

Using Maximum Entropy Algorithm to Analyze Changes in the Distribution of the Stingless Bees, *Tetragonisca angustula* (Latreille, 1811), in Response to Future Climatic Conditions

Hossam F. ABOU-SHAARA

Department of Plant Protection, Faculty of Agriculture, Damanhour University, Damanhour, 22516, EGYPT

e-mail: hossam.farag@agr.dmu.edu.eg

ORCID ID: 0000-0001-7208-6526

ABSTRACT

The stingless bees, *Tetragonisca angustula* (Latreille, 1811), have a large habitat distribution across Central and South America. These bees are considered beneficial for plant pollination and honey production. This study aims to identify the significant environmental factors affecting the distribution of these bees and the potential effects of future climatic conditions on their distribution. To achieve this objective, the study employed a modeling approach based on MaxEnt, GIS, and DIVA-GIS, using six environmental variables based on temperature and precipitation, and two future climate models for 2050: The Beijing Climate Center Climate System Model (BCC-CSM2-MR) and model Earth System Model2 (CMCC-ESM2). The model's performance was high, as the area under the curve was 0.965 ± 0.003 , and the true skill statistic was 0.64, indicating the accuracy of the outputs. The results revealed a high restriction of these bees to their native distribution and the suitability of some regions outside their native range. The study found annual precipitation to be highly important for *T. angustula* and suggests a limited potential invasion to other regions in the near future.

Keywords: MaxEnt, modeling, GIS, meliponiculture, climate change.

INTRODUCTION

The stingless bees are generally important for pollination and meliponiculture, especially in tropical communities (Roubik, 2022). The species *Tetragonisca angustula* (Latreille, 1811) (Hymenoptera: Apidae) can be found in parts of Mexico, Central, and South America up to Argentina (Batista, Ramalho, & Soares, 2003). This species is small in size and consists of two subspecies: *T. angustula fiebrigi* and *T. angustula angustula* (Wittmann, 1985; Proni & Hebling, 1996; Koling & Moretto, 2010; Francisco Santiago, Brito, Oldroyd, & Arias, 2014) with high genetic overlap between them (Castanheira & Contel, 2005). Its nests are small with a clear division of labor as the nest contains queen, workers, and forager bees (Van Veen & Sommeijer, 2000; Prato & Soares, 2013; Valadares, Vieira, Santos do Nascimento, & Sandoz, 2022). Although their ability to defend their nest in a well-organized manner, they do not sting (Wittmann, Radtke, Zeil, Lübke, & Francke, 1990; Grüter, Kärcher, & Ratnieks, 2011; Shackleton, Alves, & Ratnieks, 2018; Baudier et al., 2019). So, nests of this bee species can be kept in home gardens and inhabitant areas without problems. In fact, its ability to nest in urban areas has been noted (Velez-Ruiz, Gonzalez, & Engel, 2013). Especially this species is frequently swarming, and can nest at different locations such as pre-existing cavities in tree trunks, walls, and soil (Batista et al, 2003). This species reproduces using swarming in a similar way to the western honey bees, *Apis mellifera*, which starts with finding a new nesting site by scout bees, and there is a nuptial flight for virgin queens (Van Veen & Sommeijer, 2000). Additionally, they use surrounding landmarks to locate the nest site (Zeil & Wittmann, 1993).

Indeed, several studies have been conducted on this bee species to understand its learning behavior (Mc Cabe & Farina, 2010), foraging behavior (Velez-Ruiz et al, 2013), and chemosensory reception (Balbuena & Farina, 2020). *T. angustula* can visit various plants, which reflects its significance as a pollinator in tropical areas (Iwama & Melhem, 1979; Almeida Braga et al., 2012; de Novais, Garcêz, Absy, & dos Santos, 2015). These floral resources include several plant families, such as Fabaceae, Chenopodiaceae, and Araliaceae (Saravia-Nava, Niemeyer, & Pinto, 2018), Solanaceae, and Bignoniaceae (Urquizo et al., 2022). Besides, the honey from *T. angustula* species holds special significance for folk medicine in various areas, such as Colombia, despite the low amount of honey from its nests (Torres, Garedew, Schmolz, & Lamprecht, 2004). Due to the importance of this honey, its characteristics have been studied to evaluate its quality (Alves et al., 2012; Braghini et al., 2017). Therefore, this bee species has high economic importance in the tropics.

Considering the potential impact of climate change on living organisms, including changes in their distribution (Villemant et al., 2011; Mulieri & Patitucci, 2019; Hosni, Nasser, Al-Ashaal, Rady, Kenawy, 2020; Abou-Shaara et al., 2021; Jamal et al., 2021; Abou-Shaara & Al-Khalaf, 2022; Abou-Shaara et al, 2022), it is important to test the hypothesis of potential changes in the distribution of *T. angustula* under future climate conditions. This bee species may expand its habitat to new areas in north or South America due to these changes. Insects have also shown the ability to invade regions far from their original habitat, such as the small hive beetles *Aethina tumida* Murray

1867 (Family: Nitidulidae), which invaded the USA, Australia, and some parts of Asia despite originating in sub-Saharan Africa (Elzen et al., 1999; Hood, 2004; Neumann & Elzen, 2004; Neumann, Pettis, & Schäfer, 2016; Lee et al., 2017). Therefore, understanding the global distribution of *T. angustula* is crucial. Additionally, due to the economic importance of *T. angustula*, intentional introduction to new areas may occur, as seen with the introduction of the Brazilian stingless bee *Plebeia emerina* to Palo Alto, California, USA in 1948 (dos Santos, Acosta, Ramos, Timm, & Blochtein, 2022).

