21 July 2023

Professor Allen Moore

The Editor-in-Chief,

*Ecology and Evolution*

**Submission of a manuscript for publication in the *Ecology and Evolution***

Dear Professor Moore,

We are submitting our original research article entitled ***“Unravelling the impact of climate change on honey bees: An ensemble modelling approach to predict shifts in habitat suitability in Queensland, Australia”*** for publication in the *Ecology and Evolution.*

This paper aims to identify the most influential bioclimatic and environmental variables, assess their impact on honey bee distribution, and predict future distribution in two future time spans 2020-2039 and 2060-2079. More specifically, this study developed three models: climate-only model, environment-only model, and combined climate and environment model.

The main novelty of this paper is the employment of an ensemble modelling approach to assess the distribution of honey bees (*Apis mellifera*) in relation to bioclimatic and environmental variables.The other innovation pertains to the use of high-resolution climate data (250m). Lastly, this paper predicts the distribution of honey bees under changing climate for two future time spans: 2020-2039 and 2060-2079.

Key findings and recommendations of this research are the following:

1. Radiation of the wettest and driest quarters and the temperature seasonality are the primary bioclimatic variables that determine the habitat suitability for honey bees. Proximity to regional ecosystems (floral resources), foliage projective cover, and elevation are the most influential environmental variables for honey bee habitat suitability.
2. Due to climate change, by the 2020-2039 period, approximately 88% of highly suitable habitats for honey bees are predicted to transition from their current state to become moderate to marginally suitable areas. This transformation is predicted to result in a complete change of highly suitable habitats to different categories by the years 2060 to 2079.
3. The conversion of highly suitable habitats for honey bees in the face of climate change stresses the importance of adaptation strategies including exploration of supplementary food sources for honey bees, selective breeding, and landscape planning.

This article’s field of study is within the scope of the journal. Furthermore, the content of this paper would attract the journal’s user community.

Thank you very much for your kind consideration of this manuscript.

Kind regards

Sarasie Tennakoon (On behalf of all co-authors)

**Unravelling the Impact of Climate Change on Honey Bees: An Ensemble Modelling Approach to Predict Shifts in Habitat Suitability in Queensland, Australia**

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**Unravelling the Impact of Climate Change on Honey Bees: An Ensemble Modelling Approach to Predict Shifts in Habitat Suitability in Queensland, Australia**

Honey bees play a vital role in providing essential ecosystem services and contributing to global agriculture. However, the potential effect of climate change on honey bee distribution is still not well understood. This study aims to identify the most influential bioclimatic and environmental variables, assess their impact on honey bee distribution, and predict future distribution. An ensemble modelling approach using the BIOMOD2 package in R was employed to develop three models, i.e., a climate-only model, an environment-only model, and a combined climate and environment model. The climate-only model focused on the bioclimatic factors: radiation of the wettest and driest quarters, and temperature seasonality. By utilizing bioclimatic data from 1990 to 2009, combined with observed honey bee presence and pseudo absence data, this model predicted honey bee distribution for two future time spans: 2020-2039 and 2060-2079. The climate-only model exhibited a True Skill Statistic (TSS) value of 0.85, underscoring the pivotal role of radiation and temperature seasonality in shaping honey bee distribution. The environment-only model incorporated environmental variables: proximity to regional ecosystems (floral resources), foliage projective cover, and elevation. This model demonstrated strong predictive performance, with a TSS of 0.88, emphasizing the significance of environmental variables in determining habitat suitability for honey bees. Remarkably, the combined model had a higher TSS of 0.96, indicating that the combination of climate and environmental variables enhances the model's performance. Predictions for the 2060-2079 period revealed a concerning trend of 100% transition of highly suitable land into moderately (0.54%), marginally (17.56%) or not suitable areas (81.9%) for honey bees. These results emphasize the critical need for targeted conservation efforts and the implementation of policies aimed at safeguarding honey bees and the vital apiary industry.

Keywords: honey bees, *Apis mellifera*, climate change, species distribution modelling, ensemble modelling, BIOMOD2.

1. **Introduction**

Climate is a major factor that governs the spatial and temporal distribution of a species (Adhikari et al., 2023; Araújo et al., 2005; Pant et al., 2021). Climate change is referred to as a systematic and gradual change in average weather conditions (Weber, 2010) and these changes have serious implications on the distribution, physiology, and proliferation of a wide range of species including pollinators (Aryal et al., 2016; Vercelli et al., 2021). In order to survive under changing climatic conditions, any species has to either cope, adopt in-situ, or shift from the current geographical locations (Maggini et al., 2011). This emphasises the importance of predicting the future distribution of a species under changing climate since such predictions can inform scientists and decision makers about future risks. In turn, this would enable the development of risk mitigation strategies to reduce the impact of climate change on biodiversity.

The pollinator species that is widely used globally to enhance agricultural production is the European honey bee or the western honey bee (*Apis mellifera*) (Potts et al., 2010), hereafter referred to as the honey bee. Honey bee is ranked number one as the most frequent pollinator for crops worldwide and floral species in natural habitats (Hung et al., 2018). The threat imposed by climate change on honey bees is multi-faceted, with significant impacts on diseases, parasites, predators, parasitoids, viruses, pesticide use (Cornelissen et al., 2019; Le Conte & Navajas, 2008; Varikou et al., 2020; Vercelli et al., 2021; Zawislak et al., 2019), and most importantly, the plants on which honey bees forage (Goulson et al., 2015). These issues have a huge impact on the behaviour, physiology and distribution of honey bees (Goulson et al., 2015). The future changes in honey bees with respect to the population and geographic distribution can have impact on ecology, and agriculture. Shifts in the distribution of honey bees with changing climate imply the importance of understanding the future distribution patterns for conservation purposes, preserving the ecosystem dynamics and related social systems (Bonebrake et al., 2018; Pecl et al., 2017).

The distribution of bees is hugely impacted by climate and environmental factors. For instance, temperature and precipitation variables, vegetation parameters (leaf area index, canopy height), tree cover, and topography (slope, aspect, elevation) have been used in modelling the distribution of bumble bee species (Geue & Thomassen, 2020), whereas in addition to the bioclimatic variables, MODIS phenology product has been employed in distribution modelling of a Africanised honey bee species (Stohlgren et al., 2011). Even though no study has attempted to model the distribution of the European honey bee, several studies on land suitability assessment for honey bees have revealed that pollen and nectar sources, water sources, topography, and climatic factors determine the optimum habitat locations for honey bees (Estoque & Murayama, 2010; Maris et al., 2008).

Species Distribution Modelling (SDM), also known as ecological niche modelling or habitat suitability modelling, is gaining more popularity over the other tools of analysis available for ecologists to predict the distribution of species (Tikhonov et al., 2020). The aim of SDM is to provide an insight on the spatio-temporal assembly of a species and the anticipated future distribution against the climatic and environmental changes (Guisan & Rahbek, 2011). Most importantly, SDM can be used not only for natural ecosystems but also for human managed ecosystems (Woodin et al., 2013)**.** Several methods are available to model species distribution, including statistical regression models such as Generalized Linear Models (GLM), and machine learning algorithms for instance Random Forest (RF). The predictive performance of these approaches may vary depending upon the scenario under consideration. Thus, no method has been identified to have a consistent supremacy over the others with regard to a species, region or application (Hao et al., 2019). Therefore, the selection of an individual model has become a daunting task and has led to the use of ensemble of models that can combine the predictions of different models (Araújo & New, 2007). For species distribution modelling, BIOMOD2 package is commonly used as the ensemble software (Thuiller et al., 2016) on open-source R platform (R Core Team, 2013). Moreover, BIOMOD2 has been extensively utilized in distribution modelling of a wide range of bee species (Acosta et al., 2016; Geue & Thomassen, 2020; Lanner et al., 2022; Maia et al., 2020; Marshall et al., 2015; Tabor & Koch, 2021) yet no study has attempted to predict the distribution of *Apis mellifera* under changing climate using an ensemble approach.

Honey bees are the most commonly used species in the Australian apiary industry, making an annual contribution of $14.2 billion to the economy (Agrifutures Australia, 2022). This study models the distribution of honey bees based on bioclimatic and environmental variables and predicts their future distribution for two different time spans in the future (i.e. 2020-2039 and 2060-2079) within the context of Australia. More specifically, the objectives of this study are the following: (1) to identify the bioclimatic and environmental predictor variables that contribute the most to the distribution of honey bees, and to quantify their relative impact on honey bee distribution; (2) to assess the predictive performance of an ensemble approach in modelling the distribution of honey bees using bioclimatic and environmental variables, and (3) to investigate the potential impact of climate change on honey bee distribution under 2020-2039 (referred to as 2030) and 2060-2079 (referred to as 2070) climate conditions. This study introduces several innovations: (1) it is the first to use an ensemble approach for assessing the distribution of *Apis mellifera* in relation to bioclimatic and environmental variables; (2) it employs a relatively high-resolution climate data (250m); and (3) it evaluates the distribution of *Apis mellifera* under changing climate conditions, considering two future time spans.

**2. Materials and Methods**

2.1 Study area

As the study area, a sub-section of Southern Queensland, Australia that covers an extent of 37,650km2 encompassing the four Local Government Areas of Toowoomba, Southern Downs, Goondiwindi, and Western Downs (Figure 1) was selected. The Queensland agricultural sector contributes over $10 billion annually to the national economy (Business Queensland, 2022) and accounts for 9.7% of the country's total honey production, producing approximately 37,000 tonnes per annum (Department of Agriculture Fisheries and Forestry, 2023). Most importantly, the study area was chosen to include approximately 35% of the total managed apiary sites in Queensland’s primary honey-producing region (Queensland Spatial Catalogue, 2021), while also capturing variations in climate, topography, land cover, and land use (Queensland Spatial Catalogue, 2014).

Figure 1. Elevation map and the apiary site locations in the study area

This area exhibits significant climate variations, ranging from warm temperate conditions in Toowoomba and Southern Downs to hot arid conditions in Goondiwindi and Western Downs. For example, in Stanthorpe, Southern Downs, the mean minimum temperature during winter is 1.1oC while the mean maximum temperature in summer can reach 27.40C. The mean annual rainfall in the same area is 764.2mm. In contrast, Miles, Western Downs experiences a minimum temperature of 3.60C during winter, with a mean maximum temperature of 33.30C in summer. The mean annual rainfall in Miles is 643.4mm (Australian Bureau of Statistics, 2022). Topographical features, such as slope, aspect, and elevation, also exhibit significant differences among various localities. For instance, the elevation is higher in Southern Downs and the Toowoomba region ranging from 690m-1200m above mean sea level, while most parts of the Western Downs and Goondiwindi are situated in comparatively lower elevated areas encompassing 200m-300m above mean sea level. The land use map in the study area primarily consists of regional ecosystems (basically composed of remnant and non-remnant forests), rangelands and agriculture, collectively covering 98% of the total extent with roughly equal percentages. The land use map's secondary level classification system reveals a diverse array of land use categories, spanning residential, agricultural, mining areas, and nature conservations.

2.2 Overview of the research methods

The overview of the research methods used in this study is shown in Figure 2. The modelling procedure of this study followed the overview, data, model, assessment, and prediction (ODMAP protocol introduced by Zurell et al. (2020). The initial occurrence data were rarefied using the SpThin package in R 4.2.2. Both bioclimatic variables and environmental variables were tested for multicollinearity using the USDM package, and three variables from each category were chosen for final model development. Based on the True Skills Statistics (TSS) threshold, ensemble models were developed for climate variables, environmental variables, and a combination of climate and environmental variables. The climate model, based on climate data from 1990-2009, was projected for the time periods 2020-2039 and 2060-2079.

Figure 2. Overview of the research methods

2.3 Honey bee presence data

This study aimed to utilize two disparate categories of presence data, including managed apiary site locations and records of observations derived from different sources such as the Atlas of Living Australia (ALA) and the Global Biodiversity Information Facility (GBIF). The selection of apiary sites is based on various factors, primarily including the availability of food sources for honey bees, and consideration of climatic and topographic conditions. Consequently, the locations of managed apiary sites can be regarded as reliable indicators of geographic suitability for honey bees, akin to natural occurrences. The apiary site locations on public lands were retrieved from the Queensland Spatial catalogue, and the database contains 1,592 records. Occurrence data from 1990 to the present year were obtained using ALA and GBIF. The study period was selected to encompass the available climate data from 1990 onwards. Only human and machine observations were included, excluding preserved specimens or museum records, as these do not accurately represent the true geographic distribution of a species (Araújo & Guisan, 2006). GBIF did not have any presence or absence records of *Apis mellifera* for the study area during the specified time, while ALA had only six records of occurrences. Thus, the bulk of the presence data was acquired from the Queensland Spatial Catalogue.

The spatial resolution of the environment and climate raster layers used in this study was 250m×250m. Occurrence of multiple presence data within this resolution can lead to spatial sampling bias (Aiello‐Lammens et al., 2015), spatial autocorrelation (Pant et al., 2021) and overestimated measures of prediction accuracy (Veloz, 2009). Therefore, the SpThin package in R 4.2.2 was utilized to perform spatial thinning of the presence records (Aiello‐Lammens et al., 2015), resulting in a total of 1,595 records after removing only three records from the initial dataset. This can be attributed to the fact that the managed apiary site locations, which serve as the primary occurrence data in this study, are established while maintaining a reasonable distance between two sites in accordance with government regulations (Biosecurity Act, 2014).

