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**RT:** HOST TREE INFLUENCE ON MOPANE WORM DISTRIBUTION IN SOUTHERN AFRICA

RESEARCH ARTICLE

**Host tree-based scenario modelling for predicting a key edible insect, mopane worm *Gonimbrasia belina* (Westwood, 1894) distribution in Southern Africa**

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### **Abstract**

*Gonimbrasia belina*, known as the mopane worm, is a large edible caterpillar in tropical and subtropical regions. However, little is known about the bioecology of this species as influenced by its host trees. This study evaluated the importance of different potential host trees in understanding mopane worms' behaviour and spatial distribution. To assess their relative importance, the study compared models incorporating various mopane worm host trees and predictor variables. Using the species distribution modelling (SDM) package in R, an ensemble of random forest (RF), support vector machine (SVM), and boosted regression tree (BRT) algorithms were used to assess the spatial extent of mopane worm distribution in Southern Africa. Four host tree-based scenarios were developed to assess their relative contribution to the relative distribution of the mopane worm i.e., (1) by excluding all the potential host trees as explanatory variables and considering only the environmental variables, (2) focusing on the primary host tree, *Colophospermum mopane* as an explanatory variable together with the other environmental variables, (3) incorporating all the host trees, including *C. mopane* and (4) examining all other host trees excluding *C. mopane*. Results demonstrated that incorporating all host trees enhanced the models' predictive abilities (mean AUC

= 0.87) underscoring the significant impact of the alternative host trees on the mopane worm distribution patterns beyond just the *C. mopane*. This study highlights the significance of host trees in predicting the behaviour and distribution of mopane worm populations, providing valuable insights and decision-making for mopane worm use as an alternative protein source, conservation efforts, and land management practices.

## **Keywords**

edible insects – ensemble – entomophagy – mopani forest – species distribution modelling

## **1 Introduction**

The growing global interest in harnessing insects as a sustainable protein source has gained significant momentum in response to the impact of climate change and population on food systems (van Huis, 2015). Edible insects, in particular, have attracted considerable attention as a viable and nutritious food source, especially in regions facing food security challenges such as in Africa (Stull and Weir, 2023). This emerging trend not only addresses nutritional needs in food and feed production but also offers ecological, nutraceutical, and medicinal benefits (Kipkoech *et al.*, 2023). The Food and Agricultural Organisation of the United Nations (FAO) has recognised edible insects as a sustainable solution to address the expected food shortage, especially regarding protein, due to their high nutritional value and minimal environmental impact (Rodrigues *et al.*, 2021). Numerous studies have underscored the growing importance of edible insects in human nutrition (Mokaya *et al.*, 2023; Egonyu *et al.*, 2021; Kelemu *et al.*, 2015). Consequently, from a nutritional perspective, edible insects offer a substantial supply of protein and essential minerals such as iron,

calcium, and zinc. These attributes position them as a viable component within a range of strategies aimed at mitigating the challenges of high protein demand caused by population growth and climate change on food insecurity, a predicament already impacting several regions of the world.

In many African countries, notably those situated within the Southern Africa region, edible insects have been widely adopted as an essential protein source. *Gonimbrasia belina* (Lepidoptera: Saturniidae; Westwood, 1894) is a species of emperor moth found in warmer parts of Southern Africa (Figure 1). It is a large caterpillar, known as the mopane worm with its name mainly originating from the primary consumption of the mopane tree (*Colophospermum mopane*) (Niassy *et al.*, 2016).



FIGURE 1 (A) A cluster of mopane worm (*Gonimbrasia belina*) on a leaf of mopane tree (*Colophospermum mopane*), (B) a late instar caterpillar form of the emperor moth *G. belina*.

It is native to the region and exists in the larval stage as the mopane worm, representing the caterpillar form of the emperor moth *G. belina* (Sekonya *et al.*, 2020). Mopane worm is culturally significant and is renowned for its protein-rich composition. It plays a crucial role in the local diets and culinary traditions of countries such as Botswana, South Africa, and Zimbabwe (Thomas, 2013; Niassy *et al.*, 2018; Hlongwane *et al.*, 2020). The caterpillars are one of the most economically important insect food resources in Southern Africa with an estimated economic

value worth US \$80 million in South Africa, US \$35 million in Zimbabwe, and US\$ 3.3 million in Botswana (Bara *et al.*, 2022). The availability and viability of suitable host trees is a significant factor affecting the distribution and abundance of mopane worm throughout the Southern Africa region (Togarepi *et al.*, 2020). Host trees play a crucial role as the primary food source for mopane worm larvae. These larvae rely on the leaves of specific host trees, such as the mopane tree, due to their high nutritional value. By consuming these leaves, the larvae obtain essential nutrients that fuel their growth and development. Understanding the relationship between mopane worm and their host trees is essential for effective sustainable resource management, rearing of the species, and conservation initiatives in the region (Thomas, 2013).

The mopane worm primarily feeds on the mopane tree, *C. mopane* (Ferreira *et al.*, 2003). After developing from pupae, adult moths lay eggs on the leaves of *C. mopane* and other suitable host trees during the initial weeks of the rainy season in October. However, a secondary and smaller reproduction of caterpillars may occur in April if sufficient rainfall is received in February (Bara *et al.*, 2022). Thus the most optimal period for harvesting these caterpillars is from December to January when they have reached their maximum size and developmental stage before pupation (Kwiri *et al.*, 2020). In some countries within the Southern African sub-region such as Botswana, mopane worms naturally occur twice a year (bivoltine) while in other countries they are univoltine (Mogomotsi *et al.*, 2018). Hence there is a need to consider sustainability mechanisms that will ensure sound conservation principles.

However, the availability of mopane worm is threatened by overharvesting and the decline of its primary host tree due to climatic change and anthropogenic activities (Fakazi *et al.*, 2021). Previous efforts have explored the possibilities for sustainable harvesting, however, this has not been successful due to high demand, low yields, and erratic rainfall attributed to climate change

(Baiyegunhi *et al.*, 2016). Therefore, understanding the influence of host trees on the growth, development, and distribution of mopane worm is crucial for effective conservation and long-term viability. Diverse host species have the potential to offer habitat resilience, reduce pressure on mopane trees, enhance nutritional variation, and promote overall biodiversity (Maquia, 2021). Additionally, expanding research into alternative host trees is crucial in the quest to rear mopane worms. While previous studies have predominantly focused on the mopane tree as the preferred host (e.g. Ngarega *et al.* 2021a), the decline in mopane tree populations necessitates exploring alternative host tree species (Stevens, 2021).

In this current study, we used species distribution modelling (SDM) techniques, which have demonstrated significant value in ecological research for predicting species distributions (Cruse *et al.*, 2012). The SDM approach used in this study involves constructing an ensemble model from various algorithms, including random forest (RF), support vector machine (SVM), and boosted regression tree (BRT). The ensemble model integrates the strengths of individual algorithms, leading to enhanced model accuracy and robustness (Feng *et al.*, 2020). The RF algorithm is well suited for handling complex interactions between variables and effectively manages large datasets, making it particularly relevant to this study's objectives (Qi, 2012). The SVM algorithm demonstrates proficiency in high-dimensional spaces, offering valuable predictive capabilities (Otchere *et al.*, 2021). On the other hand, the BRT algorithm employs an iterative process to capture non-linear relationships effectively, which can significantly improve model performance (Reiss *et al.*, 2015).

