

**Ecological niche modelling of *Gargaphia decoris* (Heteroptera), a biological control agent of the invasive tree *Solanum mauritianum* (Solanales: Solanaceae).**

**Short running title:** Prospects of *Gargaphia decoris* as biological control agent of *Solanum mauritianum*.

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**ABSTRACT**

**BACKGROUND:** The South American tree *Solanum mauritianum* Scopoli (Solanaceae) is a problematic invasive plant in numerous tropical, sub-tropical and temperate regions across the globe. As conventional management approaches are not cost-effective, biological control provides an alternative approach. *Gargaphia decoris* Drake (Tingidae), is currently being implemented as a biological control agent in South Africa and New Zealand. Considering the importance of climate in the establishment and success of a biological control agent, this study used ecological niche models (ENM) to identify areas where *S. mauritianum* is a problematic invader and where suitable conditions exist for *G. decoris*. Additionally, the climate niche dynamics of *G. decoris* were investigated and ENMs projected worldwide for the year 2050 were built.

**RESULTS:** Our results indicate that most of the countries where *S. mauritianum* is problematic have suitable climatic conditions for *G. decoris*, and that the species can survive in climates with lower temperatures than the ones in its native range. For future climates ENMs predict wider regions with favourable climatic conditions for *G.*

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*decoris*. CONCLUSION: Considering the results of this study, the prospects of *G. decoris* as a biological control agent is good under present and future climates. The agent's introduction could be considered in affected countries where it has not been released.

**Key words:** Tingidae; lace bug; Bugweed; Woolly Nightshade; potential distribution.

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## 1. INTRODUCTION

*Solanum mauritianum* Scopoli (Solanales: Solanaceae), commonly known as Bugweed (South Africa), Woolly Nightshade (Australia and New Zealand) or Tobacco bush (Australia), is a perennial tree native to South America, particularly north-eastern Argentina, southern Brazil, Paraguay and Uruguay.<sup>1</sup> *Solanum mauritianum* has become naturalized in Africa, Australasia, India and islands in the Atlantic, Indian and Pacific

Oceans, presumably via the Portuguese trade routes in the early 16<sup>th</sup> century.<sup>2</sup> The tree has reached invasive status in several countries.<sup>1</sup> Within these invaded countries, *S. mauritianum* is particularly problematic in conservation areas, agricultural lands, forestry plantations and riverine habitats.<sup>3</sup> Conventional control approaches such as chemical or mechanical methods are not cost-effective at a large scale. Thus, biological control is considered one of the few sustainable options to effectively control the plant's invasion over time and space.<sup>1</sup>

The lace bug, *Gargaphia decoris* Drake (Heteroptera: Tingidae), which is native to Argentina and Brazil, was introduced for the biological control of *S. mauritianum* in South Africa in 1999 and in New Zealand in 2009, following years of exhaustive laboratory tests and risk analyses.<sup>4</sup> This lace bug causes extensive foliar damage, such as chlorosis and premature leaf abscission, has a relatively narrow potential host range that does not include other species within the genus *Solanum*, except for *S. melongena*, and exhibits very strong feeding and oviposition preferences for *S. mauritianum* in choice tests in the laboratory.<sup>5,6</sup> In South Africa, *G. decoris* has caused extensive damage to *S. mauritianum* during population outbreaks but has been deemed an inefficient agent due to its sporadic fluctuations in population density.<sup>4,7</sup> In New Zealand, its performance has been more effective and consistent over time.<sup>8</sup> In South Africa, cold winter temperatures were originally blamed for poor establishment. However, this was dismissed after thermal assessments by Barker and Byrne (2005) which found that the insect was not directly affected by the cold temperatures.<sup>9</sup> Currently, predation is considered to be a major factor constraining *G. decoris* populations.<sup>1</sup>

Regarding the other biological control agent of *S. mauritianum* (released in South Africa), *Anthonomus santacruzii* Hustache (Coleoptera: Curculionidae), low

temperature and low humidity are factors impeding its establishment.<sup>10</sup> Given this background, it is imperative that climatic aspects should be taken into account, investigated and better understood in view of the successful establishment of insect biological control agents of *S. mauritianum*.<sup>10</sup> Ecological niche models (ENM) assess the ecological requirements of species based on their known occurrences and aim to identify different regions that suit these requirements. ENMs can also be projected on future climatological reconstructions that are similar ecologically to those where the species occurs. These regions resemble, in terms of the variables provided, the fundamental niches of species, namely the complete set of environmental conditions under which they can persist.<sup>11, 12</sup> For biological control studies, ENMs based on climate parameters can be very helpful for identifying areas where an invasive species is present and where there are good prospects, in terms of climate, for the successful introduction of a potential control agent. These kinds of studies are being increasingly used to understand the potential distribution and extent of insect establishment in novel environments, including pest species and natural enemies.<sup>13, 14, 15</sup> Such information can be very valuable for determining the extent, cost and probability of success of biological control programmes. Hence, an ENM is an important tool for defining strategies for the biological control of invasive species.