2.4 Bioclimatic and environmental variables

As suggested by the literature, honey bee activity (Jiang et al., 2016), honey bee colony losses and population (Hristov et al., 2020; Le Conte & Navajas, 2008), and productivity (Smart et al., 2016) are significantly influenced by environmental and climatic factors. For this study, initially, eight environmental variables that impact honey bees and the apiary industry were selected based on existing literature. These variables included regional ecosystems/flora criterion (Sarı & Ceylan, 2017; Sarı et al., 2020), Foliage Projective Cover (FPC), land use (Ambarwulan et al., 2016), land cover, topographical features (slope, aspect, elevation), and distance to water bodies (Zoccali et al., 2017). Bioclimatic variables derived from temperature and rainfall values are often used in SDM, representing annual trends, seasonality, and extremes in these climate factors. Thirty-five bioclimatic variables at a finer scale (250m×250m) were sourced from the New South Wales (NSW) and Australian Capital Territory (ACT) Regional Climate Modelling (NARCliM) database (Hutchinson & Xu, 2015) (Appendix T1).

All the variables selected for modelling were tested for multicollinearity using the USDM (Uncertainty Analysis for Species Distribution Models) package on the R platform. Two indicators, namely the correlation coefficient and variance inflation factor (VIF), were employed as measures of multicollinearity. Multicollinearity can increase uncertainty in model parameters and decrease the predictive performance of the model (De Marco & Nóbrega, 2018). Variables with a correlation coefficient greater than 0.8 and a VIF higher than 5 were excluded from further analysis, following previous studies on SDM (Diao & Wang, 2014; Fois, Bacchetta, et al., 2018; Fois, Cuena-Lombraña, et al., 2018). All eight environmental variables were retained, while only four bioclimatic variables (i.e., Bio4, Bio15, Bio24, Bio25) remained after conducting multicollinearity testing. To mitigate overfitting, the number of predictor variables was reduced (Breiner et al., 2015) by iteratively removing the least contributing variables during the model formation process (Zeng et al., 2016). The variables used for the final model formation, along with their sources, are listed in Table 1 whilst figures 3-6 visualize these variables. ArcMap 10.8.2 was used to create raster layers with a cell size of 250m × 250m and the WGS84 projection.

Table1: Bioclimatic and environmental variables finally utilized for the ensemble modelling

Figure 3. Temperature seasonality maps of 1990-2009, 2020-2039 and 2060-2079

Figure 4. Radiation of wettest quarter (Bio24) maps of 1990-2009, 2020-2039 and 2060-2079

Figure 5. Radiation of driest quarter (Bio25) maps of 1990-2009, 2020-2039 and 2060-2079

Figure 6. Environmental variables (Distance to regional ecosystems (floral resources), Foliage projective Cover (FPC) and elevation)

2.5 Species Distribution Modelling: Ensemble approach using BIOMOD2

BIOMOD is extensively used across different locations around the world in distribution modelling of a wide range of taxa mostly using presence only data and environment and climate factors (Hao et al., 2019). BIOMOD2 permits running ten different modelling algorithms (table 2), model calibration, evaluation, building ensembles, ensemble forecasting and visualization of data and results (Thuiller et al., 2016).

Table 2: An overview of the different modelling algorithms available in BIOMOD2

Even though, some algorithms such as rectilinear envelope and distance-based envelope can handle presence-only data, most of the modelling algorithms utilise both presence and absence data. Moreover, it is proven that the presence-absence models perform better than presence-only models (Elith et al., 2006). However, collecting absence data, particularly for mobile species, and ensuring its accuracy when compared with presence data, can be a challenging task (MacKenzie & Royle, 2005). In this case, researchers rely on pseudo absence or background data to enhance the predictive performance of the model. In this study, 5,000 pseudo-absence points were generated, taking into consideration the varying number of pseudo-absence points required for each algorithm (Barbet‐Massin et al., 2012). Equal weight was assigned to the presence and absence points, and the process of generating pseudo-absences was repeated three times to alleviate random bias. To estimate the predictive power of the model, a training dataset is used, ensuring that the training data are not spatially autocorrelated with test data (Allouche et al., 2006). In cases where independent data is unavailable for training the models, the original dataset is divided into two parts: training data and testing data. The honey bee presence and pseudo-absence data were divided into training (80%) and testing (20%) sets, following the approach recommended by previous studies (Chapman et al., 2019; Hopkins, 2009; Laman et al., 2018; Senay & Worner, 2019; Waldock et al., 2022). The modelling process consists of a total of 90 model runs, which includes ten modelling algorithms, three pseudo absence generation runs, and three evaluation runs. Using the ensemble modelling option available in BIOMOD2, an ensemble species distribution model was constructed by applying multiple algorithms above a selected threshold.

2.6 Model Evaluation

Model evaluation in BIOMOD consists of an assessment of the explanatory power using a standard approach associated with each algorithm and evaluating the predictive power of the model using AUC i.e., area under the relative operating characteristic curve (ROC) (Hanley & McNeil, 1982), Cohen’s Kappa (Monserud & Leemans, 1992) and the True Skills Statistics (TSS) (Allouche et al., 2006). AUC considers two aspects: sensitivity, which is the proportion of presences correctly predicted as presence, and specificity, which is the proportion of absences correctly predicted as absences. AUC can range from 0 to 1, with a practical range of 0.5 to 1. A value of 0.5 indicates a random model, while a value of 1 indicates a perfect model (Hallgren et al., 2019). The Kappa statistic evaluates the degree to which models predict occurrence at a level that exceeds what would be expected by chance (Monserud & Leemans, 1992). The Kappa statistic can have values ranging from -1 to +1. Values of 0 or below indicate random performance, while a value of +1 indicates perfect agreement (Allouche et al., 2006). The TSS considers both omission (proportion of presences identified as absences) and commission errors (proportion of absences identified as presences), and has a range of -1 to +1, where a value of +1 indicates perfect agreement, and values of zero or less indicate performance no better than random. Unlike Kappa, TSS is not influenced by prevalence. Additionally, TSS is unaffected by the size of the validation set, and two methods with equal performance will have equal TSS scores (Allouche et al., 2006).

2.7 Model development

In this study, three models namely the climate-only model, the environment-only model, and the combined climate (1990-2009) and environment model were developed. The climate-only model was developed using the three most influential bioclimatic variables for honey bees, namely Bio4 (temperature seasonality), Bio24 (radiation of the wettest quarter), and Bio25 (radiation of the driest quarter). Only individual models with a TSS greater than 0.7 were utilized for ensemble model building. The three environmental variables with the highest contribution to the model i.e., proximity to regional ecosystems (floral resources), foliage projective cover, and elevation were used in building the environment-only model. Unlike the TSS values of individual algorithms pertaining to the climate-only model, the TSS values of algorithms in environment-only model were less than 0.7. Thus, a cut-off TSS of 0.6 was selected when building the ensemble environment-only model. The combined climate and environment model was developed by incorporating the environmental and bioclimatic variables from both environment-only and climate-only models. These variables included foliage projective cover, proximity to regional ecosystems, elevation, bio4, bio24, and bio25.

2.8 Generation of suitability maps for current and projected climate change

Suitability maps were generated using BIOMOD2 for each scenario under consideration, namely: climate-only (1990-2009), environment-only, and the combined climate and environment model. Using ensemble forecasting, suitability maps for the two future scenarios i.e., 2020-2039 and 2060-2079 were generated. Each output map was divided into four suitability classes, based on the criterion namely: highly suitable (with a probability of occurrence exceeding 75%), moderately suitable (with a probability of occurrence ranging from 50% to 75%), marginally suitable (with a probability of occurrence between 25% and 50%), and not suitable (with a probability of occurrence less than 25%). For this manual method of reclassification, the reclassify tool in ArcMap 10.8.2 was utilized.

1. **Results**
   1. Model performance

3.1.1 Climate-only model

Among the algorithms used in ensemble modelling, RF had the highest average TSS value of 0.77, followed by CTA with a value of 0.72, while SRE had the lowest TSS of 0.27. Algorithms such as ANN, GAM, GBM, GLM, MARS, and MAXENT also had average TSS values less than 0.7 (Figure 7). Consequently, these algorithms were excluded from ensemble modelling. Radiation variables including Bio24 and Bio25, had the highest contribution to the model, each accounting for 35.57% and 37.73% respectively. Bio4 or the temperature seasonality contributed to the model by 26.70%. According to the response curve pertaining to probability of honey bee occurrences and radiation in the wettest quarter, the optimum radiation for honey bees is 25Wm-2. Based on the response curve for radiation in the driest quarter, honey bee occurrences display a fluctuating pattern as the radiation increases, with sudden increases and declines but an overall increasing trend. However, the optimum radiation value for honey bees in the driest quarter or winter is observed as 16Wm-2. It is apparent that honey bee occurrences are limited when the temperature seasonality or Bio4 ranges between 1.6 and 1.7. Otherwise, the pattern remains relatively stable (Figure 8). The ensemble climate-only model exhibited strong predictive performance, achieving a TSS of 0.85, an AUC of 0.98, and a Kappa value of 0.72. The same bioclimatic variables were used to project the model’s predictions into the 2020-2039 (2030) and 2060-2079 (2070) periods.

Figure 7. TSS scores of individual algorithms and the ensemble model (climate-only)

Figure 8. Response curves of bioclimatic variables in the climate-only model

3.1.2 Environment-only model

GBM had the highest average TSS value of 0.63, while RF and ANN also performed comparatively well in modelling honey bee presence data against environmental variables, achieving an average TSS of 0.62. MARS demonstrated good performance as well, with a TSS of 0.61, slightly lower than that of GBM, RF, and ANN. On the other hand, MAXENT had a TSS of 0.6. SRE, similar to the climate-only model, demonstrated the least predictive performance, achieving a TSS of 0.31 (Figure 9). The Foliage Projective Cover made the most significant contribution to the model, accounting for 57.36% of the total. Following was the distance to regional ecosystem or floral resources, which contributed 34.10%. The elevation had the least impact on the model, contributing only 8.54% to the model. According to the response curve for regional ecosystems, honey bee occurrences are optimized near the regional ecosystems with floral resources for honey bees. There is a sharp decline as the distance from regional ecosystems increases. The probability of honey bee occurrences increases with FPC and reaches its peak when FPC is 0.3. Beyond this point, the curve remains stable. Elevation displays a rather constant pattern but with a spike between 375m and 425m (Figure 10). The ensemble environmental-only model showed strong predictive performance similar to the climate-only model, with a TSS of 0.88, an AUC of 0.98, and a Kappa value of 0.75.

Figure 9. TSS scores of individual algorithms and the ensemble model (environment-only)

Figure 10: Response curves of environmental variables in the environment-only model

3.1.3 Combined climate and environment model

Just like in the climate-only model, in the combined model, RF was the best-performing algorithm with an average TSS score of 0.76. CTA and GBM also had average TSS values of 0.72 and 0.71, respectively. Comparable to the other two models, SRE displayed the lowest TSS of 0.38 (Figure 11). To construct the combined model, a TSS threshold of above 0.7 was chosen. The greatest contribution to the model came from bio24 (radiation in wettest quarter), accounting for 27.74%, followed by distance to regional ecosystems (floral resources) and Foliage Projective Cover (FPC) with approximately equal percentages of 21.25 and 21.63 correspondingly. The contribution of Bio25 (radiation in driest quarter) accounted for 18.36%. On the other hand, bio4 (temperature seasonality) and elevation, which were the least influential variables in the model, had values of 5.44% and 5.58%, respectively. As per the combined model, the predictor variables behave similarly to the individual models. The combined climate and environment model demonstrated strong predictive performance, with a high TSS score of 0.96, a near-perfect ROC score of 0.99, and a Kappa value of 0.92. Therefore, it is evident that the prediction of honey bee occurrences can be enhanced by using both environmental and climate variables together in the same model as the predictor variables.

Figure 11. TSS scores of individual algorithms and the ensemble model (combined)

* 1. Land suitability for honey bees

Based on the climate-only model, the area classified as highly suitable experiences a drastic decline of approximately 88% from the initial period of 2000 to the projected period of 2030 (Table 3). These areas were relegated into the moderately suitable and marginally suitable categories. Furthermore, this highly suitable area is completely lost from 2030 to 2070. Conversely, the moderately suitable area demonstrates an increase of 58% from 2000 to 2030 but experiences a significant loss of 96% from 2030 to 2070, suggesting a potential future loss of areas with high and moderate suitability. The area classified as marginally suitable has more than doubled between 2030 and 2070. However, there is a decrease in the area classified as not suitable from 2000 to 2030 by 9%, followed by an increase of 15% from 2030 to 2070. It is worth noting that the not suitable area is significantly large when compared to other suitability categories.

In the context of the environment-only model, the highly and moderately suitable area, which accounts for 24% of the total extent, surpasses the same area pertaining to any other climate scenario or the combined model in size. The climate-only model for 2030 indicates a significantly lower value of only 15% for the highly and moderately suitable area, making it the second-largest value. On the other hand, the marginally and not suitable area resulted by environment-only model is comparatively smaller, representing 76% of the total extent. In comparison, this value increases to approximately 85% for the 2000 and 2030 climate scenarios as well as the combined model, with a remarkably high value of 99% projected for 2070. This indicates that the study area offers more favourable environmental conditions for honey bees compared to suitability based on climatic factors alone. When compared with the combined climate and environment model, the highly and moderately suitable areas are larger in the environment-only model, while they are smaller in the climate-only model.

Table 3: Suitable area (km2) for honey bees based on climate-only (2000, 2030, 2070), environment-only, and combined environment and climate model

The number of honey bee occurrences was recorded for each suitability class using the sample tool in ArcMap. The results show that the highest number of honey bee locations, accounting for approximately 72%, was found in the highly suitable class of the current climate-only model (2000). However, this number experiences a significant decline over the timeline from 2000 to 2070, indicating a complete loss of highly suitable areas by 2070. In contrast to the area distribution within each suitability class between the environment-only and combined models, the number of occurrences in the highly suitable area is higher in the combined model compared to the environment-only model. Only 8 honey bee occurrences were found in the not suitable area under the climate-only scenario. However, this number increases by approximately 89% in 2070, indicating a significant loss of highly and moderately suitable areas for honey bees in terms of climate.

