



Climate modelling of the potential distribution in South Africa of two *Zygogramma* species (Coleoptera: Chrysomelidae) released for the biological control of invasive weed *Tithonia rotundifolia* (Asteraceae: Heliantheae)

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Abstract Two Mexican leaf-feeding beetles, *Zygogramma piceicollis* (Stål) and *Zygogramma signatipennis* (Stål) (Coleoptera: Chrysomelidae), were released in South Africa for the biological control of the invasive species *Tithonia rotundifolia* (Mill.) S.E. Blake (Asteraceae: Heliantheae). The aim of this study was to predict the potential of these beetles to establish and spread in South Africa, using MaxEnt climate modelling that incorporated locality data recorded in Mexico between 2008 and 2019 and data from the Global Biodiversity Information Facility. *Zygogramma signatipennis* displayed a wider distribution than *Z. piceicollis* in Mexico, with some overlap between the two species. The average receiver operating characteristic curves obtained for *Z. piceicollis* and *Z. signatipennis* predicted high mean area under curve values of 0.910 and 0.885, respectively.

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Jackknife tests revealed that mean annual temperature had the highest gain when used in isolation for *Z. piceicollis*, compared with minimum precipitation of the driest month for *Z. signatipennis*. These tests also revealed that the highest and lowest contributing environmental variables for *Z. piceicollis* and *Z. signatipennis* were minimum precipitation of the driest month (37.9 and 46.7%) and maximum annual temperature of the warmest month (3.8 and 12.3%), respectively. MaxEnt modelling predicted that at least six of South Africa's nine provinces provide regions that would support the proliferation of both beetles, with conditions best suited for *Z. piceicollis*. Despite predictions that both beetles should establish throughout the range of *T. rotundifolia* in South Africa, their realized establishment has so far been poor. Other factors, besides climate, including release size, site destructions, drought, soil moisture and texture could be constraining establishment.

Keywords Agent establishment · Climate matching · MaxEnt modelling · Weed biocontrol · *Zygogramma piceicollis* · *Zygogramma signatipennis*

Introduction

Currently, over 460 insect agents have been released worldwide for the biological control of invasive alien plants, with around 70% establishing in their

new range (Hinz et al. 2019) and facilitating the control of around 65% of the targeted weed species (Schwarzländer et al. 2018). In South Africa, Zachariades (2021) reported that out of 136 species of biological control agents released against 90 weed species, about 68% were reported as fully established. Although several factors affect the success of introduced agents, a considerable number of introductions fail due to climatic incompatibility between the agents' native and introduced ranges (Clausen 1978; Goolsby et al. 2005; Harms et al. 2020).

Climatic factors, notably temperature and precipitation, play a major role in the population dynamics of insects (Kamata and Igarashi 1994; Schoonhoven et al. 2005; Harms et al. 2020). In particular, temperature directly affects the survival, developmental rates and reproduction of insect populations (Schoonhoven et al. 2005; Liebhold and Bentz 2011). Furthermore, precipitation influences the microclimatic conditions of the niches inhabited by the different insect life stages (Kamata and Igarashi 1994). Climate is thus major determinant of the distribution of insect agents and their host plants in their new ranges (Goolsby et al. 2006). Hence, climate matching is an important component of biocontrol programmes. Besides predictions of regional suitability for candidate agents, it can identify reasons for the failure or poor establishment of released agents.

Climate-matching models currently include bioclimatic models, species distribution models or ecological niche models (Hirzel and Arlettaz 2003). These models utilize species distribution and environmental data to construct a species profile that describes how environmental variables drive the known distribution (Hirzel and Arlettaz 2003). The fundamental principle underlying these models is that climate is the primary determinant of the potential range of animals and plants (Andrewartha and Birch 1954; McCarty et al. 2009). The environmental requirements of each species are characterized in terms of the unique upper and lower limits of different combinations of environmental variables, and the models are used to produce maps that describe the environmental suitability of each location for the species (Kriticos and Randall 2001; Peterson 2003; Barry and Elith 2006).