One common method to understand how climate change affects the distribution of specific organisms is through modeling approaches, such as MaxEnt (Guisan & Thuiller, 2005; Phillips, Anderson, & Schapire, 2006; Wei, Wang, Hou, Wang, & Wu, 2018; Hosni et al, 2020; Jamal et al., 2021). This involves analyzing occurrence records and environmental variables from available online sources (Phillips, 2017; Hosni et al, 2020; Abou-Shaara, Amiri, & Parys, 2022) and using other software, such as geographical information system (GIS) and DIVA-GIS (Brito, Acosta, Álvares, & Cuzin, 2009; Kalboussi & Achour, 2018; Hosni et al, 2020; Abou-Shaara & Darwish, 2021; Abou-Shaara et al., 2021; Jamal et al., 2021; Leanza, Valenti, D'Urso, & Arcidiacono, 2022; Abou-Shaara et al, 2022). Therefore, this study aims to use MaxEnt, GIS, and DIVA-GIS to identify potential changes in the global distribution of *T. angustula* under different climate conditions. Additionally, this study identifies the key environmental factors that shape the distribution of this bee species based on the modeling analysis.

METHODS

Occurrence data

The occurrence data used in this study were obtained from the Global Biodiversity Information Facility (2022) and included records from approximately 45 different sources, such as Insecta of Costa Rica (INBio) and iNaturalist. A total of 8094 occurrences were initially screened, with only those based on human observations from 2005 to 2022 being retained. Additionally, DIVA-GIS 7.5.0 (<https://www.diva-gis.org>) was utilized to filter the occurrences and remove any duplicates or inaccuracies. Furthermore, the spatial distribution of the data points was tested to ensure that those points are apart from each other at least 1 km. Ultimately, a total of 400 records were included in the analysis, which revealed that the distribution of *T. angustula* is primarily limited to Central and South America (Fig. 1).

Environmental variables

Environmental variables at 5 km² of worldclim.org (WorldClim version 2.1, Fick and Hijmans, 2017) were used. First, 4 variables (bio 8, bio 9, bio 18 and bio 19) from the available 19 variables were excluded. These particular 4 variables have known spatial issues (Samy et al., 2016; Hosni et al, 2020; Booth, 2022); especially the potential distribution is analyzed on the global scale. Three variables bio1, bio2, and bio 12 were considered as highly important because all the other variables were derived from them. Then, the remaining variables were subjected to other analyses

to find out the most important variables (Hosni et al, 2020; Abou-Shaara et al., 2021). So, the highly correlated variables were tested using a tool of Species Distribution Modeling (SDM) in the ArcGIS 10.8. Also, the Jackknife test using MaxEnt v 3.4.1 (Phillips, Dudík, Schapire, 2020) was considered to find out the variables with the highest regularized training gain values > 1.6 (Fig. 2). Finally, six variables (Table 1) were considered in the analysis to present the historic/current environmental conditions (from 1970 to 2000).

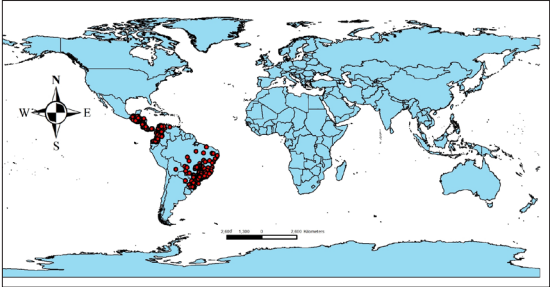


Figure 1. The distribution range of the stingless bees, *Tetragonisca angustula*, (represented by dots) on the global level.

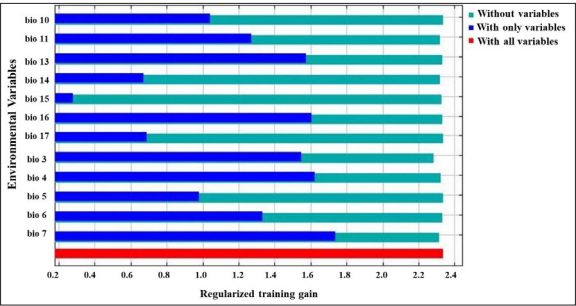


Figure 2. Jackknife test of regularized training gain for environmental variables. The highest variables are bio 7 (Temperature annual range), bio 4 (Temperature seasonality), and bio 16 (Precipitation of wettest quarter) in the regularized training gain.

Table 1. The environmental variables used in the analysis.

Variable	Abbreviation
Annual mean temperature (°C)	bio1
Mean diurnal range (Mean of monthly (max temp - min temp)) (°C)	bio2
Temperature seasonality (=standard deviation ×100)	bio4
Temperature annual range (°C)	bio7
Annual precipitation (mm)	bio12
Precipitation of wettest quarter (mm)	bio16

The same sets of variables were utilized to examine the potential distribution under future climate scenarios for the year 2050 (2041-2060). The study considered two future models under the shared socio-economic pathway 245 (ssp245) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2016): model 1) The Beijing Climate Center Climate System Model (BCC-CSM2-MR) and model 2) Earth System Model2 (CMCC-ESM2) (Table 2).

Using Maximum Entropy Algorithm to Analyze Changes in the Distribution

Table 2. Links for the used datasets in the model.

Datasets	Source
The bioclimatic factors	https://www.worldclim.org/data/worldclim21.html#
Details about the 19 bioclimatic variables	https://www.worldclim.org/data/bioclim.html
The future models (CMIP6)	https://www.worldclim.org/data/cmip6/cmip6climate.html
BCC-CSM2-MR (Institution ID: BCC) ssp245 (2.5 minutes = 5 Km2)	https://www.worldclim.org/data/cmip6/cmip6_clim2.5m.html
CMCC-ESM2 (Institution ID: CMCC) ssp245 (2.5 minutes = 5 Km2)	https://www.worldclim.org/data/cmip6/cmip6_clim2.5m.html

Modeling using MaxEnt

To examine the global distribution of *T. angustula*, the selected environmental variables were prepared using ArcGIS 10.8 to cover the world map with the GCS_WGS_1984 coordinate system. MaxEnt v 3.4.1 (Phillips et al, 2020) was utilized to analyze the potential distribution with modeling parameters previously described (Phillips, 2017; Jamal et al., 2021; Abou-Shaara et al, 2022). The model used 266 presence records for training and 134 for testing (with a random test percentage of 25%). Additionally, 10266 points were used to determine the Maxent distribution (background points and presence points). The model settings included linear/quadratic/product regularization values of 0.050, categorical regularization value of 0.250, threshold of 1.000, hinge of 0.500, cumulative output format, and 3 replicates.