Table 4: Number of honey bee occurrences by suitability class under each modelling scenario

Figure 12. Suitability maps for honey bees: Climate-only scenario in 1990-2009, 2020-2039 and 2060-2079

Figure 13. Suitability maps for honey bee habitat: environment-only and combined (Climate and Environment) scenarios

**Discussion**

4.1 Predictive performance of the models and contribution of predictor variables

The TSS, AUC, and KAPPA values of the climate-only ensemble model were 0.85, 0.98, and 0.72, respectively, indicating that the model was robust with strong predictive power. A TSS value greater than 0.8 and AUC value higher than 0.9 indicate an excellent model (Hosmer & Lemeshow, 2000; Lin & Chiu, 2018; Pittman & Brown, 2011), while a Kappa value of 0.61 to 0.8 exhibits substantial performance (Landis & Koch, 1977; Viera & Garrett, 2005), which is the case in the current scenario. Anyway, TSS is argued to be a more reliable measure in assessing the predictive performance of species distribution models. This is because TSS possesses all the advantages of Kappa while not being affected by the prevalence of a species, unlike Kappa (Allouche et al., 2006). Among the ten modelling algorithms utilized, Random Forest (RF) had the highest TSS value, which agrees with the outcome of previous studies where an ensemble approach is employed to model species distribution (Marmion, Parviainen, et al., 2009; Williams et al., 2009). SRE was excluded from further analysis due to its poor performance in predicting the honey bee distribution which was indicated by a TSS value of 0.27. SRE is not commonly used in recent literature due its lower performance when compared with other modelling algorithms used in SDM (Pecchi et al., 2019). CTA which was included in ensemble model of the current study due to a TSS value greater than 0.7, is gaining more popularity in SDM and is argued to provide a favourable trade-off, offering comparable accuracy to GLM or GAM (Thuiller et al., 2003).

On the other hand, the environment-only model, incorporating predictor variables, proximity to regional ecosystems, Foliage Projective Cover and elevation, exhibited a high predictive performance with a TSS of 0.88, an AUC of 0.98, and a kappa value of 0.75. Unlike the ensemble model, the TSS values of individual algorithms in environment-only model were less than 0.7. Therefore, a threshold value of 0.6 was chosen, while for the other two models the threshold was set as 0.7. If the presence data and the algorithms remain the same and only the predictor variables are different, the smaller TSS values in the environment-only model can be attributed to the lower effectiveness of the environmental variables in explaining the underlying patterns and relationships within the data when compared to the climatic variables. This is further confirmed by the fact that, according to the climate-only model, a higher number of honey bee occurrences align with the highly and moderately suitable classes when compared to the environment-only model. Nonetheless, the combined environment and climate model also displayed a robust predictive power with a TSS 0.96 of ROC 0.99 of and a Kappa value of 0.92. Thus, it is evident that combining climate and environmental predictor variables in a model enhances the predictive performance. Moreover, to enhance the predictive performance of the models while mitigating problems associated with SDM, such as overfitting, several precautions were taken. These included rarefying the presence data, selection of a minimum number of predictor variables, and performing cross-validation using 80% of the data for model calibration and 20% for validation (Pant et al., 2021).

According to the climate-only model, the most influential variables in the model were Bio24 and Bio25 which represent the radiation of wettest quarter and radiation of driest quarter, correspondingly. Bio4 (temperature seasonality) also exhibits a significant influence on honey bee distribution. This is consistent with previous findings that solar radiation and temperature are the two most detrimental climatic factors that contribute to bee activity (Clarke & Robert, 2018). Moreover, it has been proven that bee abundance is highest in the areas with high solar insolation (Orr et al., 2021). Compared to the significance of the other two criteria, namely proximity to regional ecosystems and Foliage Projective Cover, in constructing the environment-only model, the contribution of elevation is minimal (8.54%). Nonetheless, elevation remains a crucial factor determining honey bee activity and has been extensively utilized in literature concerning land suitability analysis for apiary sites (Fazel & Abdul, 2012; Maris et al., 2008; Sarı et al., 2020; Zoccali et al., 2017). Furthermore, it was evident that elevation holds greater importance when compared to other topographic factors such as slope and aspect. The outcome further confirms the fact that access to floral resources is a prime criterion to be considered when locating a commercial apiary site (Tennakoon et al., 2023).

4.2 Response of the spatial distribution of honey bees to climate change in Australia

By the 2020-2039 period, approximately 88% of highly suitable habitats for honey bees are projected to transition from their current state to become moderate to marginally suitable areas. Due to climate change, this transformation is predicted to result in a complete change of highly suitable habitats to different categories by the years 2060 to 2079. However, there was a contrasting trend observed in the moderately suitable area, which showed a notable increase of 58% from 1990-2009 to 2020-2039. This increase can be attributed to favourable changes in climatic factors, such as a slight decline in temperature seasonality (Bio4) and an increase in radiation during the wettest (Bio24) and driest quarters (Bio25). However, the projection from 2020-2039 to 2060-2079 revealed a significant decline in the moderately suitable area, primarily due to an increase in temperature seasonality and a drastic reduction in radiation during the driest quarter. This indicates the potential challenges that lie ahead for honey bee habitats due to changing climate. Additionally, while there is a temporary decrease in the not suitable area by the 2020-2039 period, it subsequently increases by 2060-2079, highlighting the persistence of adverse climatic conditions for honey bees. Among the three scenarios, the environment-only model exhibited the largest extent of highly and moderately suitable areas for honey bees, accounting for 24% of the total extent. This emphasizes that the environmental factors in the study area are more favourable for honey bees than the climatic factors. The combined climate and environment model revealed a decrease of approximately 9% in this value, highlighting the limitations imposed by climate factors on habitat suitability.

By 2020-2039, new moderately suitable areas have emerged in all four regions, while most of the highly suitable areas have transitioned into moderately suitable or marginally suitable lands. During the period from 2030 to 2070, a discernible westward shift can be observed in the distribution of marginally suitable areas, whereas only scattered patches of moderately suitable areas are found in Toowoomba, Western Downs and Southern Downs. Over time, the regions of Goondiwindi that were once highly and moderately suitable are predicted to transition into areas classified as marginally and not suitable.

In the suitability map produced by ensemble modelling for the 1990-2009 period, 97% of honey bee occurrence records were found within the highly suitable and moderately suitable areas. This high correspondence between the model predictions and actual occurrences further validates the accuracy of the model. However, a significant decline is observed in future projections, with the occurrence records dropping to zero by 2060-2079. Remarkably, by the same period, a substantial majority, comprising 89% of the current occurrences, will be classified as not suitable, indicating a concerning shift in habitat suitability for honey bees. Regional ecosystems with floral species suitable for honey bees are mainly confined to the eastern and southern parts of the study area, encompassing areas such as Goondiwindi, Western Downs, and Southern Downs. With the changing climate, it is predicted that the habitat suitability for honey bees will shift towards the western parts, where there are fewer favourable regional ecosystems available. This implies the vulnerability of the apiary industry, particularly in the study area, which covers a significant portion of the honey-producing region in Queensland.

4.3 Limitations of the present study and recommendations

Species Distribution Modelling (SDM) can be applied on both natural and managed ecosystems. This study aimed to assess the impact of climate change on both managed and naturally occurring honey bee colonies, yet a limitation encountered was the insufficient availability of natural honey bee occurrence records that can be derived from reliable sources. The honey bee presence data mainly consists of managed apiary site locations. While these apiary sites are presumed to capture the natural landscape attributes suitable for honey bees, it will be interesting to model honey bee distribution using other “natural” locations for the presence data.

Pesticides have a detrimental effect on honey bees, and their habitat suitability (Krupke et al., 2012; Tome et al., 2020; Williams et al., 2015; Zhu et al., 2014). In this study, the assessment of suitable locations did not consider the exposure to pesticides, which is recognized as a limitation. Therefore, it is recommended to incorporate pesticide exposure as a factor when determining suitable locations for honey bees. Furthermore, this study overlooks the aspect of habitat connectivity between suitable habitats for honey bees. It is suggested to include an analysis of the land use to assess the proximity and potential barries among habitats. Integration of habitat connectivity measures into honey bee species distribution modelling, will provide insights into how the arrangement and accessibility of suitable habitats influence honey bee populations. This information will contribute to more accurate predictions of honey bee distribution and assist in identifying priority areas for conservation and management efforts. Furthermore, this study did not take into consideration the land use changes when predicting future habitat suitability for honey bees. Therefore, it is worthwhile to combine anticipated land use changes with the projected future maps to obtain more accurate results.

**Conclusion**

In this study, an ensemble modelling approach was employed for developing three models to examine the distribution of honey bees based on various predictor variables. These models include the climate-only model, the environment-only model, and the combined climate and environment model. The climate-only model utilized the most dominant climatic factors that impact honey bee suitability such as radiation in the wettest and driest quarters, as well as temperature seasonality. On the other hand, the environment-only model incorporated the environmental variables that primarily influence honey bee habitat suitability such as proximity to regional ecosystems, foliage projective cover (FPC), and elevation. To capture the collective influence of climate and environmental factors, the combined model was developed by integrating the variables used in both the climate-only and environment-only models. Using the climate-only model, three suitability maps were projected for the time periods 1990-2009, 2020-2039, and 2060-2079. All three models demonstrated strong predictive performances with TSS values greater than 0.8. Under the 2020-2039 scenario, it is projected that 88% of the highly suitable land will transition to moderately suitable (14.84%), marginally suitable (13.46%), and not suitable (71.10%) areas, leaving only a 0.6% of the land as highly suitable. By the period of 2060-2079, the highly suitable area will undergo a complete transformation, transitioning entirely into other classes: moderately suitable (0.54%), marginally suitable (17.56%), and unsuitable (81.9%). This predicted loss of suitable habitats, particularly in terms of climate suitability, highlights the vulnerability of honey bees for climate change. Thus, this decline is anticipated to have significant impacts on natural ecosystems and commercial apiary management, which is a crucial contributor to the national economy.

The results of this study reveal a significant decline in the suitable area for honey bees under changing climate conditions. Therefore, this study stresses the importance of mitigating the impacts of climate change on honey bee habitats. Accordingly, investigating potential adaptation strategies for honey bee management in the face of climate change is crucial. Such strategies may include exploration of supplementary food sources for honey bees , selective breeding, innovative hive management techniques, and landscape planning to enhance honey bee resilience and minimize the negative impacts of changing climatic conditions. Additionally, engaging stakeholders, including beekeepers, farmers, and relevant government authorities, in addressing the challenges posed by climate change on honey bee distribution is essential. Evaluating the effectiveness of current policies and offering recommendations for promoting sustainable honey bee management and conservation efforts are key avenues for further exploration. These potential extensions would provide valuable insights into the complex interactions among climate change, environmental factors, and honey bee distribution. They would enhance our comprehensive understanding of land suitability for honey bees and contribute to the development of targeted conservation and management strategies.

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Conflict of Interest

None.

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Data Availability

Location records and predictor variables used in model development can be accessed on DOI <https://doi.org/10.5061/dryad.vdncjsz16>

Author Contributions

**Sarasie Tennakoon**: Conceptualization (equal), Data Curation (lead), Formal Analysis (lead), Methodology (equal), Software (lead), Validation (equal), Visualization (lead), Writing – Original Draft Preparation (lead), Writing – Review and Editing (equal). **Armando Apan**: Conceptualization (equal), Formal Analysis (supporting), Methodology (equal), Validation (equal), Visualization (supporting), Writing – Original Draft Preparation (supporting), Writing – Review and Editing (equal), Supervision (lead). **Tek Maraseni**: Conceptualization (equal), Writing – Review and Editing (equal), Supervision (supporting).

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References

Abou-Shaara, H., Owayss, A., Ibrahim, Y., & Basuny, N. (2017). A review of impacts of temperature and relative humidity on various activities of honey bees. *Insectes sociaux*, *64*, 455-463.

Acosta, A. L., Giannini, T. C., Imperatriz-Fonseca, V. L., & Saraiva, A. M. (2016). Worldwide alien invasion: a methodological approach to forecast the potential spread of a highly invasive pollinator. *PLoS one*, *11*(2), e0148295.

Adhikari, B., Subedi, S. C., Bhandari, S., Baral, K., Lamichhane, S., & Maraseni, T. (2023). Climate‐driven decline in the habitat of the endemic spiny babbler (Turdoides nipalensis). *Ecosphere*, *14*(6), e4584.

*Agrifutures Australia*. (2022). Rural Industries Research Development Corporation (RIRDC). Retrieved 01/07/2022 from <https://www.agrifutures.com.au/rural-industries/honey-bee-pollination/>

Aiello‐Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B., & Anderson, R. P. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, *38*(5), 541-545.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223-1232.

Ambarwulan, W., Sjamsudin, C. E., & Syaufina, L. (2016). Geographic information system and analytical hierarchy process for land use planning of beekeeping in forest margin of Bogor Regency, Indonesia. *Jurnal Silvikultur Tropika*, *7*(3), S50-S57.

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of biogeography*, *33*(10), 1677-1688.

Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in ecology & evolution*, *22*(1), 42-47.

Araújo, M. B., Pearson, R. G., & Rahbek, C. (2005). Equilibrium of species' distributions with climate. *Ecography*, *28*(5), 693-695.

Aryal, A., Shrestha, U. B., Ji, W., Ale, S. B., Shrestha, S., Ingty, T., Maraseni, T., Cockfield, G., & Raubenheimer, D. (2016). Predicting the distributions of predator (snow leopard) and prey (blue sheep) under climate change in the Himalaya. *Ecology and Evolution*, *6*(12), 4065-4075.

Australian Bureau of Statistics. (2022). Retrieved 01/05/2022 from <https://www.abs.gov.au/>

Barbet‐Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo‐absences for species distribution models: How, where and how many? *Methods in ecology and evolution*, *3*(2), 327-338.

Biosecurity Act. (2014). *Biosecurity Act*. Retrieved from <https://www.legislation.qld.gov.au/view/html/inforce/current/act-2014-007>

Bonebrake, T. C., Brown, C. J., Bell, J. D., Blanchard, J. L., Chauvenet, A., Champion, C., Chen, I. C., Clark, T. D., Colwell, R. K., & Danielsen, F. (2018). Managing consequences of climate‐driven species redistribution requires integration of ecology, conservation and social science. *Biological Reviews*, *93*(1), 284-305.