Through using the SDM approach, this research aimed to understand how specific environmental variables, particularly the presence of host trees, affect the spatial distribution of mopane worm populations in the Southern Africa region. The primary hypothesis of the study was,

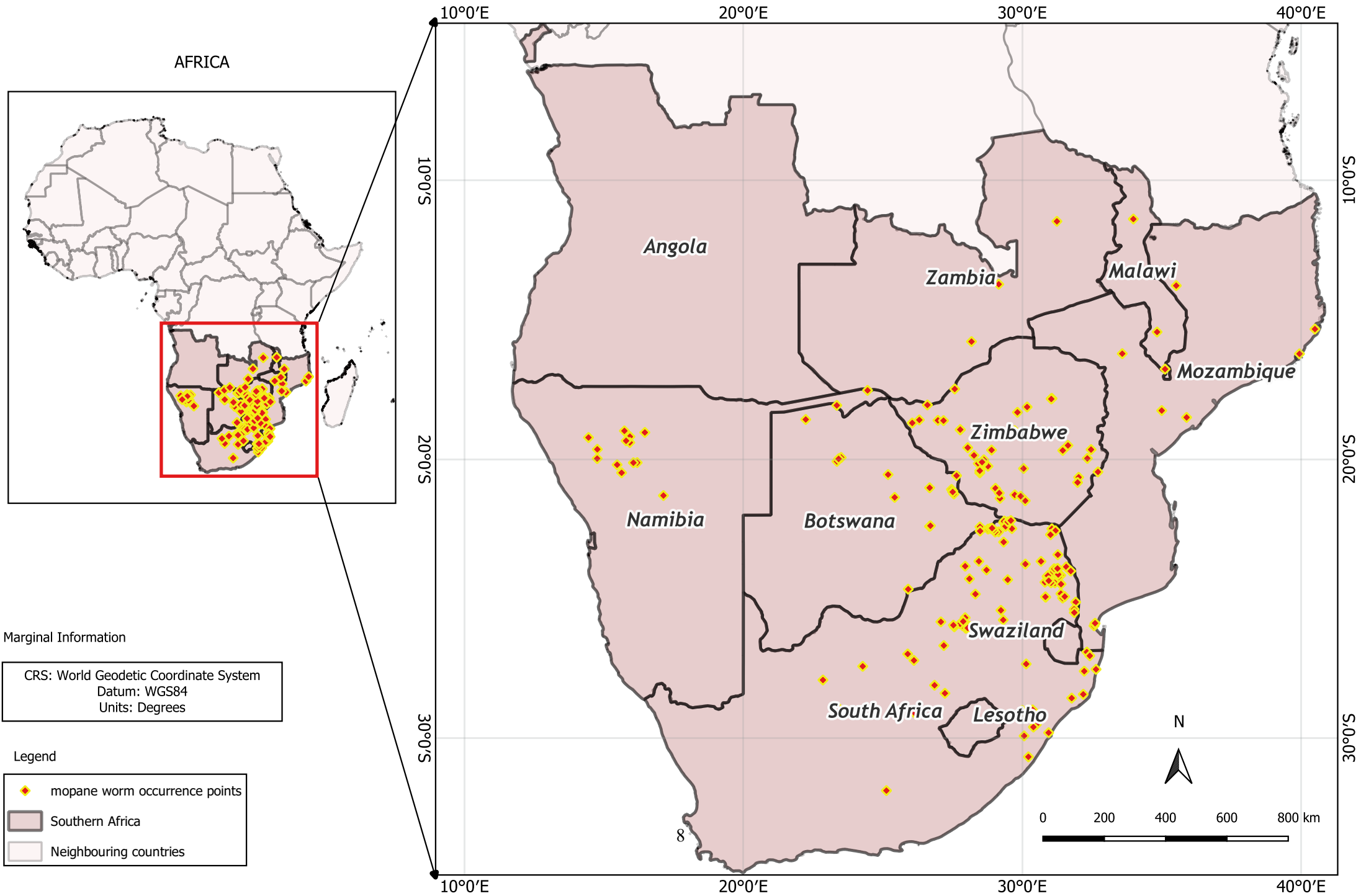
therefore, to assess the extent of the influence of host trees on the predictive ability of mopane worm habitat suitability models. By incorporating the findings of this research, researchers can better assess the suitability of alternative host trees and their potential to complement the declining *C. mopane*, thus offering alternative resources for mopane worm to thrive and ensuring the species' long-term sustainability.

## 2 Materials and methods

### *Study area*

The study was conducted in Southern Africa i.e., Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia, and Zimbabwe collectively termed as Southern Africa (**Error! Reference source not found.**). The study area is located between latitudes 34° 54' S and 4° 21' S, and longitudes 8° 58' E and 41° 18' E, covering an approximate area of 5,995,215 km<sup>2</sup>. Southern Africa is home to a variety of ecosystems, landscapes, and climatic conditions. It includes countries with coastlines such as Angola, Mozambique, Namibia, and South Africa as well as landlocked nations like Botswana, Lesotho, Malawi, Swaziland, Zambia, and Zimbabwe (Kawasaki *et al.*, 2021). The region's geography ranges from arid and semi-arid landscapes in Botswana and Namibia to lush forests and savannahs in Mozambique and Zambia (Mukwada, 2018). Southern Africa includes a diverse range of ecological habitats, such as the vast Kalahari Desert, the Okavango Delta's wetlands, the Zambezi River basin, the Miombo woodlands, the Eastern Highlands, and South Africa's various biomes (Dowsett-Lemaire, 1985). Because of the diversity of these habitats, not all of them are suitable for the sustenance of the mopane worm life cycle.

FIGURE 2 Spatial distribution of mopane worm (*Gonimbrasia belina*) in Southern Africa.





### ***Species occurrence data***

The occurrence data for the mopane worm and its potential host trees were obtained from the Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>) and the iNaturalist website (<https://www.inaturalist.org/>). The GBIF is an international network and data infrastructure funded by the world's governments aimed at providing access to data about all taxa. The facility hosts more than 2 billion records of data from all taxa, hence was ideal as the main data source for our target edible insect (mopane worm) and its potential host trees. Additionally, we utilised iNaturalist, a citizen science platform, to ensure comprehensive occurrence data for all the species. In this study, presence-only data was used and is summarised in TABLE 1 . Only records of species that had precise locations and coordinates were included in the list of occurrence data used in the analysis. To ensure data integrity, entries with missing values, duplicates, data older than 1950, due to higher susceptibility to unreliability (Perennes *et al.*, 2021), and incomplete information regarding occurrence locations were systematically excluded. This data cleaning was done using the “rgbif v.0.7.0” package developed by Chamberlain *et al.* (2022) in the R environment (R Core Team, 2023). It was also assumed that the year and the season would not affect the location of the occurrence hence this was not considered as a delimiter within the elimination criteria. However, approximately one harvest per year during the early months of the rainy season (November to January) with seldom harvests being conducted between April and May of good rainfall years. The quantity of the harvest varies from year to year mainly influenced by the presence and viability of leaves of host trees.

TABLE 1 Occurrence data of mopane worm (*Gonimbrasia belina*) and its potential host trees obtained from the Global Biodiversity Information Facility (GBIF) and iNaturalist website

Species name	Taxonomic group (Order: Family)	Species type	Number of records	Number of retained records after spatial thinning
<i>Gonimbrasia belina</i> (Westwood, 1894)	Lepidoptera: Saturniidae	edible insect	462	260
<i>Colophospermum mopane</i> (Kirk ex Benth) J. Léonard	Fabales: Fabaceae	host tree	1594	950
<i>Dichrostachys cinerea</i> (L.) Wight and Arn.	Fabales: Fabaceae	host tree	1737	856
<i>Diospyros mespiliformis</i> Hochst. ex A.DC.	Ericales: Ebenaceae	host tree	385	217
<i>Julbernardia globiflora</i> (Benth.) Troupin	Fabales: Fabaceae	host tree	369	300
<i>Sclerocarya birrea</i> (A.Rich.) Hochst.	Sapindales: Anacardiaceae	host tree	1395	648
<i>Terminalia sericea</i> Burch. ex DC.	Myrtales: Combretaceae	host tree	1353	859

### ***Mopane worm (Gonimbrasia belina) occurrence data***

A systematic spatial thinning technique was applied to the mopane worm occurrence data obtained from the GBIF and iNaturalist databases, retaining within the used dataset, points that have a distance of 1 km apart in all directions using the “spThin v.0.2.0” package (Aiello-Lammens et al., 2015). This thinning process aimed to mitigate bias caused by the clustering of points and reduce potential overfitting in the species distribution model. TABLE 1 shows the reduced number of points utilised in the analysis.