Analysis using the ArcGIS

The maps generated by MaxEnt were further analyzed using ArcGIS 10.8 (Hosni et al, 2020; Abou-Shaara et al., 2021; Abou-Shaara & Darwish, 2021; Jamal et al., 2021; Abou-Shaara et al, 2022). The final maps were categorized into four classes: Rarely suitable (0-1), Moderately suitable (1-20), Highly suitable (20-50), and Very highly suitable (50-100) (Phillips, 2017; Jamal et al., 2021; Abou-Shaara et al, 2022). Spatial analysis tools such as Raster calculator and Reclassify were used to present the final maps. For future conditions, we obtained two maps: one for BCC-CSM2-MR and the other for CMCC-ESM2. The average of the two maps was then calculated to obtain a single map for both models.

Distribution modeling

To validate the results from MaxEnt analysis, the options in DIVA-GIS 7.5 (<https://www.diva-gis.org/download>) were also used to confirm the outputs from the MaxEnt analysis. So, the envelope option (modeling/distribution modeling/envelope with percentile value of 0.025) was used to gain insights into the relationship between distribution of *T. angustula* and two key environmental variables, temperature, and precipitation. The analysis was conducted for both historic/current conditions (~1950-2000) and future conditions (~ 2100) using CCM3 model (Govindasamy, Duffy, & Coquard, 2003) at 5 km². For more information about these climatic models, please refer to <https://www.diva-gis.org/climate>.

Contribution percentages and model performance

The study presented the contribution percentage of each variable in the model and evaluated the model's performance based on the obtained outcomes (Phillips,

2017; Hosni et al, 2020; Abou-Shaara et al., 2021; Abou-Shaara & Darwish, 2021; Jamal et al., 2021; Abou-Shaara et al, 2022). The performance evaluation included values of area under the curve (AUC) of the receiver operating characteristics (ROC), rates of omission/commission, and jackknife test for the variables that contributed to the analysis. Additionally, the study calculated the True Skill Statistic (TSS) to assess the model's performance.

RESULTS

Contribution percentages and model performance

The environmental variables contributed in the model as follows: 55.4% for bio 12, 15.2% for bio 4, 14.2% for bio 16, 7.2% for bio 1, 5.4% for bio 7, and 2.6% for bio 2. The annual precipitation showed the highest impact on the suitability of *T. angustula* habitat, followed by temperature seasonality and precipitation of the wettest quarter, based on the used model. Other temperature-related variables represented 15.2%. The model's area under the curve (AUC) was high (0.965 ± 0.003) as shown in Figure 3, and the omission rate was close to the predicted omission (Fig. 4). The true skill statistic (TSS) was acceptable (0.64). These parameters indicate the accuracy of the used model in the study. Furthermore, the AUC for all the used variables was higher than 0.88 (Fig. 5). The ideal range for each variable for the occurrence of *T. angustula* was 15 to 28°C, with the most perfect range being 20 to 25°C for bio 1, 7 to 15°C, with the most perfect range being 10 to 12°C for bio 2, <500 for bio 4, 10 to 20°C for bio 7, and perfectly from 3000 to 5000 mm for bio 12, and perfectly from 1000 to 2000 mm for bio 16 (Fig. 6).

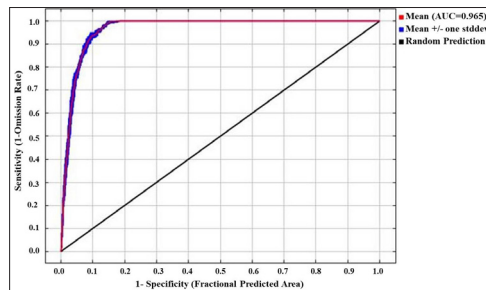


Figure 3. The receiver operating characteristic (ROC) curve for the data used in the model.

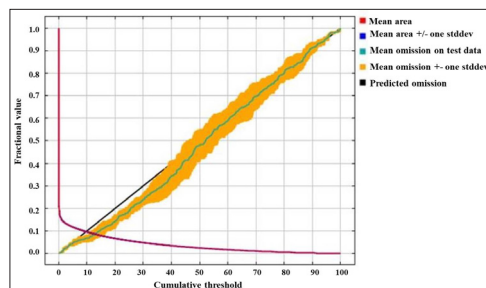


Figure 4. The average omission and predicated area for *Tetragonisca angustula*.

Using Maximum Entropy Algorithm to Analyze Changes in the Distribution

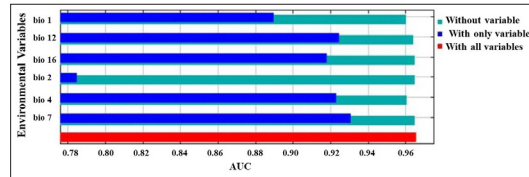


Figure 5. Jackknife test using area under the curve (AUC) on test data for the used environmental variables. bio 1: Annual mean temperature, bio 2: Mean diurnal range, bio 4: Temperature seasonality, bio 7: Temperature annual range, bio 12: Annual precipitation, and bio 16: Precipitation of wettest quarter.

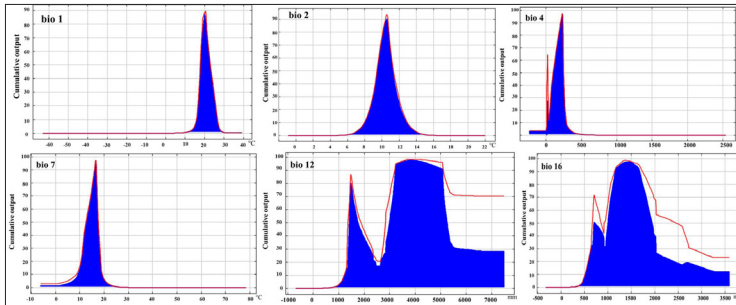


Figure 6. Response curve for bio1: annual mean temperature (°C), bio2: mean diurnal range (°C), bio 4: temperature seasonality (°C), bio 7: temperature annual range (°C), bio 12: annual precipitation (mm), and bio 16: precipitation of wettest quarter (mm).