Breiman, L. (2017). *Classification and regression trees*. Routledge.

Breiner, F. T., Guisan, A., Bergamini, A., & Nobis, M. P. (2015). Overcoming limitations of modelling rare species by using ensembles of small models. *Methods in ecology and evolution*, *6*(10), 1210-1218.

Business Queensland. (2022). *About Queensland's agriculture industry*. Retrieved 02 February 2022 from <https://www.business.qld.gov.au/industries/farms-fishing-forestry/agriculture/overview#:~:text=Queensland%27s%20agricultural%20industries%20are%20made%20up%20of%3A%20plant,of%20land%20area%20in%20Australia%20dedicated%20to%20agriculture>.

Chapman, D., Pescott, O. L., Roy, H. E., & Tanner, R. (2019). Improving species distribution models for invasive non‐native species with biologically informed pseudo‐absence selection. *Journal of biogeography*, *46*(5), 1029-1040.

Clarke, D., & Robert, D. (2018). Predictive modelling of honey bee foraging activity using local weather conditions. *Apidologie*, *49*(3), 386-396.

Cornelissen, B., Neumann, P., & Schweiger, O. (2019). Global warming promotes biological invasion of a honey bee pest. *Global change biology*, *25*(11), 3642-3655.

De Marco, P., & Nóbrega, C. C. (2018). Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. *PLoS one*, *13*(9), e0202403.

Department of Agriculture Fisheries and Forestry. (2023). *Honey bees*. Retrieved 16/05/2023 from <https://www.agriculture.gov.au/agriculture-land/farm-food-drought/hort-policy/honeybees>

Diao, C., & Wang, L. (2014). Development of an invasive species distribution model with fine-resolution remote sensing. *International Journal of Applied Earth Observation and Geoinformation*, *30*, 65-75.

Elith, J., H. Graham\*, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., & Lehmann, A. (2006). Novel methods improve prediction of species’ distributions from occurrence data. *Ecography*, *29*(2), 129-151.

Estoque, R., & Murayama, Y. (2010). Suitability analysis for beekeeping sites in La Union, Philippines, using GIS and multi-criteria evaluation techniques. *Res. J. Appl. Sci*, *5*(3), 242-253.

Fazel, A., & Abdul, R. B. M. S. (2012). Application of geographic information systems in land-use suitability evaluation for beekeeping: A case study of Vahregan watershed (Iran). *African Journal of Agricultural Research*, *7*(1), 89-97.

Fois, M., Bacchetta, G., Cuena-Lombraña, A., Cogoni, D., Pinna, M. S., Sulis, E., & Fenu, G. (2018). Using extinctions in species distribution models to evaluate and predict threats: a contribution to plant conservation planning on the island of Sardinia. *Environmental Conservation*, *45*(1), 11-19.

Fois, M., Cuena-Lombraña, A., Fenu, G., & Bacchetta, G. (2018). Using species distribution models at local scale to guide the search of poorly known species: Review, methodological issues and future directions. *Ecological Modelling*, *385*, 124-132.

Franklin, J. (2002). Enhancing a regional vegetation map with predictive models of dominant plant species in chaparral. *Applied Vegetation Science*, *5*(1), 135-146.

Geue, J. C., & Thomassen, H. A. (2020). Unraveling the habitat preferences of two closely related bumble bee species in Eastern Europe. *Ecology and Evolution*, *10*(11), 4773-4790.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

Guisan, A., & Rahbek, C. (2011). SESAM–a new framework integrating macroecological and species distribution models for predicting spatio‐temporal patterns of species assemblages. In (Vol. 38, pp. 1433-1444): Wiley Online Library.

Hallgren, W., Santana, F., Low-Choy, S., Zhao, Y., & Mackey, B. (2019). Species distribution models can be highly sensitive to algorithm configuration. *Ecological Modelling*, *408*, 108719.

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, *143*(1), 29-36.

Hao, T., Elith, J., Guillera‐Arroita, G., & Lahoz‐Monfort, J. J. (2019). A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Diversity and Distributions*, *25*(5), 839-852.

Hastie, T., & Tibshirani, R. (1987). Generalized additive models: some applications. *Journal of the American Statistical Association*, *82*(398), 371-386.

Hastie, T., Tibshirani, R., & Buja, A. (1994). Flexible discriminant analysis by optimal scoring. *Journal of the American Statistical Association*, *89*(428), 1255-1270.

Hopkins, R. L. (2009). Use of landscape pattern metrics and multiscale data in aquatic species distribution models: a case study of a freshwater mussel. *Landscape Ecology*, *24*, 943-955.

Hosmer, D., & Lemeshow, S. (2000). Applied Logistic Regression 2nd Ed. 2000 John Wiley and Sons. *New York, NY*.

Hristov, P., Shumkova, R., Palova, N., & Neov, B. (2020). Factors associated with honey bee colony losses: A mini-review. *Veterinary Sciences*, *7*(4), 166.

Huang, Z.-Y., & Robinson, G. (1995). Seasonal changes in juvenile hormone titers and rates of biosynthesis in honey bees. *Journal of Comparative Physiology B*, *165*, 18-28.

Hung, K.-L. J., Kingston, J. M., Albrecht, M., Holway, D. A., & Kohn, J. R. (2018). The worldwide importance of honey bees as pollinators in natural habitats. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1870), 20172140.

Hutchinson, M., & Xu, T. (2015). *Methodology for generating Australia-wide surfaces and associated grids for monthly mean daily maximum and minimum temperature, rainfall, pan evaporation and solar radiation for the periods 1990–2009, 2020–2039 and 2060–2079.* . <https://climatechange.environment.nsw.gov.au/-/media/NARCLim/Files/Climate-Change-Impact-Reports/ANUNARCLiM--Methodology-for-Generating-Australiawide-Surfaces-and-Associated-Grids.pdf?la=en&hash=AEB0C0C9ACFDE49EE52499559D5A398FCACC1A9B>

Hutchinson, M. F., Stein, J. L., Stein, J.A.,, Anderson, H., & Tickle, P. K. (2008). *GEODATA 9 second DEM and D8: Digital Elevation Model Version 3 and Flow Direction Grid 2008*. <http://pid.geoscience.gov.au/dataset/ga/66006>

Iverson, L. R., Prasad, A. M., Matthews, S. N., & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest ecology and management*, *254*(3), 390-406.

Jiang, J.-A., Wang, C.-H., Chen, C.-H., Liao, M.-S., Su, Y.-L., Chen, W.-S., Huang, C.-P., Yang, E.-C., & Chuang, C.-L. (2016). A WSN-based automatic monitoring system for the foraging behavior of honey bees and environmental factors of beehives. *Computers and Electronics in Agriculture*, *123*, 304-318.

Krupke, C. H., Hunt, G. J., Eitzer, B. D., Andino, G., & Given, K. (2012). Multiple routes of pesticide exposure for honey bees living near agricultural fields. *PLoS one*, *7*(1), e29268.

Laman, E. A., Rooper, C. N., Turner, K., Rooney, S., Cooper, D. W., & Zimmermann, M. (2018). Using species distribution models to describe essential fish habitat in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(8), 1230-1255.

Landis, J. R., & Koch, G. G. (1977). The measurement of observer agreement for categorical data. *biometrics*, 159-174.

Lanner, J., Dubos, N., Geslin, B., Leroy, B., Hernández-Castellano, C., Dubaić, J. B., Bortolotti, L., Calafat, J. D., Ćetković, A., & Flaminio, S. (2022). On the road: Anthropogenic factors drive the invasion risk of a wild solitary bee species. *Science of the Total Environment*, *827*, 154246.

Le Conte, Y., & Navajas, M. (2008). Climate change: impact on honey bee populations and diseases. *Revue Scientifique et Technique-Office International des Epizooties*, *27*(2), 499-510.

Lek, S., & Guégan, J.-F. (1999). Artificial neural networks as a tool in ecological modelling, an introduction. *Ecological Modelling*, *120*(2-3), 65-73.

Lin, C.-T., & Chiu, C.-A. (2018). The Relic Trochodendron aralioides Siebold & Zucc.(Trochodendraceae) in Taiwan: Ensemble distribution modeling and climate change impacts. *Forests*, *10*(1), 7.

MacKenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105-1114.

Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L., & Zbinden, N. (2011). Are Swiss birds tracking climate change?: Detecting elevational shifts using response curve shapes. *Ecological Modelling*, *222*(1), 21-32.

Maia, U. M., Miranda, L. d. S., Carvalho, A. T., Imperatriz‐Fonseca, V. L., de Oliveira, G. C., & Giannini, T. C. (2020). Climate‐induced distribution dynamics of Plebeia flavocincta, a stingless bee from Brazilian tropical dry forests. *Ecology and Evolution*, *10*(18), 10130-10138.

Maris, Mansor, S., & Shafri, H. (2008). Apicultural site zonation using GIS and Multi-Criteria Decision analysis. *Pertanika J. Trop. Agric. Sci*, *31*(2), 147-162.

Marmion, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). The performance of state-of-the-art modelling techniques depends on geographical distribution of species. *Ecological Modelling*, *220*(24), 3512-3520.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, *15*(1), 59-69.

Marshall, L., Carvalheiro, L. G., Aguirre‐Gutiérrez, J., Bos, M., de Groot, G. A., Kleijn, D., Potts, S. G., Reemer, M., Roberts, S., & Scheper, J. (2015). Testing projected wild bee distributions in agricultural habitats: predictive power depends on species traits and habitat type. *Ecology and Evolution*, *5*(19), 4426-4436.

McCullagh, P. (2019). *Generalized linear models*. Routledge.

Monserud, R. A., & Leemans, R. (1992). Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling*, *62*(4), 275-293.

Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C.-D., & Ascher, J. S. (2021). Global patterns and drivers of bee distribution. *Current Biology*, *31*(3), 451-458. e454.

Pant, G., Maraseni, T., Apan, A., & Allen, B. L. (2021). Predicted declines in suitable habitat for greater one‐horned rhinoceros (Rhinoceros unicornis) under future climate and land use change scenarios. *Ecology and Evolution*, *11*(24), 18288-18304.

Pecchi, M., Marchi, M., Burton, V., Giannetti, F., Moriondo, M., Bernetti, I., Bindi, M., & Chirici, G. (2019). Species distribution modelling to support forest management. A literature review. *Ecological Modelling*, *411*, 108817.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., & Evengård, B. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3-4), 231-259.

Pittman, S. J., & Brown, K. A. (2011). Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS one*, *6*(5), e20583.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, *25*(6), 345-353.

Queensland Spatial Catalogue. (2014). *Landsat Foliage Projective Cover - Queensland 2014*. Queensland Government. Retrieved 01/05/2023 from <https://qldspatial.information.qld.gov.au/catalogue/custom/detail.page?fid>={E3A795AC-867D-4AA2-96DA-FF6F7BC6F3CD}

Queensland Spatial Catalogue. (2021). *Managed apiary sites*. Queensland Government Retrieved 01 October 2021 from <https://qldspatial.information.qld.gov.au/catalogue/>

R Core Team, R. (2013). R: A language and environment for statistical computing.

Rangel, J., & Fisher, A. (2019). Factors affecting the reproductive health of honey bee (Apis mellifera) drones—A review. *Apidologie*, *50*(6), 759-778.

Ridgeway, G. (1999). The state of boosting. *Computing science and statistics*, 172-181.

Sarı, & Ceylan. (2017). Site suitability analysis for beekeeping via analythical hyrearchy process, Konya Example. *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, *4*, 345.

Sarı, F., Ceylan, D. A., Ozcan, M. M., & Ozcan, M. M. (2020). A comparison of multicriteria decision analysis techniques for determining beekeeping suitability. *Apidologie*, *51*(4), 481-498.

Senay, S. D., & Worner, S. P. (2019). Multi-scenario species distribution modeling. *Insects*, *10*(3), 65.

Smart, M. D., Pettis, J. S., Euliss, N., & Spivak, M. S. (2016). Land use in the Northern Great Plains region of the US influences the survival and productivity of honey bee colonies. *Agriculture, Ecosystems & Environment*, *230*, 139-149.

Specht, R. (1981). Foliage projective cover and standing biomass. *Vegetation classification in Australia*, 10-21.

Steven, M., Biscoe, P., Jaggard, K., & Paruntu, J. (1986). Foliage cover and radiation interception. *Field Crops Research*, *13*, 75-87.

Stohlgren, T. J., Jarnevich, C. S., Esaias, W. E., & Morisette, J. T. (2011). Bounding species distribution models. *Current Zoology*, *57*(5), 642-647.

Switanek, M., Crailsheim, K., Truhetz, H., & Brodschneider, R. (2017). Modelling seasonal effects of temperature and precipitation on honey bee winter mortality in a temperate climate. *Science of the Total Environment*, *579*, 1581-1587.

Tabor, J. A., & Koch, J. B. (2021). Ensemble models predict invasive bee habitat suitability will expand under future climate scenarios in Hawai’i. *Insects*, *12*(5), 443.

Tennakoon, S., Apan, A., Maraseni, T., & Altarez, R. D. D. (2023). Decoding the impacts of space and time on honey bees: GIS based fuzzy AHP and fuzzy overlay to assess land suitability for apiary sites in Queensland, Australia. *Applied Geography*, *155*, 102951.

Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package ‘biomod2’. *Species distribution modeling within an ensemble forecasting framework*.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography*, *32*(3), 369-373.

Thuiller, W., Vayreda, J., Pino, J., Sabate, S., Lavorel, S., & Gracia, C. (2003). Large‐scale environmental correlates of forest tree distributions in Catalonia (NE Spain). *Global Ecology and Biogeography*, *12*(4), 313-325.

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge, M. M., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r‐package Hmsc. *Methods in ecology and evolution*, *11*(3), 442-447.