In recent years, computer-based systems such as MaxEnt and Climex have facilitated climate-matching models, each with different advantages and shortcomings. Moreover, the majority of these models are constrained by very limited data on species presence in the native range (Merow and Silander 2014). Although the results from these models are not unique to a particular species, they remain very important, particularly when very little is known about an individual organism (Baker et al. 2000). These models thus constitute valuable tools in a variety of applications, including invasive species management, natural resource management, environmental health, agriculture and other ecological fields (Corsi et al. 1999; Scott et al. 2002; Peterson and Shaw 2003).

Native to Mexico, red sunflower, *Tithonia rotundifolia* (Mill.) S.E. Blake (Asteraceae: Heliantheae), is increasing its invasive status in South Africa, with extensive monospecific stands in over 42 quarter degree squares inhabiting roadsides, agroecosystems, rivers and natural systems (Henderson 2007, 2020; Mawela et al. 2022). Five out of South Africa's nine provinces, namely Gauteng, KwaZulu-Natal, Limpopo, Mpumalanga and North West support populations of *T. rotundifolia* (Henderson 2007, 2020; Simelane et al. 2011; Mawela and Simelane 2021; Mawela et al. 2022). A biological control programme was thus initiated in 2007 (Mawela and Simelane 2021) and culminated in release of two leaf-feeding beetles, *Zygogramma piceicollis* (Stål) and *Zygogramma signatipennis* (Stål) (Coleoptera: Chrysomelidae), from 2014 to 2019 (Mawela et al. 2022). Founder populations of the two *Zygogramma* species originated from different regions in Mexico, with somewhat different climatic conditions, suggesting that their distribution in South Africa may also vary. Additional releases of the two beetles should cover the extent of the weed's distribution in South Africa, which occurs across a range of climatic conditions from the "Lowveld" (150–600 m altitude) to the "Highveld" (1500–2100 m altitude) regions (Supplementary Figure S1).

The aim of this study was to predict the potential distribution of *Z. piceicollis* and *Z. signatipennis* in South Africa, using maximum entropy modelling (MaxEnt). The model outcomes could identify regions best suited for additional releases, as well as explain why earlier releases have resulted in either good or poor establishment success.

Materials and methods

Study area and mapping

Five roadside surveys were conducted in Mexico between late September and early November during 2008–2019, in search of insect natural enemies of *T. rotundifolia*. These incorporated seven states, namely Mexico, Puebla, Guerrero, Veracruz, Oaxaca, Chiapas and Tabasco, situated from the central region to the far south of Mexico. Locality data for sites supporting the two *Zygogramma* species were recorded, using a Garmin hand-held multi-satellite Global Positioning System (NUVI 2497 LMT) receiver with ± 5 m positional accuracy. Additional records for both species were downloaded from the Global Biodiversity Information Facility, to increase the sample size for both beetle species (GBIF 2022a, 2022b). Using the R ‘Biogeo’ package in R statistical software R v 4.0.2 (R Core Team 2020) as in Robertson et al. (2016), the presence data were ‘cleaned’ to filter out records with erroneous coordinates, as well as duplicated or inaccurate records.

The model for *Z. piceicollis* incorporated 87 ‘clean’ records, arising from 31 survey records and 353 records from the GBIF database (GBIF 2022a), while the model for *Z. signatipennis* incorporated 111 ‘clean’ records, arising from 35 survey records and 343 GBIF records (GBIF 2022b). The number of occurrence points for each *Zygogramma* species thus exceeded the minimum sample size (i.e., 23) required to construct a robust Environmental Niche Model in MaxEnt (Stockwell and Peterson 2002). MaxEnt was selected because it is a freely available software that is widely used for species distribution and environmental niche modelling (Phillips et al. 2006), with over 1000 published applications since 2006 (Merow et al. 2013). Furthermore, MaxEnt has proved to perform well compared to alternative available models (Phillips et al. 2017). MaxEnt uses a set of environmental and georeferenced occurrence locality data of a species for modelling its niche and distribution (Phillips et al. 2006). The ‘cleaned’ locality data were converted to CSV files (comma-separated values) and imported into ArcGIS online to delineate the beetles’ native range distribution.

