African bioregions at risk of further pompom weed expansion (Fig. 3D). The areas at greatest risk of pompom weed invasion based on Mucina and Rutherford (2006) and the South African National Vegetation Map (SANBI, 2024) include the lowveld (Limpopo, Mpumalanga, and KwaZulu-Natal) (Fig. 4C), mesic highveld grassland (Limpopo, Mpumalanga, and eastern parts of the Free State) (Fig. 4D), sub-escarpment grassland (KwaZulu-Natal and the eastern side of Eastern Cape) (Fig. 4E), Drakensburg grassland (KwaZulu-Natal and Eastern Cape), sub-escarpment savanna and Indian Ocean coastal belt (KZN and Eastern Cape) (Fig. 4F). South Africa has 120 threatened terrestrial ecosystem types; 14 vulnerable, 51 endangered and 55

critically endangered types, with five critically endangered types at risk of further pompom weed invasion (Fig. 4i–v).

3.2. Important environmental variables

The top five environmental predictor variables determining the areas suitable for pompom weed in ENMinvaded were maximum temperature of the warmest month, precipitation of the wettest and the coldest quarter, precipitation seasonality and temperature seasonality (Fig. 5). ENMentire, identified similar environmental predictors of pompom weed (Fig. 5).

4. Discussion

4.1. Suitable pompom weed range

The two ENM models indicated regions in northeastern South Africa that are suitable for pompom weed, with clusters in the Western Cape and the Eastern Cape. ENMinvaded projected larger suitable areas along the western edges of the distribution, particularly noticeable in the North West, Free State, parts of the Eastern Cape and Western Cape provinces compared to ENMentire. However, ENMentire projected a more suitable range in Mpumalanga and parts of Limpopo, the eastern Free State, KwaZulu-Natal, and the central Eastern Cape (Fig. 3). The models by Trethowan et al. (2011) also predicted the invasion of the wetter eastern region of South Africa, with corresponding areas in the Western and Eastern Cape Provinces deemed suitable for pompom weed. However, their invasive range ENM resulted in a more limited potential distribution, not finding the Free State region north of Lesotho suitable for pompom weed, as indicated by ENMinvaded. Their model, which uses both invasive and native range data, predicted a slightly larger area as suitable for pompom weed than ENMinvaded, with suitability extending into central North West, Free State, and a pocket in the Northern Cape province. Although ENMinvaded and ENMentire modelled similar suitable ranges for pompom weed, ENMinvaded showed an AUC statistic of 0.784, which was outperformed by ENMentire with an AUC statistic of 0.923. In contrast, the ENMs calibrated using invasive range data only, and both invaded and native range data by Trethowan et al. (2011) performed well with AUC statistics of 0.963 and 0.966, respectively. However, several studies have found that predictive models for identifying suitable areas for invasive species show improved performance when incorporating data from both native and invaded ranges (Mau-Crimmins et al., 2006; Ballesteros-Mejia et al., 2011; Sales et al., 2021). Although an invasive species may adapt to environments different from their native range due to less competition or predation, many species retain their fundamental climatic niches (Sales et al., 2021). This may be the case for pompom weed and why the ENMentire model outperformed the ENMinvaded model.

4.2. Environmental drivers

The environmental predictor variables used by Trethowan et al. (2011) were six WorldClim biovariables, obtained from Beaumont et al. (2009), a study that focused on developing ENMs for *Hieracium* species in Europe, Australia, New Zealand and North America. The environmental predictor variables included mean temperature range, maximum temperature of the warmest month, mean temperature of the coldest quarter, annual precipitation, precipitation of the driest month and precipitation seasonality. However, Trethowan et al. (2011) did not rank these variables or report how they influenced their models' outputs. Overall, there is little literature on the environmental factors that impact pompom weed growth. Goodall et al. (2011) found that soil erosion and rockiness in Gauteng grasslands significantly affected both the height and the density of pompom weed, showing that the greater the disturbance or degradation, the