Historic/current distribution of *Tetragonisca angustula*

The map (Fig. 7) illustrates that the highly suitable areas for *T. angustula* are primarily limited to Central and South America, with some regions in central Africa, Madagascar, and specific regions in south Asia. These areas in Central and South America align with the current distribution of these bees. The areas classified as highly suitable include Central and South America, south Florida, some regions in central Africa, Madagascar, coastal regions of India, Sri Lanka, specific regions in south Asia, coastal parts of Australia, and New Zealand. The moderately suitable areas include Central and South America, Florida, coastal regions of Louisiana and Mississippi, some parts in central Africa, Madagascar, coastal regions of India, Sri Lanka, some regions in south Asia, coastal parts of Australia, and specific regions in New Zealand. All other regions are considered rarely suitable for *T. angustula*.

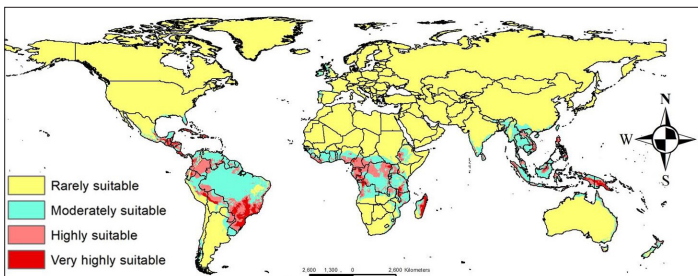


Figure 7. Map showing historic/current habitat suitable for *Tetragonisca angustula*.

Future distribution of *Tetragonisca angustula*

The map for the future distribution (Fig. 8) shows the high ability of *T. angustula* to maintain its habitat regardless of climatic changes. Still some areas outside its original range in Africa, and South Asia have potentiality to be very highly and highly suitable for these bees. With focus on north and south America (Fig. 9), still areas in south Florida showed high suitability for these bees in addition to some moderately suitable areas in south of Louisiana and Mississippi. The map for future conditions does not support any wide invasion by this bee species to nearby areas.

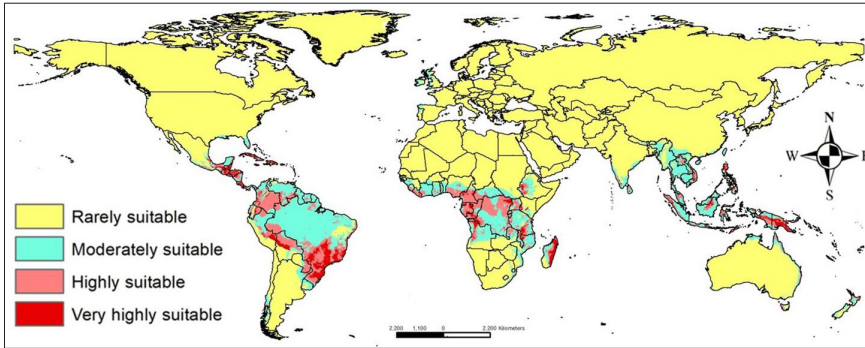


Figure 8. Map showing future habitat suitable for *Tetragonisca angustula* during 2050. The map presents the average of two future models (BCC-CSM2-MR and CMCC-ESM2).

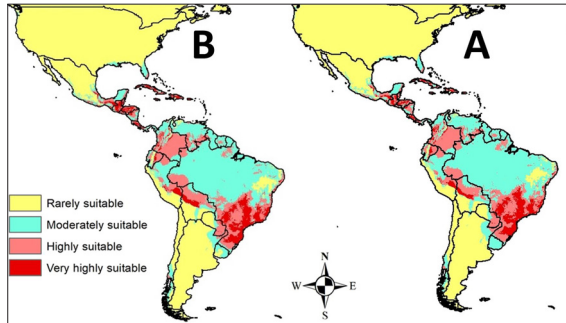


Figure 9. Map showing future habitat suitable for *Tetragonisca angustula* during 2050 in north and south America. The map presents the average of two future models (BCC-CSM2-MR and CMCC-ESM2).

Distribution modeling

The distribution modeling using the envelope option based on two key variables, annual precipitation and annual mean temperature, is presented in Figure 10. This test shows that *T. angustula* is suitable for warm environments with an annual mean temperature ranging from 17-27°C and high annual precipitation between 1000 to 5000 mm. The envelope test supports the outputs from the response curves obtained from the MaxEnt analysis. Furthermore, the outcomes from the envelope test (Fig. 11) are consistent with the results from MaxEnt, particularly in the case of temperature seasonality, which showed a suitability value <500, similar to that shown by the response curve.

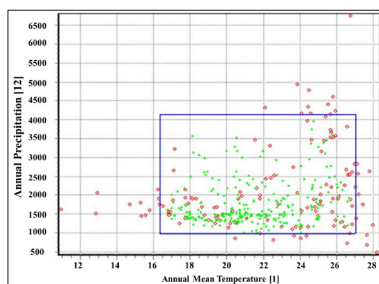


Figure 10. The distribution modelling presents an envelope with two variables: annual precipitation and annual mean temperature. The green points fall within the envelopes for the two climate variables while those fall outside one or more envelopes are shown in red.

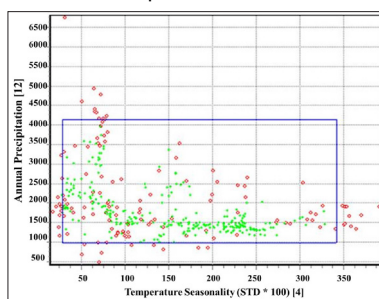


Figure 11. The distribution modelling presents an envelope with two variables: annual precipitation and temperature seasonality. The green points fall within the envelopes for the two climate variables while those fall outside one or more envelopes are shown in red.

The environmental envelope based on future climate conditions (Fig. 12) suggests that the distribution of this bees in its current habitat will require adaption to high temperature especially, annual mean temperature increased by 1-2°C than historic/current conditions. Meanwhile, this bee species will require the same amount of rainfall of the current conditions (annual mean precipitation ranges from 1000 to 5000 mm) to still adapt to its habitat. So, the potential habitat loss in the future could happen due to extremes of these factors: heat stress and the low rainfall amounts.