Environmental variables and species occurrence data

We obtained a set of bioclimatic predictor variables from the World-Clim data set (a set of global climate layers with a spatial resolution of 1 km²; <http://www.worldclim.org>) (Hijmans et al. 2005), which were used to determine the most influential variables associated with the distribution of the two beetles. These comprised raster layers with a spatial resolution of 30 arc seconds. In general, the bioclimatic variables are those environmental variables known to indicate general patterns of temperature and precipitation, including the extremity and seasonality of temperatures. Environmental variables that are highly correlated are known to reduce the accuracy of the predicted results. Therefore, Pearson correlation analysis was used to screen out environmental variables with correlation values higher than 0.8.

The selected variables included annual precipitation (Bio 12), maximum annual temperature in the warmest month (Bio 5), and both mean annual temperature (Bio 1) and minimum precipitation in the driest month (Bio 14) (Table 1). Jackknife tests for regularized training gain and area under the receiver operating characteristic (ROC) area under curve (AUC), for both *Zygogramma* species, incorporated these four variables. MaxEnt version 3.4.1 was used to predict the potential distribution of the two *Zygogramma* species in South Africa. The analysis of omission/commission was conducted to test the omission rate and predicted area, as a function of the cumulative threshold averaged over the replicate runs. The climatic suitability was categorised using colour codes where dark green indicates an unsuitable area, light green a marginally (low) suitable area, yellow a

Table 1 Estimates of the percentage contributions of four environmental variables to the MaxEnt model for *Zygogramma piceicollis* and *Zygogramma signatipennis*

Environmental variable	<i>Z. piceicollis</i>	<i>Z. signatipennis</i>
Minimum precipitation in the driest month (Bio 14)	37.9	46.7
Mean annual temperature (Bio 1)	35.3	27.8
Annual precipitation (Bio 12)	23.1	13.2
Maximum annual temperature in the warmest month (Bio 5)	3.8	12.3

moderately (average) suitable area, orange a suitable (above average) area and red a highly suitable area.

Results

Native range distribution

Field surveys conducted between 2008 and 2019 revealed that the distributions of the two *Zygogramma* species were different in their native Mexican range. *Zygogramma signatipennis* displayed the widest distribution and occurred in almost all surveyed states, while *Z. piceicollis* was concentrated in only two states, namely the coastal region of Oaxaca and inland of Chiapas (Fig. 1). *Zygogramma signatipennis* was located predominantly in the higher altitude areas of Oaxaca and Puebla States, with altitudes averaging 1500–2000 m, while *Z. piceicollis* was mainly found in relatively lower altitude (100–1700 m), humid and hotter regions of Oaxaca and Chiapas States.

Predicted distribution in introduced ranges

The average omissions and predicted areas for *Z. piceicollis* (Fig. 2a) and *Z. signatipennis* (Fig. 2b) varied with the choice of cumulative threshold. The omissions for both *Zygogramma* species are generally below the predicted omissions, although the model for *Z. piceicollis* displayed considerably more variation than that for *Z. signatipennis*. Using AUC to assess model performance, the AUC values for both *Zygogramma* species show good performance to predict their potential distribution using available data. The average ROC curves determined by MaxEnt produced mean (\pm SD) AUC values of 0.910 (\pm 0.027) for *Z. piceicollis* (Fig. 2c) and 0.885 (\pm 0.005) for *Z. signatipennis* (Fig. 2d). The performance of the model was thus slightly higher for *Z. piceicollis* than for *Z. signatipennis*.