### ***Host tree occurrence data***

Various tree species documented in the literature as suitable host trees were considered as potential host trees in this study due to their critical role in the distribution and abundance of mopane worms throughout Southern Africa (Togarepi *et al.*, 2020). The analysis of the relationship between mopane worm and these host trees is fundamental to improving our understanding of resource management, potential mopane worm rearing opportunities, and critical conservation efforts in the region (Thomas, 2013). By considering the significance of these host trees, the study contributed to a comprehensive understanding of the interplay between the mopane worm and their crucial habitat resources.

The selection of suitable host trees was informed by a user-defined criterion that ensured the development of robust models i.e. the species needed to have a minimum of 100 occurrence records within the spatial extent of Southern Africa. This approach was informed by the need to include documented substitute host tree species for mopane worm that were predominantly found in Southern Africa. Consequently, the host tree *Uapaca kirkiana* which has been reported in Shen *et al.* (2023) as one of the main hosts of mopane worm was excluded from the analysis as it did

not meet the threshold number of 100 occurrence points within the spatial extent of Southern Africa, resulting in a consideration of only the top 6 host trees (TABLE 1 ). Similarly, spatial thinning was done for the host tree occurrence data at a 1km radial distance. Figure 3 represents the selected host trees present in Southern Africa.

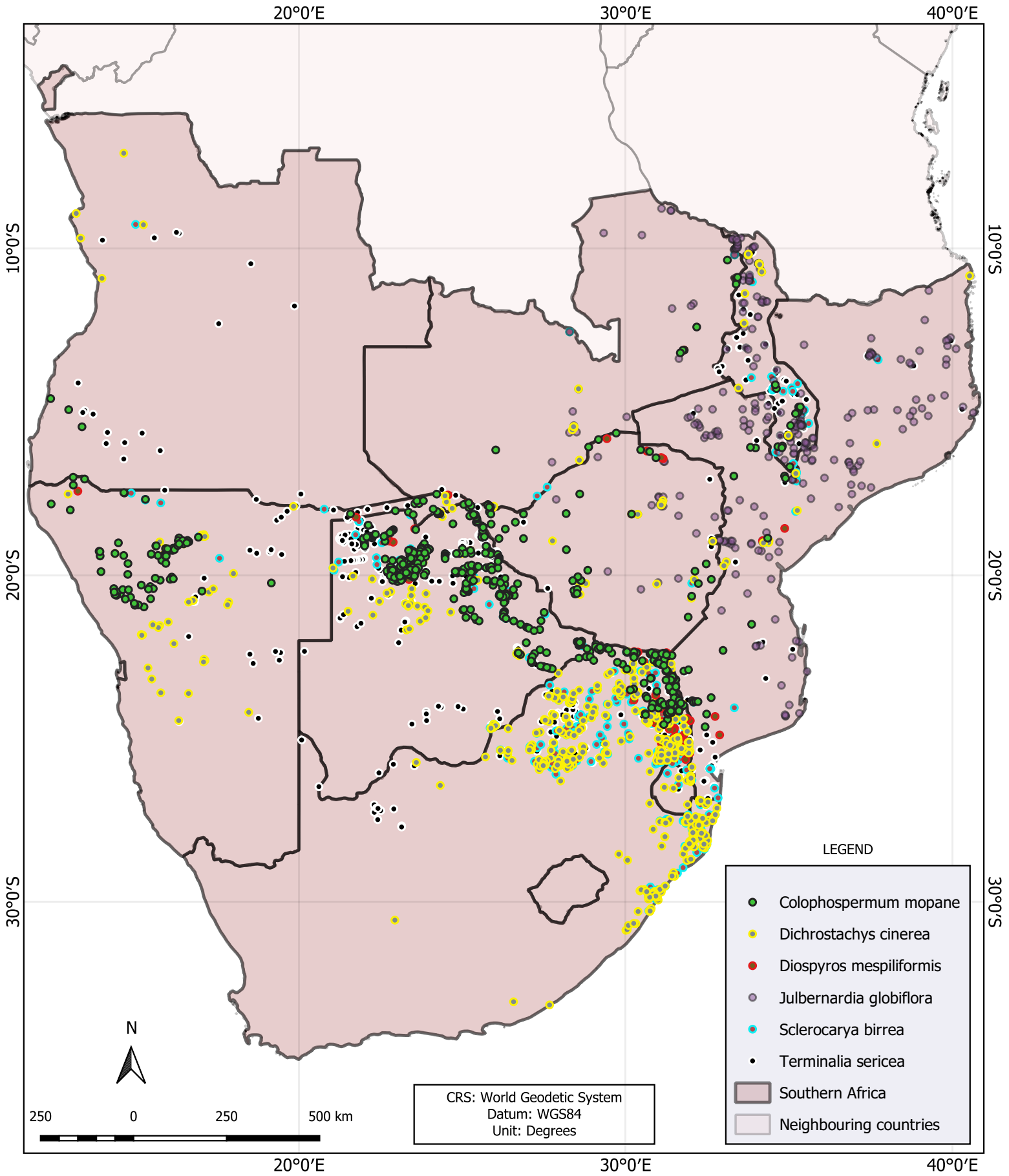
### ***Predictor variables***

#### Bioclimatic variables

Bioclimatic variables are environmental variables that are used to describe the ecological conditions of various species in a given area (Title and Bemmels, 2018). They have been used predominantly to perform SDM, such as in this study, as they offer crucial knowledge in understanding species' ecological niches (Mtengwana *et al.*, 2021).

We considered 19 bioclimatic variables in running both host tree distribution models and the mopane worm model scenarios. The bioclimatic variables used in this study were freely obtained from the WorldClim database (<https://www.worldclim.org/>) at a spatial resolution of 30 arc seconds (i.e.  $1 \times 1$  km). The 19 bioclimatic variables were clipped to the Southern Africa region and were later subjected to a collinearity test in R. The test employed a hierarchical approach, i.e. Pearson's correlation test and the variance inflation factor (VIF). Supplementary Table S1 shows the bioclimatic variables that were used together with the other predictor variables for various host tree models and the mopane worm model scenario.

FIGURE 3 Spatial distribution of mopane worm (*Gonimbrasia belina*) suitable host trees.



## Edaphic variables

Edaphic variables were used in the study as they have proven valuable for assessing the ecological niche requirements of tree species and comprehending the factors that influence their geographic distribution in numerous studies on host tree species distribution models (Maes *et al.*, 2019; Pecchi *et al.*, 2019; Pelletier *et al.*, 2019). The behaviour of mopane worm larvae, specifically their burrowing into the ground and pupating during dry seasons, suggests their preference for favourable soil conditions (Shen *et al.*, 2023). This behaviour indicates that the larvae actively seek out soil environments that are conducive to their pupation process, potentially characterised by specific moisture levels or other soil properties that support successful development (Styles and Skinner, 1996).

Soil variables used in the study were downloaded from various sites, as shown in TABLE 2 . These variables were also tested alongside other predictor variables and filtered according to the thresholds set for Pearson's correlation and VIF. TABLE 2 gives a detailed account of the considerations for the soil variable for each host tree and mopane worm scenario model. These soil variables were resampled and projected to the same dimensions of Southern Africa in preparation for use in the models.

TABLE 2 Edaphic variables used in various models in this study.

Soil Variable	Source	Resolution	Time	Modeled species
OpenLandMap soil ph in H2O	Google Earth Engine catalogue (Hengl, 2018)	250 m	NA	All modelled species
Soil subsurface moisture (susm)	NASA-USDA Enhanced SMAP Global Soil Moisture Data <a href="https://earth.gsfc.nasa.gov/hydro/data/nasa-usda-global-soil-moisture-data">https://earth.gsfc.nasa.gov/hydro/data/nasa-usda-global-soil-moisture-data</a> (Google Earth Engine catalogue)	10 km	Average of 10 years	<i>C. mopane</i> (Rains, 2017) <i>J. globiflora</i> (Gwate and Ndou, 2022) <i>T. sericea</i> – both subsurface and surface soil moisture can be used but susm was considered (Nakanyala and Hipondoka, 2020) <i>D. cinerea</i> (Musimba, 2020)
Soil surface moisture (ssm)	NASA-USDA Enhanced SMAP Global Soil Moisture Data <a href="https://earth.gsfc.nasa.gov/hydro/data/nasa-usda-global-soil-moisture-data">https://earth.gsfc.nasa.gov/hydro/data/nasa-usda-global-soil-moisture-data</a> (Google Earth Engine catalogue)	10 km	Average of 10 years	<i>S. birrea</i> (Dzikiti <i>et al.</i> , 2022) <i>Mopane worm</i> – after filtering <i>D. mespiliformis</i> (Wakawa <i>et al.</i> , 2022)
Africa Surface lithology	RCMRD- Geoportal <a href="https://geoportal.rcmr.org/layers/">https://geoportal.rcmr.org/layers/</a>	~95 m	NA	All modelled species

NA = Not Applicable.