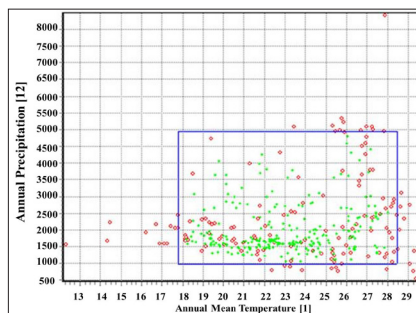


Figure 12. The distribution modelling presents an envelope with two variables in the future (~ 2100): annual precipitation and annual mean temperature. The green points fall within the envelopes for the two climate variables while those fall outside one or more envelopes are shown in red.

DISCUSSION

The performance of the model was high as value of area under the curve (AUC) was close to 0.965 which more than 0.75 (Swets, 1988; Mulieri & Patitucci, 2019; Hosni et al, 2020; Abou-Shaara et al., 2021; Abou-Shaara & Darwish, 2021). Additionally, the acceptable value for TSS is equal or above 0.5 (Hosni et al, 2020), in the model such value was 0.64, which indicates the acceptable performance of the model. The contribution of the used environmental variables in the model showed high importance of precipitation for the distribution of *T. angustula* followed by temperature. The highest three variables contributed in the model were annual precipitation, temperature seasonality and precipitation of the wettest quarter. This can help in explaining the distribution of *T. angustula* in the tropics where rainfall and high temperature are available year-round. The distribution of *T. angustula* requires perfectly high annual precipitation from 3000-5000 mm, and annual mean temperature most preferably between 20-25°C.

The results for the historic/current conditions are fit with the actual distribution of *T. angustula* in Central and South America from Mexico up to Argentina. Also, the analysis showed the possibility of some specific areas in Central Africa and South Asia to be very highly suitable for *T. angustula*. Also, some areas in the south of USA were classified as highly suitable for *T. angustula* as well as many areas mainly in central Africa, and South Asia. It is expected that these specific areas have rainfall amounts and temperatures suitable for the distribution of *T. angustula*. Although *T. angustula* is not currently occur outside its native range, but those areas are expected to be ready for hosting it if arrived to them. It is known that some other stingless bee species occur in Africa such as *Hypotrigona gribodoi* Magretti (Hymenoptera: Apidae) (Byarugaba 2004; Eardley, Gikungu, & Schwarz, 2009; Eardley & Urban 2010; Pauly & Hora, 2013) and *Meliponula ferruginea* which is source of honey (Popova et al., 2021) and in Australia such as *Tetragonula carbonaria* (Hymenoptera: Apidae) (Smith, Heard, Beekman, & Gloag, 2017).

In fact, *T. angustula* has the ability to compete with other bee species for nesting, particularly in recovering forests (Batista et al, 2003). Therefore, introducing *T. angustula* to areas where other stingless bee species and established pollinators exist could lead to biological imbalances in those areas. However, in areas classified as very highly suitable to moderately suitable and lacking in pollinators, introducing *T. angustula* could help solve pollination problems and provide economic benefits. However, it should be noted that *T. angustula* may not be able to establish itself in the long term in new environments, as was the case with *P. emerina* when introduced to California, USA (dos Santos, Acosta, Ramos, Timm, & Blochtein, 2022). Thus, any introduction strategies should be well-planned and thoroughly studied.

Under future conditions during 2050, the model predicts that *T. angustula* will maintain its current historic distribution without observable changes, and no changes are expected in very highly to moderately suitable areas. The model predicts that the nearest areas to be invaded by *T. angustula* are located in the extreme south of the

USA, especially in the south of Louisiana and Mississippi, and Florida. However, this bee species is not expected to invade other areas in Africa or Asia unless introduced passively or intentionally by pollination experts or researchers. If *T. angustula* were to invade the USA, it is not expected to pose a high threat to other pollinators, especially since stingless bees are not native to the USA. However, its ability to establish itself for long periods is uncertain, as *T. angustula* has shown susceptibility to pesticides (Quiroga-Murcia, Zotti, de Polan a, & Pech-Pech, 2017) and can be impacted by their massive use in new areas. Additionally, *T. angustula* can inhabit urban areas (Fierro, Cruz-Lopez, Sanchez, Villanueva-Gutierrez, & Vandame, 2012), which could be problematic for its establishment in new environments due to human removal. The used model does not support the wide invasion of this bee species to new areas. A study on another insect species, *Plecia nearctica* (Diptera, Bibionidae), did not show a wide distribution inside the USA in the near future compared to its current distribution (Abou-Shaara et al, 2022). In contrast, other modeling studies supported the invasion of some insects to new regions, such as small hive beetles (Jamal et al., 2021), large hive beetles (Abou-Shaara et al., 2021), and the Asian hornet (Abou-Shaara & Al-Khalaf, 2022). The variations between these species are mainly due to their environmental needs in terms of temperature and precipitation.

The distribution modeling supports the outputs from MaxEnt and indicates that *T. angustula* requires an annual mean temperature ranging from 17-27 C, coupled with high annual precipitation between 1000 to 5000 mm. In line with this, Proni & Hebling (1996) found that *T. angustula* can maintain brood temperature at 28.6 C during winter (with air temperature 10.5  - 24.4 C) and 31.6 C during summer (with air temperature 20.1 - 36.3 C), indicating the species' preference for warm weather conditions. *T. angustula* has also been shown to forage under high air temperature in urban environments (Velez-Ruiz et al, 2013), further supporting its ability to adapt to warm weather conditions. Moreover, Malerbo-Souza & Halak (2016) found that *T. angustula* can forage in temperatures as low as 17.8 C without collecting pollen, while those with pollens can forage at 19.6 C, indicating the species' adaptation to tropical conditions. However, foraging behavior is not impacted by relative humidity (Malerbo-Souza & Halak, 2016), similar to honey bees (Abou-Shaara, 2014; Abou-Shaara, Owayss, Ibrahim, & Basuny, 2017). The distribution modeling suggests that *T. angustula* needs to adapt to higher air temperature to maintain its current distribution under future conditions. In contrast, any low rainfall amounts in the future could limit the distribution of *T. angustula*, which requires high annual precipitation.