Validation of the models revealed that the predicted and realized distributions in the native range were generally aligned for both *Z. piceicollis* (Fig. 3a)

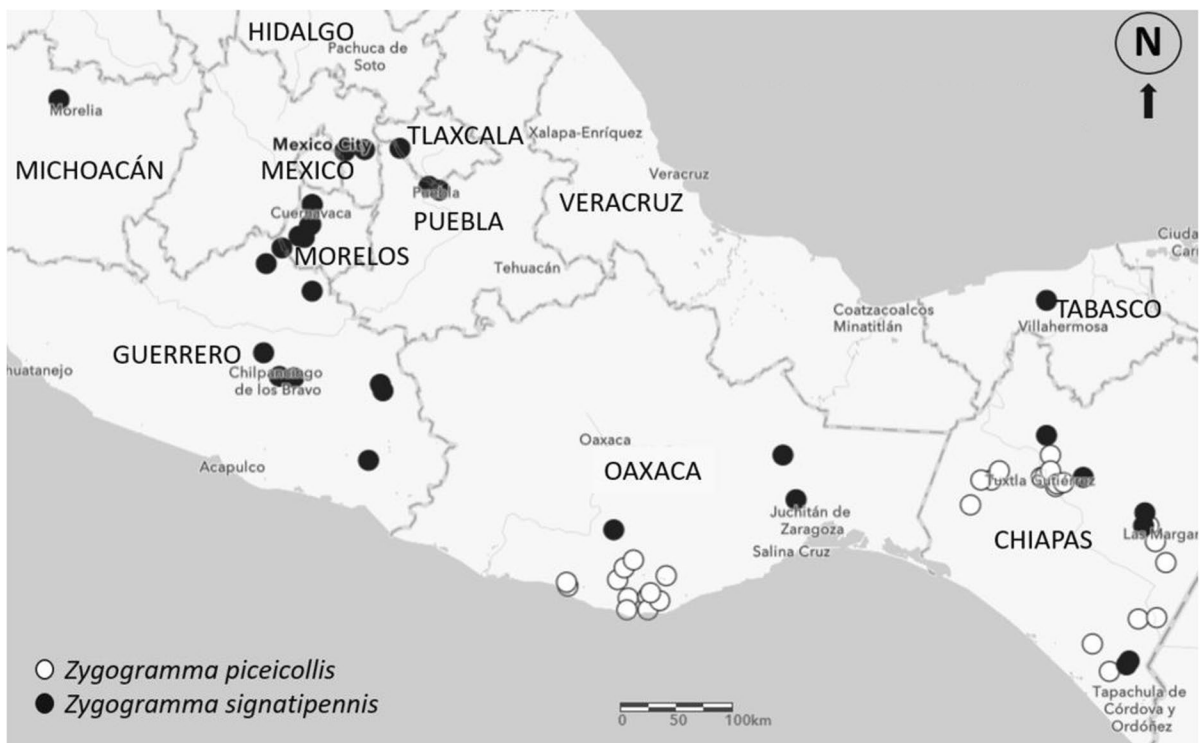


Fig. 1 Distribution of *Zygogramma piceicollis* and *Zygogramma signatipennis* in their native Mexican range, based on surveys conducted between 2008 and 2019. Constructed using

ArcGIS online basemap. Sources: Environmental Systems Research Institute (Esri); DeLorme Publishing Company; Here Technologies; MapmyIndia