Although ENMs are useful for understanding and predicting species distributions across landscapes or different times, they also have limitations. The successful establishment of a non-indigenous species in a new environment depends on many factors, among them predators, food availability, and climatic similarity.<sup>16</sup> Of these, ENMs take into account climatic similarity under the assumption that species are conservative in their climatic requirements across space and time but this assumption has been challenged by evidence of climatic niches shifting during invasions.<sup>16, 17, 18</sup> A

niche shift is a change in the limits of the environmental space occupied by a species.<sup>17</sup> Therefore, the recognition of differences in the environmental spaces occupied by a species in native and invaded areas and of the climatic variables involved can provide important insight into understanding the results of ENMs and awareness of their potential limitations.

The aims of this study were: i) to identify within the regions where *S. mauritianum* is known to be a problematic invader, areas with suitable climatic conditions for the introduction of *G. decoris* as a biological control agent; ii) to identify, within the areas where *G. decoris* has been successfully introduced, the variables which differ more with respect to the climate of the native range and, therefore, the variables to which the species exhibits more plasticity and could adapt more easily when the conditions are different to the ones in its native range; and iii) to generate a worldwide ecological niche model of *G. decoris* projected onto future climates (period 2050), considering the invasive nature of *S. mauritianum*.

## 2. MATERIALS AND METHODS

### 2.1 *Species data*

Two occurrence datasets were compiled for *G. decoris*, one with native range records (from Argentina and Brazil) and another with its entire distribution, including native and non-native records. The native record dataset was compiled with the aim of recognizing areas where the species is established and where the climatic conditions are different from the ones in the native area. If the non-native records were found to occur in regions predicted by the model (built with the native records) to have novel climatic

conditions or non-suitable conditions, then the climatic conditions in these areas differ to the ones in the native range.

To avoid biases due to spatial autocorrelation, occurrences less than 10 km apart were discarded. The final datasets (Appendix A) used to train the models were constituted by 13 and 45 records (including only native records and all records, respectively) compiled from specimens held at the Museo de La Plata (Argentina) and from the literature.<sup>1, 6, 8, 19, 20, 21, 22, 23, 24, 25</sup> Three records from New Zealand were personally communicated to the authors by Fowler (2018).

## 2.2 Variable selection

To build the models, we used the set of 19 bioclimatic variables (Appendix B) available from the WorldClim database.<sup>26</sup> For the models developed in regions where *S. mauritianum* is a problematic invader, the resolution of the layers used was 2.5 arc-min (~5 km), and for the models developed on a global scale for future climates (excluding South America, its native range), it was 5 arc-min (~10 km). To project future climate (for the 2040-2069 period, referred to as 2050), three Global Climate Models (GCM) were used, CCSM4, GISS-E2-R and MIROC5, with two very different representative concentration pathways (RCP): RCP 2.6 and RCP 8.5. A Representative Concentration Pathway (RCP) considers a wide range of possible changes in future climates depending on how much greenhouse gas (GHG) is released in the years to come. RCP 2.6 predicts milder changes, assuming that global GHG emissions will peak between the years 2010-2020 and subsequently decline substantially, while RCP 8.5 predicts the most catastrophic scenario, in which emissions will continue to rise during the current century (IPCC 2013).

As climatic surrogates and in order to avoid issues with multi-collinearity we performed a principal component analysis (PCA) of the 19 Worldclim variables clipped to the extent of a polygon.<sup>27</sup> The polygon of the calibration area of the ENM trained with the native records encompassed all the ecoregions where these records are distributed with a buffering zone of 50 km (Appendix C).<sup>28</sup> Likewise, the polygon of the calibration area of the ENM trained with all the records comprised all the ecoregions where these are distributed with a buffering zone of 50 km as well (Appendix D). For the areas where the models were projected, the polygons used to clip the variables for the PCA included the extent of the countries where *S. mauritanum* is a problematic invader, or in the case of future projections, included the extent of the world. PCA analysis was performed using the 'PCARaster' function in ENMGadgets Rpackage.<sup>29</sup> The PCAs used to train the models had a cumulative variation of >90% for the first four principal components (PC), so we used them as climatic predictors (Appendices E, F). For the first two PCs in the model built with the native records, the variables with highest contributions were Mean Temperature of Coldest Quarter (Bio11), Annual Mean Temperature (Bio1) and Min Temperature of Coldest Month (Bio6) and Annual Precipitation (Bio12), Precipitation of Wettest Month (Bio13) and Precipitation of Wettest Quarter (Bio16), respectively; and for the model built with the full distribution, these were Mean Temperature of Coldest Quarter (Bio11), Annual Mean Temperature (Bio1) and Annual Precipitation (Bio12), Precipitation of Wettest Month (Bio 13) and Precipitation of Wettest Quarter (Bio16), respectively.

### 2.3 Ecological niche models

ENMs were prepared using Maxent v3.4.1k. and were developed with the two occurrence datasets (native and entire) and 10000 random background points

representing the distribution of environmental conditions in the training area following the recommendations of Phillips & Dudík (2008).<sup>30, 31</sup> In order to avoid over-parameterization, the models trained with the native and with the entire dataset were tuned by exploring the performance of different beta-regularization multiplier values (0.5 to 4) and of different feature classes (L, H, LQ and LQH). Model performance for each combination of regularization multiplier and feature class were evaluated, following the recommendations of Shcheglovitova and Anderson (2013), through the omission rate and the area under the curve (AUC), and by analyzing the model predictions in the known distribution of the species.<sup>32</sup> Optimal model complexity was estimated using a regularization multiplier of 1.5 and the feature classes LQ for the models trained with the native records (Appendix G, Table I), and using 2.5 and the H feature class for the models trained with the full dataset (Appendix G, Table II).