It is important to acknowledge that the decision to consider between soil subsurface moisture and soil surface moisture for the various host trees was contingent upon the scholarly sources cited in Table 2. The various citations given, expound upon the distinct root systems associated with each tree species.

## Topographic data

The digital elevation model (DEM) utilised in this study was obtained from the Google Earth engine platform. The primary data source for the DEM was the shuttle radar topography mission (SRTM), which provides elevation data with a spatial resolution of 30 meters (Farr *et al.*, 2007). The DEM data used in the study had gaps, and it was necessary to address these gaps by filling the 'NoData' raster cells in the DEM file. In quantum GIS (QGIS Version 3.28, 2022), the 'FillNoData' function within the GDAL plugin was employed, utilizing the nearest neighbour interpolation technique. This process allowed for the estimation of values in the missing areas in the DEM raster. The resampled and projected DEM raster, representing the general altitude of Southern Africa, was then aligned with the masking raster layer file for further analysis as a predictor variable.

## Land use/ land cover

Land use and land cover (LULC) are essential factors in describing the ecological niche of mopane worm. Several studies have examined how LULC affects mopane worm distribution and highlighted the influence of human activities on the presence and abundance of mopane worm (Gondo *et al.*, 2019; Ndlovu *et al.*, 2019).

Assessing the impact of LULC on the population of mopane worm is crucial, as it can result in both positive and negative consequences. Positively, LULC provides information about the various land cover types and uses, such as agricultural use, which has been noted to favour mopane worm populations. Conversely, the distribution of mopane worm can be indirectly affected by human activities associated with land use, such as habitat modification or landscape fragmentation and degradation (Mugari *et al.*, 2019).



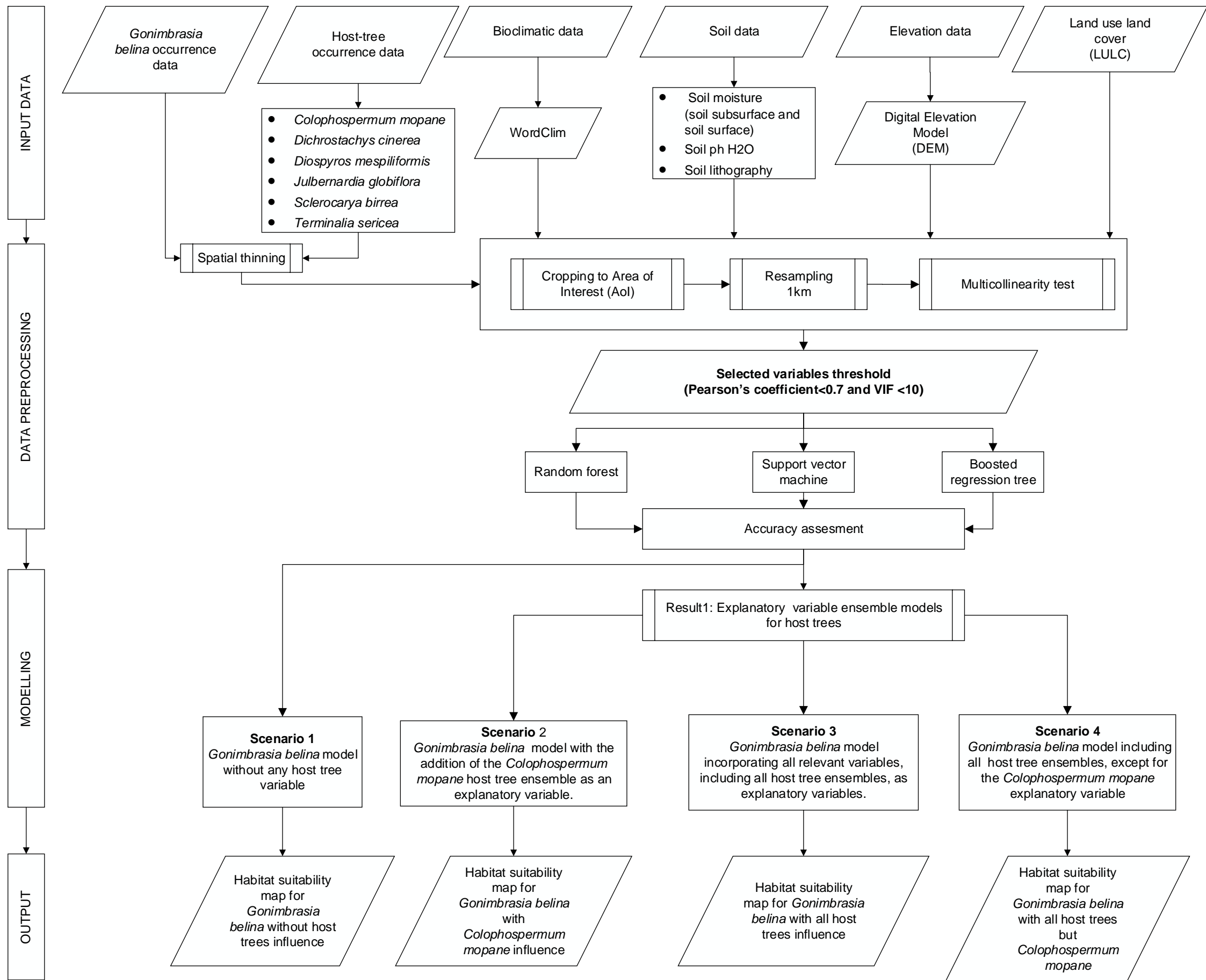


FIGURE 4 A systematic flowchart illustrating the methodological processes employed for modelling all the mopane worm host trees and mopane worm. The four main processes employed to develop the key models for this study were (1) input data, involving the collection of all relevant data types for the study (2) data preparation, which entailed data cleaning and selection of predictor variables (3) modelling, encompassing the use of ensembles and (4) generating various outputs aligned with the study's objectives.

The LULC raster layer was utilised in all four case model scenarios presented in Figure 4. The LULC raster image employed in this study was clipped to the geographic extent of Southern Africa and was obtained at a spatial resolution of approximately  $1 \text{ km} \times 1 \text{ km}$ . The primary data source for the consensus global land cover dataset was the EarthEnv website, which is supported by the NCEAS (National Center for Ecological Analysis and Synthesis), NASA (National Aeronautics and Space Administration), NSF (National Science Foundation), and Yale University. The data source contains 12 distinct land cover classes such as open water, snow/ice, urban/built up, cultivated and managed vegetation, herbaceous vegetation, and shrubs among others.

This dataset was selected due to its close alignment with the intended model resolution and its established importance in the context of monitoring and modelling biodiversity, ecosystems, and climate dynamics at a global scale (Tuanmu and Jetz, 2014). The LULC raster layer was later resampled and projected accurately to the dimensions of the mask file used (bioclim 4), in the R software.

### ***Variable selection and multicollinearity analysis***

#### Multicollinearity test for predictor variables

In SDM, overfitting is a common issue that can arise due to multicollinearity between predictor variables. Overfitting occurs when a model performs well on the training data but fails to generalise to independent data (Zhang *et al.*, 2019). To address this issue, one approach is to identify and eliminate the highly correlated variables from the models. Two common methods used for this purpose are the VIF and Pearson's correlation coefficient. The VIF assesses the extent to which multicollinearity raises the slope estimate variance (Liou and Muluaem, 2019).