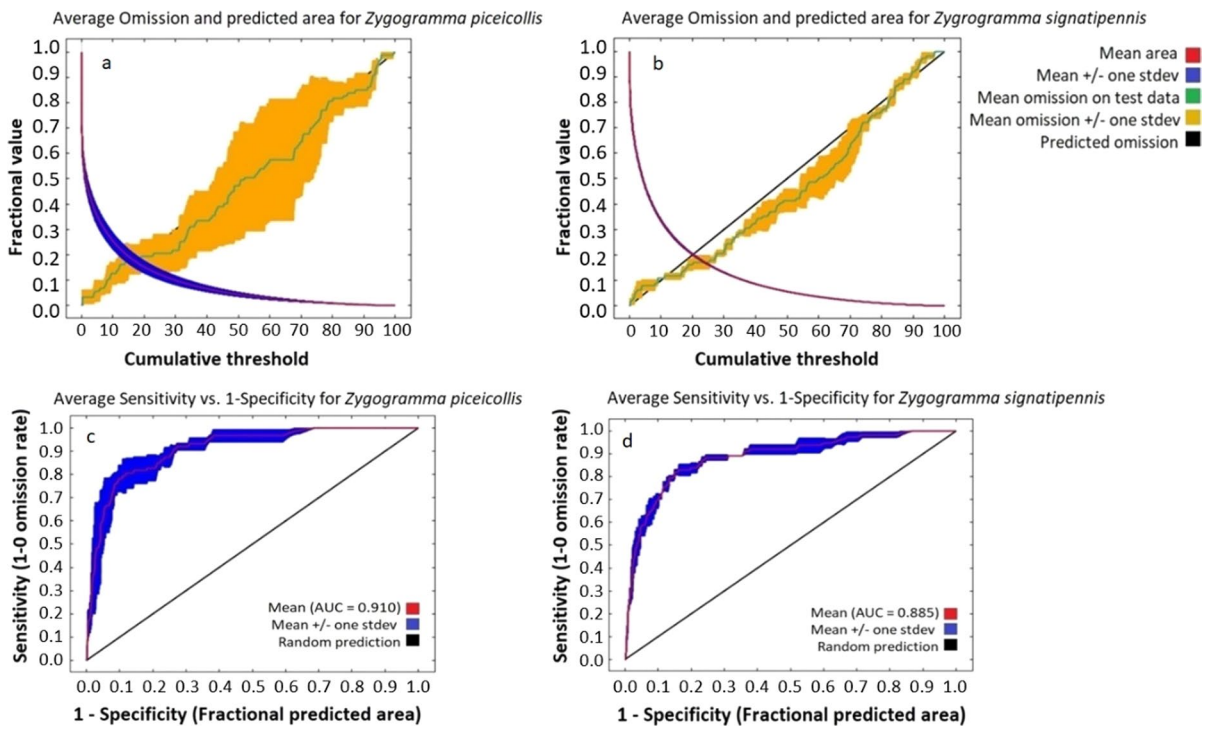


Fig. 2 Average omission and predicted area (a and b) and average sensitivity vs. 1-specificity (c and d) for *Zygodramma piceicollis* (left) and *Zygodramma signatipennis* (right). Constructed using MaxEnt (version 3.4.1)

and *Z. signatipennis* (Fig. 3b). Similarly, MaxEnt predicted a wide distribution of the two *Zygodramma* beetle species in South Africa. The Jackknife test of variable importance for *Z. piceicollis* revealed that

mean annual temperature has the highest gain when used in isolation, therefore providing the most useful information by itself. Minimum precipitation in the driest month decreased the gain the most when