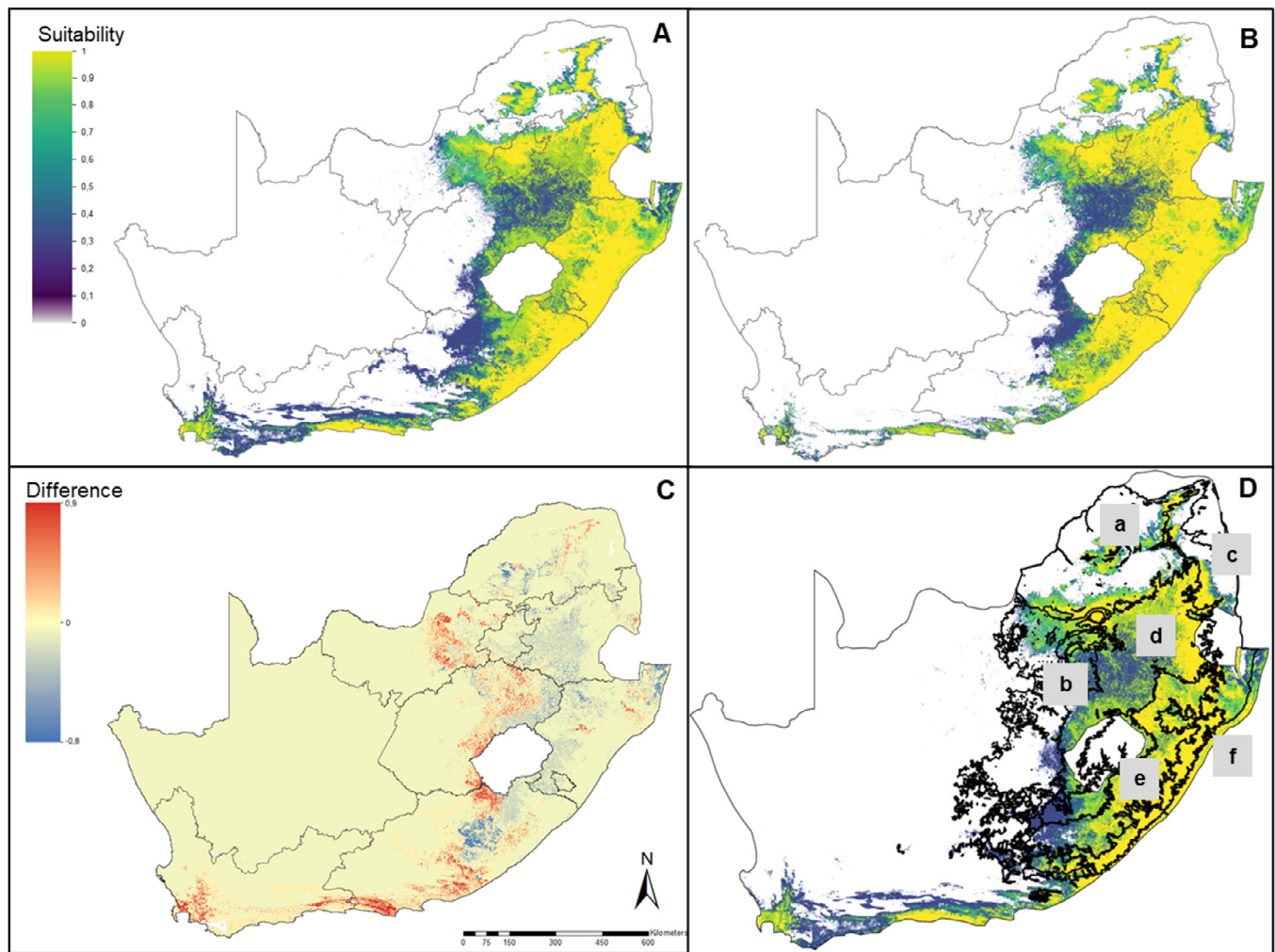


Fig. 3. Ecological niche models of pompom weed calibrated using A) ENMinvaded and B) ENMentire, highlighting the areas of greatest difference between the two models and mapped at 1 km resolution. ENMinvaded AUC statistic = 0.783 and ENMentire AUC statistic = 0.923. C) The difference in area suitable for pompom weed between ENMinvaded and ENMentire: red shows the areas deemed more suitable by ENMinvaded, while blue shows the areas deemed more suitable by ENMentire. D) ENMentire suitability range overlaid with six sensitive South African bioregions at risk of further pompom weed expansion: a) Central Bushveld Bioregion, b) Dry Highveld Grassland Bioregion, c) Lowveld Bioregion, d) Mesic Highveld Grassland Bioregion, e) Sub-Escarpment Grassland Bioregion, and f) Sub-Escarpment Savanna Bioregion.

greater the pompom weed invasions. Additionally, denser stands of pompom weed were found in areas subject to frequent fires, as high fire frequency allows the emergence of pompom before native grasses (Goodall et al., 2011). Mean annual rainfall showed no significant effect on density or height; however, Goodall et al. (2011) only assessed pompom weed sites in Gauteng and not across the entire invaded range of pompom weed. The environmental factors influencing the distribution of pompom weed in South Africa remained unknown before the study done by Szewczuk (2025) on the distribution of pompom weed. There, it was found that pompom weed distribution was primarily driven by elevation and temperature seasonality, mean temperature of the coldest quarter, temperature annual range, maximum temperature of the warmest month and rainfall seasonality. The top five environmental variables of ENMinvasive and ENMentire similarly identified the maximum temperature of the