The model trained with the native dataset was validated through the jackknife approach. This methodology was specifically designed to evaluate the predictive accuracy of models built with a small number of occurrences (fewer than 25 records).<sup>33</sup> It is based on removing one record from the dataset and building a model using the remaining  $n-1$  records. The ability of each  $n-1$  model to predict the record excluded is tested. To do this, the  $n-1$  models are converted into binary presence–absence maps using a threshold. We used the ‘minimum training presence threshold’. As many  $n-1$  models are built as records exist. The significance of the models is tested using the P value program, and if  $P \leq 0.05$  the model is validated.<sup>33</sup> The models trained with the full dataset were validated by applying the partial receiver operating characteristic procedure (pROC). For each species, 1000 random iterations with 50 % sub-sampling were performed to evaluate if the real models were statistically significantly better than



random (higher than 1.0) ( $P < 0.001$ ).<sup>34</sup> These evaluations were carried out in Niche Toolbox.<sup>35</sup>

Discriminatory ability was measured through the area under the curve of the receiver operating characteristic plot (AUC/ROC), which ranges from 0 to 1. Values closer to 1 indicate a better prediction, values of 0.5 correspond to a prediction equal to random, and values lower than 0.5 a prediction worse than random.

Current and future models were converted into binary maps. Values above the ‘minimum training presence logistic threshold’ (MTP) were considered as presence, and values below this threshold as absence.<sup>33</sup> The MTP indicates values above which the climate conditions are suitable for the survival of the modelled species and guarantees that all actual presences of the target species are predicted as suitable. A multivariate environmental similarity surface (MESS) analysis was conducted to identify the regions with environmental conditions outside the range of the training area, i.e. with novel climatic conditions in the models trained with the native dataset and with the entire dataset. Cells on the binary map where the MESS analysis recovered novel climates were identified. For future models, the full dataset was used to train the models. Consensus maps were built in which the regions where the three GCMs matched were recovered. This procedure was performed for the two RCPs considered.

Current binary maps were superimposed on a map of the areas where *S. mauritanum* is problematic in order to investigate areas where the establishment of *G. decoris* would be more relevant.<sup>1</sup>

#### 2.4 Direct climate comparisons

A direct climate comparison was performed for the records in areas where the MESS analysis of the model trained with the native records identified novel climates. The raw

environmental data of the 19 bioclimatic variables were extracted for the ecoregions occupied by these records and from the native range of distribution. This information was used to build and compare boxplots for each region. The World Wildlife Fund (WWF) hierarchical classification was followed to identify ecoregions.<sup>28</sup>

### 3. RESULTS

#### 3.1 Present ENM for regions where *S. mauritanum* is a problematic invader

Jackknife validation indicated that the ENM built with native records was robust, yielding predictions statistically significantly better than random ( $P < 0.001$ ) and the performance of the model was very good with an AUC of 0.894. Based on model projections, all releases of *G. decoris* in South Africa (Fig. 1a) and New Zealand (Fig. 2a) where establishment has been confirmed had suitable habitat conditions, except for two records of *G. decoris* in KwaZulu-Natal, South Africa in areas predicted by the model as being unsuitable. Some of the release sites where the establishment of the lace bug has not been confirmed are in Gauteng, KwaZulu-Natal and Eastern Cape provinces. The MESS analysis determined small areas with novel climatic conditions in the northeast and southwest of South Africa. In New Zealand (Fig. 2a) the model indicated that the North Island is climatically suitable for *G. decoris*, as well as the western side of the South Island, though most of this region had environmental conditions outside the training area. Areas where *S. mauritanum* is problematic and where the model found suitable climates for the establishment of *G. decoris* were located mainly in patchy regions throughout Madagascar and on the margins of the Mascarene islands (Fig. 1a); in northern Uganda and southeastern Kenya (Fig. 1c); in most of Australia and in central Papua New Guinea (Fig. 2a); in most of India and, just a few central pixels, in Sri Lanka (Fig. 2c); and in the USA in the state of California

(Fig. 3a). For most of these regions suitable climatic conditions outside the range of the training area were found.

The ENM built with the full distribution, including native and non-native records of *G. decoris*, proved to be significantly better than random (AUC ratio of 1.37) and exhibited a very good model performance with an AUC of 0.91. Models built with all the records exhibited a similar pattern to those built with only the native records but, as expected, predicted wider areas with suitable conditions and fewer areas with novel climatic conditions. Most of South Africa (Fig. 1b) except for the central area, and most of New Zealand (Fig. 2b) except for central regions in the South and North Islands, were determined to have suitable conditions. With respect to the other areas where *S. mauritianum* is problematic, suitable climates for the establishment of *G. decoris* were also found in central and southern Madagascar and in the north of Reunion Island and most of Mauritius (Fig. 1b); in most of Uganda and in Kenya towards the south and west (Fig. 1d); in the central part of Australia (Fig. 2b); throughout the majority of India and all Sri Lanka (Fig. 2d); and in the USA in some parts of Florida and in all the western areas (Fig. 3b). In Madagascar, Reunion Island, India, Sri Lanka and the USA, suitable climatic conditions outside the range of the training area were found, however, most of these were only a few pixels. In Papua New Guinea, *S. mauritianum* is a serious problem but no climatically suitable areas for *G. decoris* were identified (Fig. 2b).