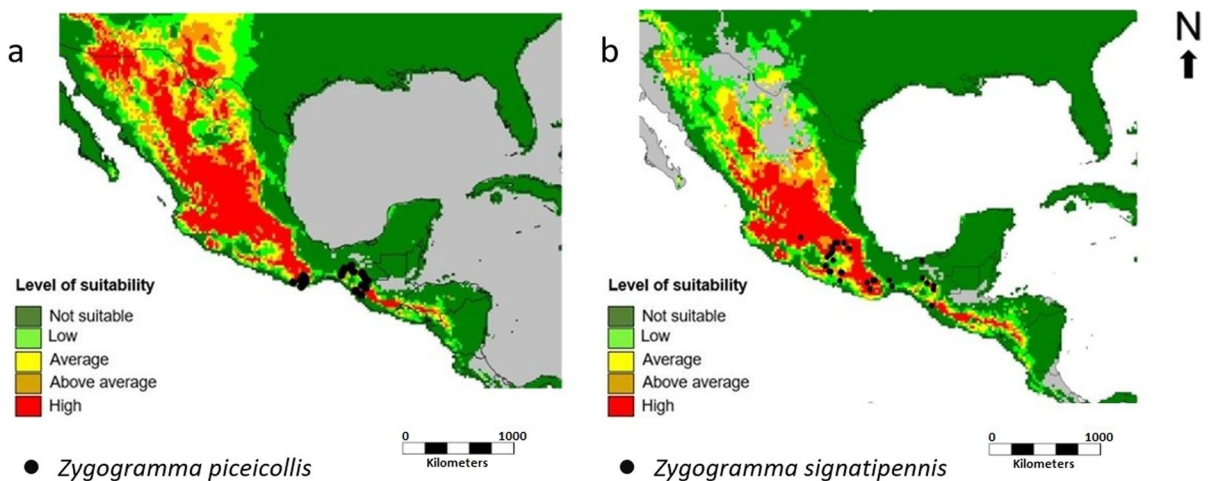


Fig. 3 Validation of the MaxEnt models, using the predicted and realized distribution of *Zygodramma piceicollis* (a) and *Zygodramma signatipennis* (b) in their native Mexican range

omitted, implying that it provides the most information that is absent in the other variables (Fig. 4). Minimum precipitation in the driest month had the highest contribution to the model for *Z. piceicollis* (37.9%), while the lowest contributing factor was maximum annual temperature in the warmest month (3.8%) (Table 1). With regard to *Z. signatipennis*, the Jackknife test revealed that minimum precipitation in the driest month provided the highest gain when used in isolation (Fig. 4) while minimum precipitation in the driest month decreased the gain the most when omitted. Minimum precipitation in the driest month had the highest contribution to the model for *Z. signatipennis* (46.7%) while the lowest contributing factor was maximum annual temperature in the warmest month (12.3%) (Table 1).

The *Z. piceicollis* model predicted that regions with the highest suitability (i.e., regions shaded in red) are in the provinces of Gauteng, Mpumalanga, Free State, North West, Limpopo, KwaZulu-Natal, Western Cape and Eastern Cape. However, some areas in the North West and Free State provinces ranged from moderately suitable to suitable while the Northern Cape, Western Cape and Eastern Cape provinces ranged from unsuitable to suitable (Fig. 5a). The *Z. signatipennis* model similarly

predicted that areas with the highest suitability are in KwaZulu-Natal (inland region), Mpumalanga, Limpopo, North West, Gauteng and Free State provinces, and some areas in the Western Cape and Northern Cape provinces (Fig. 5b). However, the Eastern Cape Province displayed only above average suitability for *Z. signatipennis*.

Discussion

Geographic features are known to play a major role in success or failure of biological control programs through differential responses of biocontrol agents and the targeted invasive weeds to both biotic and abiotic factors (Harms et al. 2020). The objective of this study was to predict the potential for *Z. signatipennis* and *Z. piceicollis* to establish and spread throughout the invaded range of *T. rotundifolia* in South Africa. *Tithonia rotundifolia* remains a major invasive weed in five provinces of South Africa (Henderson 2007). While there might be scepticism towards the release of almost identical biocontrol agents that attack the same niche, the realized distributions of *Z. signatipennis* and *Z. piceicollis* were different in Mexico. Accordingly, this may present a better chance for both