warmest month as well as temperature and rainfall seasonality to determine the potential range of pompom weed, which aligns well with the results of Szewczuk (2025). This highlights that maximum temperature has a crucial role in restricting regions that are suitable for pompom weed, particularly in the warmer climates of South Africa. When comparing the predicted suitable region to the different bioregions of South Africa, there is alignment to the distribution of mesic highveld grassland in the North West, Limpopo, Gauteng and

Mpumalanga provinces and the sub-escarpment grassland in Kwa-Zulu-Natal and the eastern half of the Eastern Cape (Fig. 4). Additional grassland and savanna biotypes at risk are the central bushveld, dry highveld grassland, lowveld, and sub-escarpment savanna (Mucina and Rutherford, 2006) (Fig. 4). The results suggest that pompom weed is inclined to invade regions distinguished by more open grassy regions within the country, which adds further pressure to an already threatened grassland biome.

4.3. Implications for future management

4.3.1. Biocontrol

There are several biocontrol agents with the potential to control pompom weed: the stem- and leaf-deforming thrips *Liothrips tractabilis* Mound and Pereyra (Thysanoptera: Phlaeothripinae) (Mound and Pereyra, 2008), biotrophic rust fungi *Puccinia conoclinii* Seym. and *Puccinia eupatorii* Dietel (Uredinales: Pucciniaceae) (McConnachie et al., 2011), and the flower-feeding moth *Cochylis campuloclinium* Brown (Lepidoptera: Tortricidae) (McConnachie and McKay, 2015). The rust fungus, *P. eupatorii*, from Argentina was discovered on pompom weed in Gauteng in 2006 and has spread to most areas invaded by pompom weed (McConnachie et al., 2011). The optimum temperature for infection of pompom weed by *P. eupatorii* is 18 °C