Beside the economic value of *T. angustula* as source of honey and as pollinator to many plants, it can be used in greenhouse as well. A study showed *T. angustula* is an effective strawberry pollinator in greenhouse causing significant improvement in the crop (Malagodi-Braga & Kleinert, 2004). This is advantageous over honey bees, which are not as effective in greenhouse settings. Considering the potential impact of future climatic conditions and global warming, it is likely that *T. angustula* will continue to play a significant role as a plant pollinator, both within and outside of its current distribution range.

CONCLUSION

This study modeled the distribution of *Tetragonisca angustula* under various environmental conditions. The species currently has multiple cryptic species within its geographical range; thus, the modeling results are applicable to all of them. The model suggests that *T. angustula* is unlikely to spread widely beyond its original range in central and South America. However, some areas in the southern USA, such as Florida, Louisiana, and Mississippi, could be potential hotspots for the species. The model also identifies certain areas in Africa and South Asia that could be suitable for *T. angustula* if introduced. Moreover, the model highlights the importance of high annual precipitation for the distribution of *T. angustula*. The model predicts that *T. angustula* will maintain its original distribution in 2050, but the species will require high adaptability to heat stress and potential low rainfall amounts in the future. Therefore, further studies on thermal biology of *T. angustula* and methods to increase its adaptability to harsh environmental conditions are recommended. *T. angustula* has shown potential as a greenhouse pollinator, which is advantageous over *Apis mellifera* in such settings. Thus, introducing and maintaining *T. angustula* in areas with few pollinators or pollination problems could be a potential solution to address the decline of pollinators. Additional studies on *T. angustula* as a pollinator for greenhouse crops are also advised. Finally, the study recommends conducting more modeling studies using different time periods and future climate scenarios.

REFERENCES

- Abou-Shaara, H.F. (2014). The foraging behaviour of honey bees, *Apis mellifera*: a review. *Veterinari medicina*, 59(1), 1-10.
- Abou-Shaara, H.F. & Al-Khalaf, A.A. (2022). Using maximum entropy algorithm to analyze current and future distribution of the Asian hornet, *Vespa velutina*, in Europe and North Africa under climate change conditions. *Journal of the Entomological Research Society*, 24(1), 07-21.
- Abou-Shaara, H.F. & Darwish, A.A.E. (2021). Expected prevalence of the facultative parasitoid *Megaselia scalaris* of honey bees in Africa and the Mediterranean region under climate change conditions. *International Journal of Tropical Insect Science*, 41(2), 3137-3145.
- Abou-Shaara, H.F., Alashaal, S.A., Hosni, E.M., Nasser, M.G., Ansari, M.J., & Alharbi, S.A. (2021). Modeling the invasion of the large hive beetle, *Oplostomus fuliginus*, into north Africa and South Europe under a changing climate. *Insects*, 12(4), 1-12.
- Abou-Shaara, H.F., Amiri, E., & Parys, K.A. (2022). Tracking the effects of climate change on the distribution of *Plecia nearctica* (Diptera, Bibionidae) in the USA using MaxEnt and GIS. *Diversity*, 14(8), 690.
- Abou-Shaara, H.F., Owayss, A.A., Ibrahim, Y.Y., & Basuny, N.K. (2017). A review of impacts of temperature and relative humidity on various activities of honey bees. *Insectes sociaux*, 64(1), 455-463.
- Almeida Braga, J., Oliveira Sales, É., Soares Neto, J., Menezes Conde, M., Barth, O. M., & Lorenzon, M.C. (2012). Floral sources to *Tetragonisca angustula* (Hymenoptera: Apidae) and their pollen morphology in a Southeastern Brazilian Atlantic Forest. *Revista de Biología Tropical*, 60, 1491-1501.
- Alves, E.M., Fonseca, A.A.O., dos Santos, P.C., Bitencourt, R.M., Sodré, G.D.S., & de Carvalho, C.A.L. (2012). Physico-chemical and sensorial stability of *Tetragonisca angustula* honey. *Magistra*, 24, 185-193.
- Balbuena, M.S., & Farina, W.M. (2020). Chemosensory reception in the stingless bee *Tetragonisca angustula*. *Journal of Insect Physiology*, 125(2), 104076.