Tome, H. V., Schmehl, D. R., Wedde, A. E., Godoy, R. S., Ravaiano, S. V., Guedes, R. N., Martins, G. F., & Ellis, J. D. (2020). Frequently encountered pesticides can cause multiple disorders in developing worker honey bees. *Environmental Pollution*, *256*, 113420.

Varikou, K., Kasiotis, K. M., Bempelou, E., Manea-Karga, E., Anagnostopoulos, C., Charalampous, A., Garantonakis, N., Birouraki, A., Hatjina, F., & Machera, K. (2020). A pesticide residues insight on honeybees, bumblebees and olive oil after pesticidal applications against the olive fruit fly Bactrocera oleae (Diptera: Tephritidae). *Insects*, *11*(12), 855.

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence‐only niche models. *Journal of biogeography*, *36*(12), 2290-2299.

Venables, W. N., & Ripley, B. D. (2013). *Modern applied statistics with S-PLUS*. Springer Science & Business Media.

Vercelli, M., Novelli, S., Ferrazzi, P., Lentini, G., & Ferracini, C. (2021). A qualitative analysis of beekeepers’ perceptions and farm management adaptations to the impact of climate change on honey bees. *Insects*, *12*(3), 228.

Viera, A. J., & Garrett, J. M. (2005). Understanding interobserver agreement: the kappa statistic. *Fam med*, *37*(5), 360-363.

Waldock, C., Stuart‐Smith, R. D., Albouy, C., Cheung, W. W., Edgar, G. J., Mouillot, D., Tjiputra, J., & Pellissier, L. (2022). A quantitative review of abundance‐based species distribution models. *Ecography*, *2022*(1).

Weber, E. U. (2010). What shapes perceptions of climate change? *Wiley Interdisciplinary Reviews: Climate Change*, *1*(3), 332-342.

Williams, G. R., Troxler, A., Retschnig, G., Roth, K., Yañez, O., Shutler, D., Neumann, P., & Gauthier, L. (2015). Neonicotinoid pesticides severely affect honey bee queens. *Scientific reports*, *5*(1), 14621.

Williams, J. N., Seo, C., Thorne, J., Nelson, J. K., Erwin, S., O’Brien, J. M., & Schwartz, M. W. (2009). Using species distribution models to predict new occurrences for rare plants. *Diversity and Distributions*, *15*(4), 565-576.

Woodin, S. A., Hilbish, T. J., Helmuth, B., Jones, S. J., & Wethey, D. S. (2013). Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. *Ecology and Evolution*, *3*(10), 3334-3346.

Yee, T. W., & Mitchell, N. D. (1991). Generalized additive models in plant ecology. *Journal of vegetation science*, *2*(5), 587-602.

Zawislak, J., Adamczyk, J., Johnson, D. R., Lorenz, G., Black, J., Hornsby, Q., Stewart, S. D., & Joshi, N. (2019). Comprehensive survey of area-wide agricultural pesticide use in southern United States row crops and potential impact on honey bee colonies. *Insects*, *10*(9), 280.

Zeng, Y., Low, B. W., & Yeo, D. C. (2016). Novel methods to select environmental variables in MaxEnt: A case study using invasive crayfish. *Ecological Modelling*, *341*, 5-13.

Zhu, W., Schmehl, D. R., Mullin, C. A., & Frazier, J. L. (2014). Four common pesticides, their mixtures and a formulation solvent in the hive environment have high oral toxicity to honey bee larvae. *PLoS one*, *9*(1), e77547.

Zoccali, P., Malacrinò, A., Campolo, O., Laudani, F., Algeri, G. M., Giunti, G., Strano, C. P., Benelli, G., & Palmeri, V. (2017). A novel GIS-based approach to assess beekeeping suitability of Mediterranean lands. *Saudi journal of biological sciences*, *24*(5), 1045-1050.

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera‐Arroita, G., & Guisan, A. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261-1277.

**Tables**

Table1: Bioclimatic and environmental variables finally utilized for the ensemble modelling

|  |  |  |
| --- | --- | --- |
| **Predictor Variable** | **Rationale** | **Source** |
| **Bioclimatic variables** | | |
| Bio4 (Temperature seasonality) | Temperature has a huge impact on honey bee mortality (Switanek et al., 2017), activity (Abou-Shaara et al., 2017; Huang & Robinson, 1995), and reproduction (Rangel & Fisher, 2019) | New South Wales (NSW) and Australian Capital Territory (ACT) Regional Climate Modelling (NARCliM) (Hutchinson & Xu, 2015) |
| Bio24  (Radiation of wettest quarter (Wm-2)  Bio25  (Radiation of driest quarter (Wm-2) | Having a significant amount of solar radiation is particularly desirable during winter because the rate at which bees leave the hive (bee egress rate) is influenced by temperature and radiation. Previous studies have observed a reduced bee egress rate when exposed to low temperatures and limited solar radiation (Clarke & Robert, 2018). Solar radiation is also associated with defensive behaviour of honey bees (Southwick & Moritz, 1987) |  |
| **Environmental Variables** | | |
| Regional Ecosystems (Floral resources) | Honey bees gather nectar and pollen from various flowering species, which are crucial for their survival and honey production. Hence, honey bees are present in areas where they have access to floral resources. Furthermore, when choosing a location for an apiary, it is essential to consider the availability of food sources (nectar/pollen) for honey bees. The Queensland regional ecosystems database contains information about vegetation communities in a specific bioregion. Regional ecosystems refer to vegetation communities in a bioregion that consistently correspond to specific combinations of geology, landform, and soil (Sattler and Williams 1999, Vegetation Management Act 1999). This database, therefore, serves as an excellent resource to identify the floral species suitable for honey bees in a particular ecosystem. The same methodology used to rate regional ecosystems by Tennakoon et al. (2023) was used in the present study. | Regional Ecosystems Maps – Queensland Spatial Catalogue: Queensland Government (https://qldspatial.information.qld.gov.au) |
|  |  |  |
| Foliage Projective Cover (FPC) | FPC refers to the proportion of the ground surface taken up by the vertical projection of foliage (Queensland Spatial Catalogue, 2014). Foliage is an important factor related with honey bee foraging being an indicator of food sources available for honey bees and the incoming solar radiation (Specht, 1981; Steven et al., 1986). | Queensland Spatial Catalogue: Queensland Government (https://qldspatial.information.qld.gov.au) |
| Elevation | Elevation is closely correlated with floral resources and climatic factors that affect honey bees. | GEODATA 9 Second Digital Elevation Model (DEM-9S) Version 3 from Geoscience Australia (<https://ecat.ga.gov.au>) (Hutchinson et al., 2008) |

Table 2: An overview of the different modelling algorithms available in BIOMOD2

|  |  |
| --- | --- |
| Model | Overview |
| Artificial Neural Networks (ANN) | ANNs are non-linear models with several parameters (Thuiller et al., 2009) and are based on the function of the human brain (Lek & Guégan, 1999). This is an effective rule-based, machine learning algorithm gaining more popularity in SDM (Marmion, Luoto, et al., 2009). |
| Classification Tree Analysis (CTA) | CTA being an alternative machine learning algorithm to regression techniques uses a tree-based analysis system (Franklin, 2002; Venables & Ripley, 2013). This offers the benefit of capturing non-additive behavior and intricate interactions. Nonetheless, CTA tends to generate excessively intricate models, which can result in misleading interpretations (Breiman, 2017). |
| Generalized Additive Model (GAM) | GAM is a non-parametric extension to GLM (Hastie & Tibshirani, 1987). GAMs are better suited for more complex non-linear relationships between species and predictor variables that cannot be addressed by GLM (Yee & Mitchell, 1991). |
| Generalized Boosting Method (GBM) | GBM, a machine learning algorithm, exhibits high efficiency in data fitting, possess non-parametric characteristics, and leverages the strengths of various contemporary statistical techniques (Ridgeway, 1999). |
| Generalized Linear Model (GLM) | GLMs are mathematical expansions of linear models (McCullagh, 2019). GLMs can accommodate non-linear relationships and various statistical distributions that characterize spatial data and are closely connected to conventional techniques employed in linear modelling (Marmion, Luoto, et al., 2009). |
| Multivariate Adaptive Regression Spines (MARS) | MARS is an extension to linear regression models and important when there are large number of explanatory variables with low-order interactions (Thuiller et al., 2009). |
|  |  |
|  |  |
| Flexible Discriminant Analysis (FDA) | FDA is a classification method and important in performing classification among multiple groups (Hastie et al., 1994). |
| MAXENT.Phillips.2 | This is a specific implementation of the MaxEnt algorithm with additional features and improvements. Maxent is a machine learning algorithm that offers a precise mathematical framework, making it highly suitable for modelling species distributions (Phillips et al., 2006). |
|  |  |
| Random Forest (RF) | RF is capable of effectively managing correlated variables, accommodating larger datasets, processing a vast number of input variables, and handling missing data (Breiman, 2017). RF is regarded as one of the most precise algorithm in SDM (Iverson et al., 2008). |
|  |  |
| Surface Range Envelope (SRE) | Widely employed in SDM, yet has shortcomings such as the inability to achieve the same level of performance as certain alternative modelling techniques (Elith et al., 2006). Anyway, it continues to be favoured due to its simplicity and comprehensibility (Pecchi et al., 2019). |

Table 3: Suitable area (km2) for honey bees based on climate-only (2000, 2030, 2070), environment-only, and combined environment and climate model

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Classification | Climate-only | | | | | | Environment-only | | Combined (Environment and Climate) | |
| **1990-2009**  **(2000)** | | **2020-2039**  **(2030)** | | **2060-2079**  **(2070)** | |
| **Area (km2)** | **Percent**  **(%)** | **Area**  **(km2)** | **Percent**  **(%)** | **Area**  **(km2)** | **Percent**  **(%)** | **Area**  **(km2)** | **Percent**  **(%)** | **Area**  **(km2)** | **Percent**  **(%)** |
| Highly Suitable | 1,832 | 4.86 | 227 | 0.6 | 0 | 0 | 3,748 | 9.96 | 2,056 | 5.47 |
| Moderately Suitable | 3,546 | 9.42 | 5,588 | 14.84 | 207 | 0.54 | 5,159 | 13.72 | 3,476 | 9.24 |
| Marginally suitable | 2,936 | 7.80 | 5,068 | 13.46 | 6,611 | 17.56 | 4,486 | 11.93 | 2,980 | 7.92 |
| Not suitable | 29,336 | 77.92 | 26,767 | 71.10 | 30,832 | 81.90 | 24,220 | 64.39 | 29,101 | 77.37 |
| Total | **37,650** | **100** | **37,650** | **100** | **37,650** | **100** | **37,613** | **100** | **37,613** | **100** |

Table 4: Number of honey bee occurrences by suitability class under each modelling scenario

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Classification | Climate-only | | | | | | Environment-only | | Combined (Environment and Climate) | |
| **1990-2009**  **(2000)** | | **2020-2039**  **(2030)** | | **2060-2079**  **(2070)** | |
| **Number** | **Percent**  **(%)** | **Number** | **Percent**  **(%)** | **Number** | **Percent**  **(%)** | **Number** | **Percent**  **(%)** | **Number** | **Percent**  **(%)** |
| Highly Suitable | 1,140 | 71.93 | 18 | 1.13 | 0 | 0 | 745 | 47.03 | 1,054 | 66.54 |
| Moderately Suitable | 395 | 24.92 | 547 | 4.51 | 1 | 0.001 | 618 | 39.02 | 413 | 26.07 |
| Marginally suitable | 42 | 2.65 | 206 | 13.00 | 173 | 10.92 | 170 | 10.73 | 79 | 4.99 |
| Not suitable | 8 | 0.5 | 814 | 51.36 | 1411 | 89.02 | 51 | 3.22 | 38 | 2.40 |
| Total | **1,585** | **100** | **1,585** | **100** | **1,585** | **100** | **1,584** | **100** | **1,584** | **100** |

**Figures**

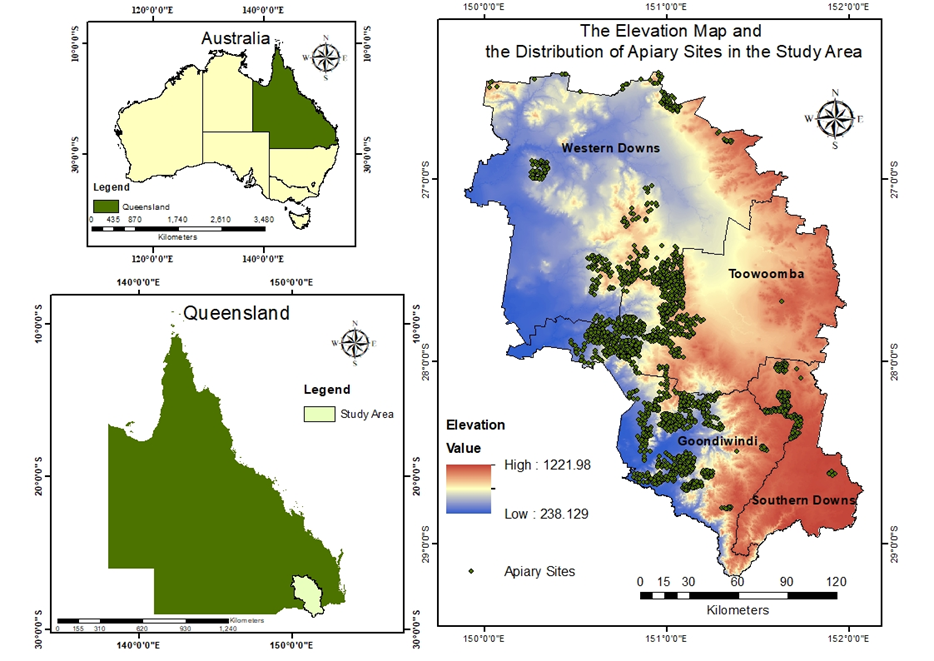


Figure 1. Elevation map and the apiary site locations in the study area

Honey bee presence data

n = 1,598

Spatial Thinning

(SpThin package in R4.2.2)