The Pearson's correlation was set at  $|r| > 0.7$  while the VIF correlation was set at 10 following Makori *et al.* (2017). These thresholds help in identifying and removing variables with strong correlations. The 'car' package in the statistical software R, as described in Salmerón *et al.* (2019), was employed to carry out the elimination of highly correlated variables.

In the study, every model scenario had a set of predictor variables as described in the previous subsections, with the number of predictor variables ranging from 10-18, with host-tree scenario 4 having the highest number of variables used (Supplementary Figure S10). Notably, the DEM predictor variable was excluded from 2 out of the 10 models conducted in the study. This decision was made during the collinearity test process, where it was identified that the DEM variable exhibited high collinearity with other variables in those specific models using the set VIF threshold. Therefore, to ensure the models' accuracy and avoid multicollinearity issues, the DEM variable was removed from those analyses. The two models included that of the *J. globiflora* and *S. birrea* host trees.

#### Visualising multicollinearity tests output using a dendrogram

Understanding the relationships between predictor variables in statistical analysis requires the ability to visualise their multicollinearity. Various statistical techniques have been used to visualise multicollinearity outputs, with dendrogram plots being one of the most effective ways (Ahmadalipour and Moradkhani, 2018).

In the case of predictor variable tests for mopane worm host trees described in this study, dendrogram plots were specifically generated from sample extract information of proposed environmental layers within each model. These plots provide valuable insights into the

interrelationships between predictor variables, enabling a comprehensive understanding of potential multicollinearity effects in the analysis (Supplementary Figures S1-S7).

### ***Predicting host tree distribution in Southern Africa***

A total of 6 models representing potential host trees of mopane worm distribution were run in R within the sdm package (Naimi *et al.*, 2022). Each model was treated independently of others and multiple model runs were done for each host tree to achieve satisfactory model outputs that were later used as explanatory variables in three host-tree scenarios.

Several algorithms were tested in their ability to accurately model the host tree distribution, and three modelling techniques generally outperformed all SDM models. The three model algorithms that were chosen due to their good performance were support vector machine (SVM), boosted regression tree (BRT), and random forest (RF).

The difficulty of obtaining absence data has led to the widespread use of presence-only models with pseudo-absence (Downie *et al.*, 2013). Semiautomatic generation of ‘background’ points together with ‘presence-only’ data were used in the host tree and mopane worm model scenarios. Different presence-to-background point ratios were used for the various host tree models to achieve the best model performance, reduce biases, and champion equitable ratios of presence-to-background point data as shown in TABLE 3

TABLE 3 The ratios of the presence to background data used for each of the host tree modelling scenarios

Host tree model	Presence to background ratio data
<i>Colophospermum mopane</i>	1:5
<i>Dichrostachys cinerea</i>	1:10
<i>Diospyros mespiliformis</i>	1:10
<i>Julbernardia globiflora</i>	1:5
<i>Sclerocarya birrea</i>	1:10
<i>Terminalia sericea</i>	1:5

The explanatory variable derived from each mopane worm host tree model was an ensemble model of the best three performing algorithms, which were decided using accuracy metrics. Utilizing a weighted average of the best-performing model, ensemble models optimised the prediction accuracy of the various machine learning techniques (Vorsino *et al.*, 2014). To produce the ensemble models, the weighted area under the curve (AUC) was employed, with a threshold value of 0.7, to determine which models to include. The AUC has been commonly used in the selection of model algorithms for an optimal solution of an ensemble (Kumar *et al.*, 2023).

The QGIS software was used in the reclassification and generation of all host tree suitability maps for visualization purposes. The reclassification of the suitability raster layers exported from the R environment followed the class limits described by Azrag *et al.* (2022) i.e.  $\leq 0.2$  unsuitable,  $0.21 \leq 0.4$  low suitability,  $0.41 \leq 0.6$  moderate suitability, and  $0.61 \leq 1$  high suitability.

### ***Predicting mopane worm (Gonimbrasia belina) distribution in Southern Africa***

Four different model scenarios were employed with the primary model using mopane worm presence-only observations without any mopane worm host tree as an explanatory variable, scenario 1. The other three scenarios had the presence of mopane worm in addition to (1) *C. mopane* host tree (scenario 2), (2) all host trees (scenario 3), and (3) all host trees, except *C. mopane* (scenario 4) as described in the methodology flowchart (**Error! Reference source not found.**). The primary scenario 1 model, served as the base-comparison model. Several model runs were conducted to achieve optimal model performance, establishing precedence for the ratio of presence to background data points in the subsequent models. Given that the focus species was mopane worm, the only modification made in the consecutive models was the number of predictor variables added.

Scenario 1 model set the three main algorithms to be ensemble as BRT, RF, and SVM. The rest of the models used the same algorithms for consistency. These models were similarly run in R software using the SDM package (Naimi *et al.*, 2022), and the ensembles were produced using the weighted AUC accuracy metric. Each ensemble model for all four model scenarios had all three algorithms used regardless of the AUC threshold value of inclusion set for the host trees.

Subsequently, the resulting suitability raster layers of all four modelling scenarios were exported to QGIS software for reclassification using the same classification criteria employed to generate the suitability maps for the host trees described by Azrag *et al.* (2022). The process was followed by map generation based on the reclassified layers.

### ***Model evaluation***

Effective model evaluation is a crucial step in assessing the accuracy and reliability of modelling outcomes. In this study, the model accuracies were rigorously tested utilizing a robust 10-fold cross-validation approach. This method has consistently demonstrated its effectiveness in providing a comprehensive and reliable evaluation of a model's performance (Dutschmann *et al.*, 2023).

In this study, the metrics used to evaluate model performance included a variety of indicators such as AUC, correlation (COR), true skill statistic (TSS), and deviance. The model's overall capacity to distinguish between positive and negative instances is measured by the AUC. The values of the AUC range from 0 to 1. Higher AUC values indicate stronger discrimination ability (Mohammadi *et al.*, 2019). COR offers insights into the relationship's strength and direction with values ranging from -1 to +1. Better model performance is indicated by a higher absolute value of COR (Handel, 2015; Smith and Santos, 2020).

The TSS is a combined sensitivity and specificity metric. TSS values range between -1 and +1, with higher values indicating better classification performance (Parikh *et al.*, 2008). On the other hand, deviance is a measure of a model's goodness of fit. It quantifies the difference between the observed data and the model's predictions. Lower deviance values indicate better fit, suggesting that the model accurately captures the data's patterns (MacKenzie *et al.*, 2018a).

In this study, particular emphasis was placed on maximizing the TSS and AUC values while considering the tradeoff between COR and deviance. The focus was on achieving optimal discrimination between positive and negative instances (AUC) and accurately capturing the relationship between predicted and actual values (COR) of the host trees and mopane worm

(MacKenzie *et al.*, 2018b). By prioritizing TSS and AUC, the analysis sought to strike a balance between these key indicators to ensure a comprehensive evaluation of the model's performance.

### 3 Results

#### *Host tree suitability in Southern Africa*

Among the evaluated host tree models, the *D. mespiliformis* model consistently exhibited the highest performance across all three model algorithms (RF, SVM, and BRT). Specifically, the RF algorithm achieved the highest goodness of fit (AUC = 0.97 and TSS = 0.88; Table 4).

On the other hand, *T. sericea* consistently demonstrated the lowest performance among the studied host tree models, with the BRT algorithm yielding the lowest AUC and a TSS (Table 4). The *C. mopane* model closely followed the performance of the *D. mespiliformis* model, achieving high values for AUC and TSS across all three algorithms used.



TABLE 4 Accuracy metrics of host tree models utilizing random forest (RF), support vector machine (SVM), and boosted regression tree (BRT) algorithms. The model accuracies include the area under the curve (AUC), correlation (COR), true skill statistic (TSS), and deviance.