Using Maximum Entropy Algorithm to Analyze Changes in the Distribution

- Batista, M.A., Ramalho, M., & Soares, A.E. (2003). Nesting sites and abundance of Meliponini (Hymenoptera: Apidae) in heterogeneous habitats of the Atlantic Rain Forest, Bahia, Brazil. *Lundiana: International Journal of Biodiversity*, 4(4), 19-23.
- Baudier, K.M., Ostwald, M.M., Grüter, C., Segers, F.H., Roubik, D.W., Pavlic, T.P., ... & Fewell, J.H. (2019). Changing of the guard: mixed specialization and flexibility in nest defense (*Tetragonisca angustula*). *Behavioral Ecology*, 30, 1041-1049.
- Booth, T.H. (2022). Checking bioclimatic variables that combine temperature and precipitation data before their use in species distribution models. *Austral Ecology*, 47(7), 1506-1514.
- Braghini, F., Chiapetti, E., S Júnior, J.F., Mileski, J.P.F., de Oliveira, D.F., Morés, S., ... & Tonial, I.B. (2017). Quality of honeys from honey bee (*Apis mellifera*) and Jataí (*Tetragonisca angustula*) marketed in the micro-region of Francisco Beltrão-PR. *Revista de Ciências Agrárias*, 40(1), 279-289.
- Brito, J.C., Acosta, A.L., Álvares, F., & Cuzin, F. (2009). Biogeography and conservation of taxa from remote regions: An application of ecological-niche based models and GIS to North-African Canids. *Biological Conservation*, 142(12), 3020-3029.
- Byarugaba, D. (2004). Stingless bees (Hymenoptera: Apidae) of Bwindi impenetrable forest, Uganda and Abayanda indigenous knowledge. *International Journal of Tropical Insect Science*, 24(1), 117-121.
- Castanheira, E.B., & Contel, E.P.B. (2005). Geographic variation in *Tetragonisca angustula* (Hymenoptera, Apidae, Meliponinae). *Journal of Apicultural Research*, 44(3), 101-105.
- de Novais, J.S., Garcêz, A.C.A., Absy, M.L., & dos Santos, F.D.A.R. (2015). Comparative pollen spectra of *Tetragonisca angustula* (Apidae, Meliponini) from the Lower Amazon (N Brazil) and caatinga (NE Brazil). *Apidologie*, 46(4), 417-431.
- dos Santos, C.F., Acosta, A.L., Ramos, J.D., Timm, J.M., & Blochtein, B. (2022). Scientific note: a stingless bee species attempting to invade a foreign region. *Apidologie*, 53(3), 1-4.
- Eardley C.D., & Urban, R. (2010). Catalogue of Afrotropical bees (Hymenoptera: Apoidea: Apiformes). *Zootaxa*, 2455(1), 1–548.
- Eardley, C.D., Gikungu, M., & Schwarz, M.P. (2009) Bee conservation in Sub-Saharan Africa and Madagascar: diversity, status and threats. *Apidologie*, 40(3), 355–366.
- Elzen, P.J., Baxter, J.R., Westervelt, D., Randall, C., Delaplane, K.S., Cutts, L., & Wilson, W.T. (1999). Field control and biology studies of a new pest species, *Aethina tumida* Murray (Coleoptera, Nitidulidae), attacking European honey bees in the Western Hemisphere. *Apidologie*, 30(5), 361-366.
- Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E. (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development*, 9(5), 1937-1958.
- Fick, S.E., & Hijmans, R.J. (2017). WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(2), 4302-4315.
- Fierro, M.M., Cruz-Lopez, L., Sanchez, D., Villanueva-Gutierrez, R., & Vandame, R. (2012). Effect of biotic factors on the spatial distribution of stingless bees (Hymenoptera: Apidae, Meliponini) in fragmented neotropical habitats. *Neotropical Entomology*, 41(2), 95-104.
- Francisco, F.O., Santiago, L.R., Brito, R.M., Oldroyd, B.P., & Arias, M.C. (2014). Hybridization and asymmetric introgression between *Tetragonisca angustula* and *Tetragonisca fiebrigi*. *Apidologie*, 45(1), 1-9.
- GBIF (2022). <https://www.gbif.org/occurrence/download/0412234-210914110416597>, (01 August 2022
- Govindasamy, B., Duffy, P.B., & Coquard, J. (2003). High-resolution simulations of global climate, part 2: effects of increased greenhouse gases. *Climate Dynamics*, 21(5), 391-404.
- Grüter, C., Kärcher, M.H., & Ratnieks, F.L.W. (2011). The natural history of nest defence in a stingless bee, *Tetragonisca angustula* (Latreille) (Hymenoptera: Apidae), with two distinct types of entrance guards. *Neotropical entomology*, 40(1), 55-61.
- Guisan, A., & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8(9), 993-1009.

- Hood, W.M. (2004). The small hive beetle, *Aethina tumida*: a review. *Bee world*, 85(3), 51-59.
- Hosni, E.M., Nasser, M.G., Al-Ashaal, S.A., Rady, M.H., & Kenawy, M.A. (2020). Modeling current and future global distribution of *Chrysomya bezziana* under changing climate. *Scientific Reports*, 10, 4947.
- Iwama, S., & Melhem, T.S. (1979). The pollen spectrum of the honey of *Tetragonisca angustula angustula* Latreille (Apidae, Meliponinae). *Apidologie*, 10(3), 275-295.
- Jamal, Z.A., Abou-Shaara, H.F., Qamer, S., Alotaibi, M.A., Khan, K.A., Khan, M.F., Bashir, M.A., Hannan, A., AL-Kahtani, S.N., Taha, E.A., Anjum, S.I., Attaullah, M., Raza, G., & Ansari, M.J. (2021). Future expansion of small hive beetles, *Aethina tumida*, towards North Africa and South Europe based on temperature factors using maximum entropy algorithm. *Journal of King Saud University – Science*, 33(1), 101242.
- Kalboussi, M., & Achour, H. (2018). Modeling the spatial distribution of snake species in northwestern Tunisia using maxi-mum entropy (Maxent) and Geographic Information System (GIS). *Journal of Forestry Research*, 29, 233-245.
- Koling, D.F., & Moretto, G. (2010). Mitochondrial discrimination of stingless bees *Tetragonisca angustula* (Apidae: Meliponini) from Santa Catarina state, Brazil. *Apidologie*, 41(4), 454-462.
- Leanza, P.M., Valenti, F., D'Urso, P.R., & Arcidiacono, C. (2022). A combined MaxEnt and GIS-based methodology to estimate cactus pear biomass distribution: application to an area of southern Italy. *Biofuels, Bioproducts and Biorefining*, 16(1), 54-67.
- Lee, S., Hong, K.J., Cho, Y.S., Choi, Y.S., Yoo, M.S., & Lee, S. (2017). Review of the subgenus *Aethina* Erichson s. str. (Coleoptera: Nitidulidae: Nitidulinae) in Korea, reporting recent invasion of small hive beetle, *Aethina tumida*. *Journal of Asia-Pacific Entomology*, 20(2), 553-558.
- Malagodi-Braga, K.S., & Kleinert, A.D.M.P. (2004). Could *Tetragonisca angustula* Latreille (Apinae, Meliponini) be effective as strawberry pollinator in greenhouses?. *Australian Journal of Agricultural Research*, 55(7), 771-773.
- Malerbo-Souza, D.T., & Halak, A.L. (2016). Flight activity of stingless bees *Tetragonisca angustula* (Hymenoptera: Apidae: Meliponini) during in the year. *Entomotropica*, 31(39), 319-331.
- Mc Cabe, S.I., & Farina, W.M. (2010). Olfactory learning in the stingless bee *Tetragonisca angustula* (Hymenoptera, Apidae, Meliponini). *Journal of Comparative Physiology A*, 196(7), 481-490.
- Mulieri, P.R. & Patitucci, L.D. (2019). Using ecological niche models to describe the geographical distribution of the myia-sis-causing *Cochliomyia hominivorax* (Diptera: Calliphoridae) in southern South America. *Parasitology Research*, 118, 1077-1086.
- Neumann, P., & Elzen, P.J. (2004). The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): Gaps in our knowledge of an invasive species. *Apidologie*, 35(3), 229-247.
- Neumann, P., Pettis, J.S., & Schäfer, M.O. (2016). Quo vadis *Aethina tumida*? Biology and control of small hive beetles. *Apidologie*, 47(3), 427-466.
- Pauly, A., & Hora, Z.A. (2013). Apini and Meliponini from Ethiopia (Hymenoptera: Apoidea: Apidae: Apinae). *Belgian Journal of Entomology*, 16, 1-35.
- Phillips S.J., Dudík M., & Schapire, R.E. (2020). Maxent software for modeling species niches and distributions (Version 3.4.1). Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Accessed on 2020-3-20.
- Phillips, S.J. (2017). A Brief Tutorial on Maxent. Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/
- Phillips, S.J., Anderson, R.P., & Schapire, R.E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological modeling*, 190(3-4), 231-259.
- Popova, M., Gerginova, D., Trusheva, B., Simova, S., Tamfu, A.N., Ceylan, O., ... & Bankova, V. (2021). A preliminary study of chemical profiles of honey, cerumen, and propolis of the African stingless bee *Meliponula ferruginea*. *Foods*, 10, 997.
- Prato, M., & Soares, A.E.E. (2013). Production of sexuals and mating frequency in the stingless bee *Tetragonisca angustula* (Latreille) (Hymenoptera, Apidae). *Neotropical entomology*, 42, 474-482.