### 3.2 Direct climate comparisons

From the North Island of New Zealand, there are two records, from Waikato and the Bay of Plenty, in regions where the MESS analysis of the model trained with the native records identified climatic conditions outside the range of those present in the

native distribution of *G. decoris* (Fig. 2a). These regions correspond to the ecoregion of North Island temperate forests (NITF). The variables identified with a high discrepancy between the NITF ecoregion and the native range of distribution are all related to temperature (Fig. 4, Table 1): Annual Mean Temperature (Bio1), Temperature Seasonality (Bio4), Max Temperature of Warmest Month (Bio5), Min Temperature of Coldest Month (Bio6), Mean Temperature of Wettest Quarter (Bio8), Mean Temperature of Warmest Quarter (Bio10) and Mean Temperature of Coldest Quarter (Bio11). For all these variables, the boxplots do not overlap. Additionally, for Mean Diurnal Range (Bio2), Isothermality (Bio3), Precipitation of Warmest Quarter (Bio18) and Precipitation of Coldest Quarter (Bio19), the records from the Bay of Plenty and Waikato have values outside the range of the native distribution boxplots and, again, most of these variables are related to temperature (Appendix H).

### 3.3 Future worldwide ENM (period 2050)

The worldwide consensus maps for future projections (2050) under the two RCP scenarios (2.6 and 8.5) are very similar, with some differences in the extent of the areas predicted as suitable (Fig. 5a, b). Most of Africa (Fig. 5a, b) was determined to support suitable conditions. The pattern is very similar to the present climate model for Uganda and Madagascar, much broader for Kenya and South Africa, while for Mauritius, conditions change and become unsuitable (Fig. 1b, d). For Oceania (Fig. 5a, b), the consensus maps predicted a similar but wider pattern than the current model except for New Zealand, where suitable areas became narrower. For Australia (Fig. 5a, b), the suitable region was wider, and for Papua New Guinea a few pixels exhibit suitable conditions in contrast with the present model where there were none (Fig. 2b). In Asia (Fig. 5a, b), suitable conditions are found mainly in the south and west of the

continent; for India (in the areas where *S. mauritianum* is particularly problematic) and Sri Lanka, suitable areas become narrower (Fig. 2d). Most of Europe (Fig. 5a, b) is predicted to support suitable conditions for both consensus maps. Finally, for North and Central America (Fig. 5c, d), the consensus map for the 8.5 RCP scenario is much wider than the 2.6 RCP scenario, as it predicts suitable conditions in areas of southern North America and northern Central America. The consensus map for the RCP 2.6 scenario is very similar to the present climate model for North America (Fig. 3b), but wider.

#### 4. DISCUSSION AND CONCLUSIONS

In the ENM trained with the native records, there are two established populations of *G. decoris* in South Africa that are in areas predicted by the model as unsuitable. Both these records fall outside the suitable area by 1.2 and 11 km. One possible reason for these outliers is that they are in regions with specific micro-climates. Another reason could be that the model might be somewhat overfitted. When the model was tuned, different regularization multipliers were considered. Regularization multipliers control model complexity: a lower regularization multiplier is likely to result in a more restricted and potentially overfitted model, whereas a larger regularization multiplier is likely to result in a less restrictive prediction. In New Zealand, there were many areas outside the training range where the climate had no analogs. The conditions outside the range in the training data were treated by Maxent as if they were at the limit of the training range, by “clamping” the variables.<sup>36</sup> Due to the “clamping” in the exploratory models built with regularization multipliers higher than the one used, many of the areas with conditions outside the training range were predicted as suitable. These models were therefore unrealistic and had poor predictive ability, which is why we opted for a model that might be slightly overfitted. This should be taken into account

when interpreting the ENM trained with the native records. Most of the release sites with unconfirmed establishment fell within the areas predicted to have suitable conditions, and the ones outside this range were quite close (the farthest is 22 km away), so considering that the model might be somewhat overfitted, the possibilities of successful establishment should not be discarded.<sup>1</sup>

It should be also noted that although some of the release sites with unconfirmed results were in areas predicted as suitable, these populations are not necessarily successfully established. ENMs do not consider features that can be crucial for the establishment of a species, such as biotic interactions (i.e. predators, competitors or presence of host plants), and, particularly in the case of *G. decoris*, abiotic features such as shadow exposure. It is worthwhile mentioning that *G. decoris* significantly reduces the photosynthetic output of *S. mauritianum* in both shaded and sunny habitats, and although the impact is greater in sunny environments the insect prefers shaded ones.<sup>37,</sup>

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The ENM built with only the native records predicted narrower areas with suitable conditions, whereas the model built with all the records (entire distribution) was wider. ENMs identify areas that are ecologically similar to those where the species is known to occur.<sup>11</sup> The inclusion of non-native records results in wider predictions since these records are distributed in areas with climates quite dissimilar to those in the native range.