Host tree species name	Model algorithm	AUC	COR	TSS	Deviance
<i>Diospyros mespiliformis</i>	RF	0.97	0.80	0.88	0.22
	SVM	0.95	0.74	0.82	0.28
	BRT	0.96	0.72	0.84	0.35
<i>Colophospermum mopane</i>	RF	0.97	0.83	0.85	0.31
	SVM	0.93	0.73	0.77	0.46
	BRT	0.92	0.71	0.74	0.57
<i>Sclerocarya birrea</i>	RF	0.96	0.74	0.83	0.26
	SVM	0.92	0.64	0.75	0.35
	BRT	0.90	0.62	0.68	0.41
<i>Julbernardia globiflora</i>	RF	0.94	0.70	0.79	0.45
	SVM	0.90	0.58	0.72	0.62
	BRT	0.91	0.61	0.71	0.64
<i>Dichrostachys cinerea</i>	RF	0.95	0.70	0.80	0.29
	SVM	0.90	0.56	0.70	0.41
	BRT	0.88	0.56	0.64	0.44
<i>Terminalia sericea</i>	RF	0.93	0.71	0.74	0.47
	SVM	0.88	0.59	0.65	0.60
	BRT	0.86	0.56	0.59	0.71

## Spatial distribution of host tree suitability in Southern Africa

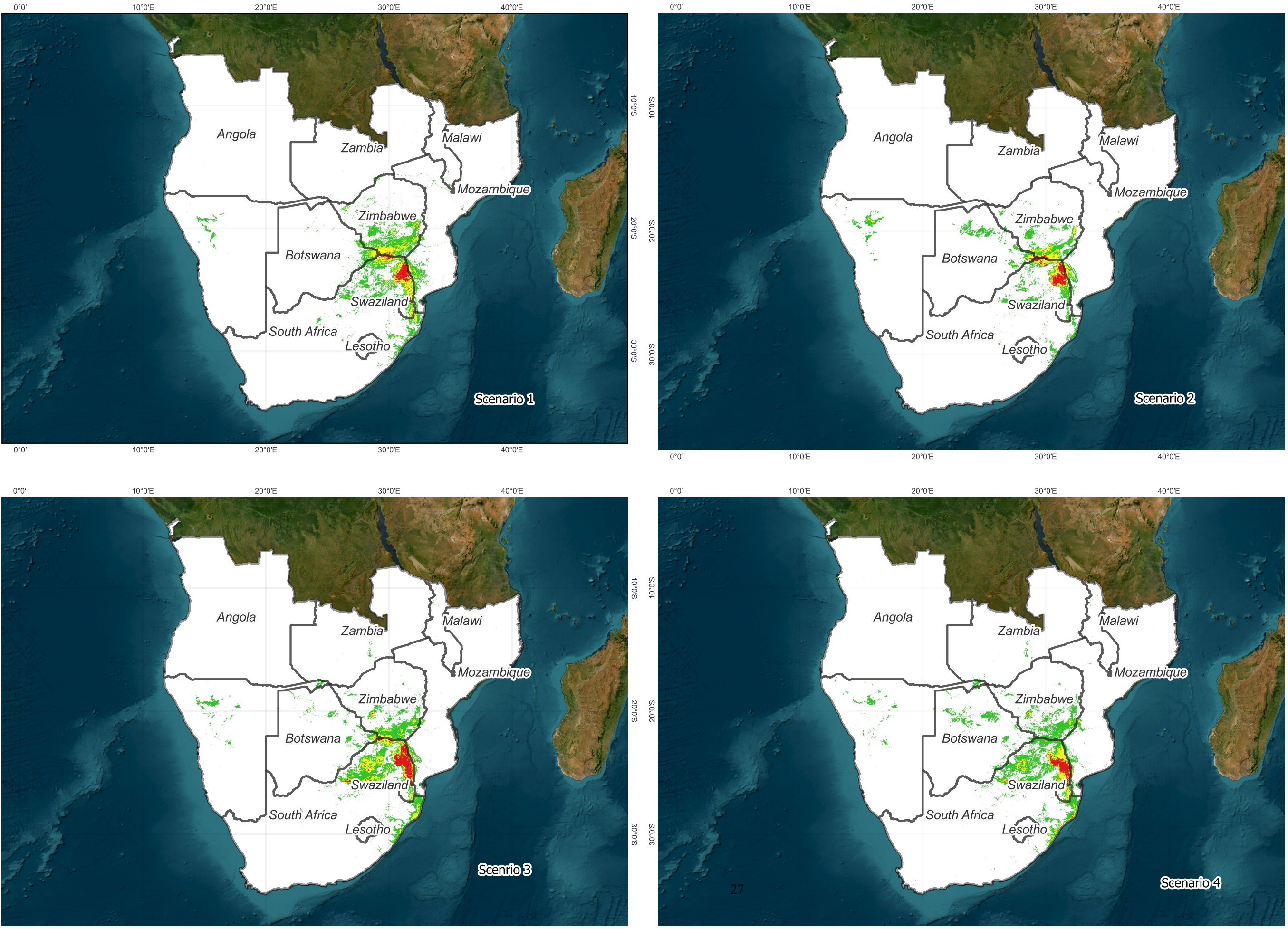
The suitable areas for the survival of each mopane worm host tree revealed distinct spatial patterns. For instance, the *C. mopane* showed high suitability in northern Botswana. Additionally, high suitability regions for *C. mopane* were in the Southern parts of Zimbabwe, the northeastern regions of South Africa, the south-western areas of Mozambique and the northwestern parts of Namibia (Figure 5). Conversely, the remaining countries in the Southern Africa region exhibited regions of moderate to low suitability, and unsuitable for the survival of *C. mopane*.

The assessment of *T. sericea*'s suitability in Southern Africa revealed that the host tree thrives in northern Botswana and the northeastern regions of South Africa. On the other hand, other countries like Malawi displayed relatively low suitability for *T. sericea*, while regions in Angola, Lesotho, Namibia, and Zambia were mostly unsuitable for the host tree (Figure 5). Whereas *D. mespiliformis* showed a high suitability preference in the bordering region encompassing Zimbabwe, South Africa, and Mozambique, the highest suitability for *D. mespiliformis* was observed in the northeastern part of South Africa. Most parts of the Southern Africa region exhibited a higher degree of unsuitability for the tree's survival.

Similarly, *S. birrea* showed high suitability in the northeastern part of South Africa and along the shores of the Southwest Indian Ocean. However, regions such as Namibia, Angola, and Zambia were deemed unsuitable for *S. birrea* within the study area. The rest of the countries within the study area exhibited a range of suitability from low to unsuitable for *S. birrea* (Figure 5).

For *J. globiflora*, high suitability was observed in Mozambique and Malawi. Parts of Zimbabwe, and along the border with Mozambique, showed varying levels of suitability. Mozambique was highly suitable for the *J. globiflora*. However, most of the Southern Africa

FIGURE 5 Mopane worm (*Gonimbrasia belina*) host tree suitability in Southern Africa developed using ensemble model techniques in species distribution model (SDM) with random forest (RF), boosted regression tree (BRT) and support vector machine (SVM) model algorithms. The base map used is the Esri World Satellite Imagery accessible within the QGIS environment.



N

**LEGEND**

- Unsuitable
- Low suitability
- Moderate suitability
- High suitability
- Southern Africa
- Satellite World\_Imagery

CRS: World Geodetic System  
Datum: WGS84

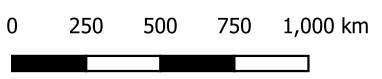
Unit: Degrees

**Scenario 1**  
The *G. belina* model incorporated all relevant variables except for the host trees ensemble.

**Scenario 2**  
The *G. belina* model included all other variables, with the addition of the *C. mopane* host tree ensemble as an explanatory variable.

**Scenario 3**  
The *G. belina* model incorporated all relevant variables, including all host tree ensembles, as explanatory variables.

**Scenario 4**  
The *G. belina* model included all explanatory variables, encompassing various host tree ensembles, except for the *C. mopane* explanatory variable



region was identified as unsuitable for *J. globiflora*, with patches of low suitability observed across Zambia (Figure 5).

Lastly, the suitability of *D. cinerea* was similar to *D. mespiliformis*, which exhibited a high level of suitability in South Africa, particularly in the northern regions and along the Southwest Indian Ocean. In contrast, the rest of the region showed unsuitable areas for *D. cinerea* survival, with Botswana and Zimbabwe having a few areas of moderate suitability transitioning into unsuitable regions (Supplementary Figure S13).