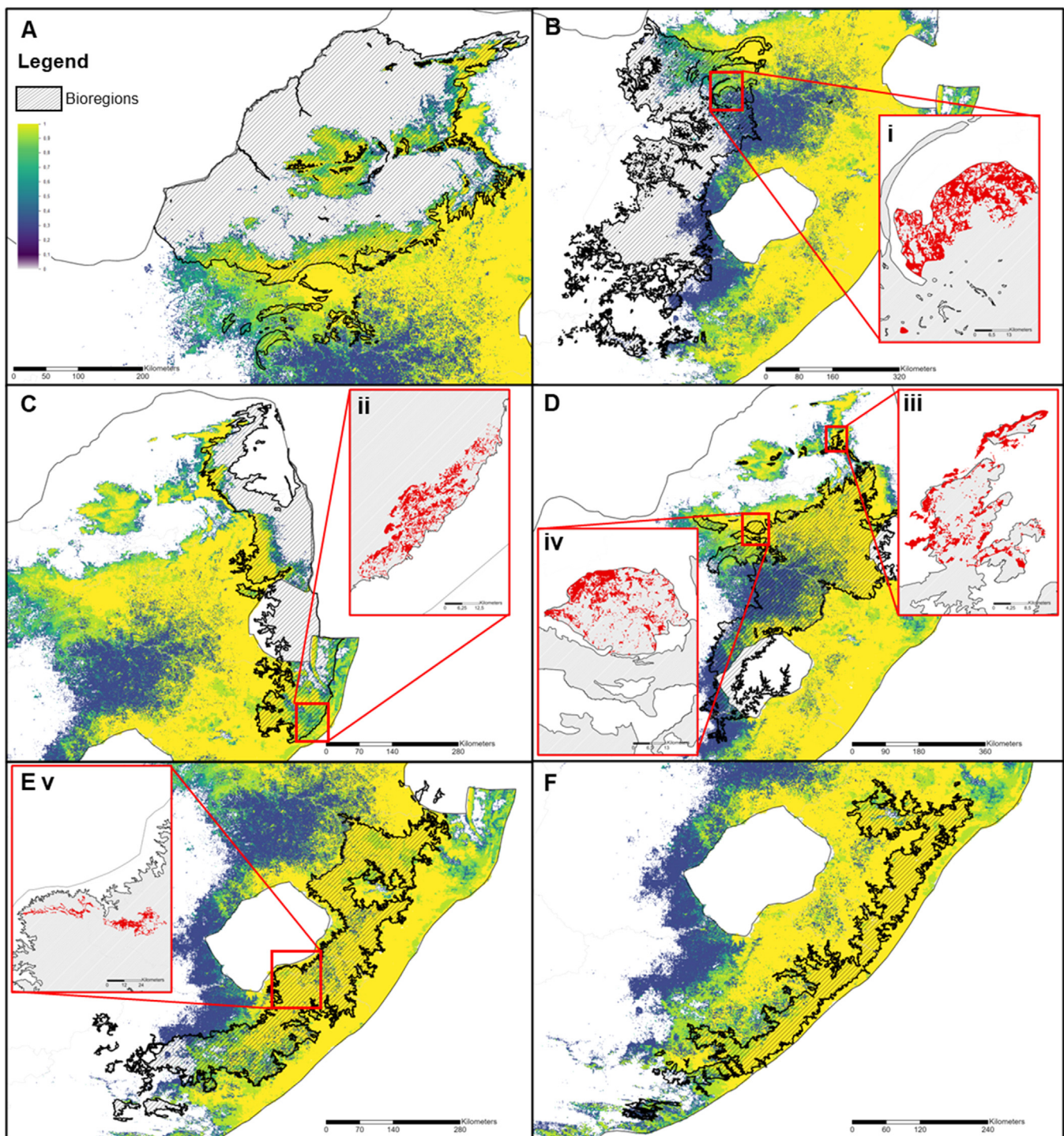


Fig. 4. The ecological niche model of pompom weed calibrated using ENMentire overlaid with six sensitive South African bioregions at risk of further pompom weed expansion: A) Central Bushveld Bioregion, B) Dry Highveld Grassland Bioregion, C) Lowveld Bioregion, D) Mesic Highveld Grassland Bioregion, E) Sub-Escarpment Grassland Bioregion, and F) Sub-Escarpment Savanna Bioregion. These bioregions contain critically endangered ecosystem types which include: i) Vredefort Dome Granite Grassland, ii) Zululand Coastal Thornveld, iii) Woodbush Granite Grassland, iv) Egoi Granite Grassland, and v) Mabela Sandy Grassland. Further details on the vulnerable and endangered ecosystem types that fall within these bioregions are in the Appendix.