Seven of the eleven temperature-related bioclimatic variables were clearly different in their value ranges between the native region and the NITF ecoregion, New Zealand (boxplots with no overlap). Among these are the two variables, Mean Temperature of Coldest Quarter (Bio11) and Annual Mean Temperature (Bio1), which contribute the most to PCI in both models (built with native records and entire

distribution). Moreover, the minimum and maximum temperatures of these seven variables were always lower in the NITF ecoregion than in the native range, differing by approximately 10 °C for the minimum, 5.5 °C for the maximum and 6 °C for the median temperatures. Furthermore, for eleven of the nineteen bioclimatic variables (Bio1-6, Bio8, Bio10-11 and Bio18-19), the climatic conditions of the records in the Bay of Plenty and Waikato are outside the ranges of the boxplot from the native region. Because of the dataset sizes we were not able to apply quantitative methods to measure the climatic niche shift, though the magnitude of the differences observed in the temperature related variables implied a mismatch between the climatic niche of the native and non-native ranges. With this background, ENMs should be conscientiously interpreted as they may be misrepresenting the regions where *G. decoris* could be introduced.

To date, cold winter temperatures were believed to be one of the reasons for the low population densities in South Africa, as low temperatures reduce the quality of *S. mauritianum* foliage.<sup>1</sup> All the previous evidence suggests that this is not so. At least in New Zealand, all the temperature-related variables are much lower than in the native range, with *G. decoris* having established readily at many of these sites.<sup>8</sup> The aforementioned evidence suggests a change in the climatic niche occupied by *G. decoris* and the possibility that it can establish in regions with climates colder than those in its native range.

Our ENM indicates that most of the countries where *S. mauritianum* is problematic have areas with suitable climatic conditions for the establishment of *G. decoris*. These countries include South Africa, Madagascar, Kenya, Uganda, Eswatini, India, Sri Lanka, Australia (QLD coastline), New Zealand North and South Island, and the United States (California). Cowie et al (2018) calculated the climatic matches for

biological control in the countries where *S. mauritianum* is problematic.<sup>1</sup> Most of the regions with suitable conditions according to our study would also present a good climatic match. However, there are some exceptions. The Gauteng province (South Africa) and the state of California (United States), have the lower climatic match percentages, but in our models have suitable conditions. On the other hand, New South Wales and Victoria coastlines (Australia), New Caledonia and the state of Florida (United States), have high climatic match percentages but in our models have unsuitable conditions.

The projected ENM (2050) suggests that regions experiencing problematic *S. mauritianum* invasions may support the establishment of *G. decoris*. Considering the results of this study, *G. decoris* has good prospects as a biological control agent both in the present and in the future. Its implementation could be considered in affected countries where it has not yet been released.

We have discussed some situations in which the results of our ENM should be cautiously interpreted in the context of models built for a biological control agent as they might affect their success and efficiency. These situations include models that might be overfitted, parameters not considered by the models and ENMs built for biological control agents whose abilities to adapt to different climatic conditions are not really known, among other possible situations. Therefore, a good or bad climatic match should always be interpreted with caution and contrasted with other lines of evidence. Hence, further efforts to understand relevant aspects of the biology and ecology of *G. decoris* are necessary to understand its potential as a biological control agent.



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## 7. TABLES

**Table 1.** Information on the climatic variables in the ecoregions occupied by *Gargaphia decoris* in the native range and in the NITF ecoregion (New Zealand). Variables in grey and with an asterisk are variables with high discrepancy.

## 8. FIGURE LEGENDS

**Fig. 1** Suitability in Africa for the areas where *Solanum mauritianum* is considered a problematic invader for the establishment of *Gargaphia decoris*. a-b. South Africa, Madagascar, Mauritius and Reunion islands; c-d. Uganda and Kenya. Red areas represent suitable conditions with climatic conditions not outside the native range; orange areas suitable conditions with novel climatic conditions; blue dots confirmed records, green pentagons unconfirmed records, cross-hatching indicates areas where *Solanum mauritianum* is considered a problematic invader. a&c. Models trained with native records (a with detail of the two confirmed records outside the red area); b&d. Models trained with the full dataset

**Fig. 2** Suitability in Australiasia for the areas where *Solanum mauritianum* is considered a problematic invader for the establishment of *Gargaphia decoris*. a-b Australia, New Zealand and Papua New Guinea. c-d India and Sri Lanka. Red areas represent suitable conditions with climatic conditions not outside the native range; orange areas suitable conditions with novel climatic conditions; blue dots confirmed records, cross-hatching

indicates areas where *Solanum mauritianum* is considered a problematic invader. a&c.

Models trained with native records; b&d. Models trained with the full dataset

**Fig. 3** Suitability of North America for the establishment of *Gargaphia decoris*. Red areas represent suitable conditions with climatic conditions not outside the native range; orange areas suitable conditions with novel climatic conditions; cross-hatching indicates areas where *Solanum mauritianum* is considered a problematic invader. a. Model trained with native records; b. Model trained with the full dataset

**Fig. 4** Boxplots representing variables with high discrepancy of the ecoregions occupied by *Gargaphia decoris* in the native range of distribution and the NITF ecoregion. Boxes represent the upper and lower 25% of the scores and are separated by the median, whiskers indicate the variability outside the upper and lower quartiles. Dots indicate values for the established populations in New Zealand.