#### ***Mopane worm (Gonimbrasia belina) habitat suitability in Southern Africa***

Based on the statistical analysis of the mean AUC and mean TSS values obtained from different mopane worm model scenarios, it was observed that the scenario incorporating all host trees (scenario 3) exhibited the highest mean AUC value of 0.87 and mean TSS value of 0.68 (Table 5). Contrarily, the model that did not incorporate any host tree (scenario 1) as an explanatory variable exhibited the lowest mean AUC (0.85) and mean TSS (0.61) values (Table 5).

TABLE 5 Accuracy metrics of mopane worm (*Gonimbrasia belina*) habitat suitability models in Southern Africa with four different model scenarios using support vector machine (SVM), random forest (RF), and boosted regression tree (BRT) algorithms. The model accuracies include the area under the curve (AUC), correlation (COR), true skill statistic (TSS), and deviance

Model scenarios	Model algorithm	AUC	COR	TSS	Deviance
Scenario 1	RF	0.90	0.60	0.68	0.38
	SVM	0.81	0.45	0.55	0.48
	BRT	0.85	0.47	0.60	0.48
Scenario 2	RF	0.90	0.59	0.69	0.38
	SVM	0.83	0.44	0.62	0.50
	BRT	0.87	0.51	0.65	0.48
Scenario 3	RF	0.91	0.61	0.72	0.37
	SVM	0.82	0.52	0.65	0.45
	BRT	0.88	0.55	0.67	0.45
Scenario 4	RF	0.91	0.60	0.69	0.38
	SVM	0.81	0.46	0.58	0.49
	BRT	0.88	0.53	0.68	0.45

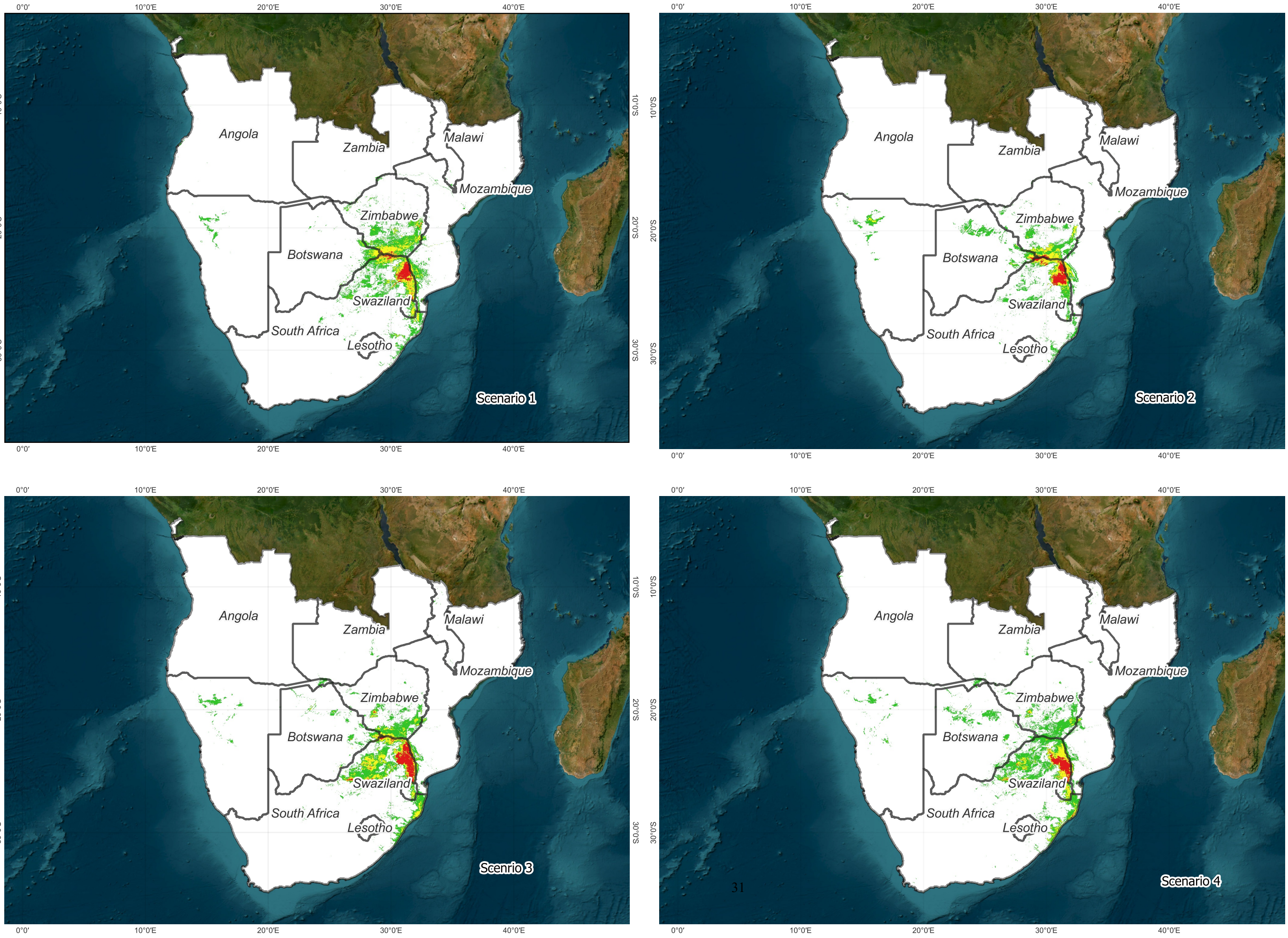
Comparatively, the ensemble model which incorporated all the host trees (scenario 3) demonstrated superior predictive performance in predicting the distribution of mopane worm, as evidenced by the higher accuracy metrics achieved compared to the other scenarios. The ensemble model which only had the alternative host trees to the *C. mopane* (scenario 4) also exhibited favourable results, representing a robust alternative for predicting suitable areas for the survival of mopane worm across all evaluated metrics. The base model which did not incorporate any host tree variables (scenario 1), displayed commendable predictive capabilities. The model scenario that only incorporated *C. mopane* as the sole host tree (scenario 2), improved the base model (scenario 1) though to a lesser extent as compared to the other scenario models (scenario 3 and scenario 4).

#### Spatial distribution of mopane worm (*Gonimbrasia belina*) suitability in Southern Africa

The four different scenarios considered for the study yielded similar habitat suitability patterns for mopane worm across the Southern Africa region. When considering other predictor variables with the exclusion of any host tree explanatory variable, the habitat suitability map revealed that mopane worm exhibited low to high suitability primarily in the northeastern part of South Africa and low to moderate suitability in Southern Zimbabwe. Conversely, the remaining regions of Southern Africa showed unsuitable areas for mopane worm survival with some parts of Namibia showing patches of low suitability (Figure 6).

In contrast, when including the primary host tree as an explanatory variable, slight differences were observed with respect to the spatial extent of high suitability categories most especially in the northern part of South Africa. The suitability map that included *C. mopane* as the only host tree, revealed that areas along the boundary of Mozambique South Africa, and Zimbabwe exhibited high suitability for the survival of mopane worm, with the immediate surrounding

FIGURE 6 Suitability of mopane worm (*Gonimbrasia belina*) in Southern Africa. The base map used is the Esri World Satellite Imagery accessible within the QGIS software.



N

**LEGEND**

- Unsuitable
- Low suitability
- Moderate suitability
- High suitability
- Southern Africa
- Satellite World\_Imagery

CRS: World Geodetic System  
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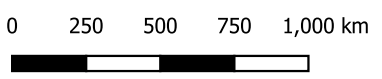
Unit: Degrees

**Scenario 1**  
The *G. belina* model incorporated all relevant variables except for the host trees ensemble.

**Scenario 2**  
The *G. belina* model included all other variables, with the addition of the *C. mopane* host tree ensemble as an explanatory variable.

**Scenario 3**  
The *G. belina* model incorporated all relevant variables, including all host tree ensembles, as explanatory variables.