Bioclimatic variables

n = 35

Environmental variables

n = 8

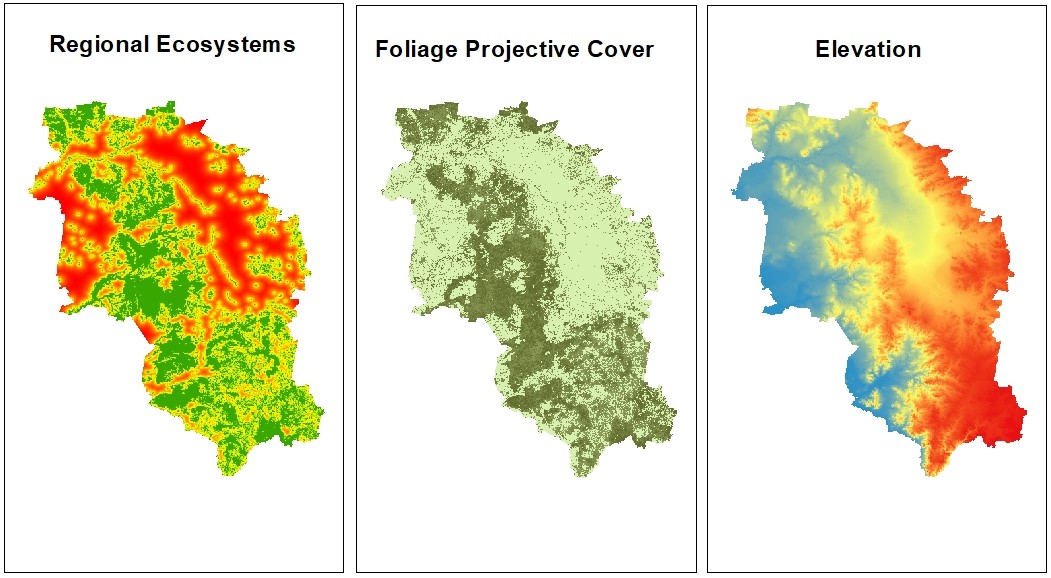
Spatial Autocorrelation

(USDM package in R4.2.2)



Bioclimatic variables

n = 3



Environmental variables

n = 3

ANN

CTA

FDA

GAM

GBM

GLM

MARS

MAXENT

RF

SRE

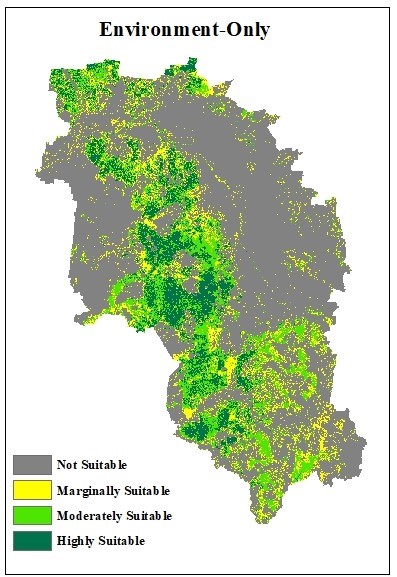
Species distribution modelling algorithms

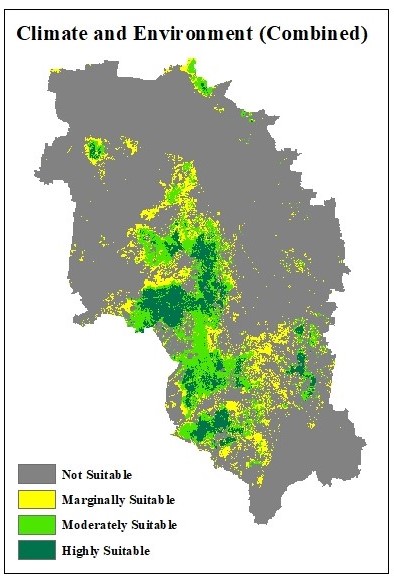
Ensemble Modelling

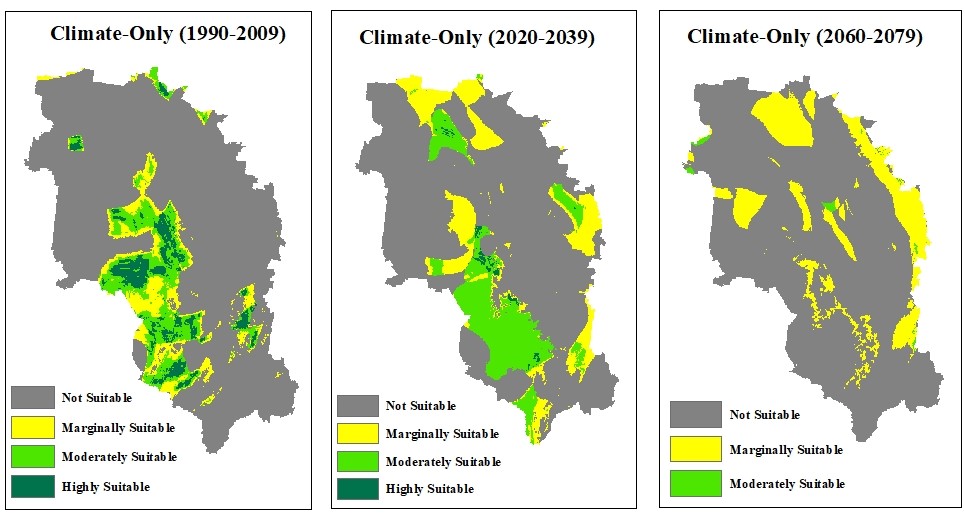
Climate-only model

Environment-only model

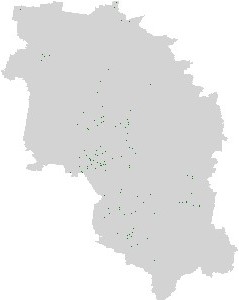
Combined climate and environment model







2000, 2030, and 2070



n = 1,595

Figure 2. Overview of the research methods

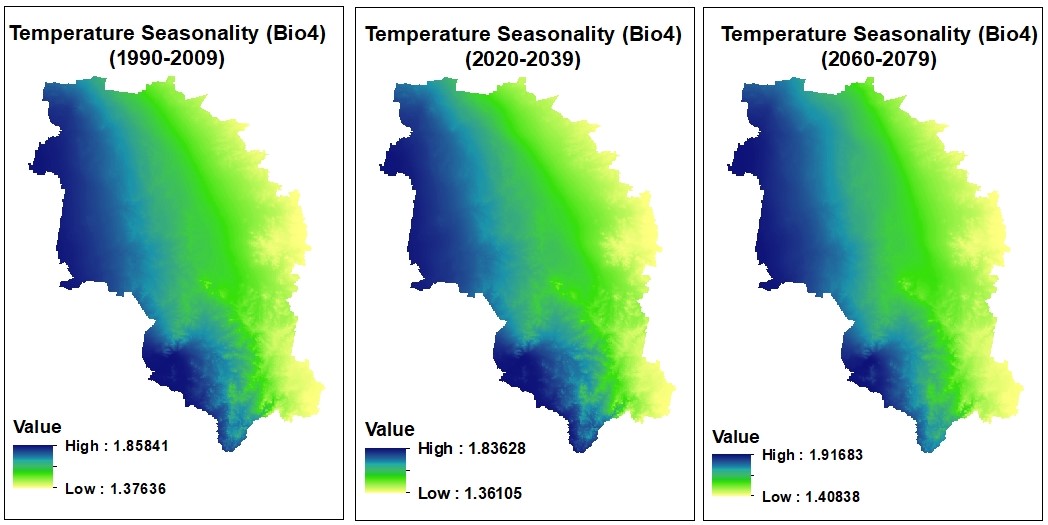


Figure 3. Temperature seasonality maps of 1990-2009, 2020-2039 and 2060-2079

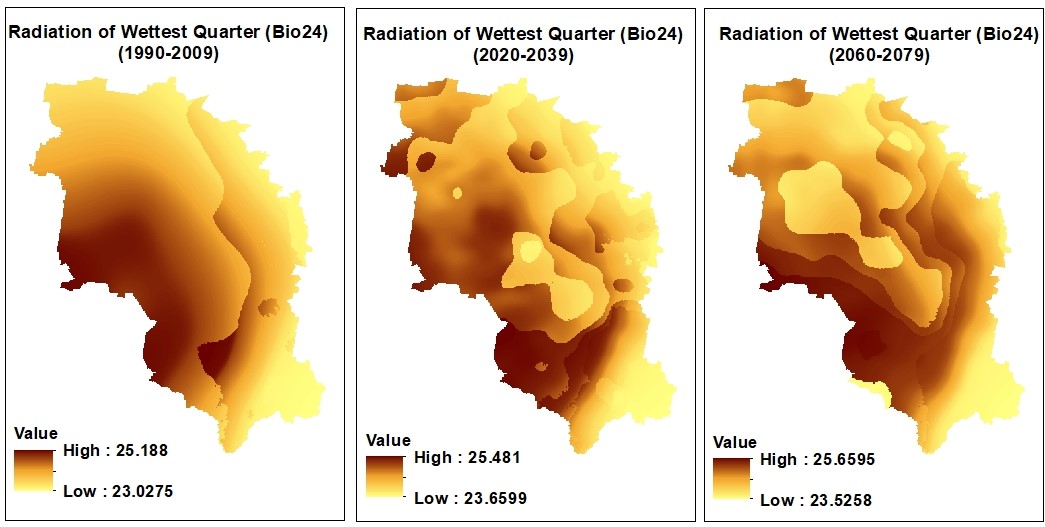


Figure 4. Radiation of wettest quarter (Bio24) maps of 1990-2009, 2020-2039 and 2060-2079

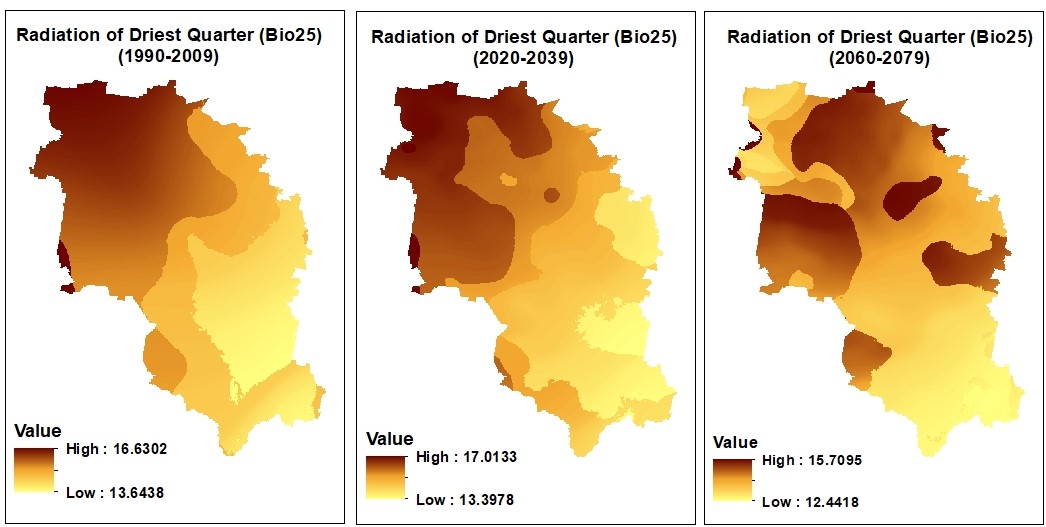


Figure 5. Radiation of driest quarter (Bio25) maps of 1990-2009, 2020-2039 and 2060-2079

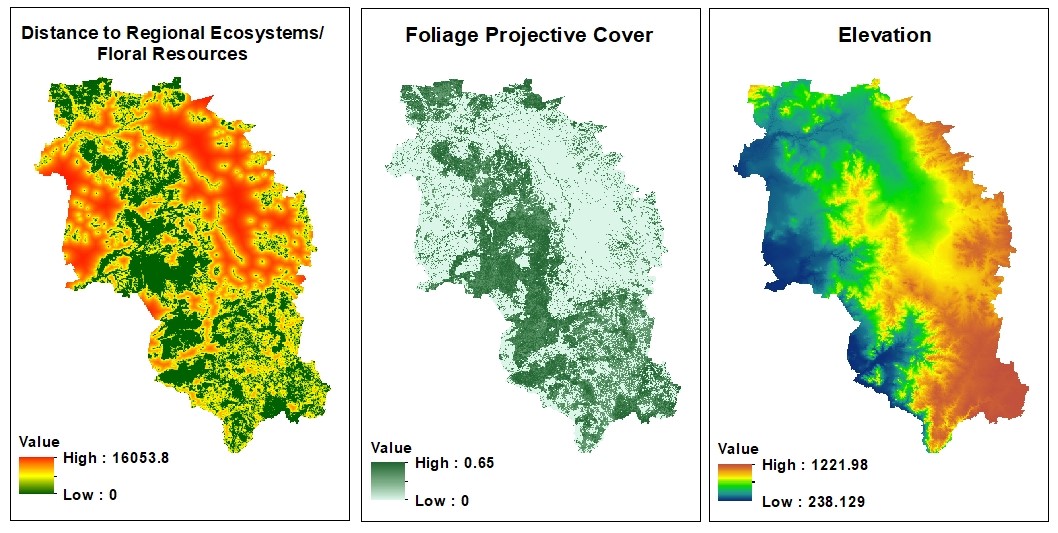


Figure 6. Environmental variables (Distance to regional ecosystems (floral resources), Foliage projective Cover (FPC) and elevation)