**Fig. 5** Consensus maps (period 2050), on the left using RCP 2.6, on the right using RCP 8.5. The darker the colour, the more GCM models predict novel climate conditions for the area. a-b. Africa, Asia, Oceania and Europe. c-d. Central and North America.

## 8. SUPPORTING INFORMATION

Appendix A: Distributional information

Appendix B: Bioclimatic variable

Appendix C: Native range of distribution in light green, calibration area of the ENM trained with the native dataset in dark green.

Appendix D: Calibration area of the ENM trained with the full dataset in dark green.

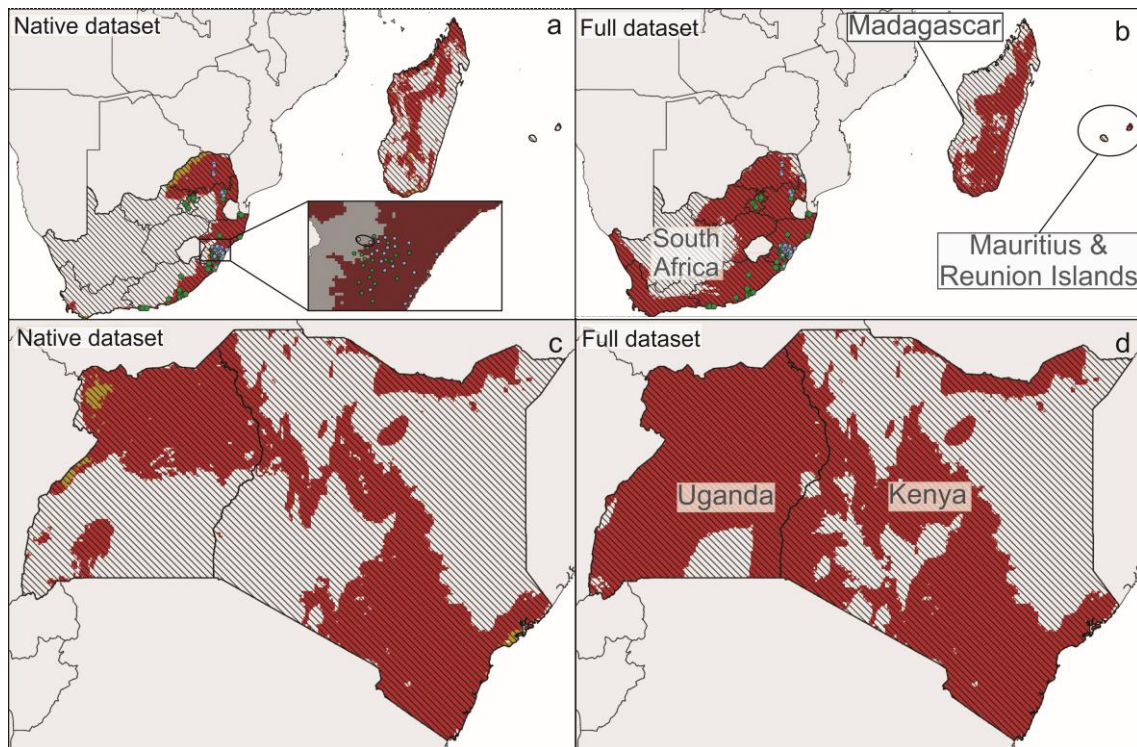
Appendix E: Results of the PCA used to train the ENM built with the native dataset.