**Scenario 4**  
The *G. belina* model included all explanatory variables, encompassing various host tree ensembles, except for the *C. mopane* explanatory variable



regions showing moderate to low suitability. Additionally, certain areas in Namibia showed low to moderate suitability for mopane worm distribution, while the remaining parts of Southern Africa were unsuitable (Figure 6). The relative importance of the *C. mopane* tree was recorded as the highest compared to the other environmental variables (Supplementary Figure S10) across other different host tree scenarios (Supplementary Figures S8-S12).

When incorporating all mopane worm host trees into the model, there was a noticeable increase in the spatial extent of highly suitable areas for mopane worm survival as compared to the scenario where only the *C. mopane* host tree was considered. Nevertheless, the model that included all host trees exhibited a slightly larger spatial area suitable for the mopane worm compared to the model that lacked any host tree as an explanatory variable, with patches of low to moderate suitability in Botswana. The relative variable importance for each mopane worm host tree indicated varying degrees of influence on the distribution of mopane worm with *D. cinerea* showing high relative importance as compared to the primary host tree, *C. mopane* (Supplementary Figure S9).

Lastly, in the absence of the *C. mopane* tree, the spatial extent of suitable regions for mopane worm mirrored that of the scenario with all host trees as explanatory variables (scenario 3), with a range of suitability varying from low to high. Notably, slightly more areas in the northern part of South Africa exhibited moderate to low suitability.



## 4 Discussion

Numerous empirical studies have indisputably revealed the biotic interdependence present in several insect species and their host trees (Wardhaugh, 2014; Du *et al.*, 2020). In a study conducted by Kusia *et al.* (2021), the maximum entropy (MaxEnt) model was leveraged to delineate the distribution of *Saturniids* based on their associations with their host trees, to comprehend the complicated biological relationship between the species and their host trees, among other things. Additionally, in a study done by Shen *et al.* (2023), numerous ensemble models of various host trees, alongside other pertinent biotic interactions were integrated into a Bayesian network, facilitating the present and future prediction of mopane worm. Aligned with these scientific endeavours, our study adopted a modelling paradigm to comprehensively grasp the ecological relationships governing mopane worm to their host trees.

### ***Influence of host trees on the distribution of mopane worm (Gonimbrasia belina) in Southern Africa***

In contrast to earlier studies that primarily centred on individual host trees and the impacts of climate change on the population and distribution of mopane worm, our research specifically concentrated on harnessing host tree-based models collaboratively and comparatively for predictive purposes (Ngarega *et al.*, 2021b). There is a noticeable dearth of research that investigates the interactions between mopane worms and various host trees. This unique approach enabled a comprehensive gauge of the collective influence of diverse host trees, facilitating a more holistic comprehension of mopane worm distribution patterns. Moreover, our study adopted a powerful modelling technique, affording us a meticulous exploration of potential interactions among predictor variables that might have been overlooked in previous investigations.

The outcomes derived from the host tree models and their corresponding suitability locations in Southern Africa offer essential insights for stakeholders when determining suitable areas for rearing the edible mopane worm. By comparing the relative importance rankings of each host tree, decision-makers can identify the most influential host trees in shaping mopane worm distribution. Understanding the comparative significance of each host tree allows decision-makers to prioritise the selection of rearing sites where the most critical host trees are prevalent such as the *C. mopane* and the *D. cinerea* host trees.

The study also made several noteworthy contributions to the existing knowledge of mopane worm distribution. Firstly, it revealed that incorporating the primary host tree, *C. mopane* in our model, significantly improved the predictive capabilities of the mopane worm (scenario 2) as compared to models without any host tree information. Further enhancement in predictive abilities was observed with the inclusion of multiple host trees, as seen in scenario 3, encompassing all host trees. This finding is consistent with previous research indicating that certain host trees can significantly influence the presence and abundance of insect species (Mráček *et al.*, 2005). It also reinforces the ecological importance of *C. mopane* as a key predictor for mopane worm presence, consistent with previous research (Kwiri *et al.*, 2020; Nematodzi *et al.*, 2023).

These findings underscore the potential significance of alternative host trees, particularly *D. cinerea*, which demonstrated the highest relative variable importance among all host trees and other environmental variables included in the model development. This suggests that *D. cinerea* may exert a relatively stronger influence on mopane worm distribution patterns compared to all other host trees considered. This could signify the importance of *D. cinerea* as a mirror replacement to the *C. mopane* in case of its extinction or of its limited supply. It's worth noting that our initial study did not originally intend to examine the sole impact of *D. cinerea*. Based on

the outcomes arising from our initial hypothesis, we performed a fifth host-tree-based mopane worm model, focusing solely on the influence of *D. cinerea*. In the findings, the relative importance value for *D. cinerea* slightly exceeded 0.8, in contrast to scenario 2, which exclusively featured *C. mopane* with a value of approximately 0.7. The detailed results of this additional scenario are presented in Supplementary Figure S12. This would contribute to a deeper exploration of the ecological dynamics surrounding mopane worm habitat and distribution.

### ***Implications and limitations of the study***

The study's findings have significant implications for conservation efforts, especially considering the concerning decline in *C. mopane* trees caused by multiple factors, such as climate change and elephant damage in various regions (Simbarashe and Farai, 2018). Additionally, the decline of mopane worm populations can largely be attributed to the overharvesting of the edible caterpillar by communities (Langley *et al.*, 2020). Earlier studies also indicate that rainfall patterns, distribution, occurrence, temperature and occurrence of droughts, impact of natural enemies and predators also influence the occurrence and distribution of the mopane worm. As vast forests of *C. mopane* trees are no longer inhabited by mopane worms this indicates the greater importance of identifying and defining the level of importance of other host trees as well as other non-host factors in determining mopane worm abundance in Southern Africa.

Furthermore, recent studies point to the fact of declining populations associated with larvae failing to burrow and pupate due to frequent droughts and low soil moisture at the time of pupation. Hence, there is a need for future studies to conduct laboratory tests that derive and identify thresholds of drought and soil texture that inhibit the burrowing of the mopane worm into the soil to complete its life cycle. Therefore, the habitat suitability maps presented in the research can serve

as a valuable tool to guide targeted conservation measures in addressing these challenges. These maps identify regions with high suitability for the survival of mopane worm and their host trees, providing essential information for conservation initiatives to focus their efforts on protecting these areas.

Another key implication is the recognising the importance of *C. mopane* as a critical predictor variable for guiding targeted conservation strategies. By focusing on the conservation of this primary host tree, we can support the long-term viability of the species. However, our study's examination of the collective impact of multiple host trees, with *D. cinerea* notably achieving a high relative importance rank, provides invaluable insights for formulating comprehensive management plans aimed at conserving other alternative host trees. Understanding how different host trees contribute to mopane worm distribution allows for a more holistic approach to conservation efforts.

Despite the valuable insights gained from our study, it is acknowledged that the findings are specific to Southern Africa. Therefore, caution should be exercised when extrapolating the results to other regions with different ecological conditions and host tree species. Similarly, the use of a coarse spatial resolution of 1km might have restricted our ability to capture fine-scale spatial variations in mopane worm distribution and its associations with specific host trees. While the study focuses on mopane worm host tree species, it acknowledges other potential limiting environmental hazards, including forest fires and pesticide use as common agricultural practices, as well as other ecological interactions such as predation, competition, and mutualism, that could impact mopane worm distribution. These factors and interactions may not have been fully accounted for in the models. Further research and refinement in these areas is warranted to enhance

the accuracy and precision of the ecological relationships between mopane worm and individual host trees.

## **5 Conclusions**

The study provided valuable insights into the predictive abilities of the mopane worm distribution in Southern Africa, particularly within diverse host tree scenarios. The incorporation of multiple mopane host trees has notably enhanced the model's predictive accuracy as evidenced by the empirical evidence derived from our research, further elucidating the important role mopane host trees play in influencing the model's performance. These findings can inform conservation efforts, land management strategies, and decision-making processes aimed at preserving suitable habitats for mopane worm populations. Furthermore, the research underscores the imperative of establishing comprehensive policy frameworks to regulate the harvest and trade of mopane worms within respective country jurisdictions considering the potential loss of host trees to climate change and logging. Moreover, further research is needed to explore the ecological relationships and potential synergistic effects of multiple host trees and other landscape indicators on mopane worm distribution.

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