with a minimum dew period of six hours (McConnachie et al., 2011). Goodall et al. (2012) assessed *P. eupatorii* on pompom weed over five growing seasons, with three seasons experiencing above-average rainfall (2004/05, 2007/08, 2008/09) and one experiencing a drought with below-average rainfall (2006/07). Goodall et al. (2012) found that *P. eupatorii* did particularly well during the 2007/08 and 2008/09 above-average rainfall seasons, and the effectiveness of *P. eupatorii* diminished during the drought. This suggests that moisture plays an

important role in the efficacy of *P. eupatorii*, which, along with the cooler temperature required for infection, suggests that the cooler and wetter eastern side of South Africa that is suitable for pompom weed is likely to be suitable for *P. eupatorii* too. The thrips, *L. tractabilis*, was first released in 2013 at sites in Gauteng, North West and Limpopo provinces and has since established at several pompom weed sites in Gauteng and North West (McConnachie and McKay, 2015). The flower-feeding moth, *C. campuloclinium*, was approved for

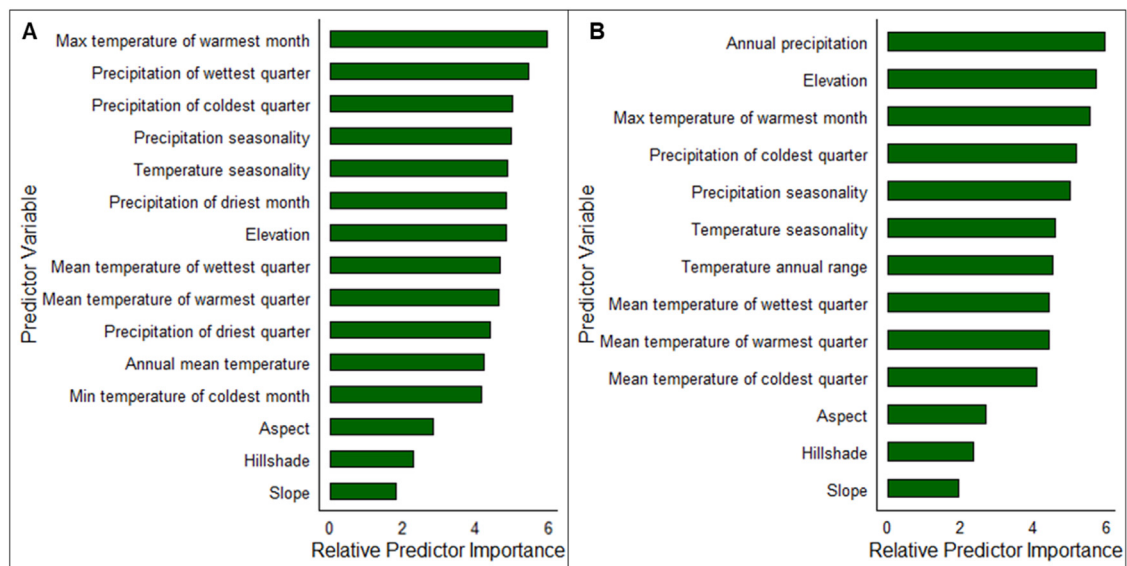


Fig. 5. Relative importance of variables used in the Ecological niche models for predicting pompom weed's potential range, calibrated using A) invasive range data (ENMinvaded) and B) the native and invaded range data combined (ENMentire).

release in 2015 (McConnachie and McKay, 2016), but the release has yet to be achieved (Zachariades et al., 2021). Trethowan et al. (2011) mapped the potential range of *L. tractabilis* and *C. campuloclinium* in comparison to pompom weed, which showed minimal overlap. Their models largely predicted *L. tractabilis* occurrences across the Northern Cape and parts of the Western Cape and *C. campuloclinium* over the central Northern Cape. However, Trethowan et al. (2011) acknowledged that the small size of the native datasets for *L. tractabilis* and *C. campuloclinium* underestimated the two biocontrol agents' possible range. Post-release data has, however, been recorded for *L. tractabilis* establishment at pompom sites in Gauteng and North West, that are cooler, and with higher altitudes (Ramanand et al., 2017). Additionally, Ramanand et al. (2017) tested the lower thermal developmental threshold of *L. tractabilis* at two outdoor sites in KwaZulu-Natal: a site in Pietermaritzburg (no frost) and a site in Cedara (frost area). This threshold was estimated to be 9.6 °C with 546.9 days needed to complete development, and *L. tractabilis* was predicted to complete 3–9 annual generations within the SAPIA pompom weed distribution (Ramanand et al., 2017). This suggests that *L. tractabilis* has the potential to maintain populations wherever pompom weed is established within the projected suitable range of ENMentire, but more research is needed to confirm this.