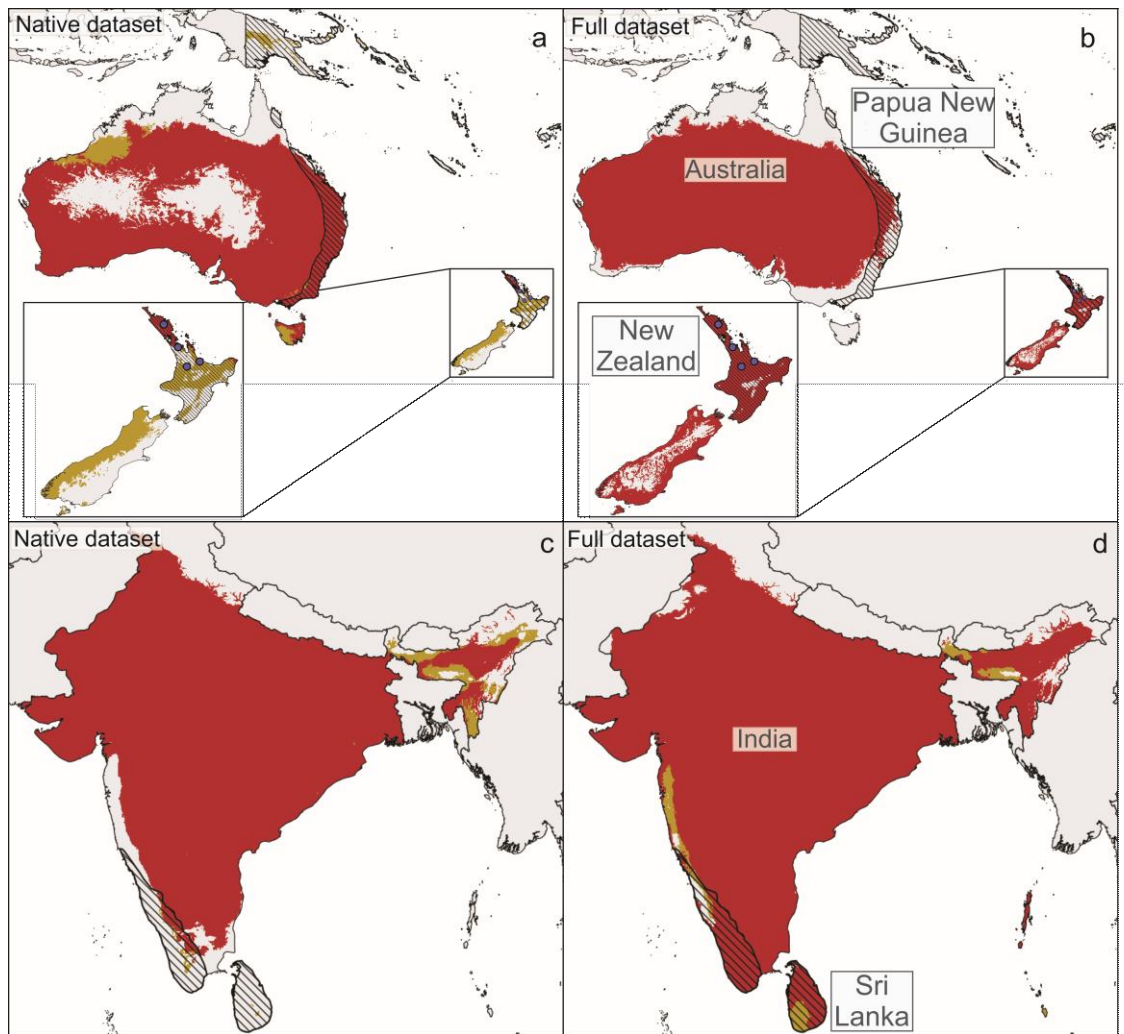
Appendix F: Results of the PCA used to train the ENM built with the full dataset.

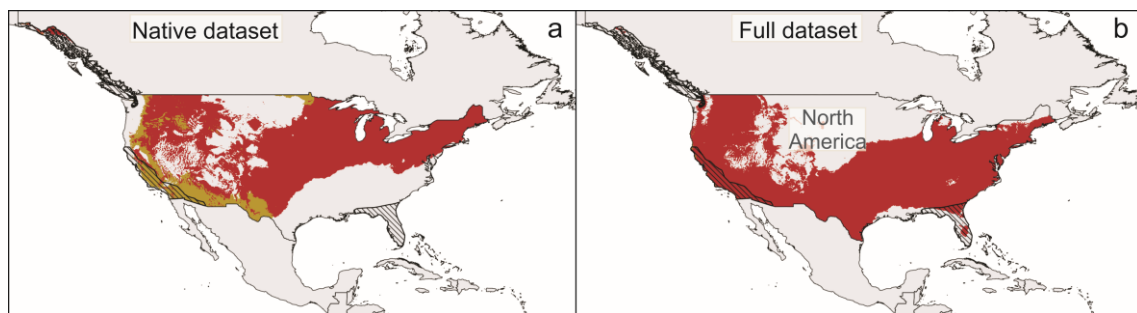
Appendix G: Model evaluation information, Table I: native dataset, Table II: full dataset. Best model performances for the criteria considered are in red, orange and yellow (in decreasing order of performance). The chosen settings are in blue.