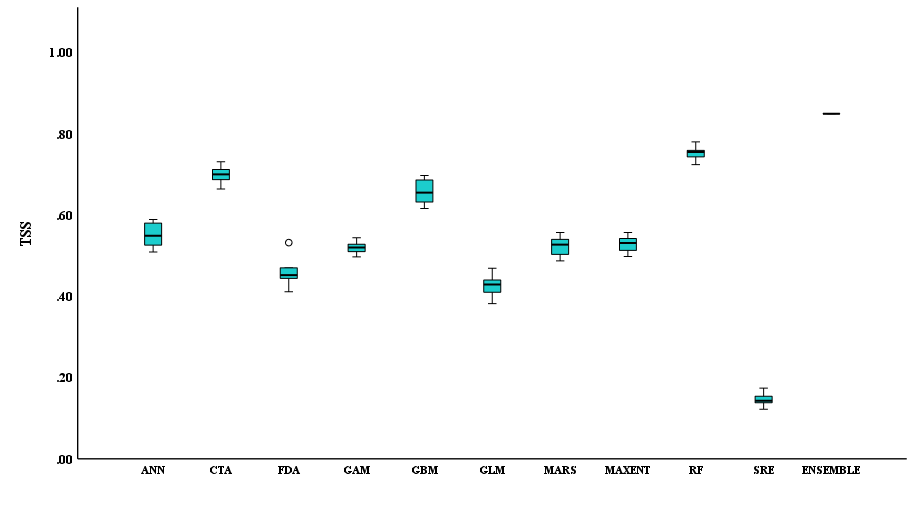
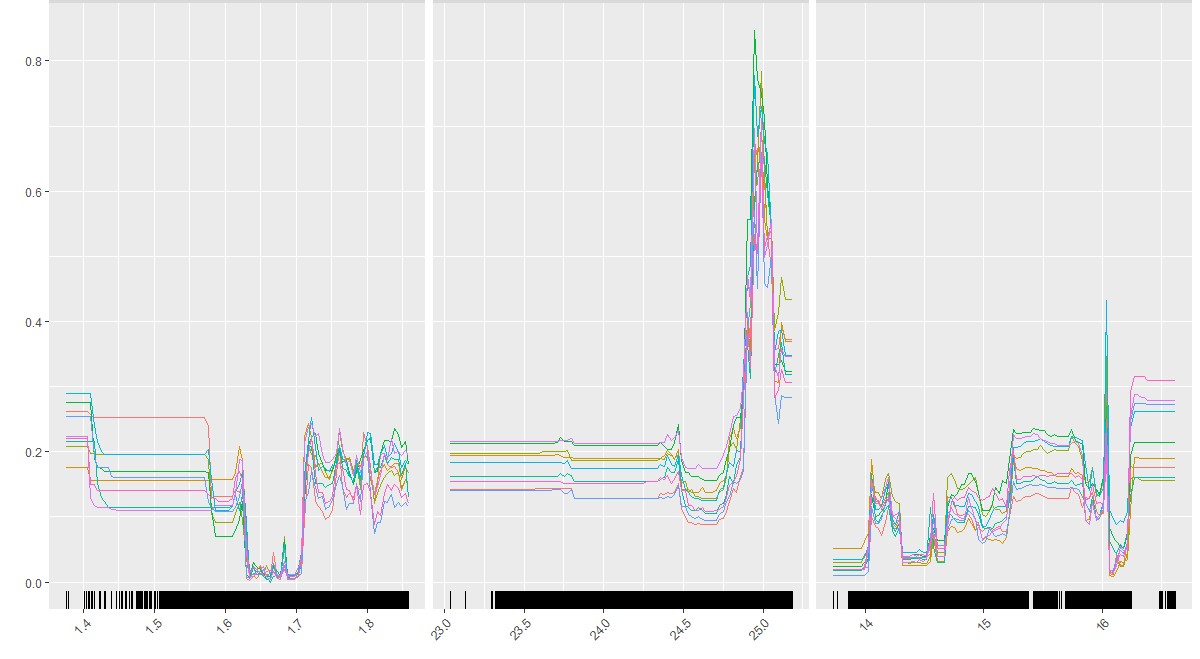


Figure 7. TSS scores of individual algorithms and the ensemble model (climate-only)



**Bio25 (Radiation of the driest quarter)**

**Contribution: 37.73%**

**Bio24 (Radiation of the**

**wettest quarter) Contribution: 35.57%**

**Bio4 (Temperature seasonality)**

**Contribution: 26.7%**

Figure 8. Response curves of bioclimatic variables in the climate-only model

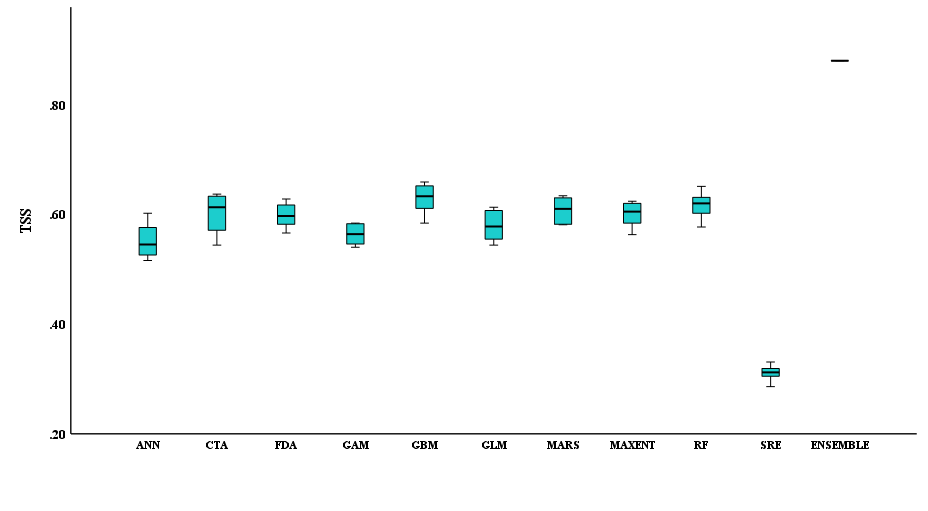
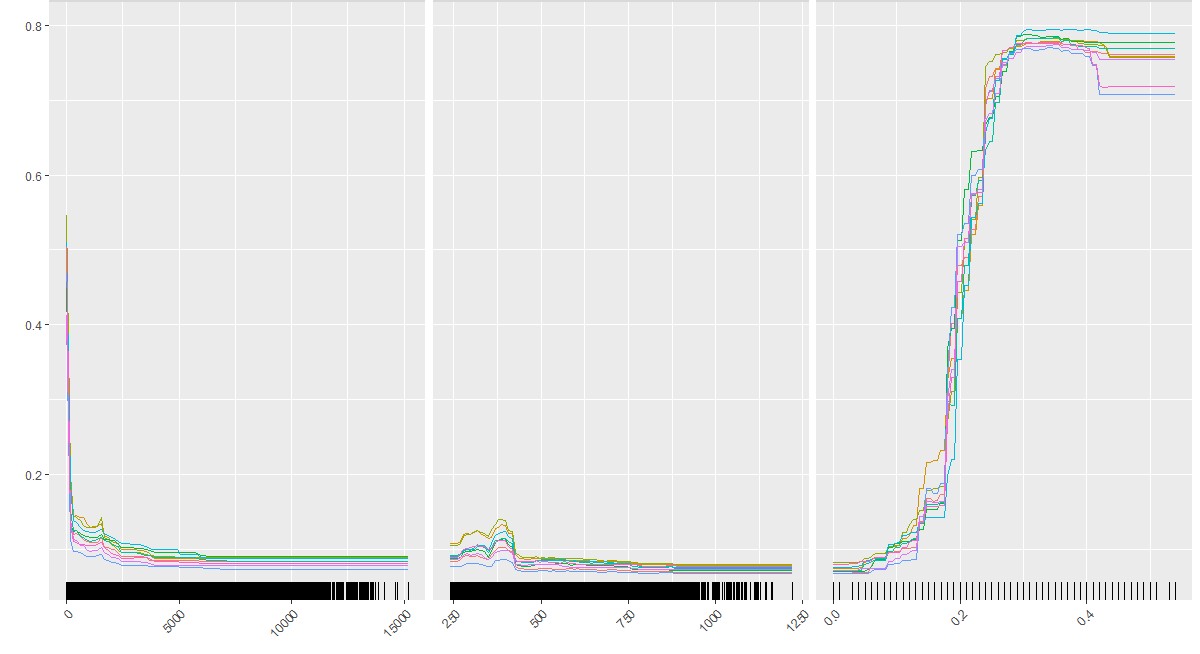


Figure 9. TSS scores of individual algorithms and the ensemble model (environment-only)



**FPC**

**Contribution: 57.36%**

**Elevation**

**Contribution: 8.54%**

**Distance to Regional Ecosystems (Floral resources)**

**Contribution: 34.1%**

Figure 10: Response curves of environmental variables in the environment-only model

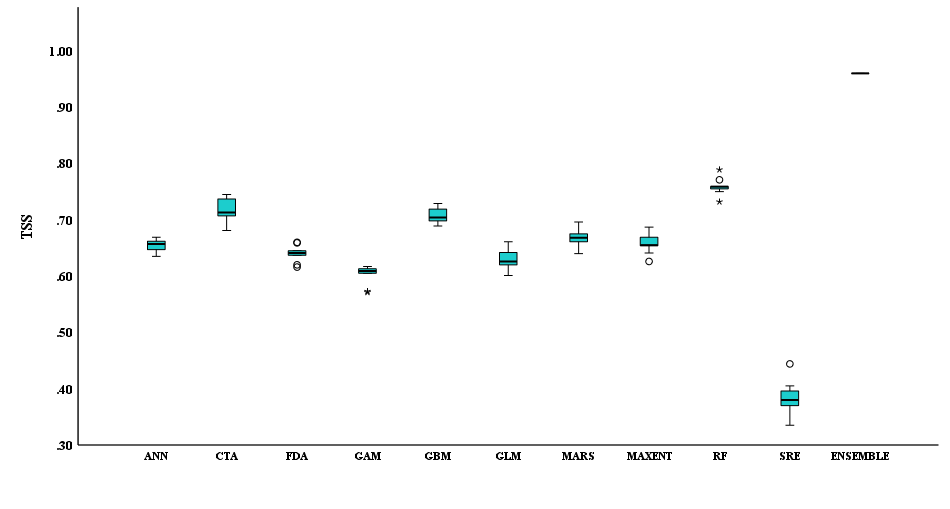


Figure 11. TSS scores of individual algorithms and the ensemble model (combined)

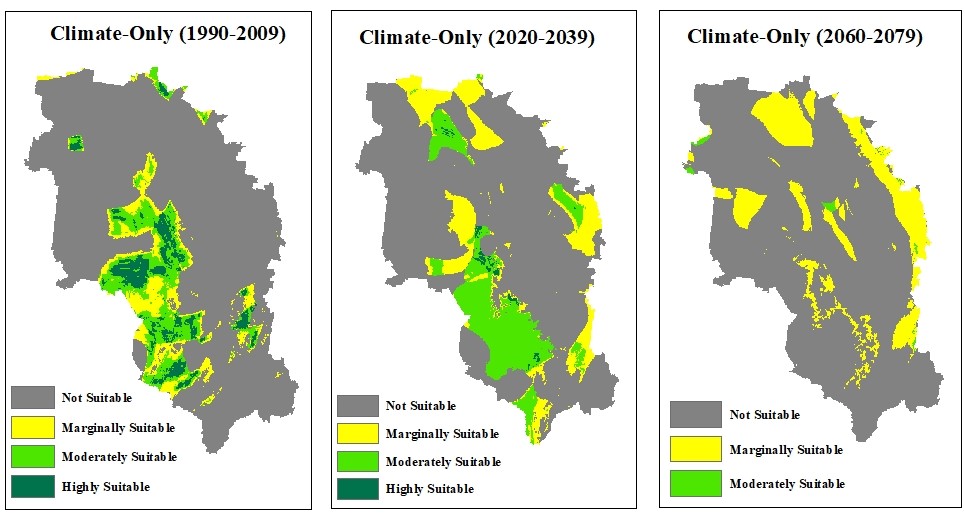


Figure 12. Suitability maps for honey bees: Climate-only scenario in 1990-2009, 2020-2039 and 2060-2079

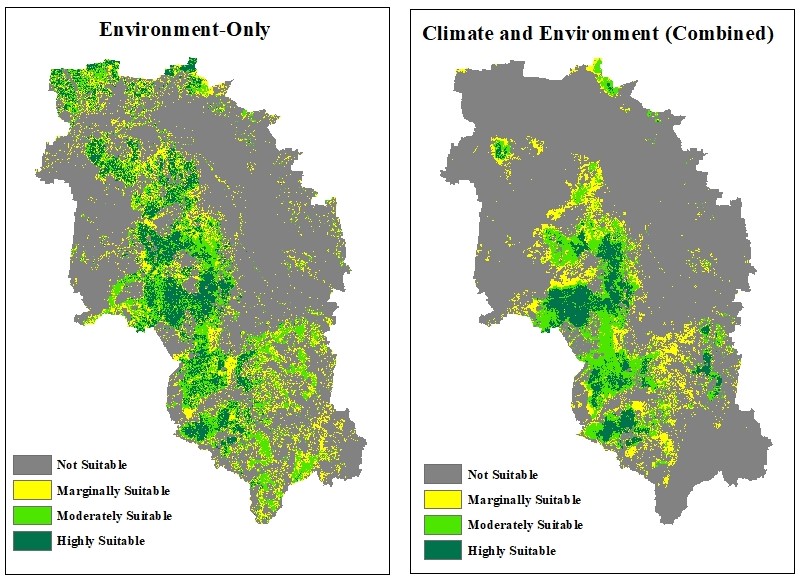


Figure 13. Suitability maps for honey bee habitat: environment-only and combined (Climate and Environment) scenarios

**Appendices for**

**Unravelling the Impact of Climate Change on Honey Bees: An Ensemble Modelling Approach to Predict Shifts in Habitat Suitability in Queensland, Australia**