4.3.2. Climate change and other drivers

The future spread of pompom weed in South Africa is likely to be influenced further by factors such as overgrazing, rising atmospheric CO₂ levels, climate change and bush encroachment. The response of pompom weed to varying concentrations of CO₂ is unknown. But considering that *Parthenium hysterophorus* L. (Asteraceae), an invasive weed related to pompom weed, demonstrates increased growth and reproduction under elevated CO₂ conditions (Cowie et al., 2020), it is plausible to assume that pompom weed might react in a similar manner, increasing the risk of further pompom weed expansion. However, rising CO₂ levels have also facilitated the expansion of woody plants in South African savannas (Stevens et al., 2016). Additionally, other factors such as overgrazing not only lead to rangeland degradation, creating opportunities for invasive species such as pompom weed, but also lead to bush encroachment (O'Connor et al., 2014; Belayneh and Tessema, 2017). The spread of pompom weed may likely be hampered by the decline of grasslands due to the increase in woody cover. Additionally, with the projected rise in mean annual temperatures of 2.5–3.5 °C (Kikstra et al., 2022;

Engelbrecht et al., 2024), the potential range of pompom weed may shrink, as maximum temperature is an important negative driver of the weed's distribution. However, climate models predict a large part of South Africa (excluding the west coast) to become wetter with increased rainfall (Knoesen et al., 2009), which may encourage the spread of pompom weed west into central South Africa, as the results of this study have shown pompom weed to be positively related to rainfall seasonality. These range shifts due to climate change will also affect the success of the biocontrol agents. More research is required into how pompom weed will respond to changes induced by rising atmospheric CO₂ levels, climate change and bush encroachment.

4.3.3. Focal areas for management

Management efforts should focus on grassland and savanna ecosystem types at risk within pompom weeds' suitable range to prevent the further spread of pompom weed. Ecosystem types that fall into the critically endangered category should be targeted first, followed by the endangered and then vulnerable types (Appendix). In particular, the critically endangered Egoli Granite Grassland ecosystem type (Mesic Highveld Grassland Bioregion) in central Gauteng falls within the known epicentre of pompom weed as described in Szewczuk (2025); the remnants of this vegetation type should be the priority for pompom weed control. The small populations in the Western and Eastern Cape may be small enough for eradication, followed by monitoring to prevent a resurgence.

5. Conclusion

The two ENMs developed in this study provide valuable insights into the potential expansion and spread of pompom weed in South Africa. The models indicate that beyond its current distribution, pompom weed has the potential to spread extensively into the remaining regions of Gauteng, the eastern areas of the North West province, Mpumalanga, KwaZulu-Natal, the eastern portion of the Eastern Cape, and along the east coast extending into the Western Cape toward Cape Town. While the model predicts some climatic suitability in parts of the Western Cape, observations suggest pompom weed retains a summer flowering pattern even in winter rainfall regions and its ability to persist under cold, wet winter conditions is uncertain. Of the two models, ENMentire, calibrated using the entire range data, produced the most accurate habitat suitability map with an AUC of 0.923. In contrast, ENMinvaded was calibrated solely using