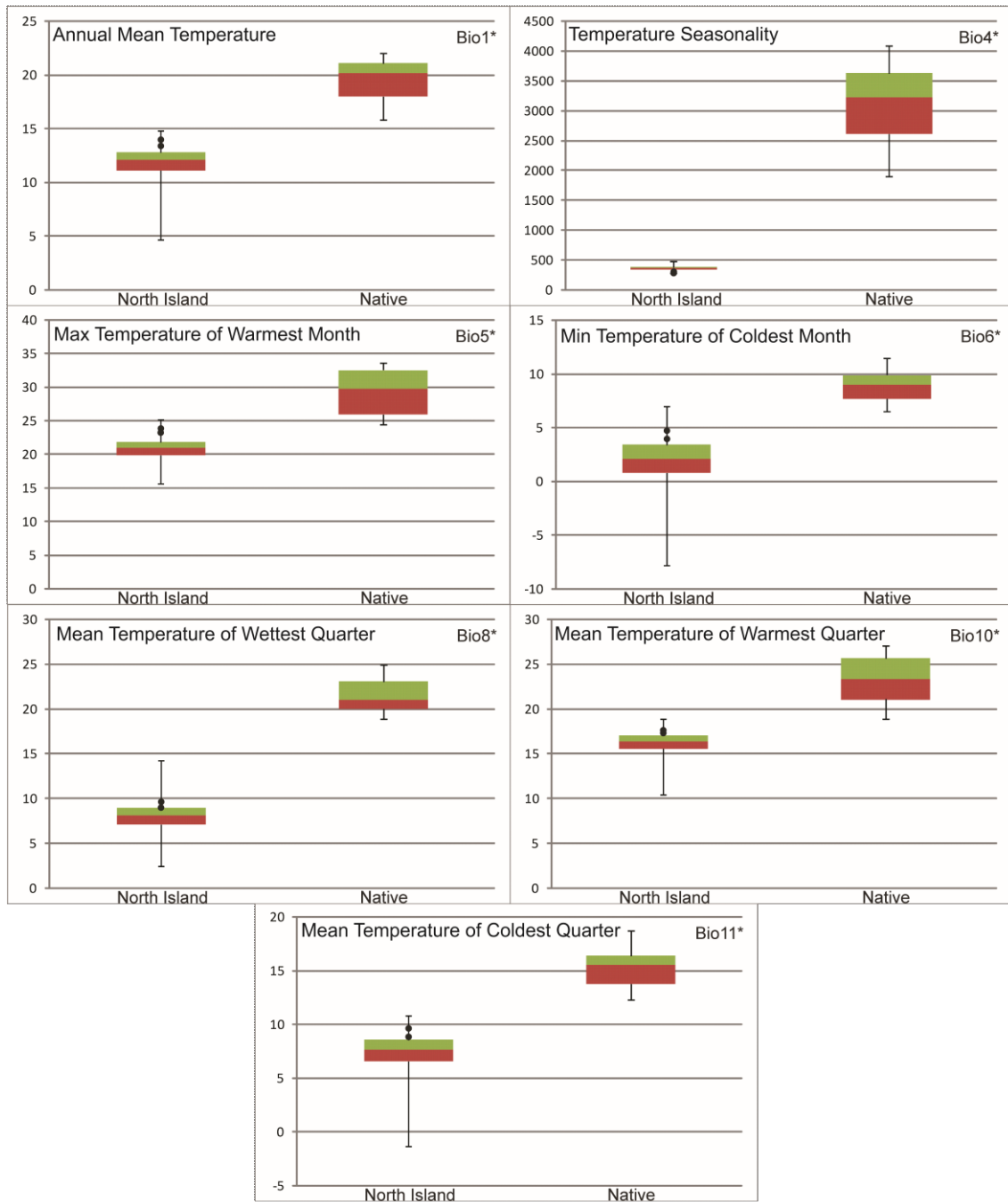
Appendix H: Boxplots representing variables without high discrepancy.

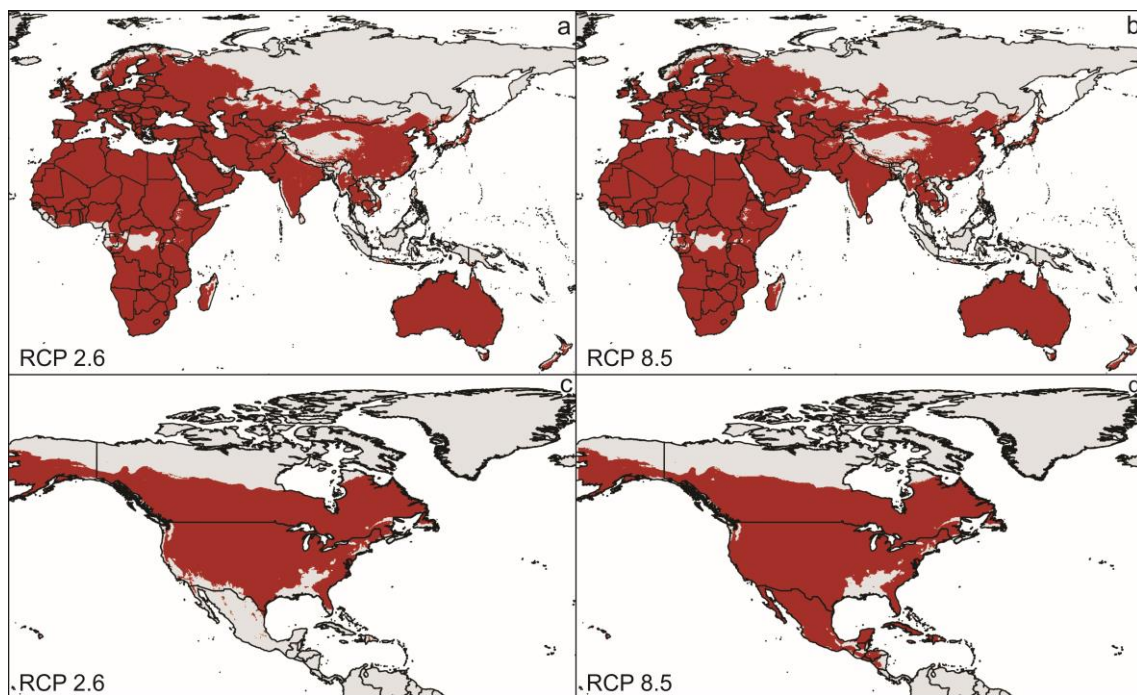












*Solanum mauritianum* is an invasive weed that is causing serious problems in many regions of the world. Through ecological niche models prospects of *Gargaphia decoris* as biocontrol agent are explored.