Appendix T1: Thirty-five bioclimatic variables used for multicollinearity testing (Sourced from the New South Wales (NSW) and Australian Capital Territory (ACT) Regional Climate Modelling (NARCliM) database) (Hutchinson & Xu, 2015)

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Variable Number** | **Variable** | **Minimum temp (°C)** | **Maximum temp (°C)** | **Rainfall (mm month-1)** | **Radiation (W m-2d-1)** | **Pan evaporation (mm d-1)** |
| Bio01 | Annual mean temperature (°C) | × | × |  |  |  |
| Bio02 | Mean diurnal temperature range (mean(period max-min)) (°C) | × | × |  |  |  |
| Bio03 | Isothermality (Bio02 ÷ Bio07) | × | × |  |  |  |
| Bio04 | Temperature seasonality (C of V) | × | × |  |  |  |
| Bio05 | Max temperature of warmest week (°C) |  | × |  |  |  |
| Bio06 | Min temperature of coldest week (°C) | × |  |  |  |  |
| Bio07 | Temperature annual range (Bio05-Bio06) (°C) | × | × |  |  |  |
| Bio08 | Mean temperature of wettest quarter (°C) | × | × | × |  |  |
| Bio09 | Mean temperature of driest quarter (°C) | × | × | × |  |  |
| Bio10 | Mean temperature of warmest quarter (°C) | × | × |  |  |  |
| Bio11 | Mean temperature of coldest quarter (°C) | × | × |  |  |  |
| Bio12 | Annual precipitation (mm) |  |  | × |  |  |
| Bio13 | Precipitation of wettest week (mm) |  |  | × |  |  |
| Bio14 | Precipitation of driest week (mm) |  |  | × |  |  |
| Bio15 | Precipitation seasonality (C of V) |  |  | × |  |  |
| Bio16 | Precipitation of wettest quarter (mm) |  |  | × |  |  |
| Bio17 | Precipitation of driest quarter (mm) |  |  | × |  |  |
| Bio18 | Precipitation of warmest quarter (mm) | × | × | × |  |  |
| Bio19 | Precipitation of coldest quarter (mm) | × | × | × |  |  |
| Bio20 | Annual mean radiation (W m-2) |  |  |  | × |  |
| Bio21 | Highest weekly radiation (W m-2) |  |  |  | × |  |
| Bio22 | Lowest weekly radiation (W m-2 |  |  |  | × |  |
| Bio23 | Radiation seasonality (C of V) |  |  |  | × |  |
| Bio24 | Radiation of wettest quarter (W m-2) |  |  | × | × |  |
| Bio25 | Radiation of driest quarter (W m-2) |  |  | × | × |  |
| Bio26 | Radiation of warmest quarter (W m-2) | × | × |  | × |  |
| Bio27 | Radiation of coldest quarter (W m-2) | × | × |  | × |  |
| Bio28 | Annual mean moisture index |  |  | × |  | × |
| Bio29 | Highest weekly moisture index |  |  | × |  | × |
| Bio30 | Lowest weekly moisture index |  |  | × |  | × |
| Bio31 | Moisture index seasonality (C of V) |  |  | × |  | × |
| Bio32 | Mean moisture index of wettest quarter |  |  | × |  | × |
| Bio33 | Mean moisture index of driest quarter |  |  | × |  | × |
| Bio34 | Mean moisture index of warmest quarter | × | × | × |  | × |
| Bio35 | Mean moisture index of coldest quarter | × | × | × |  | × |

Appendix T2: The ODMAP protocol followed for the development of honey bee species distribution models and prediction of habitat suitability in future

| **ODMAP Section/**  **Subsection** | **ODMAP Elements** |
| --- | --- |
| **OVERVIEW** | |
| *Authorship* | * **Authors:** Sarasie Tennakoon, Armando Apan, and Tek Maraseni * **Contact e-mail:** [sarasie.tennakoon@gmail.com](mailto:sarasie.tennakoon@gmail.com), sarasie.tennakoon@usq.edu.au * **Title:** Unravelling the Impact of Climate Change on Honey Bees: An Ensemble Modelling Approach to Predict Shifts in Habitat Suitability in Queensland, Australia |
| *Model objective* | * **Objective:** Identify the most influential bioclimatic and environmental variables and quantify their relative importance on honey bee distribution.   Predict habitat suitability for honey bees in two future time-spans: 2020-2039 and 2060-2079.   * **Target outputs:** Habitat suitability maps based three climate scenarios: 1990-2009, 2020-2039 and 2060-2079, environmental variables and a combined climate and environment variables. |
| *Taxon* | European honey bee, *Apis mellifera*, Apis, Apidae, Hymenoptera, Insecta |
| *Location* | Queensland, Australia |
| *Scale of analysis* | * **Spatial extent (Lon/Lat):** 150012’ - 151097’ E, 27077’ - 27068’ S, covering an extent of 37,650 km2 in Southern Queensland, Australia * **Spatial Resolution:** 250m * **Temporal extent/time period:** Honey bee occurrence data- 1990 to present; environmental data - present, and bioclimatic variables – 1990-2009, 2020-2039 and 2060-2079 * **Type of extent boundary:** Political (Local Area Boundaries) |
| *Biodiversity data overview* | * **Observation type:** Managed apiary site locations (records), human observations, machine observations * **Response/Data type:** Presence-only |
| *Type of predictors* | Bioclimatic and environmental variables |
| *Conceptual model / hypothesis* | * **Hypothesis about species-environment relationships:** Distribution of a species is in equilibrium with the environmental and climatic factors that have an influence on that species. Honey bee distribution is mainly influenced by the bioclimatic variables, radiation in wettest and driest quarters, and temperature seasonality and the environmental variables proximity to regional ecosystems (floral resources), foliage projective cover and elevation. |
| *Assumptions* | * Species’ distribution is at equilibrium with their environment * Species presence data are a representative sample of the species distribution across the study area * Pseudo absence data/background data can be treated as absence data * All the key predictor variables of the species under consideration are accounted for in the model |
| *SDM algorithms* | **Algorithms:**  Artificial Neural Network (ANN)  Classification Tree Analysis (CTA)  Flexible Discriminant Analysis (FDA)  Generalised Additive Model (GAM)  Generalised Boosting Model (GBM)  Generalised Linear Model (GLM)  Multiple Adaptive Regression Splines (MARS)  Maximum Entropy (MAXENT)  Random Forest (RF)  Surface Range Envelope (SRE)   * **Model complexity:** Ten modelling algorithms were used * **Model averaging:** The models with TSS>0.7 were used to develop ensemble models pertaining to climate-only and the combined climate and environment scenarios whereas the models with a TSS>0.6 were incorporated in building the environment only model |
| *Model workflow* | * Included honey bee presence data pertaining to both human managed systems and natural occurrences * The presence data were rarefied using the SpThin package in R to reduce sample bias. * Initially, 8 environmental variables and 35 bioclimatic variables were selected and tested for multicollinearity using USDM (Uncertainty Analysis for Species Distribution Models) package in R to avoid model overfitting and reduce uncertainty in model parameters. * Variables with a correlation coefficient >0.8 and variance inflation factor (VIF) >5 were excluded from further analysis. * The most influential 3 bioclimatic variables and the 3 environmental variables were retained following a stepwise removal of the least contributing variables. * Five-thousand pseudo absence data were generated, and this process was repeated for three times to avoid random bias. * Presence and absence data were divided into training (80%) and testing data (20%). * The raster layers were processed to have a cell size of 250m×250m and projected to WGS84 coordinate system using ArcMap 10.8.1 * The modelling process consisted of 90 model runs that included ten modelling algorithms, three pseudo absence generation runs, and three evaluation runs. * Using the ensemble modelling option available in BIOMOD2, an ensemble species distribution model was constructed by applying multiple algorithms above a selected threshold. * Three models namely the climate-only model, the environment-only model, and the combined climate (1990-2009) and environment model were developed. * The climate-only model was developed using the three most influential bioclimatic variables for honey bees, namely Bio4 (temperature seasonality), Bio24 (radiation of the wettest quarter), and Bio25 (radiation of the driest quarter). * The three environmental variables with the highest contribution to the model i.e., proximity to regional ecosystems (floral resources), foliage projective cover, and elevation were used in building the environment-only model. * The combined climate and environment model was developed by incorporating the environmental and bioclimatic variables from both environment-only and climate-only models. These variables included foliage projective cover, proximity to regional ecosystems, elevation, bio4, bio24, and bio25. * Suitability maps were generated using BIOMOD2 for each scenario under consideration, namely: climate-only (1990-2009), environment-only, and the combined climate and environment model. Using ensemble forecasting, suitability maps for the two future scenarios i.e., 2020-2039 and 2060-2079 were generated. |
| *Software, codes, and data* | * **Modelling platform:** BIOMOD2 package on R (Version 4.2.2) * **Code:** Code is shared in DRYAD data repository * **Data:** Data is shared in DRYAD data repository |
| **DATA** | |
| *Biodiversity data* | * **Taxon names:** *Apis mellifera* * **Taxonomic reference system:** N/A * **Ecological level:** Species level * **Data source:**   Honey bee presence data were derived from the Queensland Spatial Catalogue and Atlas of Living Australia (time period from: 1990 to present)   * **Sampling design:** N/A * **Sample size:** 1,595 presence records collected from the study area in Southern Queensland, Australia * **Absence data:** Five-thousand pseudo-absence data were generated * **Data cleaning and filtering:** SpThin package in R was used to rarefy the presence data |
| *Data partitioning* | * The honey bee presence and pseudo-absence data were divided into training (80%) and testing (20%) sets |
| *Predictor variables* | * **Predictor variables:**  1. Bioclimatic variables — Temperature seasonality (BIO4), Radiation in wettest quarter (BIO24), and Radiation in driest quarter (BIO25) 2. Environmental variables — Proximity to regional ecosystems (floral resources), Foliage Projective Cover, and Elevation  * **Data sources:**  1. Bioclimatic variables: New South Wales (NSW) and Australian Capital Territory (ACT) Regional Climate Modelling (NARCliM) 2. Regional ecosystems and foliage projective cover: Queensland Spatial Catalogue: Queensland Government (<https://qldspatial.information.qld.gov.au>) 3. Elevation: GEODATA 9 Second Digital Elevation Model (DEM-9S) Version 3 from Geoscience Australia (https://ecat.ga.gov.au)  * **Data processing:** The raster layers were extracted, projected, and resampled using Arcmap10.8.1 * **Spatial resolution of raw data:** 250m, 25m * **Projection:** WGS84 |
| **MODEL** | |
| *Variable pre-selection* | * Thirty-five bioclimatic variables and eight environmental variables were selected. * The variables with correlation coefficients >0.8 and VIF>5 were removed from further analysis. Only 4 bioclimatic variables and all 8 environmental variables were retained based on the results of multicollinearity testing. * The most influential variables were retained following a process of removing the least contributing variables. |
| *Multicollinearity* | * Multicollinearity among the predictor variables were tested using the USDM (Uncertainty Analysis for Species Distribution Models) package in R. |
| *Model settings* | * Default settings for BIOMOD2 |
| *Model estimates* | * **Model coefficient:** TSS, ROC and KAPPA * **Variable importance:** Importance of predictor variables in the three different models were calculated |
| *Model averaging / ensembles* | * To develop climate-only and the combined model, the models with a TSS>0.7 were selected whereas to develop the environment-only model, the algorithms with TSS>0.6 were selected. |
| *Non-independence* | * No test was performed to test for non-independence of the models. |
| **ASSESSMENT** | |
| *Performance statistics* | * **Performance statistics estimated on training data:** Model performances were assessed using the TSS scores |
| *Plausibility checks* | * **Response plots:** Ecological plausibility was tested using the response curves for the predictor variables. |
| **PREDICTION** | |
| *Prediction output* | * The continuous probability maps were classified into four categories as highly suitable, moderately suitable, marginally suitable and not suitable. |
| *Uncertainty quantification* | * **Algorithmic uncertainty:** Ensemble forecasting was employed to reduce model-based uncertainty and consensus method was utilized to combine outputs of individual algorithms * **Reality check:** On-ground reality was validated against the existing locations of managed apiary sites and honey bee occurrences. |

Appendix T3: Performance of models resulting from different combinations of predictor variables

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | TSS | ROC | KAPPA | Variable Importance |
| Climate Only |  |  |  |  |
| Bio4 + Bio24 + Bio25 | 0.85 | 0.98 | 0.72 | Bio4 36.42%  Bio24 36.73%  Bio25 26.86% |
| Environment Only |  |  |  |  |
| RE + Elevation + Distance to roads | 0.80 | 0.95 | 0.60 | RE 40.84%  Elevation 1.9%  Distance to roads 57.29% |
| RE + Elevation + Aspect | TSS value of each algorithm < 0.6 |  |  |  |
| RE + Elevation + Slope | TSS value of each algorithm < 0.6 |  |  |  |
| RE + Elevation + Distance from trees | TSS value of each algorithm < 0.6 |  |  |  |
| RE + Elevation + Distance to water | TSS value of each algorithm < 0.6 |  |  |  |
| RE + Elevation + FPC (TSS cut off 0.6) | 0.88 | 0.98 | 0.75 | RE 34.10%  Elevation 8.54%  FPC 57.36% |
| RE + FPC (TSS cut off 0.6) | 0.80 | 0.96 | 0.64 | RE 25.82%  FPC 74.18% |
| Climate + Environment |  |  |  |  |
| RE + FPC + Bio4 + Bio24 + Bio25 | 0.93 | 0.99 | 0.89 | RE 19.90%  FPC 21.42%  Bio4 7.19%  Bio24 32.34%  Bio25 19.15% |
| RE + FPC + Elevation+ Bio4 + Bio24 + Bio25 | 0.92 | 0.99 | 0.87 | RE 16.76%  FPC 24.10%  Elevation 5.57%  Bio4 5.01%  Bio24 29.63%  Bio25 18.93% |