Using Maximum Entropy Algorithm to Analyze Changes in the Distribution

- Proni, E.A., & Hebling, M.J.A. (1996). Thermoregulation and Respiratory Metabolism in two Brazilian Stingless Bee Subspecies of Different Climatic Distribution, *Tetragonisca angustula fiebrigi* and *T. angustula* (Hymenoptera: Apidae: Meliponinae). *Entomologia generalis*, 20(4), 281-289.
- Quiroga-Murcia, D.E., Zotti, M.J., de Polanía, I.Z., & Pech-Pech, E.E. (2017). Toxicity evaluation of two insecticides on *Tetragonisca angustula* and *Scaptotrigona xanthotricha* (Hymenoptera: Apidae). *Agronomía Colombiana*, 35(3), 340-349.
- Roubik, D.W. (2022). Stingless bee (Apidae: Apinae: Meliponini) ecology. *Annual Review of Entomology*, 68(1), 2023.
- Samy, A.M., Elaagip, A.H., Kenawy, M.A., Ayres, C.F., Peterson, A.T., & Soliman, D.E. (2016). Climate change influences on the global potential distribution of the mosquito *Culex quinquefasciatus*, vector of West Nile virus and lymphatic filariasis. *PloS one*, 11(10), e0163863.
- Saravia-Nava, A., Niemeyer, H.M., & Pinto, C.F. (2018). Pollen types used by the native Stingless bee, *Tetragonisca angustula* (Latreille), in an Amazon-Chiquitano transitional forest of Bolivia. *Neotropical entomology*, 47(6), 798-807.
- Shackleton, K., Alves, D.A., & Ratnieks, F.L. (2018). Organization enhances collective vigilance in the hovering guards of *Tetragonisca angustula* bees. *Behavioral Ecology*, 29(5), 1105-1112.
- Smith, J.P., Heard, T.A., Beekman, M., & Gloag, R. (2017). Flight range of the Australian stingless bee *Tetragonula carbonaria* (Hymenoptera: Apidae). *Austral Entomology*, 56(1), 50-53.
- Swets, J.A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285-1293.
- Torres, A., Garedew, A., Schmolz, E., & Lamprecht, I. (2004). Calorimetric investigation of the antimicrobial action and insight into the chemical properties of "angelita" honey—a product of the stingless bee *Tetragonisca angustula* from Colombia. *Thermochimica Acta*, 415(1-2), 107-113.
- Urquiza, O.N., Cardozo-Alarcón, F., Adler, M., Lozano, R., Calcina-Mamani, S., Collao-Alvarado, K., ... & Pinto, C.F. (2022). Pollen Preference Patterns by *Tetragonisca angustula* (Apidae: Meliponini) in a Boliviano-Tucumano Forest. *Neotropical Entomology*, 51(2):649-659.
- Valadares, L., Vieira, B.G., Santos do Nascimento, F., & Sandoz, J.C. (2022). Brain size and behavioral specialization in the jataí stingless bee (*Tetragonisca angustula*). *Journal of Comparative Neurology*, 530(13), 2304-2314.
- Van Veen, J.W., & Sommeijer, M.J. (2000). Colony reproduction in *Tetragonisca angustula* (Apidae, Meliponini). *Insectes sociaux*, 47, 70-75.
- Velez-Ruiz, R.I., Gonzalez, V.H., & Engel, M.S. (2013). Observations on the urban ecology of the Neotropical stingless bee *Tetragonisca angustula* (Hymenoptera: Apidae: Meliponini). *Journal of Melittology*, 15, 1-8.
- Villemant, C., Barbet-Massin, M., Perrard, A., Muller, F., Gargominy, O., Jiguet, F. & Rome, Q. (2011). Predicting the invasion risk by the alien bee-hawking Yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. *Biological Conservation*, 144(9), 2142-2150.
- Wei, B., Wang, R., Hou, K., Wang, X., & Wu, W. (2018). Predicting the current and future cultivation regions of *Carthamus tinctorius* L. using MaxEnt model under climate change in China. *Global Ecology and Conservation*, 16, 1-11.
- Wittmann, D. (1985). Aerial defense of the nest by workers of the stingless bee *Trigona* (*Tetragonisca*) *angustula* (Latreille)(Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology*, 16(2), 111-114.
- Wittmann, D., Radtke, R., Zeil, J., Lübke, G., & Francke, W. (1990). Robber bees (*Lestrimelitta limao*) and their host chemical and visual cues in nest defense by *Trigona* (*Tetragonisca*) *angustula* (Apidae: Meliponinae). *Journal of Chemical Ecology*, 16(2), 631-641.
- Zeil, J., & Wittmann, D. (1993). Landmark orientation during the approach to the nest in the stingless bee *Trigona* (*Tetragonisca*) *angustula* (Apidae, Meliponinae). *Insectes sociaux*, 40(4), 381-389.