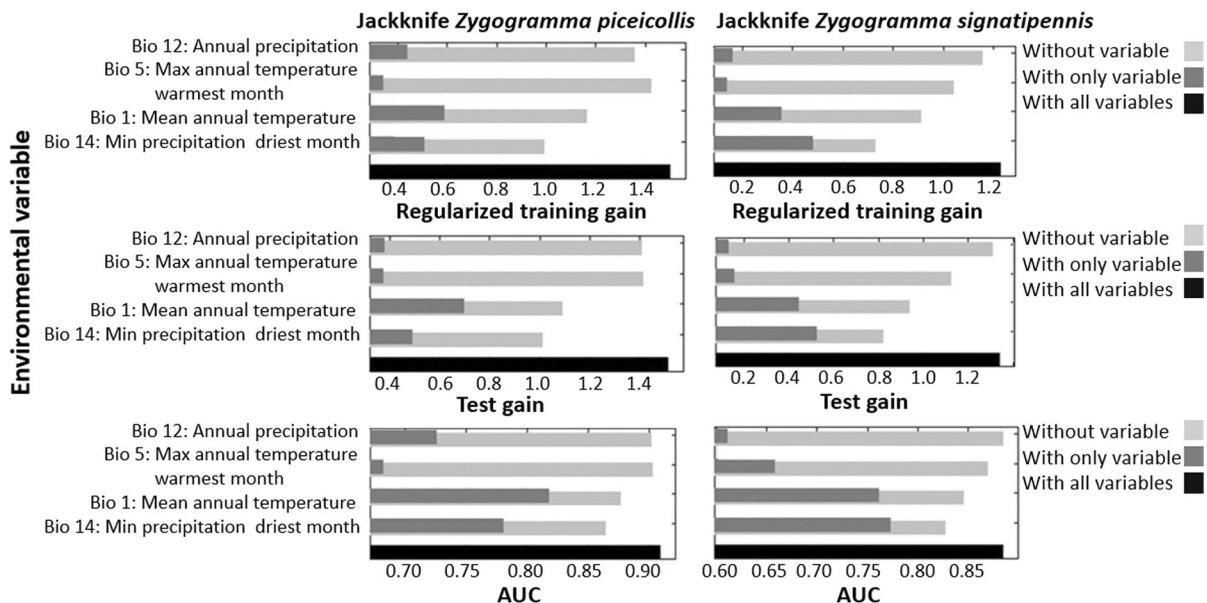


Fig. 4 Jackknife tests for evaluation of the relative importance of environmental variables, using regularised training gain, test gain, and AUC for *Zygogramma piceicollis* (left) and *Z. signatipennis* (right)

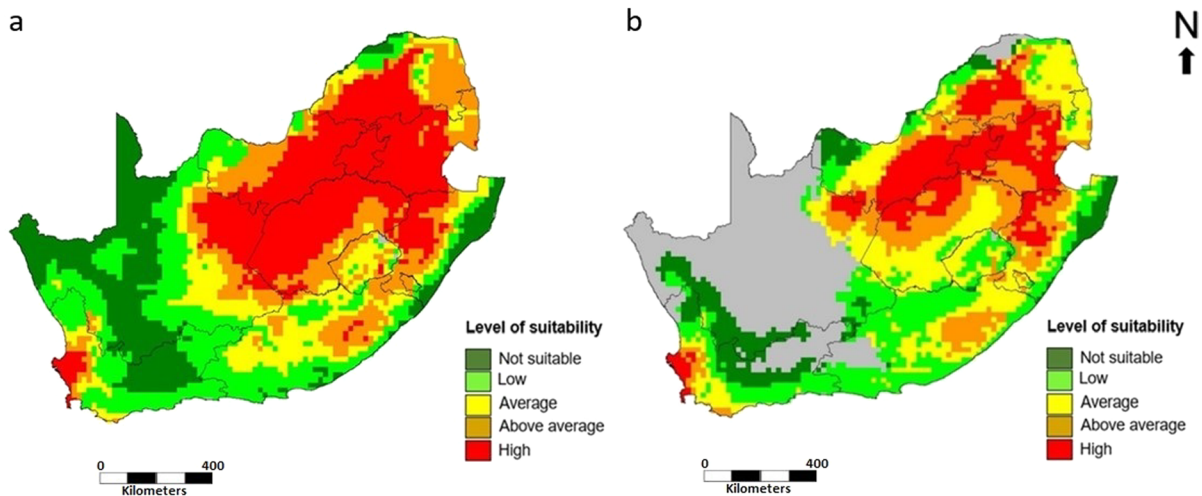


Fig. 5 Potential distribution of *Zygotogramma piceicollis* (a) and *Zygotogramma signatipennis* (b) in South Africa, using MaxEnt modelling