data from the invaded range, achieving an AUC of only 0.783. The most important environmental variables shown to influence the projected suitable range of pompom weed were elevation, annual precipitation, the maximum temperature of the warmest month, precipitation seasonality and temperature seasonality. Pompom weed can likely survive in colder, frost-prone areas in winter due to its perennial rootstock. As such, the grassland biome and the cooler savannas on the east coast are at most risk of further pompom invasion. Pompom weed monitoring and management priority areas were identified based on the sensitive (critically endangered, endangered or vulnerable) grassland and savanna ecosystem types that fall within pompom weeds' suitable range. While the models developed here were limited to South Africa, Botswana is likely at low risk due to arid conditions in the southern areas bordering South Africa. In contrast, grasslands and open savannas in Zimbabwe and Mozambique may be suitable for pompom weed. A broader regional modelling effort, similar to that of [Trethowan et al. \(2011\)](#), would help assess the potential suitability of these neighbouring countries. This study builds on and refines [Trethowan et al. \(2011\)](#) previous predictions of the suitable range for pompom weed in South Africa by incorporating a more comprehensive dataset and updated climate variables, resulting in a more spatially refined and ecologically relevant projection of pompom weed's potential range. Furthermore, including a wider range of environmental predictors and exploring their contributions to the models has improved the understanding of the factors driving pompom weed's distribution. Overall, this research offers a more ecologically informed and management-relevant prediction of pompom weed's future distribution.

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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

Alekzandra Mari Szewczuk: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marcus J. Byrne:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Ed T.F. Witkowski:** Writing – review & editing, Supervision, Project administration, Conceptualization.

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Appendix. The grassland and savanna ecosystem types based on [Mucina and Rutherford \(2006\)](#) and the South African National Vegetation Map ([SANBI, 2024](#)) classified as critically endangered, endangered or vulnerable should receive pompom weed management priority

Vegetation Type	Bioregion	Biome	Threat Status
Egoli Granite Grassland	Mesic Highveld Grassland Bioregion	Grassland	CR
Mabela Sandy Grassland	Sub-Escarpment Grassland Bioregion	Grassland	CR
Vredefort Dome Granite Grassland	Dry Highveld Grassland Bioregion	Grassland	CR
Woodbush Granite Grassland	Mesic Highveld Grassland Bioregion	Grassland	CR
Zululand Coastal Thornveld	Lowveld Bioregion	Savanna	CR
East Griqualand Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Eastern Highveld Grassland	Mesic Highveld Grassland Bioregion	Grassland	EN
Income Sandy Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
KaNgwane Montane Grassland	Mesic Highveld Grassland Bioregion	Grassland	EN
KwaZulu-Natal Sandstone Sourveld	Sub-Escarpment Savanna Bioregion	Savanna	EN
Lebombo Summit Sourveld	Lowveld Bioregion	Savanna	EN
Legogote Sour Bushveld	Lowveld Bioregion	Savanna	EN
Marikana Thornveld	Central Bushveld Bioregion	Savanna	EN
Midlands Mistbelt Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Mooi River Highland Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Mthatha Moist Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Northern Escarpment Dolomite Grassland	Mesic Highveld Grassland Bioregion	Grassland	EN
Northern Zululand Mistbelt Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Paulpietersburg Moist Grassland	Mesic Highveld Grassland Bioregion	Grassland	EN
Southern KwaZulu-Natal Moist Grassland	Sub-Escarpment Grassland Bioregion	Grassland	EN
Tsakane Clay Grassland	Mesic Highveld Grassland Bioregion	Grassland	EN
Tzaneen Sour Bushveld	Lowveld Bioregion	Savanna	EN
Vaal-Vet Sandy Grassland	Dry Highveld Grassland Bioregion	Grassland	EN
Western Highveld Sandy Grassland	Dry Highveld Grassland Bioregion	Grassland	EN
Dry Coast Hinterland Grassland	Sub-Escarpment Grassland Bioregion	Grassland	VU
Eastern Free State Clay Grassland	Mesic Highveld Grassland Bioregion	Grassland	VU
Moist Coast Hinterland Grassland	Sub-Escarpment Grassland Bioregion	Grassland	VU
Northern KwaZulu-Natal Moist Grassland	Sub-Escarpment Grassland Bioregion	Grassland	VU
Rand Highveld Grassland	Mesic Highveld Grassland Bioregion	Grassland	VU
Soweto Highveld Grassland	Mesic Highveld Grassland Bioregion	Grassland	VU
Ngongoni Veld	Sub-Escarpment Savanna Bioregion	Savanna	VU

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