beetle species to proliferate and exert a greater impact on *T. rotundifolia* throughout its invaded range. Hoffmann et al. (1998) reported that, while the leaf-feeding beetle *Leptinotarsa defecta* Dunal (Coleoptera: Chrysomelidae) was localised and scarce, its congener *L. texana* Dunal proliferated in high densities with a wider distribution following their release as biocontrol agents of *Solanum elaeagnifolium* Cavaniilles (Solanales: Solanaceae) in South Africa. Furthermore, two leaf-feeding beetle species in the genus *Galerucella* have played a major role in the biological control of purple loosestrife, *Lythrum salicaria* L. (Myrtales: Lythraceae) in the USA (Blossey 1992; Moore 2009).

The models also suggest that the native range distributions of both *Zygotogramma* species could be more extensive than indicated by the available distribution records. Depending on the presence of their host plants, both beetle species could potentially occur from the southern states of the USA, through Central America and into South America (Supplementary Figs. S2 and S3). It is therefore anticipated that the slight difference in the distribution of the two beetle species in their native range may collectively increase the area under which they will be distributed in South Africa.

The model predicted that the minimum precipitation in the driest month would largely determine the potential distribution of both *Zygotogramma* species in South Africa. Given the differential contribution of

this variable to the two models, the predicted distribution of the two *Zygotogramma* species varied slightly. These results indicate a very good match for the predicted omission rate for both *Zygotogramma* species. An AUC mean above 0.8 is considered reliable in terms of model accuracy (Araujo et al. 2005). Hence, the high AUC values reported for both *Zygotogramma* species, based on available data, are good predictors of their presence.

Although the two *Zygotogramma* species originated from different provinces of Mexico, with differing climatic conditions, their predicted distribution in South Africa is similar. Areas predicted to be highly suitable for the establishment of both *Zygotogramma* species are largely consistent with the distribution of the target weed, *T. rotundifolia*, in South Africa (Mawela and Simelane 2021). Globally, patches of high suitability were predicted in some countries ranging from central to north-eastern Africa, southern Europe as well as South East Asia (Supplementary Figs. S2 and S3). Since *T. rotundifolia* is also invasive in the humid and sub-humid tropics of South America, South East Asia, as well as tropical and subtropical Africa (Lazarides et al. 1997; Meyer 2000; Varnham 2006), these models may be applicable to other countries interested in utilizing the two biocontrol agents (Supplementary Figs. S2 and S3).

Although the models predicted that both *Zygotogramma* species would establish throughout the distribution of *T. rotundifolia* in South Africa, their

realized establishment has so far been poor (Mawela and Simelane 2021). While the AUC values for both *Zygogramma* species suggested good model performance, it is clear that such models have limitations since they rely entirely on climate-related features and meteorological data from the locations used (Sutherst 2003). In particular, there are several variables besides climatic factors (e.g., soil conditions, habitat preferences, landscape features, predation and parasitism) that are not factored into these models and could influence the distribution and persistence of these beetles in South Africa (Patrick and Olckers 2014; Devegili et al. 2019). Soil type and soil moisture that affect the survival of the subterranean pupae (Beirne 1970) could explain the disparity between the predicted and realized results. Chang et al. (2008) reported that moisture could directly alter the water balance in insects, which may affect their growth and population dynamics. Indeed, the minimum precipitation of the driest month was determined to be the most important variable in the models. Low rainfall during the dry winter months throughout much of South Africa may result in low soil moisture that is suboptimal for the beetles and either prevents establishment or constrains population proliferation. Further studies on the biology of the two *Zygogramma* species (e.g., thermal physiology, ecological needs) are thus required to elucidate their potential as bio-control agents for *T. rotundifolia* in South Africa and other invaded countries.

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Author contributions KVM: conceptualization, investigation, data curation, formal analysis, writing—original draft; DOS: conceptualization and project administration, supervision, writing—review and editing; TO: supervision, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Data availability All raw data generated or analysed during this study can be obtained by contacting the corresponding author.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

Informed consent Not applicable.

Institutional review board Not applicable.

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